MODELLING AND MAPPING FISHING IMPACT AND THE CURRENT AND POTENTIAL BIOMASS OF CORAL-REEF FISHES IN SOUTH FLORIDA

Phase 2 Final Technical Report prepared by:

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Contents

Summary

To assist in the management of fisheries and marine habitats in Florida, The Nature Conservancy (TNC) contracted Florida International University (FIU) to map coral reef fish and fisheries on the Florida reef tract from Martin County, FL to the Dry Tortugas. The aims of Phase 1, led by Rachel Zuercher and Alastair Harborne were to model and map fishing impact, model and map current fish biomass, and assess the potential benefit of conservation and management measures, such as the potential biomass on a reef following the cessation of fishing. Following completion of Phase 1 in September 2019, the project was extended for a Phase 2 to allow for further refinements to the products and modelling of sections of the reef tracts (e.g. Biscayne National Park, Middle Keys, and the Dry Tortugas) and individual species.

Using federally collected fish survey data from the NCRMP Reef Visual Census (RVC), the project had access to 4,176 fish surveys from coral reef and pavement (non-accreting hardbottom) habitats across the Florida reef tract. These data were collected following the RVC protocol, where divers record and estimate size for all fish species encountered. The fish survey data set were split, and fish data from 2090 sites were used to statistically model fishing impact. This fishery-independent data set was used to model the biomass, at each site, of species that are included in the federally managed snapper-grouper fishery complex. These are species commonly landed in both commercial and recreational fisheries. The biomass data were modelled in relation to 24 potential predictor variables, such as the distance and size of nearby fish markets (market gravity) and sea surface temperature. These analyses demonstrated that both human-related and biophysical gradients, particularly depth, reef complexity and coral cover, are important factors affecting the biomass of fishery species. The human influence on fish populations, assumed to be through fishing, was best correlated with the number of recreational fishermen within 50 km of a reef (based on the zip code that a fishing license was purchased under), the number of marina slips within 10 km of a reef, and market gravity, with fish biomass generally decreasing as the number of recreational fishermen, number of marina slips, and market gravity increased. Using only the three fishing-related variables (i.e. considering biophysical influences as homogeneous across the region), the model was used to extrapolate relative fishing impact (specifically the total cumulative impact of fishing on the fish assemblage) to all coral reef and pavement habitat sites across the Florida reef tract, and generate a continuous map at a resolution of 1 ha reef cells.

Estimates of fishing impact were then used as a key data layer, along with 15 environmental variables, to model the current biomass of all surveyed reef-fish species (total biomass, excluding sharks and rays), of the snapper-grouper fishery complex, all fished species, herbivorous species, species in the marine life fishery complex (species collected for aquaria), Hogfish (*Lachnolaimus maximus*), Yellowtail Snapper (*Ocyurus chrysurus*), and Stoplight Parrotfish (*Sparisoma viride*). using the remaining 2,086 sites where survey fish data were available. The snapper-grouper model demonstrated that biomass decreased with increasing fishing impact, and was also affected strongly by depth, complexity, and net primary productivity at the site. The models of herbivores and species in the marine life complex suggested that the overall biomass of those groups is not strongly affected by fishing. The models for all fish species and groups were then used to extrapolate estimates of current biomass (on, in the case of single species, abundance) across the reef tract to generate previously unavailable maps. Models were also generated for seven areas of the reef tract: the Coral ECA, Biscayne National Park, the Upper Keys, Middle Keys and Lower Keys, the Dry Tortugas region, and the entire Florida Keys National Marine Sanctuary. These area-specific models highlight local drivers of fish biomass.

Finally, the model of current biomass was adjusted to represent two potential management scenarios: the establishment of a no-take reserve and coral restoration. To simulate a reserve (i.e. to estimate the biomass possible on a reef given no fishing impacts with the current biophysical conditions), fishing impact was reduced to zero in the model. To simulate coral restoration, we increased coral cover to 15% and reef complexity by 15 cm. This allowed the production of maps estimating patterns of potential biomass across the region. Finally, using maps of predicted current and potential biomass under a simulated no-take reserve, the project generated a map of the predicted time of recovery following the cessation of fishing.

The maps generated by this project represent the first spatially explicit, continuous maps of fishing impact and current and potential biomass for the Florida reef tract. These maps, which are available on the Mapping Ocean Wealth data portal, can be provided to management agencies to support reef and fishery-related decisions. For example, as marine managers weigh multiple considerations, fishing impact and estimates of current and potential biomass can highlight potential reefs for protection. For instance, areas with low levels of conflict with fishing activity, a large potential for increased fish biomass following the cessation of fishing, or relatively intact fish assemblages that could be protected from any increases in anthropogenic impact. Furthermore, the models allow planners to examine a wider range of management scenarios for their effects on fish biomass. For example, the models can show the spatially explicit potential benefits of coral restoration (adding coral cover and complexity), engineering solutions (adding structure), and replanting mangroves (adding nursery habitat). The project team is now working on publishing the results of the models and potential management scenarios in a scientific journal.

1. Introduction

1.1. The reefs of Florida

The Florida coral reef tract stretches for ~550km across the counties of Martin, Palm Beach, Broward, Miami-Dade, and Monroe (Fig. 1). Monroe County includes the Florida Keys, a barrier reef that extends ~400 km southwest along an island archipelago from Key Biscayne near Miami to the Dry Tortugas region west of Key West (Ault et al. 2005). These reef areas have been extensively studied, and readers are referred to introductory texts for more detailed information (e.g. Dustan 2000, Riegl and Dodge 2008, Walker and Gilliam 2013, Shinn and Lidz 2018). Briefly, oceanographic conditions are considered marginal for coral growth, especially areas heavily influenced by water generated in Florida Bay and moving into the Atlantic (Riegl and Dodge 2008). Consequently, the best developed reefs are more isolated from Florida Bay, such as areas east of Key Largo. Forereefs often have a distinct spur and groove zone, there are multiple patch reefs further inshore, and the reefs support ~50 species of coral and over 500 species of fishes (Riegl and Dodge 2008).

The reefs of south Florida represent an economically vital resource. In 12 months during the years 2000-2001, reef-related expenditures generated $504 million in sales in Palm Beach County, $2.1 billion in Broward County, $1.3 billion in Miami-Dade County, and $490 million in Monroe County (Johns et al. 2001). These expenditures provided 6,300 jobs in Palm Beach County, 35,500 jobs in Broward County, 18,600 jobs in Miami-Dade County and 10,000 jobs in Monroe County. The reefs support commercial and recreational fishing industries with rich histories in the Florida Keys and Southeast Florida (Ault et al. 1998, Shivlani 2014). However, like many reefs close to large urban populations, the marine ecosystem of south Florida is threatened by myriad stressors. These stressors include coral bleaching driven by climate change (Manzello 2015), coral diseases (Precht et al. 2016), overfishing of reef-associated species such as grouper and snapper (Ault et al. 1998, McClenachan 2009), loss of grazing species (Chiappone et al. 2002), decreasing water quality (Ward-Paige et al. 2005), anchor damage (Davis 1977), and invasive species such as lionfish (Ruttenberg et al. 2012). The stressors interact with natural threats, including

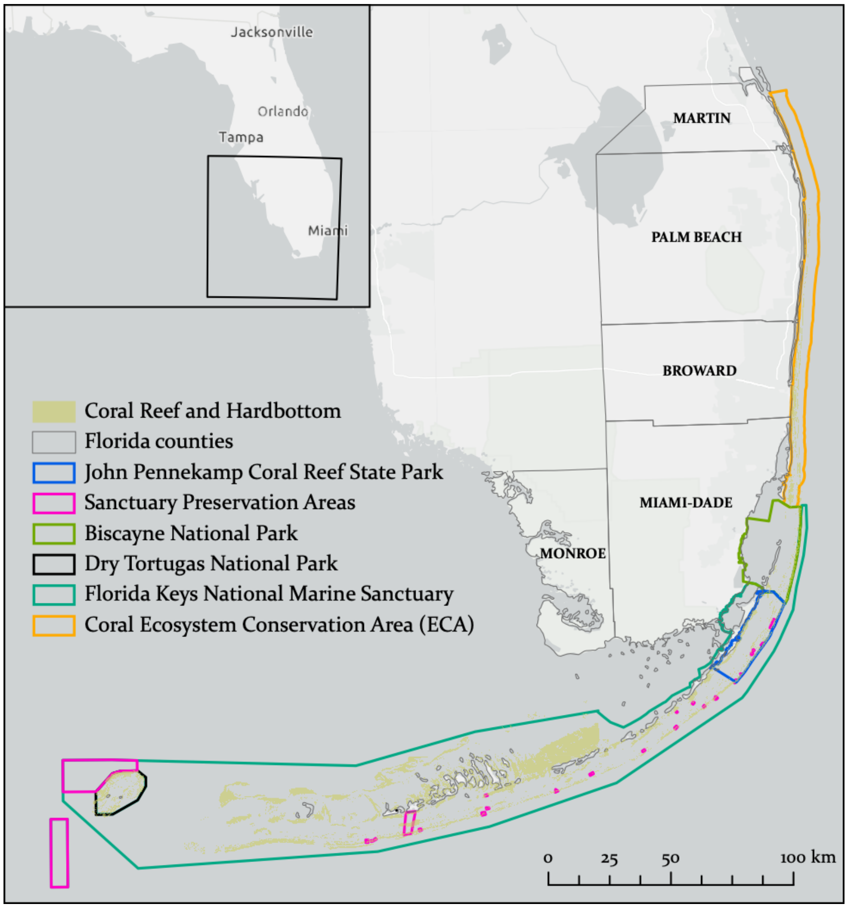

Fig. 1. Map of the Florida reef tract and major management areas.

damage from hurricanes (Blair et al. 1994) and cold-water thermal anomalies (Kemp et al. 2016). This combination of natural and anthropogenic stressors has led to increasing concerns of large-scale loss of coral cover (Palandro et al. 2008) and negative carbonate budgets leading to long-term loss of reef structure (Toth et al. 2018). Consequently, understanding the resilience of the system has been a major research focus (Maynard et al. 2017).

Efforts to ameliorate threats to the reef tract have been extensive, including the establishment of a Florida Keys National Marine Sanctuary (FKNMS) that is managed by the National Oceanic and Atmospheric Administration (NOAA) (Fig. 1). Other parts of the reef are protected by the Dry Tortugas National Park and Biscayne National Park (managed by the National Park Service within the Department of Interior) and John Pennekamp Coral Reef State Park (managed by the Florida Department of Environmental Protection) (Ault et al. 2005). Fisheries are managed by the Florida Fish and Wildlife Conservation Commission (FWC). In 1997, the FKNMS established a network of no-take marine reserves, comprising 22 Sanctuary Preservation Areas (SPAs; mean size = 0.85 km^2) and a larger (18.7 km^2) Western Sambo Ecological Reserve (Bohnsack et al. 2007) (Fig. 1). These no-fishing areas, along with other regulations, have been successful at increasing fish populations and sizes (Bohnsack et al. 2007, Bohnsack 2011, Ault et al. 2013) and fish recruitment (Sponaugle et al. 2012b) within their boundaries. Protection of South Florida's reef has been augmented by the building of numerous artificial reefs (Baine 2001) and increasing efforts at reef restoration (van Woesik et al. 2018, Ladd et al. 2019).

1.2. Mapping fishing and fish biomass in south Florida

Like coral reefs, the ecosystem services that humans derive from reefs, including food provisioning from fisheries, are under threat from the wide range of human-caused stressors discussed above. This makes it imperative that we incorporate these services into marine management decisions (Arkema et al. 2015). To facilitate this goal, The Nature Conservancy established the Mapping Ocean Wealth initiative[1] to spatially quantify the benefits that ocean ecosystems provide today. Under this umbrella, the project described here aimed to map and model reef fish and fisheries in South Florida to provide quantitative estimates of fish biomass, an important component of ecosystem benefits. The work provides analogous data to projects assisting marine management in Micronesia (Harborne et al. 2018) and The Bahamas. The data are publicly available on the Mapping Ocean Wealth data portal[2].

1.3. Project aims

The original aims of the Florida mapping project were to create the following products:

- A model and map of each of the following:
    - Fishing impact (unitless, fishery-independent estimate of cumulative fishing impact)
    - Current biomass (estimated biomass of fish on the reef)
    - Potential biomass (estimated biomass of fish possible on the reef in the absence of fishing)
    - Estimated effects of additional management on fish biomass (i.e. estimates of potential fish biomass following simulated management actions such as increasing reef complexity)
    - Likely recovery times for reef fish assemblages to recover to reef carrying capacity

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[1] https://oceanwealth.org
[2] https://maps.oceanwealth.org

- Guidance on how to use the models and maps to support area-based fisheries management and conservation activities

The project was officially started on May 31, 2018 and was planned to conclude on August 31, 2019. However, following a range of stakeholder meetings where the results of Phase 1 were discussed, it was decided that models of fish biomass in specific reef areas (e.g. the Upper and Lower Keys) and species-specific models would be useful. Therefore, the project was extended for a Phase 2 through September 30, 2020. This report is the final technical report of Phase 2.

2. Methods and data

2.1. Methods overview

The major products of the project, namely the models and maps of fishing impact and current and potential biomass, use a range of data inputs and are interlinked (Fig. 2). Details of the fish survey data and predictive data layers are provided in subsequent sections, but the first step was to model fishing impact using metrics derived from fish survey data in relation to environmental (e.g. wave exposure) and socio-economic (e.g. number of recreational fishers) variables. The model of fishing impact used data independent of the data used to model biomass to ensure robust statistical models (i.e. we did not derive fishing impact from a dataset, then use the fishing impact metric to model biomass with the same dataset). The model of fishing impact was limited to locations where fish survey data were available, but it was used to extrapolate values across the region using continuous data layers of each significant explanatory variable, thus deriving a continuous map of fishing impact.

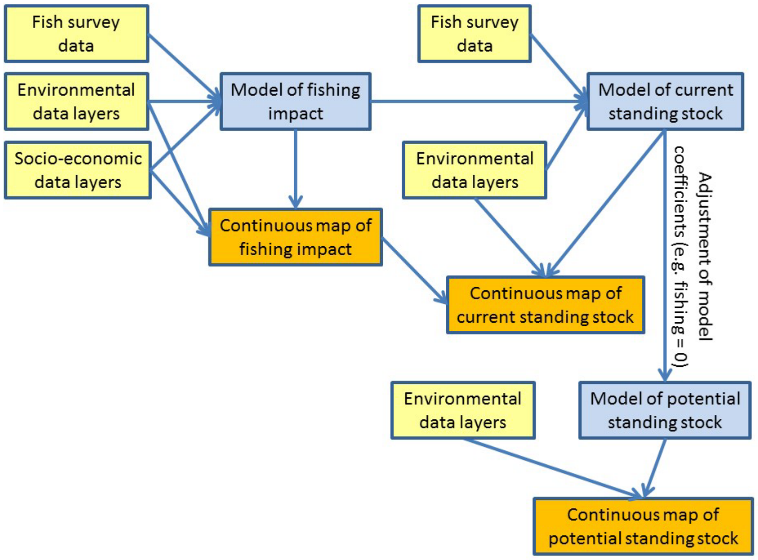

Fig. 2. Overview of the methods for modelling and mapping fishing impact and fish biomass. Yellow boxes represent input data, blue boxes represent output models, and orange boxes represent output maps.

The predicted values of fishing impact were then a key input into the model of current biomass. Predicted fishing impact was combined with environmental data to model the biomass of the fish assemblage as recorded during fish surveys. The model was then combined with continuous variables throughout the Florida reef tract and derive a continuous map of current biomass. Finally, the coefficients of the model of current biomass were adjusted to estimate potential biomass under different management initiatives. This report includes the results of adjusting fishing impact to zero, simulating the effects of a no-take reserve or other fisheries management tool, and providing estimates of potential biomass on a reef given its biophysical conditions. It also includes increasing coral cover and complexity (i.e. the maximum hard cover relief) to simulate a coral restoration effort. Other management approaches could potentially be modelled, or the models could be used to simulate some of the potential effects of climate change (increasing sea surface temperatures). These adjusted models could then be combined with all significant environmental data layers to generate a continuous map of potential biomass under different management scenarios.

2.2. Approach to modelling fishing impact

Researchers typically use fishery-dependent (e.g. catch data) or fishery-independent (e.g. underwater fish counts) data to assess fishing impact. While catch data are available for the state of Florida, they lack the spatial resolution required for the models and maps produced by this project. Furthermore, there are concerns about the reliability of fisheries-dependent data sets focused on recreational fishing, a major component of reef fisheries in Florida. Consequently, this project used fishery-independent data derived from surveys of fish assemblages at sites across the Florida reef tract. Where survey data are available there are many different options for inferring fishing impact, and many approaches have been discussed in the general fisheries literature (e.g. Jennings 2005, Shin et al. 2005, Shin et al. 2010). The use of indicators of fishing impact has subsequently extended into coral reef fisheries and has included maximum size or age at female maturation as an indicator of vulnerability (Jennings et al. 1999, Stallings 2009, Taylor et al. 2014a), and measuring fishing impacts by the calculation of size-spectra (Graham et al. 2005), average length of caught fish (Kronen et al. 2010), mean size of parrotfishes (Vallès and Oxenford 2014, Vallès et al. 2015), and mean length, trophic level and density of large fishes (Guillemot et al. 2014). While we have explored several of these indicators, including length-based metrics, this report provides models and maps of fishing impact based on the biomass of species that are part of the federally permitted snapper-grouper complex, a group that is economically and socio-culturally important for both commercial and recreational fisheries in Florida (NOAA 1983, Seeteram et al. 2019). During testing, this metric appeared superior to other indicators of fishing impact.

Critically, the maps of fishing impact generated by the project represent relative, unitless patterns of estimated total exploitation impact, as opposed to absolute fishing rates as measured by metrics such as catch per unit effort. This distinction is important because the project highlights areas that have been heavily impacted by fishing (e.g. low biomass of groupers and snappers), rather than identifying areas that are currently being heavily fished. Highly impacted sites may also be currently heavily fished, but equally these sites may be lightly fished because catches are limited and fishermen have moved to more profitable locations. However, light fishing impact may be sufficient to limit any recovery of heavily impacted sites. Equally, some sites may currently be heavily fished, but have little evidence of fishing impact (e.g. large biomass of groupers and snappers) because the site has only recently been exploited. Furthermore, the metric of fishing impact used in this report is scaled from 0-1 based on maximum and minimum values predicted within the geographic range of the Florida reef tract. This scale would change if more heavily fished sites were included from elsewhere within the region, such as from the heavily fished reefs of Jamaica (Hughes 1994) or if more pristine sites were included, such as the reefs in Exuma Cays Land and Sea Park in The Bahamas. Consequently, it is important to recognise that references to high or low fishing impact are high or low for the Florida reef tract, and that a fishing impact value of 0 does not mean that the fish assemblage shows no impacts of fishing. Rather, an impact value of 0 signifies the lowest fishing impact on the Florida reef tract. Additionally, it is important to note that equal values of fishing impact on pavement habitats versus high complexity coral reef habitat do not signify that equal number of fishermen have been or are exploiting that site. Instead, it is simply that the cumulative impact on the snapper-grouper assemblage is equal with the same proportion of fish removed (but this will likely be a lower absolute biomass of snapper and grouper on a pavement habitat). However, for clarity the maps for coral-reef habits and hard-bottom pavements are displayed separately because, although they may be equally close to large human populations (a key driver of fishing pressure), fishing effort may not be equally distributed between habitat types.

2.3. Fish survey data sets

The derivation of the maps and models produced by the project was entirely parameterised using existing fish survey data collected by NOAA's National Coral Reef Monitoring Program (NCRMP) Reef Visual Census (RVC) survey in the Dry Tortugas, the Florida Keys, and Southeast Florida (Table 1, Fig. 3). As such, the survey technique was consistent across all survey data used. Survey sites were split to provide a wide geographic range of data for both the fishing impact and biomass models. Notably, NCRMP has not surveyed the region between Key West and the Dry Tortugas, nor do large numbers of surveys exist for pavement areas in the Florida Keys. However, our models are able to extrapolate fishing impact and fish biomass estimates to those regions using NCRMP surveys done in areas with similar biophysical conditions. While we note that benthic assemblages on pavement habitats in the northern latitudes of the Florida reef tract are distinct from those in the Florida Keys, the biophysical variables included in our models capture the aspects of this variability that are relevant to fishing impact and fish biomass (Walker and Gilliam 2013, Ames 2017).

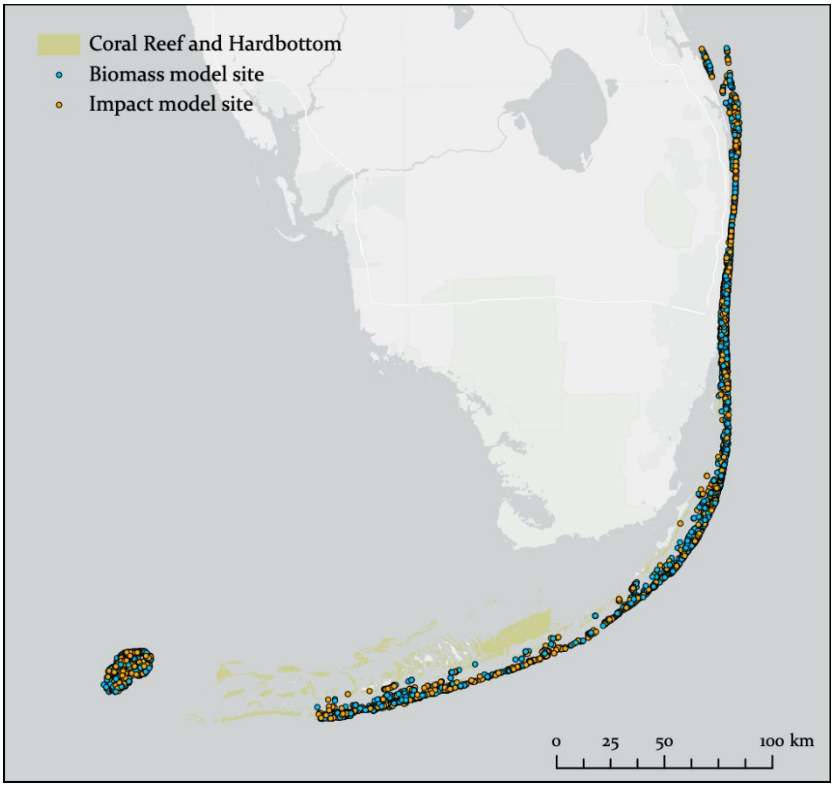

Fig. 3. Location of NCRMP RVC survey sites used in the fishing impact (orange) and biomass (blue) models.

Table 1. Summary of fish survey data used for the project.

Region	Dates	Number of sites	Fishing impact model	Biomass model
SEFCRI	2005-2018	1430	716	714
Florida Keys	2005-2018	1960	963	997
Dry Tortugas	2005-2018	786	411	375
Total		**4176**	**2090**	**2086**

Briefly, the NCRMP data were collected to assess reef health across the region and document species composition, size, abundance, density and related metrics of the fish assemblage (NOAA 2017). For this survey, divers count all fish species using the Reef Visual Census (RVC) point count method and size them to the nearest cm[3] (Bohnsack and Bannerot 1986, Brandt et al. 2009). At each survey site, two pairs of divers conduct point counts in the water column above a 7.5 meter radius circle on the reef surface. At each site, benthic cover (e.g. cover of live coral) is measured using point intercept transects and complexity is estimated based on the maximum vertical relief of the substrate.

We calculated the biomass of each fish recorded using a set of allometric parameters derived from a range of sources including Stevens (2018), Bohnsack and Banner (1988) and FishBase (Froese and Pauly 2010). Data were extracted for every survey as kg 177 m^{-2} (the area of an RVC point count), then converted to kg ha^{-1} for map presentation. A list of all fish species recorded in the RVC surveys and included in this project and whether they are part of the federal snapper-grouper fishery complex can be found in Appendix 1. In summary, the snapper-grouper complex includes groupers, snappers, grunts, triggerfishes, porgies, and several others. These are species landed in commercial fisheries across the Caribbean region (Ault et al. 1998), and are popular species for recreational fisheries (O'Toole et al. 2011).

2.4. Modelling current biomass

We modelled biomass across the Florida reef tract for five focal fish groups: species in the snapper-grouper complex; all fished species; herbivorous fishes; species in the marine life complex (saltwater fishes harvested nonlethally for commercial aquarium wholesale and retail dealers); and total biomass which includes all species documented in RVC surveys (with the exception of sharks and rays, but for clarity subsequently referred to as ‘Total biomass’). Sharks and rays seen during the surveys were removed from the data set as the survey technique is not well suited to capturing shark abundances and a single shark can significantly increase the biomass for a single survey site.

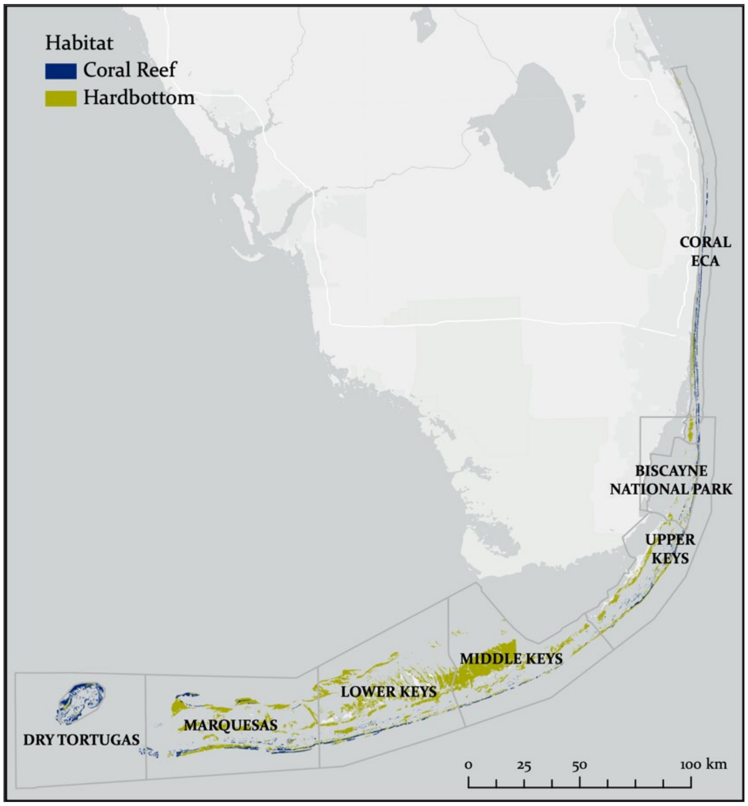

Fig. 4. Locations of the reef sections modeled separately within Phase 2 of the project. Map also shows distribution of coral reef and non-accreting hardbottom (pavement) habitats.

We also generated area-specific models of current biomass for sections of the Florida reef tract: the Coral ECA; Biscayne National Park; the Upper Keys; Middle Keys; and Lower Keys; the Dry Tortugas (Fig. 4); and the entire FKNMS (Fig. 1). Because no surveys were conducted in the Marquesas, we did not generate area-specific models for that region. While the

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[3] For some species, when more than 10 individuals are counted, only minimum, maximum and estimated mean size are recorded.

reef-tract scale model of current biomass provides the most complete overview of the drivers of fish biomass, it may be of interest to some end users to see smaller-scale, local drivers. For example, at a reef tract scale sea surface temperature may be important given the variability from Martin County to the Dry Tortugas, but these temperatures will be less important in individual sections where variability is negligible. Similarly, fishing impact varies significantly along the reef tract, but tends to be more homogeneous within a single section. Thus the models for current biomass were run for each reef section to show these local drivers, although reef-tract scale estimates of fishing impact were used in these area-specific models. Inevitably these models are less robust because they only use a subset of the data (sites surveyed in that reef section) and therefore any resulting maps are less useful for interpretation than the full reef-scale map. Consequently, only the full reef tract maps are presented in this report.

In addition, we developed models and maps of the current abundance of individual species. Such maps provide detail that is inevitably lost in maps of total reef fish biomass, and can provide species-specific guidance for management. Models were created for all common species found on the reef tract, but for clarity in this report we only show the results for one ecologically important species (Stoplight Parrotfish, *Sparisoma viride*) and two economically important species (Yellowtail Snapper, *Ocyurus chrysurus* and Hogfish, *Lachnolaimus maximus*). Models for other species are available on request.

2.5. Mapping Florida's reefs

Establishing the extent of reef areas along the Florida reef tract was critical for the project, and we used the maps generated by the Florida Fish and Wildlife Conservation Commission (FWC; Fig. 5). The Unified Florida Reef Tract Map (UFRTM) is a compilation of various remote and field-based mapping efforts and uses a thematically rich habitat classification scheme (FWC 2016). Level 2 of the classifications scheme was appropriate for identifying the habitats that would be included in the modelling and mapping work. We include coral reef and pavement habitats assigned the following Level 2 classifications: Aggregate Reef, Individual or Aggregated Patch Reef, Spur and Groove, Ridge (coral habitats), Reef Rubble, Colonized Reef Rubble, Pavement, Colonized Pavement, and Pavement with Sand Channels (hardbottom / pavement habitats) (Fig. 5). We excluded habitats in less than 2 m water depth to exclude pavement habitats especially unsuitable for coral growth, and because several of the geospatial data layers of biophysical variables are lacking data in very nearshore areas. This yields a Coral Reef and Pavement habitats layer with a diverse range of coral-supporting habitats. To address the possibility that distinct processes affect fish biomass on coral reef (e.g. Aggregate Reef) versus low-relief pavement habitats (e.g. Colonized Pavement), we ran separate experimental models for each of these habitat groups. Results suggested that similar factors were influencing biomass across all coral and pavement habitats, and so no separate Coral Reef or Pavement models are presented here. Habitat type from Level 2 of the UFRTM classification scheme was also used as a categorical variable in the fishing impact and biomass models.

The UFRTM products are vector coverages, with habitats represented by polygons of varying size. However, to accurately model the Florida reef tract, the project required a raster (grid) coverage of identically sized cells. Rasterizing a vector map requires a spatial resolution to be specified, which represents a trade-off of tractability versus accuracy. For example, as the cells become larger, there are fewer of them across the region and this improves computation times. However, small areas of reef may be lost as they are grouped with surrounding seagrass habitat. Smaller cells allow for a more accurate representation of the habitat distributions and allow the models to represent subtler gradients in environmental factors, but computation time is increased. Furthermore, very small cells may not be well parameterized because of the limitations of the explanatory data sets. Experimentation indicated that 100 x 100 m (1 hectare) cells represented an appropriate grid size that retains habitat detail, but is computationally tractable (~150,000 cells). Consequently, all maps products from the project are at a 1 ha resolution.

Other habitats not considered by the project, such as seagrass meadows, or areas of unconsolidated sediment with some coral cover, may have significant fish stocks and be exploited by fisheries. Rather than being unimportant, their exclusion is a function of a lack of data to parameterize the models adequately, and the potential for significant inter-habitat variations in how fish assemblages respond to fishing and environmental gradients. However, the modelling and mapping techniques described in this report could be extended to other habitats if additional data were available.

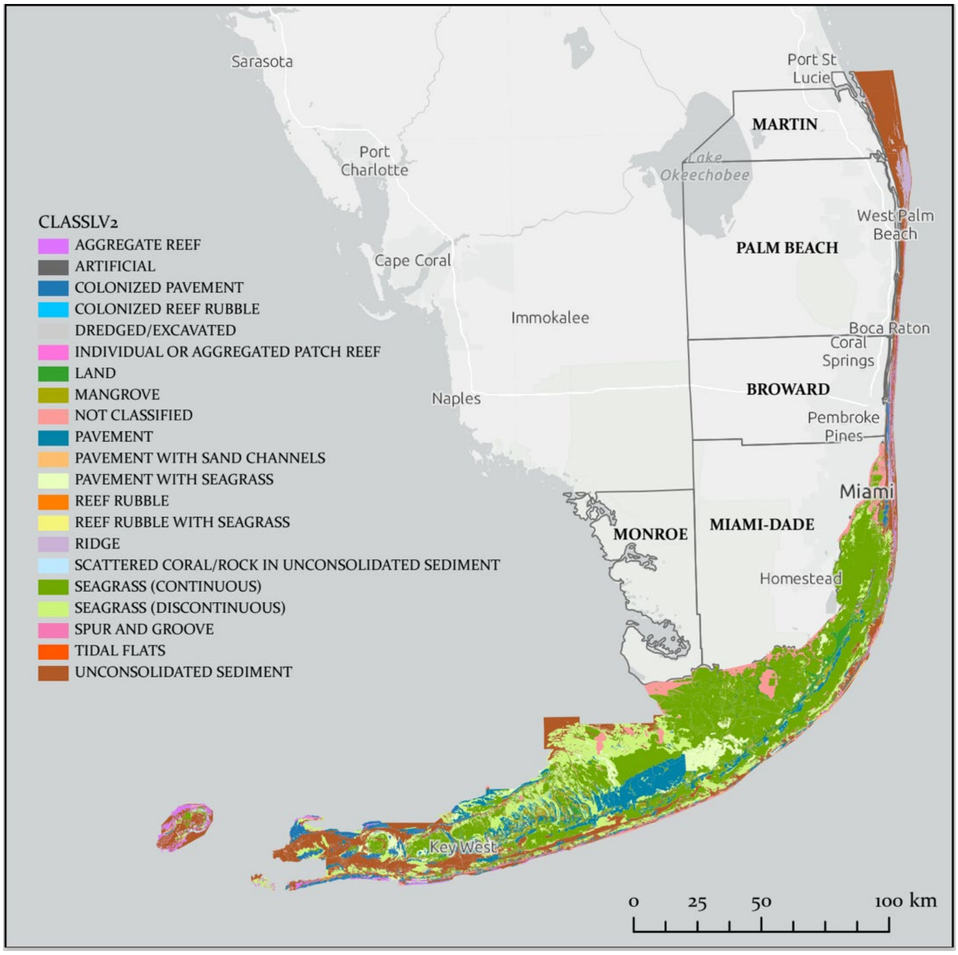

Fig. 5. Classification Level 2 of the Unified Florida Reef Tract Project map, including the coral reef and pavement habitats included in the project.

2.6. Derivation of explanatory variables

The response variable at each fish survey site (e.g. biomass of species in the snapper-grouper complex) was modelled against a range of explanatory variables to assess the significant factors driving response variability across sites. These models were then used to extrapolate fishing impact and biomass across the entire reef tract. Consequently, the project required continuous data layers of numerous potentially important explanatory variables (Table 2 and 3). Note that two explanatory variables (coral cover and complexity) are available from the *in situ* fish surveys, and from NOAA NCRMP benthic surveys, but cannot be mapped continuously in Florida. For example, deriving a continuous data layer for coral cover requires information on a complex range of variables including recruitment, grazing pressure, wave exposure, and the frequency of cyclones and bleaching events (Williams et al. 2015b). These data, and an understanding of how they interact to affect coral cover and the resilience of reefs, are not available. Therefore, coral cover and complexity were included in the models to assess whether they are important factors, but during the mapping extrapolation across unsurveyed cells this parameter was represented by the regional (Dry Tortugas, Florida Keys or Southeast Florida) mean values for each UFRTM classification Level 2 habitat type. A full description of the derivation of each variable, and a justification for its inclusion, is provided in Appendix 2.

Table 2. Variables used to model fishing impact at each survey site, including brief details of their derivation. Due to inter-variable correlations, not all variables were included in final models.

Variable	Description	Derivation
Area of reef within 20 km	Area of reef and pavement habitat within 20 km of reef cell	UFRTM habitat maps
Area of reef within 200 km	Area of reef and pavement habitat within 200 km of reef cell	UFRTM habitat maps
Artificial reefs	The number of artificial reefs within 1 km of reef cell	Data provided by various state and county government agencies
Availability of nursery habitat	Reef connectivity to mangrove and seagrass nursery habitat (separate layers for mangroves and seagrass)	Use of algorithm (Mumby 2006) in combination with UFRTM habitat maps
Coral cover	Coral cover at survey site	From fish survey data set
Depth	Depth of data collection	From fish survey data set
Distance to deep water habitats	Distance to 30m depth contour	30m contour derived from data available in Sbrocco and Barber 2013
Distance to fish spawning aggregation	Distance to nearest known snapper or grouper spawning aggregation	Location data for spawning aggregations provided by Todd Kellison (NOAA NMFS) and Ben Binder (FIU)
Community fishing engagement and reliance	Metrics of fishing engagement and economic reliance on fishing by fishing community	Data provided by Michael Jepson (NOAA NMFS) (Jepson and Colburn 2013)
Fishery activity: commercial	The number of Class 1 federal snapper-grouper permits within 50 km of reef cell; the average annual landings (lbs) of snapper-grouper complex species by county from 2012-2016	Data provided by NOAA NMFS SEFSC
Fishery activity: charter	The number of federal snapper-grouper permits assigned to charter vessels within 25 km of reef cell	Data provided by NOAA NMFS SEFSC
Fishery activity: recreational	The number of marine recreational fishing license holders within 50 km of reef cell	Data provided by the FWC
Fishery activity: tourism-related	The estimated number of tourism reef fishing days per year on a reef cell	Data on tourist hotel units publicly available from FGDL[4]; estimates of tourist fishing days by county from Johns et al. 2001
Gravity of all potential fish markets (within a 500km radius)	Market gravity defined as population size divided by the square of travel time (a proxy for distance)	From Cinner et al. 2018

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[4] Florida Geographic Data Library; https://fgdl.org/metadataexplorer/

Habitat type	Level 2 classification of reef habitat type	UFRTM habitat maps
Human population	Number of people within 20 km and 50 km of a reef cell	LandScan human population data[5]
Human population per area reef	Number of people within *x* km divided by area of fishable reef within *x* km	LandScan human population data
Latitude	Latitude of survey site	From fish survey data set
Longitude	Longitude of survey site	From fish survey data set
Marina slips	The number of marina slips with 10 km	FWC data layer available online
Month	Month of data collection	From fish survey data set
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents provided by Claire Paris (University of Miami)
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2012-2016	Oregon State University-modelled product derived from satellite data
Protected status	Whether the site is a no-take area or open to fishing; level of fishing protection	FWC and NOAA databases of marine protected areas
Complexity	Reef complexity	From fish survey data set
Sea surface temperature (SST)	Mean temperature of the coldest month	NOAA's CoRTAD satellite-based ocean temperature dataset[6]
Wave exposure	Wave exposure based on fetch and mean wind data	Data layer provided by I. Chollett (see Chollett et al. 2012)
Year	Year of data collection	From fish survey data set

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[5] https://landscan.ornl.gov/

[6] https://www.nodc.noaa.gov/SatelliteData/Cortad/

Table 3. Variables used to model biomass at each survey site, including brief details of their derivation. Due to inter-variable correlations, not all variables were included in final models.

Variable	Description	Derivation
Area of reef within 20 km	Area of reef and pavement habitat within 20 km of reef cell	UFRTM habitat maps
Area of reef within 200 km	Area of reef and pavement habitat within 200 km of reef cell	UFRTM habitat maps
Artificial reefs	The number of artificial reefs within 1 km of reef cell	Data provided by various state and county government agencies
Availability of nursery habitat	Reef connectivity to mangrove and seagrass nursery habitat (separate layers for mangroves and seagrass)	Use of algorithm (Mumby 2006) in combination with habitat maps
Coral cover	Coral cover at survey site	From fish survey data set
Depth	Depth of data collection	From fish survey data set
Distance to deep water habitats	Distance to 30m depth contour	30m contour derived from data available in Sbrocco and Barber 2013
Distance to fish spawning aggregation	Distance to nearest known snapper or grouper spawning aggregation	Location data for spawning aggregations provided by Todd Kellison (NOAA NMFS) and Ben Binder (FIU)
Fishing impact	Predicted fishing impact on 0-1 scale	From this project's fishing impact model
Habitat type	Level 2 classification of reef habitat type	UFRTM habitat maps
Latitude	Latitude of survey site	From fish survey data set
Longitude	Longitude of survey site	From fish survey data set
Month	Month of data collection	From fish survey data set
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents provided by Claire Paris (University of Miami)
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2012-2016	Oregon State University-modelled product derived from satellite data
Protected status	Whether the site is a no-take area or open to fishing; level of fishing protection	FWC and NOAA databases of marine protected areas
Complexity	Reef complexity	From fish survey data set
Sea surface temperature (SST)	Mean temperature of the coldest month	NOAA's CoRTAD satellite-based ocean temperature dataset
Wave exposure	Wave exposure based on fetch and mean wind data	Data layer provided by I. Chollett (see Chollett et al. 2012)
Year	Year of data collection	From fish survey data set

2.7. Additional considerations for modelling potential biomass

As described previously, the map and model of potential biomass represents a hypothetical data layer of the potential biomass of fish at any location with no fishing (i.e. with the fishing impact variable in the model reduced to 0). The map of potential biomass represents a target carrying capacity that might be reached within a well-enforced no-take reserve, or following implementation of another fisheries management tool, after sufficient time has elapsed to allow fish abundances to recover. However, there are myriad factors that will alter the carrying capacity, such as habitat quality that may be altered by disturbances (Abesamis et al. 2014), and this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors.

The time needed for fishes to fully recover in no-take reserves and reach a putative carrying capacity is an important research topic (Abesamis et al. 2014), encompassing complex questions of variability among fish families (McClanahan et al. 2007), predator-prey interactions that may lead to some species decreasing in abundance because of increasing abundances of carnivores (Micheli et al. 2004), and increasing abundances of herbivores increasing habitat quality by grazing macroalgae (Mumby and Harborne 2010). Noticeable differences in fish stocks are often visible within a few years (Halpern and Warner 2002, Russ et al. 2008), but up to 40 years may be needed for some predatory fishes (Russ and Alcala 2004). Providing additional insight into the recovery of species under scenarios of fishing cessation is beyond the scope of the project, but we provide broad spatial estimates of when biomass might recover using estimates of the ratio of current to potential biomass and recent, generic insights into the recovery of reef fishes. A global analysis of reef fish stock has provided an estimated relationship between the ratio of current to potential biomass and time to "recovery", defined as reaching 90% of potential biomass (Fig. 6) (MacNeil et al. 2015). We used this relationship to estimate the time it would take each 1 ha cell to reach the threshold of 90% of potential biomass. Since our metric of fishing impact is relative to the Florida Reef Tract (Section 2.2), our estimates of fish biomass on reefs with 0 fishing impact are likely to underestimate the true carrying capacity of these reefs. Consequently, our model likely underestimates the time to recovery for those sites.

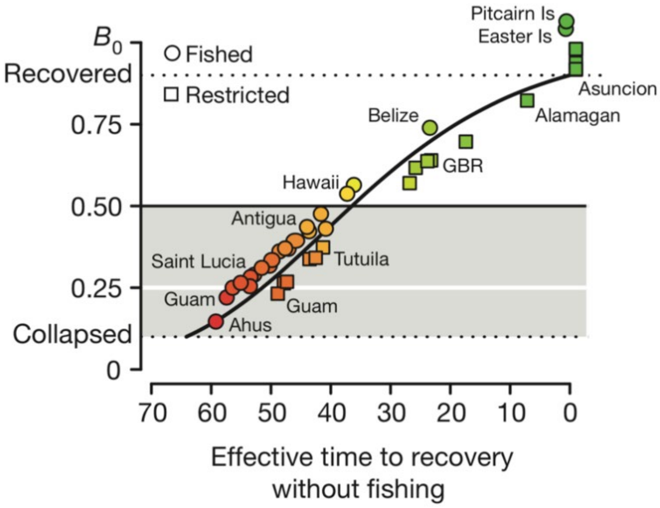


Fig. 6. The relationship between time to recovery (90% of potential biomass) following the cessation of fishing and current fishery status. Points highlight reef sites used to parameterize the relationship. Graph from MacNeil et al. (2015).

2.8. Statistical analyses

For models of both fishing impact and biomass, the final data set consisted of univariate response variables (e.g. biomass of species in the snapper-grouper fishery complex), and a large number of categorical and continuous explanatory variables. The relationships among explanatory and response variables may be curvilinear and include significant interactions that are difficult to predict *a priori*. Consequently, we use boosted regression trees (BRTs) during the modelling process. Explaining the mathematical basis of BRTs is beyond the scope of this report, and readers are referred to Elith et al. (2008) for an excellent introduction to the topic. Briefly, BRTs relate a response variable to explanatory variables by recursive binary splits (e.g. sites with high and low human populations) using an adaptive algorithm. BRTs essentially create an additive regression model and the relationships between the variables are visualised in a series of intuitively obvious graphs. Critically, BRTs have many advantages that are useful for the project including handling different types of predictors, accommodating missing data, being insensitive to outliers, fitting complex nonlinear relationships, automatically handling interactions, and being robust to fitting a large number of explanatory variables (Elith et al. 2008). Finally, models can easily be used to predict values at other locations, as required to transition from the models based on fish survey data to continuous reef tract-wide maps of fishing impact and biomass.

BRTs are generally insensitive to collinearity among explanatory variables (Soykan et al. 2014), but all explanatory variables (Tables 2 and 3) were first tested for correlations, and variables were removed so that there were no inter-variable correlations >0.8 and no variable inflation factors (VIFs) >12.0. The remaining variables were then included in the BRT, along with a variable comprised of random numbers. This variable was included as a guide to which variables were most 'significant' (Soykan et al. 2014); variables which had less explanatory power than this random number variable were removed from the model to generate a final, minimal model including only the most important variables. BRT parameters (learning rate, tree complexity, and bag fraction) were calculated for each model by testing each across a series of values, and then using the values that gave the lowest model deviance (Elith et al. 2008). Model performance was assessed using the amount of deviance explained and the correlation between observed and model-predicted values.

3. Results

3.1. Fishing impact model

Inter-variable correlations among the range of variables proposed for inclusion (Table 2) revealed that longitude was highly correlated with sea surface temperature, and so longitude was removed from the model. Similarly, latitude was highly correlated with several socio-economic variables, and removed from the model. The two scales at which we calculated the area of reef habitat were correlated, and we retained the 20 km-scale as it more closely aligns with the scale at which most reef fish ecological processes occur. The two scales of the human population variable (20 km, 50 km), the variable representing the population per area of fishable reef, our metric of tourism-related fishing, and the number of recreational fishermen within 50 km were all highly correlated. We chose to include the variable capturing the number of recreational fishermen within 50 km. A much higher percentage of Monroe County residents engage in fishing activities relative to residents of Miami-Dade, Broward, Palm Beach, and Martin counties. As such, we determined that the number of recreational fishermen (as opposed to the overall number of people) better captures fishing impact, rather than general anthropogenic impacts. We included this variable at the 50 km scale to best capture the distance that recreational fishermen might travel to fish (including travel over land), though few quantitative data exist to describe recreational fishing practices in south Florida. Finally, several additional fishing-related variables were highly correlated. In these cases, the variable with the finest spatial resolution was retained in the model. The biomass of snapper-grouper complex species underwent a $\log(x + 1)$ transformation prior to inclusion in the model to improve normality of residuals while preserving zero values in the dataset.

The fishing impact model resulted from a boosted regression tree analysis that provided a series of partial dependency plots that can be interpreted similarly to regression lines on traditional scatterplots (Fig. 7). Three human-related variables, the number of marina slips under 45 feet in length within 10 km of a reef cell, the number of recreational fishermen within 50 km of a reef cell, and total market gravity of a reef cell explained significant variation in the biomass of species in the snapper-grouper complex (4.6%, 3.3%, and 3.2% of explained variance, respectively). Additionally, 11 biophysical variables were important for explaining variation in snapper-grouper species biomass, including reef complexity (29.4%), depth (11.2%), oceanic net primary productivity (6.1%), reef area within 20km (5.2%), year (4.5%), sea surface temperature (4.3%), distance to fish spawning aggregation (3.8%), coral cover (3.7%), habitat classification (3.4%), wave exposure (3.3%), month (2.5%), and distance to deep water (2.3%).

This model was then used to predict fishing impact in every 1 ha cell along the reef tract considered by the project. Predictions were made from the model by classifying the significant variables into two categories. First, the number of recreational fishermen, marina slips, and market gravity variables were considered to relate entirely to fishing impact (generally higher fishing impact where recreational fishing population, accessibility via marinas, and the demand of local markets are highest). Values unique to each 1 ha cell (i.e. actual values for each cell) were used for these three variables. In contrast, the remaining variables were considered to be environmental or temporal drivers of fish abundance. The values of these variables in every 1 ha cell were set to their mean or the most common month and median year of data collection (August, 2014). This ensured that the predictions only represented the effects of fishing on the snapper-grouper complex, and not environmental gradients, as required for the map of fishing impact. Actual values of each variable in each cell would have been used if the aim was to predict actual biomass of species: but in this step we only wanted to investigate the effect of fishing on fish biomass, although we control for environmental variables when building the model.

It is important to note that fishing impact was not adjusted for habitat type. There are few data on how fishing effort is partitioned across habitats along the Florida reef tract, and whether the efficacy of gear such as fish traps varies among Florida's habitats (Wolff et al. 1999). In the absence of the necessary data, all habitat types are considered to be equally impacted by fishing. However, actual catches are likely to vary between habitats because of the higher abundance of fish on some habitats, but fishing impact reflects the proportional reduction in biomass. These habitat differences in fish biomass are accounted for in the maps of current and potential biomass because we have quantifiable links between, for example, reef complexity that is lower on pavements and higher on coral reef sites.

The fishing impact model explained 55% of the variability in the data set, and the correlation between observed and predicted values was 0.75 This exploratory power is considered acceptable given the challenges of the project: combining multiple data sets across a large geographic area and using a relatively crude fishery-independent metric of fishing impact.

Following predictions of human influences on the biomass of species of the snapper-grouper complex in each 1 ha cell, the predicted values were back transformed and then rescaled to range from 0 (lowest fishing impact on the reef tract) to 1 (highest fishing impact on the reef tract) and plotted (Map 1). As stated previously, it is important that these values are considered to reflect cumulative fishing impact relative to other areas on the Florida reef tract rather than an absolute measure of current fishing effort.

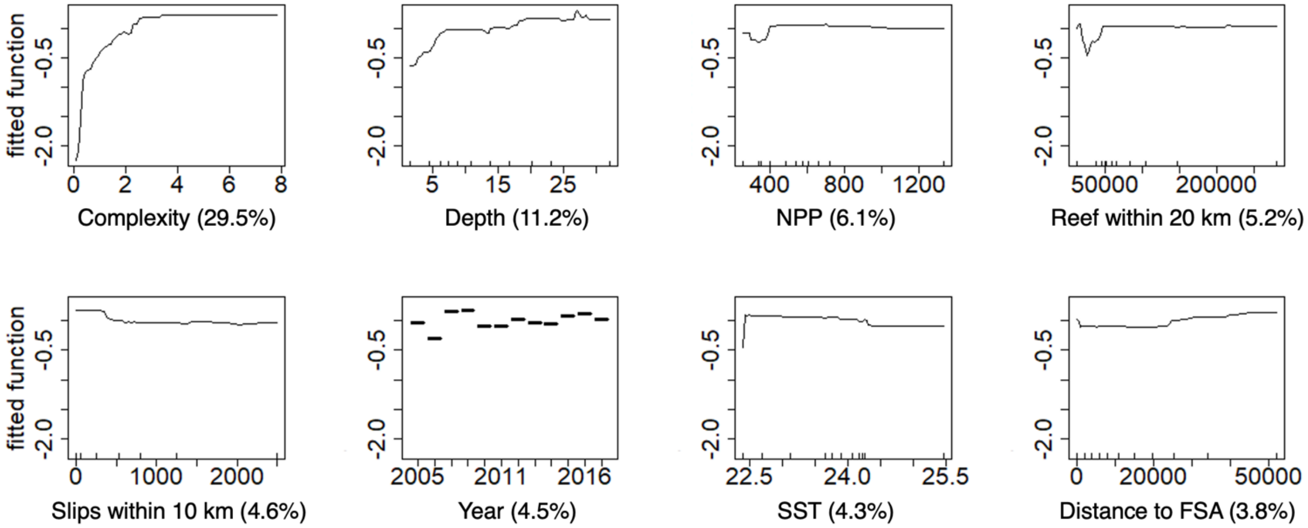
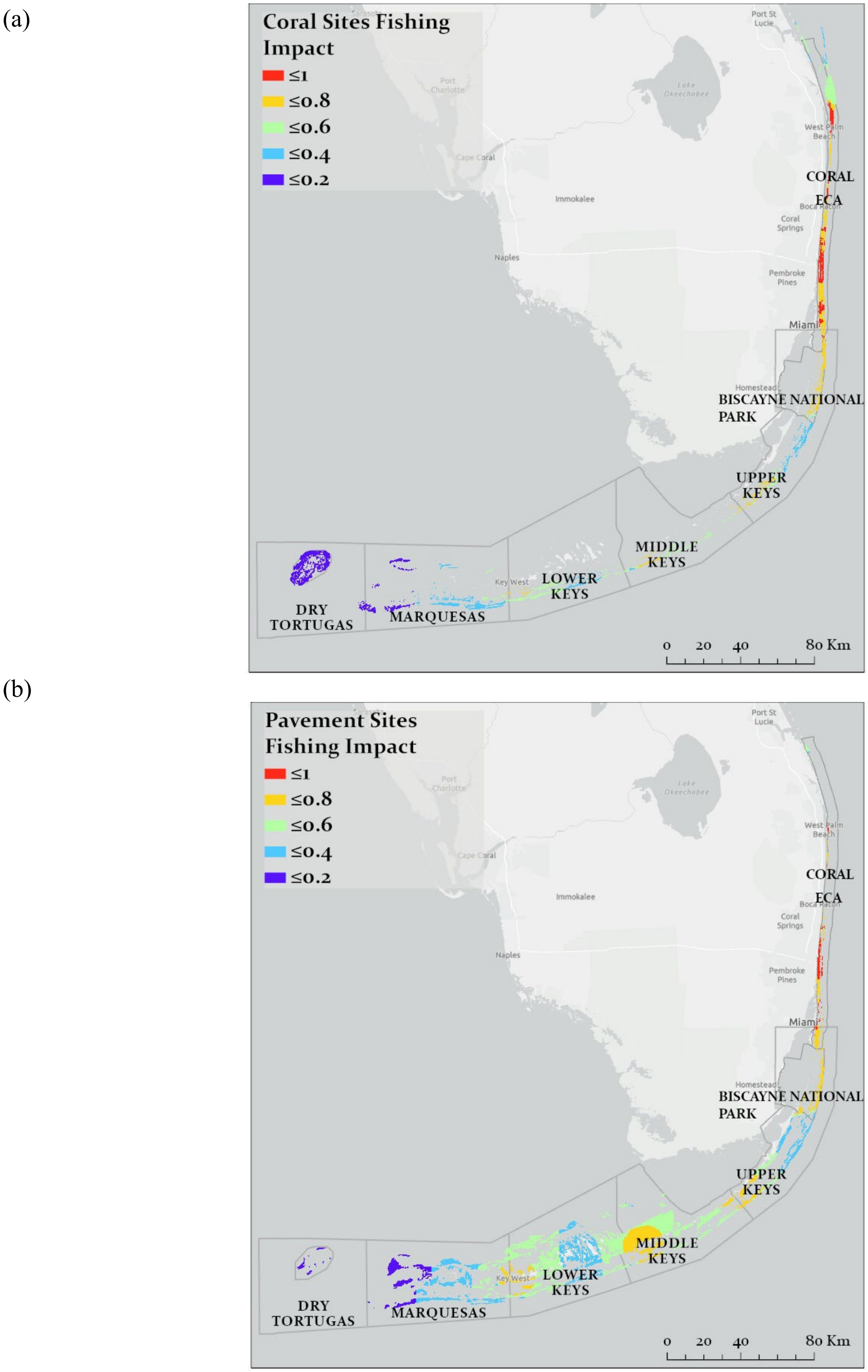


Fig. 7. Relationships between the top eight significant variables and the biomass of species in the snapper-grouper fishery complex as modelled by boosted regression trees. Values of log biomass of snapper-grouper species on the y-axis are normalised as opposed to showing actual biomass. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable.



Map 1. Spatial distribution of predicted relative fishing impact (0 = low fishing impact) across the Florida reef tract on (a) coral-reef habitats and (b) pavement habitats.

3.3. Interpretation of the fishing impact model

The model for fishing impact (Fig. 7) shows that the biomass of snapper-grouper complex species typically decreased with increasing nearby populations of recreational fishermen and with the number of marina slips under 45 feet within a 10 km radius (representing fishing access). This is consistent with expectations and the literature (e.g. Cinner et al. 2013, Cinner et al. 2016). Similarly, increasing numbers of recreational fishermen within 50 km of a reef cell and increasing market gravity influencing that cell decreased the abundance of snappers-grouper complex species. The limited deviance explained by habitat class (3.2%) suggests there may be limited difference in fishing pressure across habitats including pavement and coral sites.

The biomass of snapper-grouper species was also affected by environmental gradients, and tended to be higher on deeper reefs, on more complex habitats, and on reefs with higher net primary productivity. The relationship between biomass and depth is consistent with other literature finding that depth is a major factor in determining the fish assemblage on the Florida reef tract (Ames 2017). The importance of the complexity variable reflects the well-established effect of structure on fish assemblages (Graham and Nash 2013). The importance of complex reefs for supporting fisheries underscores the importance of maintaining positive carbonate budgets for providing ecosystem services (Rogers et al. 2014), and reflects widespread concern about the loss of complexity on Caribbean reefs (Alvarez-Filip et al. 2009). This structure is predominantly created by coral, and thus fish biomass increased with increasing coral cover. Coral cover also has a range of other benefits to fish, including providing settlement habitat to juveniles (Coker et al. 2014). The relationship between the biomass of fishes in the snapper-grouper complex was influenced by the area of reef within 20 km, although the relationship is complex (Fig. 7). Reef area has multiple effects on fishes, including providing nursery habitats, increased productivity, and greater environmental diversity (Dames et al. 2020). Year was also a significant variable, but how these changes reflect actual changes in fishing pressure versus other temporal patterns (e.g. variations in surveyors or fish recruitment) are unclear.

3.4. Current biomass model

Correlations among the variables intended for inclusion in the current biomass model (Table 3) led us to drop several variables, similar to those dropped for the fishing impact model. The total biomass response variable was log transformed to improve normality of residuals, and biomass variables with zeros in the dataset underwent a $\log(x+1)$ transformation to preserve zero values. Models were generated to predict the biomass for the following species groups: the snapper-grouper complex; all species (i.e. total biomass excluding sharks and rays); fished species; herbivorous species; and marine life species (Table 4) (see species list in Appendix 1).

As an example of the results, the biomass model for the snapper-grouper complex species generated a boosted regression tree analysis that provided a series of partial dependency plots (Fig. 8). This model was then used to predict the biomass of snapper-grouper species in every 1 ha cell considered by the project (Map 2). Values specific to each reef cell were used for every variable, except that month and year were set to August 2014 (the most common month and median year for fish surveys in the dataset). The model explained 53.7% of the variability in snapper-grouper complex biomass, and the correlation between observed and predicted values was 0.74. This explanatory power is considered acceptable given the challenges of the project: combining multiple data sets over a relatively large geographic area. Results of BRT models predicting the biomass of other fish species groups are summarized (Table 4) and the resulting maps shown (Map 3). The partial dependency plots and can be found in Appendix 3.

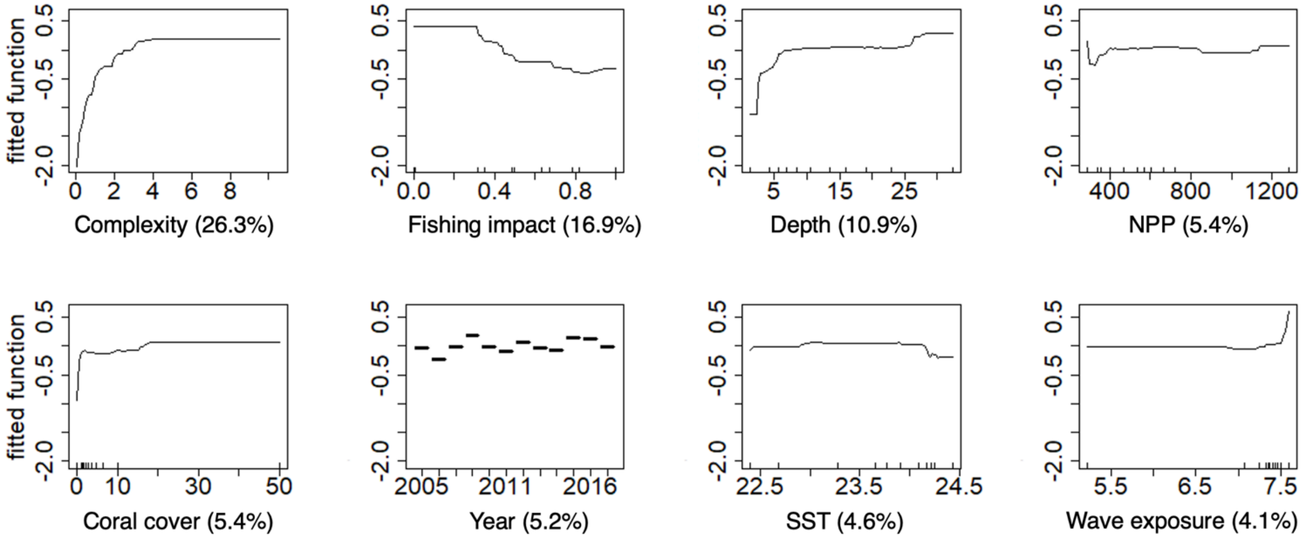
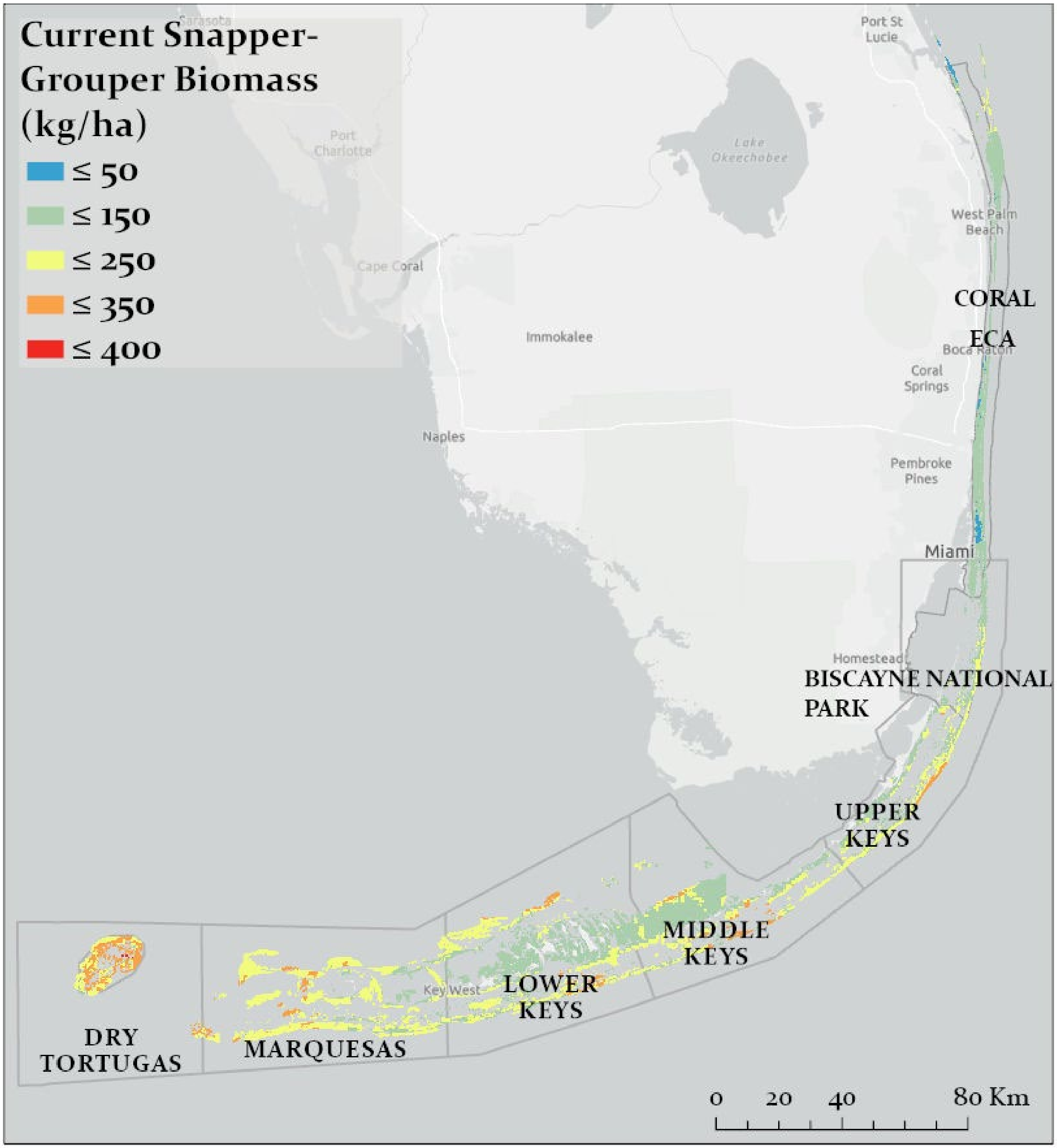


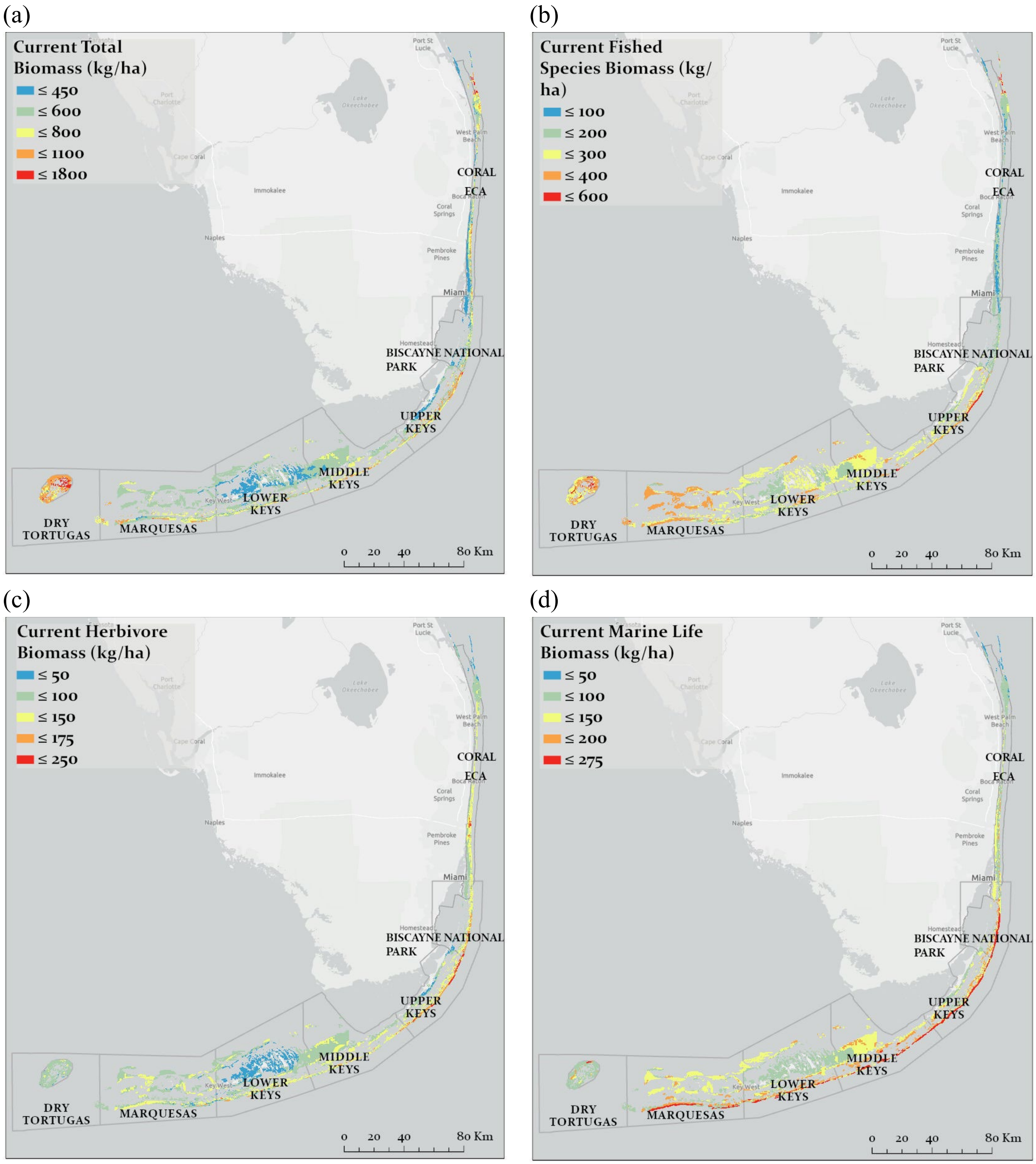
Fig. 8. Relationships between the top eight significant variables and the current biomass of species in the snapper-grouper complex as modelled by boosted regression trees. Values of log biomass of snapper-grouper species on the y-axis are normalised as opposed to showing actual biomass. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable.



Map 2. Spatial distribution of estimated current biomass of all species in the snapper-grouper complex (kg ha^{-1}) on the Florida reef tract.

Table 4. Comparison of boosted regression tree results of all biomass models.

Species Group	Variance explained	Correlation between observed and predicted values	Top five explanatory variables (and percentage of variance explained)
Total biomass	56.4%	0.76	Reef complexity (34.3%), Depth (11.3%), Year (7.7%), Wave exposure (6.1%), Coral cover (5.1%)
Fished species	52.2%	0.73	Reef complexity (31.8%), Fishing impact (9.1%), Depth (7.4%), Year (6.3%) Wave exposure (5.2%)
Snapper-grouper species complex	53.7%	0.74	Reef complexity (26.3%), Fishing impact (16.9%), Depth (10.9%), Net primary productivity (5.4%), Coral cover (5.4%)
Herbivores	67.2%	0.81	Reef complexity (21.0%), Year (9.3%), Distance to deep water (8.8%), Depth (8.5%), Coral cover (8.1%)
Marine life species	55.1%	0.75	Reef complexity (31.7%), Distance to deep water (11.4%), Year (8.7%), Depth (8.0%), Coral cover (7.2%)



Map 3. Spatial distribution of estimated current biomass of (a) total biomass, (b) fished species, (c) herbivores, and (d) marine life species (kg ha^{-1}) on the Florida reef tract.

3.5. Interpretation of the current biomass model

The metric of fishing impact derived by the project appeared to capture important properties of variability in fishing across the Florida reef tract; when used to predict fish biomass in an independent data set it showed declining fish biomass with increasing fishing impact (Fig. 8). Furthermore, this negative relationship with fishing impact was not seen for herbivorous and marine life species that are not heavily fished in Florida (Table 4, Appendix 3).

As found in the fishing impact model, fish biomass in the biomass model increased in more complex habitats, and also deeper habitats. Fish biomass varied with net primary productivity, although this relationship is complex (Fig. 8). Snapper-grouper biomass was higher on reefs with more coral cover, and this trend was particularly clear as coral cover increased from <1% to ~4%. Snapper-grouper biomass also increased with increasing reef habitat within 20 km. In addition to these variables that vary among habitats, habitat type itself was an important factor. Finally, year was a significant factor in the model, but there was no evidence of fish biomass consistently increasing or decreasing over time.

3.6. Area-specific models of current biomass

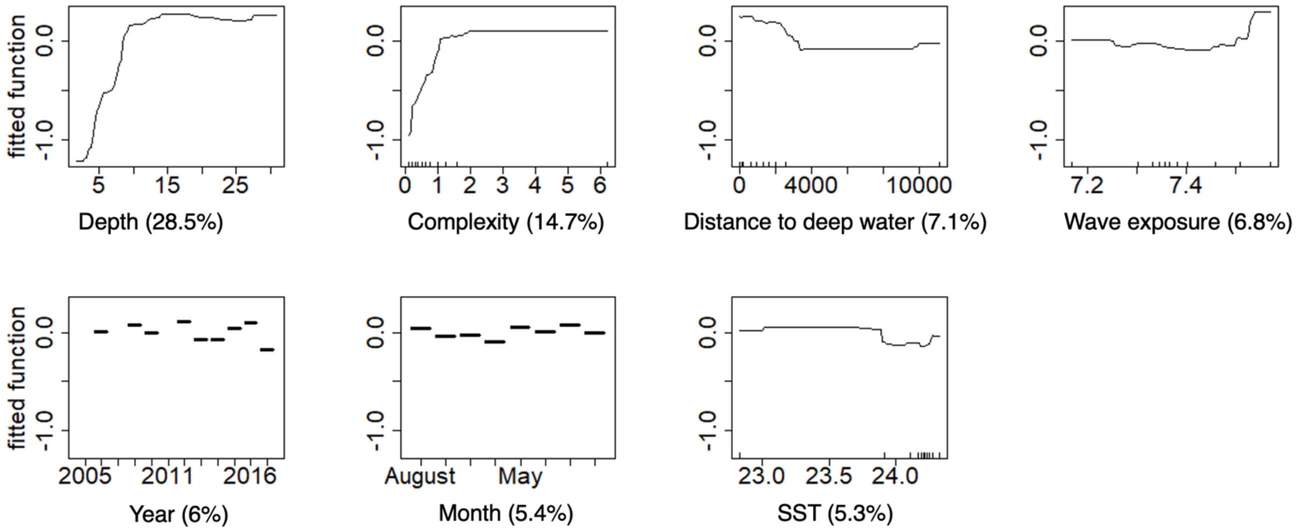
Area-specific models of current biomass were calculated for each group of species, but only the models for total biomass are shown here for brevity (Fig. 9). All of these models can be used to generate maps, but we recommend using the reef-tract-scale maps for visualization and conservation planning because they use the full data set. Rather, the models are primarily for examining relatively small-scale drivers of fish biomass.

The models for the six sections of the Florida reef tract, plus the entire FKNMS, demonstrated some differences among locations, but still highlight the primary importance of reef complexity as a driver of fish biomass. Similarly, fish biomass typically increased with increasing coral cover and depth. In general, variables that vary at the scale of the entire reef tract but not at more local scales, such sea surface temperature, wave exposure, and net primary productivity were less important in these models. However, for example, there appeared to be thresholds of wave exposure and connectivity to seagrass nurseries in the Middle Keys. Fishing impact also varies to a limited degree within each area, and its importance was limited. Larval connectivity only appeared to be important in the Lower Keys, possibly because of higher settlement rates (Sponaugle et al. 2012a).

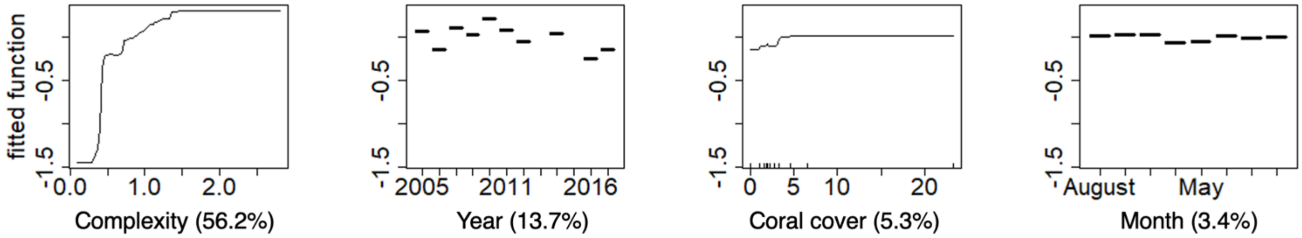
3.7. Species-specific models of current biomass

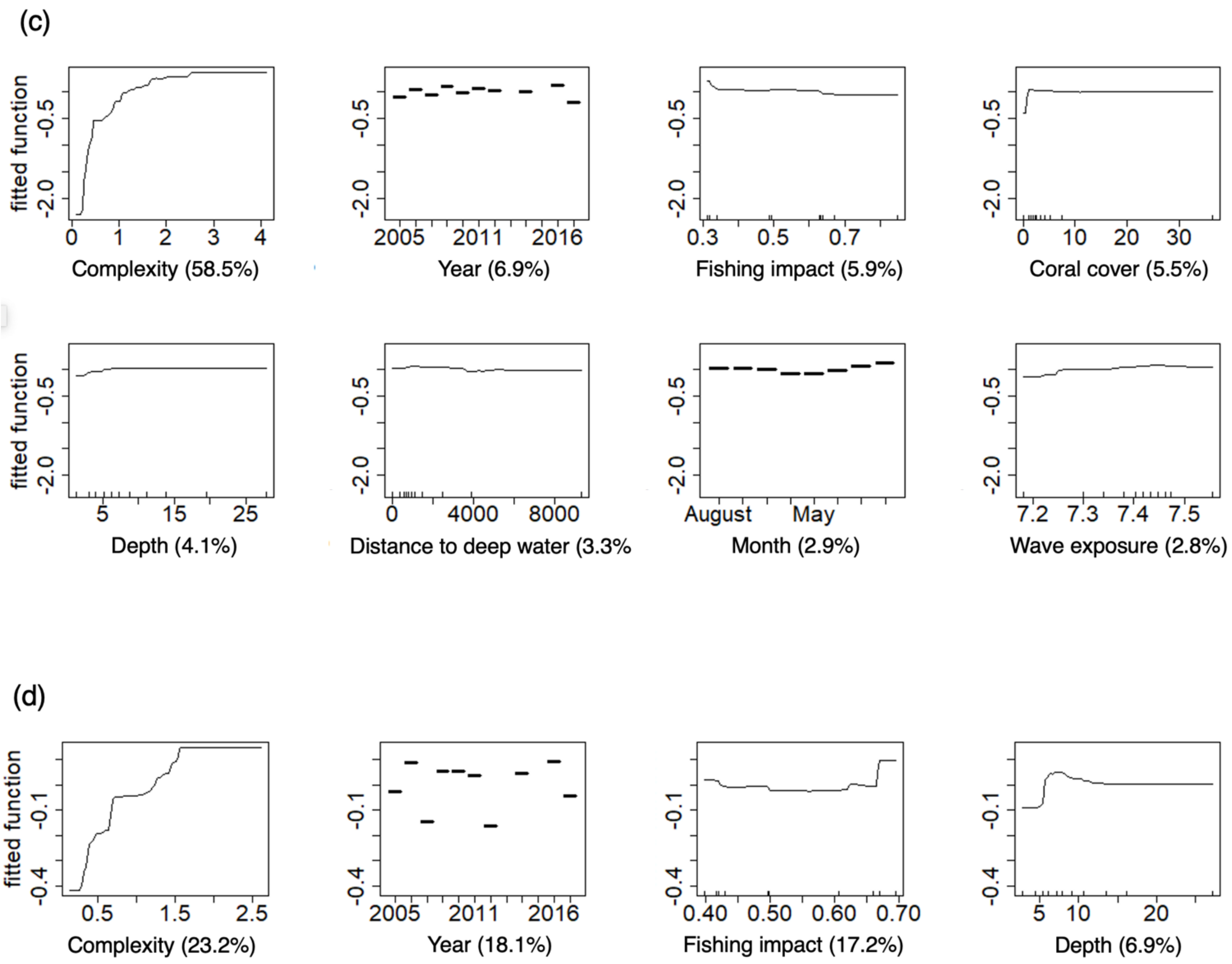
The models and maps of Hogfish, Yellowtail Snapper, and Stoplight Parrotfish abundance (Fig. 10, Map 4) provide some information on the natural history of each species. For example, Hogfish are less reliant on structure than many other species, but appear to use seagrass as nursery or foraging habitat. As expected, Yellowtail Snappers are heavily impacted by fishing, but also increase on more complex, shallow reefs. Finally, the density of Stoplight Parrotfish reflects much of what is known about their biology. For example, they are more abundant on shallow, complex reefs (Bozec et al. 2013), and appear to benefit from connectivity to seagrass nursery areas (Harborne et al. 2016).

(a)

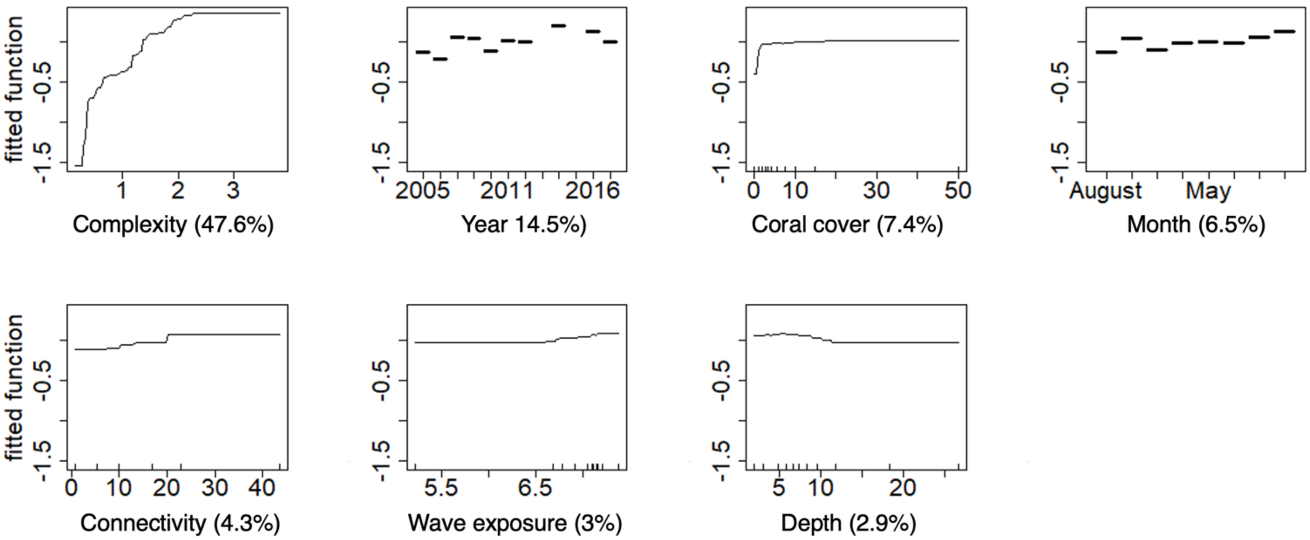

fitted function
0.0
-1.0
5
15
25
Depth (28.5%)
0
1
2
3
4
5
6
Complexity (14.7%)
0
4000
10000
Distance to deep water (7.1%)
7.2
7.4
Wave exposure (6.8%)
2005
2011
2016
Year (6%)
August
May
Month (5.4%)
23.0
23.5
24.0
SST (5.3%)

(b)

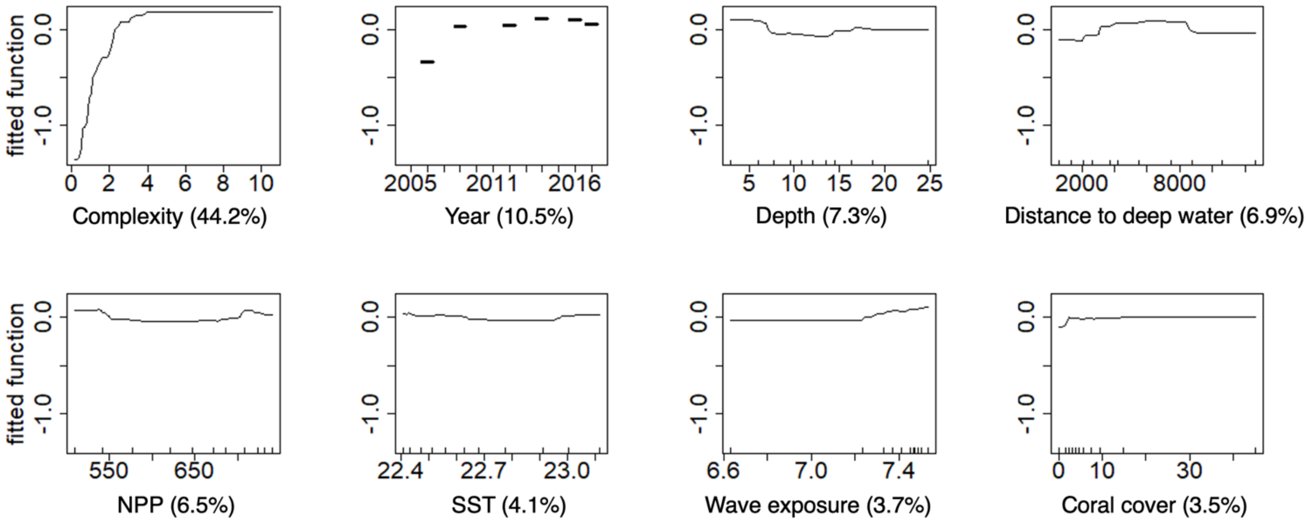

fitted function
-0.5
-1.5
0.0
1.0
2.0
Complexity (56.2%)
2005
2011
2016
Year (13.7%)
0
5
10
20
Coral cover (5.3%)
August
May
Month (3.4%)


(c)
fitted function
-0.5
-2.0
0 1 2 3 4
Complexity (58.5%)
2005 2011 2016
Year (6.9%)
0.3 0.5 0.7
Fishing impact (5.9%)
0 10 20 30
Coral cover (5.5%)
5 15 25
Depth (4.1%)
0 4000 8000
Distance to deep water (3.3%
August May
Month (2.9%)
7.2 7.3 7.4 7.5
Wave exposure (2.8%)
(d)
fitted function
-0.1
-0.4
0.5 1.5 2.5
Complexity (23.2%)
2005 2011 2016
Year (18.1%)
0.40 0.50 0.60 0.70
Fishing impact (17.2%)
5 10 20
Depth (6.9%)

(e)


fitted function
-1.5
-0.5
1
2
3
Complexity (47.6%)
2005
2011
2016
Year 14.5%)
0
10
30
50
Coral cover (7.4%)
August
May
Month (6.5%)
0
10
20
30
40
Connectivity (4.3%)
5.5
6.5
Wave exposure (3%)
5
10
20
Depth (2.9%)

(f)


fitted function
0.0
-1.0
0
2
4
6
8
10
Complexity (44.2%)
2005
2011
2016
Year (10.5%)
5
10
15
20
25
Depth (7.3%)
2000
8000
Distance to deep water (6.9%)
550
650
NPP (6.5%)
22.4
22.7
23.0
SST (4.1%)
6.6
7.0
7.4
Wave exposure (3.7%)
0
10
30
Coral cover (3.5%)

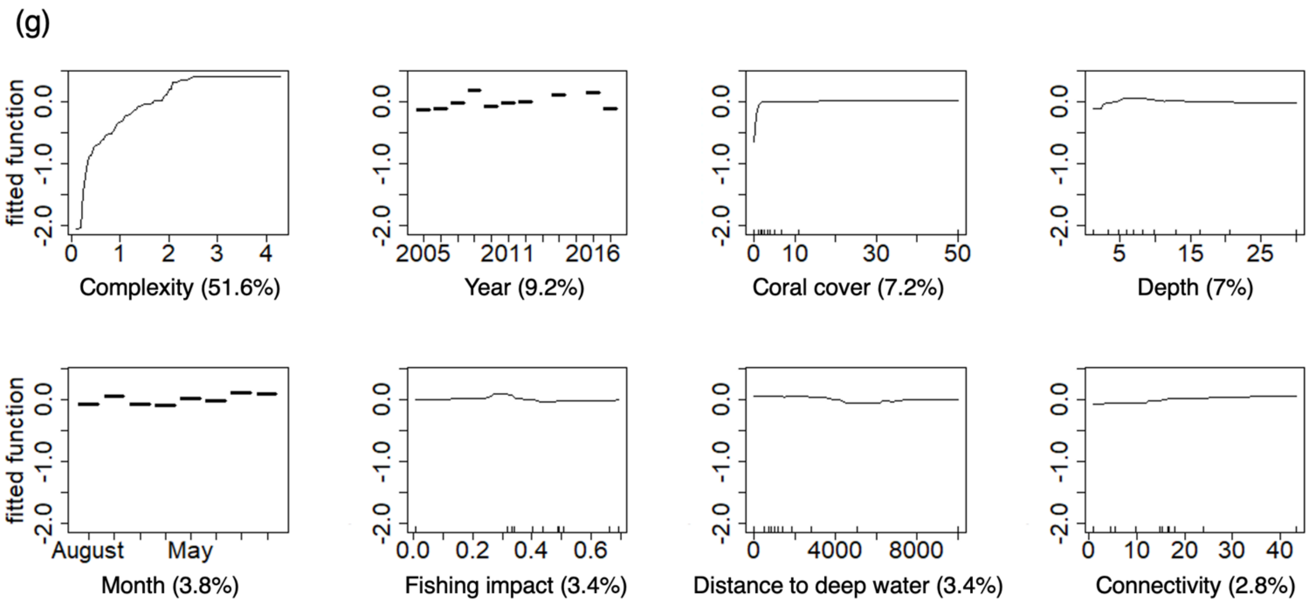
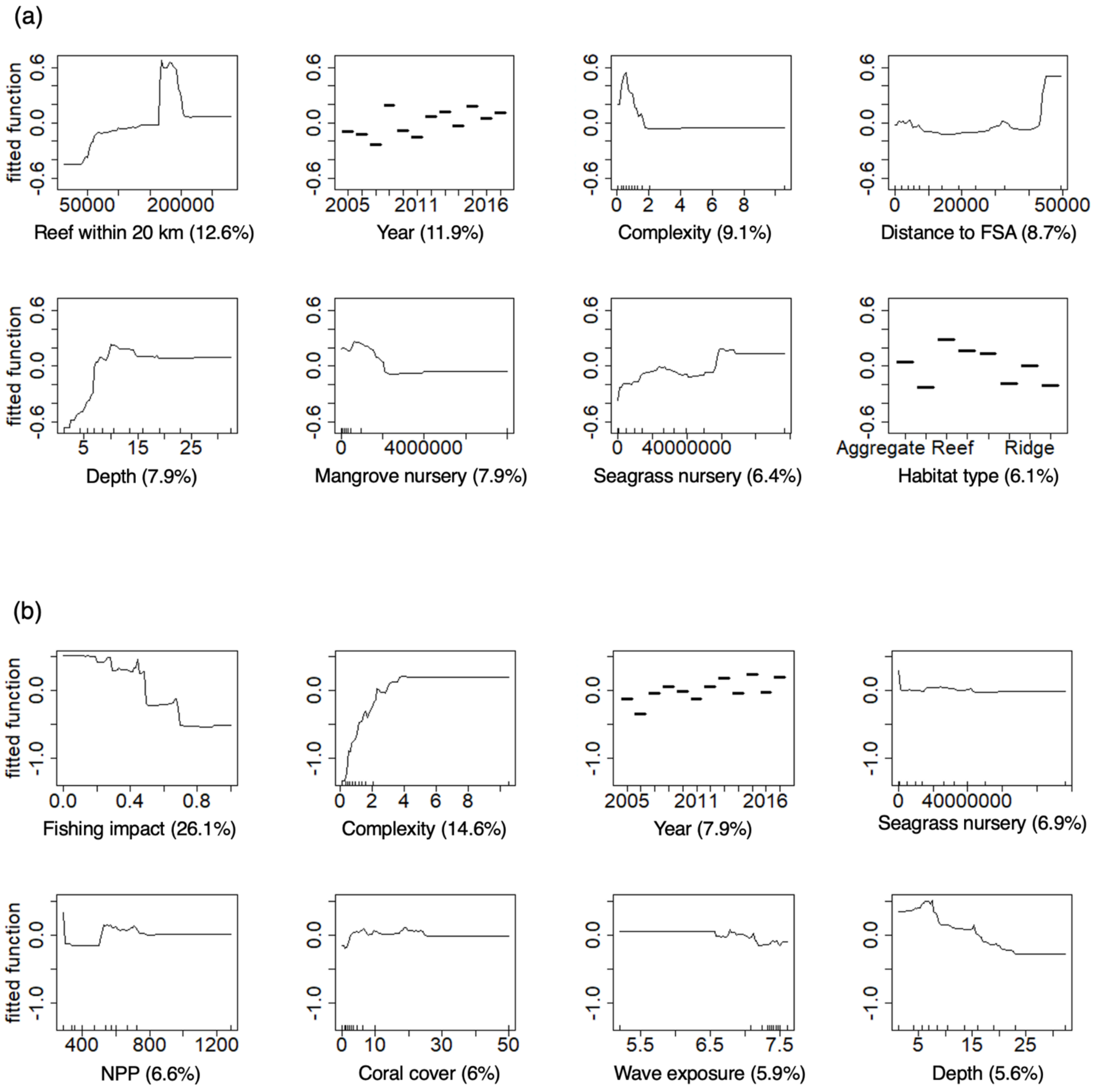


Fig. 9. Relationships between the top eight significant variables (unless the final model contained fewer variables) and the current total biomass modelled by boosted regression trees for (a) Coral ECA; (b) Biscayne National Park; (c) Upper Keys; (d) Middle Keys; (e) Lower Keys; (f) the Dry Tortugas; and (g) the entire FKNMS. Values of log fish biomass on the y-axis are normalised as opposed to showing actual biomass values. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable.


(a)
fitted function
-0.6
0.0
0.6
50000
200000
Reef within 20 km (12.6%)
2005
2011
2016
Year (11.9%)
0
2
4
6
8
Complexity (9.1%)
0
20000
50000
Distance to FSA (8.7%)
5
15
25
Depth (7.9%)
0
4000000
Mangrove nursery (7.9%)
0
40000000
Seagrass nursery (6.4%)
Aggregate Reef
Ridge
Habitat type (6.1%)
(b)
fitted function
-1.0
0.0
0.0
0.4
0.8
Fishing impact (26.1%)
0
2
4
6
8
Complexity (14.6%)
2005
2011
2016
Year (7.9%)
0
40000000
Seagrass nursery (6.9%)
400
800
1200
NPP (6.6%)
0
10
30
50
Coral cover (6%)
5.5
6.5
7.5
Wave exposure (5.9%)
5
15
25
Depth (5.6%)

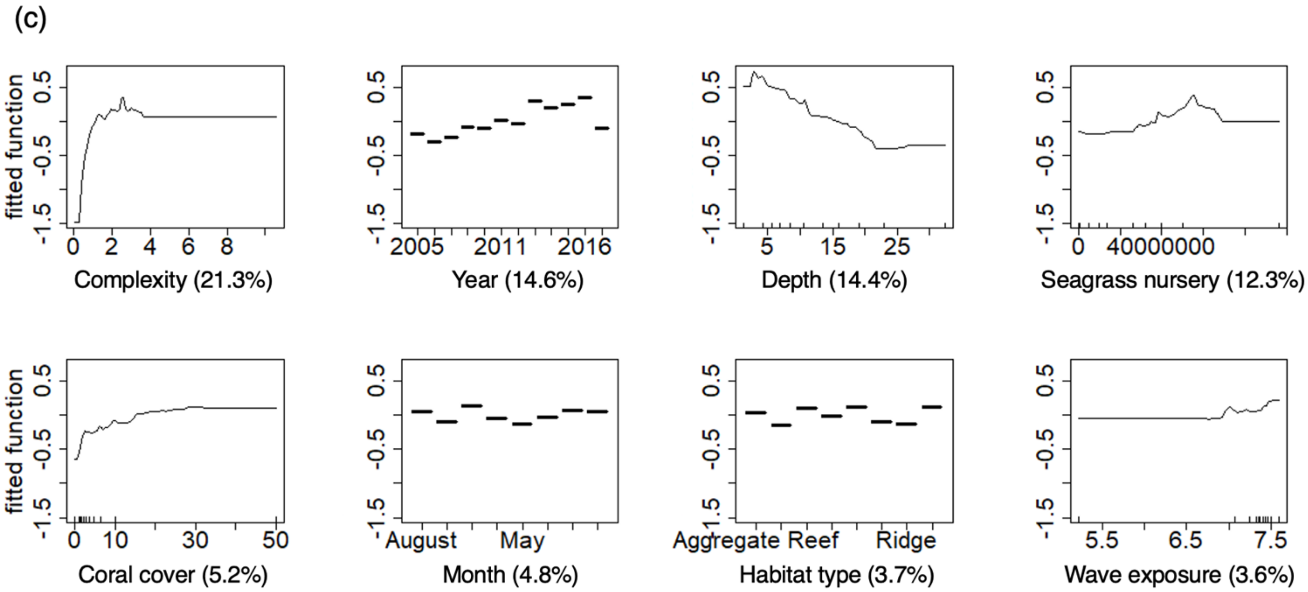
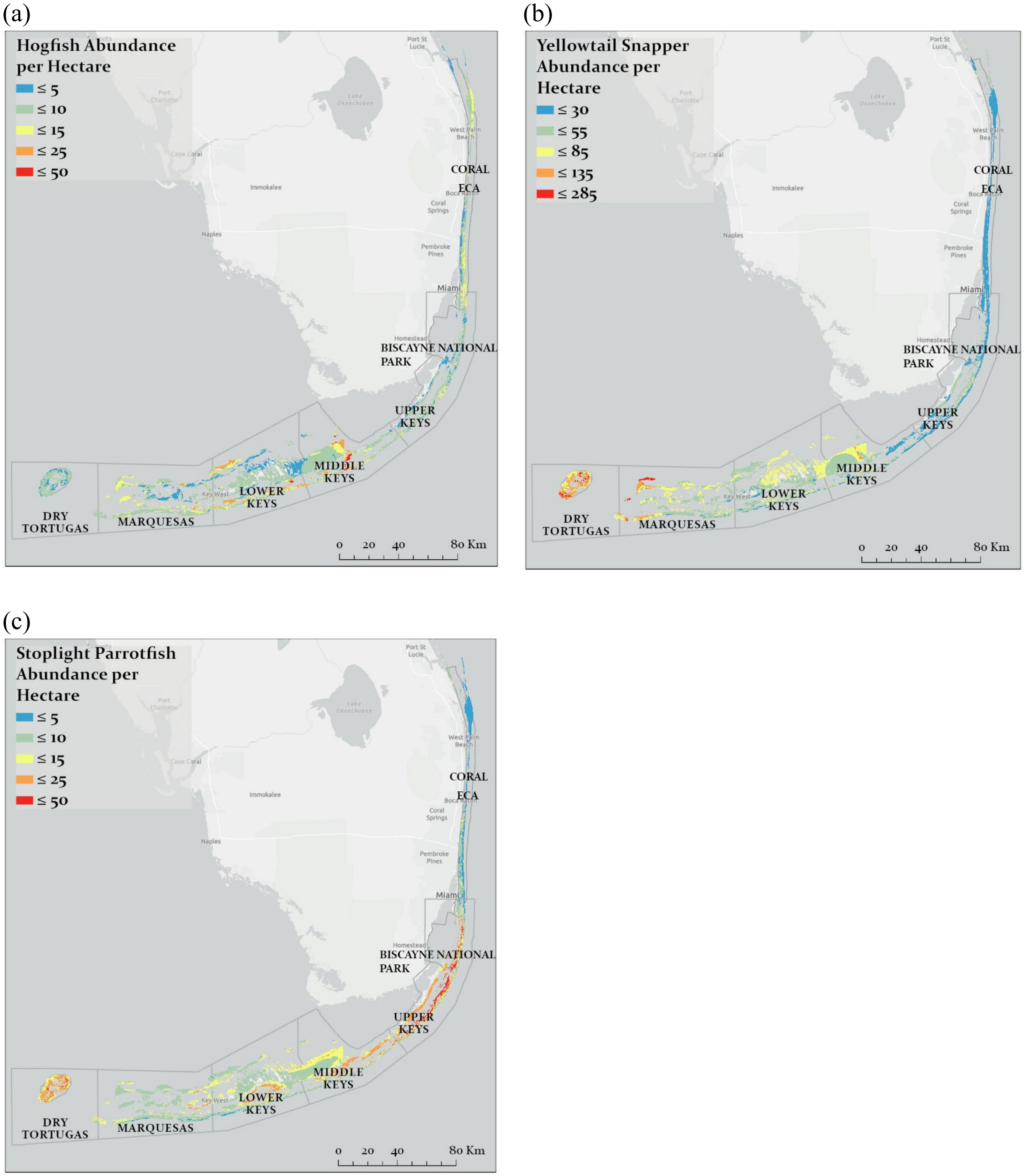


Fig. 10. Relationships between the top eight significant variables and the current density of (a) Hogfish, (b) Yellowtail snapper, and (c) Stoplight Parrotfish as modelled by boosted regression trees. Density values on the y-axis are normalised as opposed to showing actual density values. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable.

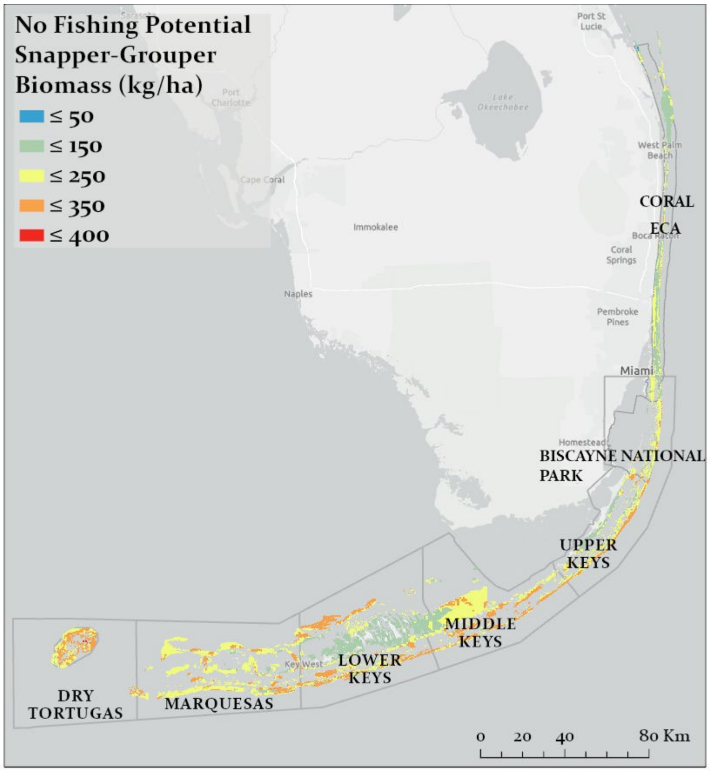


Map 4. Spatial distribution of estimated current density of (a) Hogfish, (b) Yellowtail Snapper, and (c) Stoplight Parrotfish (individuals ha^{-1}) on the Florida reef tract.

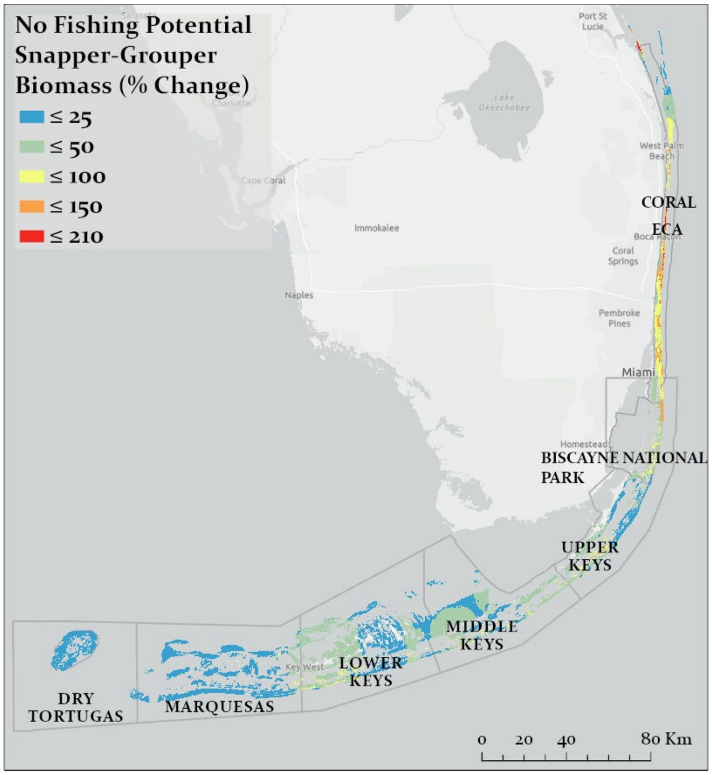
3.8. Generating a map of potential biomass

The map of potential biomass for species in the snapper-grouper complex (Map 5a) represents a hypothetical data layer of the potential biomass of fish at any location with no fishing impact. It was created by predicting the biomass in each 1 ha cell with fishing impact set to 0 (as opposed to the value actually predicted by the fishing impact model). Note that rather than setting fishing to a true value of 0, this product is for a fishing impact of 0 as determined by current levels assessed along the reef tract. It is likely that the current index of 0 in Florida does not represent a truly natural biomass of fishes in the region, because of the wide ranging footprint of commercial and recreational fishing (Ault et al. 1998). Consequently, reefs untouched by fishing for a long period may be able to support more fishes than shown here (Map 5a), and carrying capacities will increase if reef health recovers (e.g. higher coral cover and complexity). The map of potential biomass represents a carrying capacity that might be reached within a well-enforced no-take reserve under current reef conditions. Because of the complex social-ecological processes on reefs, this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors. This map should also not be viewed as any particular proposal by the authors for additional no-take areas. Rather, it indicates potential increases of biomass. Given that the project has also estimated the current biomass of fishes in this group (Map 2), the change under a no-fishing scenario can also be expressed as the potential percentage gain (Map 5b).

(a)



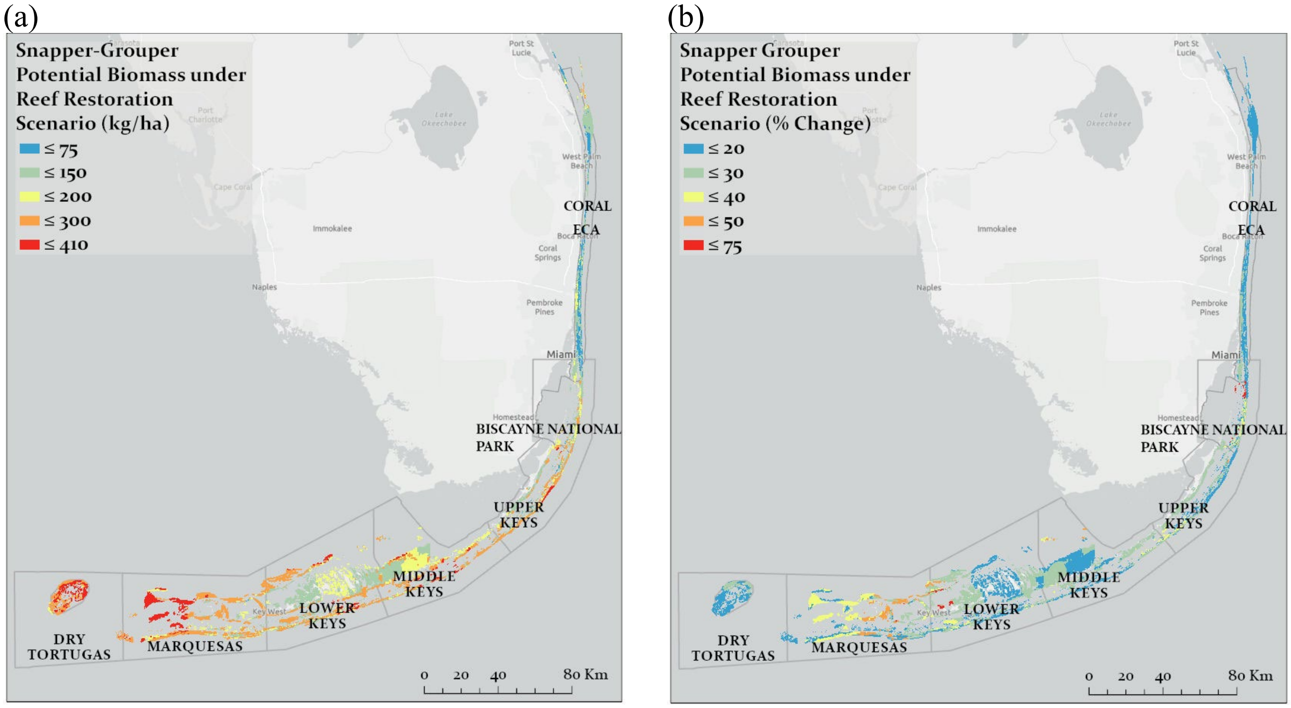
(b)



Map 5. Spatial distribution of (a) predicted potential biomass (kg ha^{-1}) of all species in the snapper-grouper complex in the absence of fishing across the Florida reef tract and (b) percentage increase of snapper-grouper biomass compared to current estimates.

3.9 Exploring potential benefits of other management actions

The models presented above allow us to explore the potential benefits of additional management actions. Map 6 illustrates the predicted potential biomass of the snapper-grouper complex species under a management scenario informed by the Restoring Seven Iconic Reefs management initiative proposed by NOAA. Our scenario increases coral cover to 15% and increases reef complexity (i.e. average maximum hard relief) by 15 cm. This simulates a coral restoration program that also increases reef complexity over time.



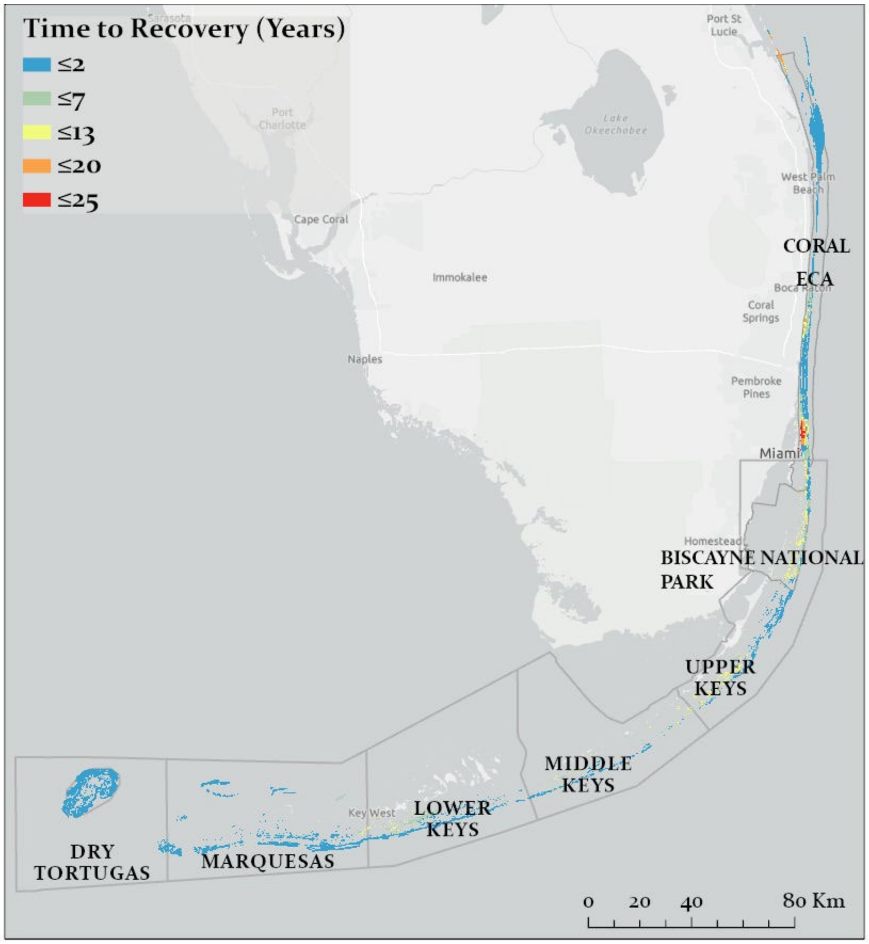
Map 6. Spatial distribution of (a) predicted potential biomass (kg ha^{-1}) of all species in the snapper-grouper complex with an increase of coral cover to 15% and an increase in complexity of 15 cm and (b) percentage increase of snapper-grouper biomass compared to current estimates.

3.10. Generating maps of fish assemblage status and time to recovery

Previous studies have suggested that the ratio of current to potential fish biomass provides some insights into the status of the fishery and some ecological processes (McClanahan et al. 2011, Karr et al. 2015). For example, when this ratio falls below 0.5 it is possible that the reef is approaching an unsustainable fishery and potentially some thresholds of ecosystem processes. Conversely, reefs where this ratio is >0.9 are considered to be virtually intact and with effectively no impacts on reef functioning (MacNeil et al. 2015). Although the majority of reefs on the Florida reef tract appear to be above the 0.5 threshold, this should be interpreted with caution because whether these thresholds are similar throughout the world is not clear. Consequently, negative impacts on reef functions may still occur when current biomass is at a higher proportion of potential biomass.

A global analysis of reef fish has provided an estimated relationship between the ratio of current to potential biomass and time to "recovery", defined as reaching 90% of potential biomass (MacNeil et al.

2015). The project used this relationship to estimate the time it would take each 1 ha cell to reach this threshold of 0.9 of potential biomass of all reef fish species, where potential biomass is the biomass under a scenario with 0 fishing impact (Map 7). Note that this was only done for coral reef sites, as the recovery curve is only parameterized for coral reefs. Our results show that for some areas in the region, reefs may not recover following the cessation of fishing for decades. However, these results should be interpreted with caution because of the relatively limited impact of fishing on many of the species included in the total biomass on Florida's reefs (e.g. parrotfishes, damselfishes, morays). Time to recovery for species in the snapper-grouper complex are likely to be much longer because the group is heavily targeted by commercial and recreational fisheries, and recovery is complex given the functional extinction of many spawning aggregations. Unfortunately there are currently no published recovery curves available to characterize recovery of just the snapper-grouper assemblage that this work shows is most impacted by fishing and thus will take longest to recover. Furthermore, these estimates do not account for any other changes, positive or negative, associated with marine environments, such as improved habitat quality or biophysical changes due to climate change. For example, if coral cover increased further then the potential fish biomass also increases and it would take longer to reach these higher levels. Furthermore, the threshold of 0.9 of potential biomass may not include full recovery of some ecologically or economically important species. These caveats underscore the need to expand management initiatives as soon as possible.



Map 7. Spatial distribution of the predicted time to recovery (90% of predicted potential biomass of all reef fish species, measured in years) following the cessation of fishing across the coral sites of the Florida reef tract.

4. Summary of patterns highlighted in the maps

The maps of fishing impact and biomass (Maps 1 and 2) highlight the expected patterns of high fishing impact in southeastern Florida adjacent to major population centers such as Miami and Ft. Lauderdale, and relatively low impact in the remote Dry Tortugas. Known centers of commercial and recreational fishing in the Florida Keys such as Islamorada, Marathon and Key West show increased fishing impact, though impact across the Keys remains lower than in the southeast region. In the Keys, impact is slightly lower in John Pennekamp State Park and in the vicinity of the more sparsely populated Cudjoe, Big Torch and Little Torch, Big Pine and No Name Keys. The areas of high and medium fishing impact showed decreased current biomass estimates, but the biomass of fishes was also affected by complex interactions of other factors including depth, complexity and primary productivity. Consequently, the distribution of fish biomass along the Florida reef tract shows significant heterogeneity.

Additionally, fishing impact was shown to impact different groups of fishes differently. As expected, fished species, including those in the snapper-grouper complex, were more strongly impacted by fishing than herbivores or the fish assemblage overall (which includes many small, unfished species). The models allow us to explore the impact of fishing on individual species, and other species groups of interest identified by the management community.

5. Participation in meetings with state and federal management agencies

One of the Services and Deliverables in the project contract was participation in an inception meeting. Though no formal inception meeting took place, Harborne and Zuercher attended several informal meetings. In addition, Harborne and Zuercher have attended and presented interim results at numerous meetings with state and federal resource managers including:

- Florida Fish and Wildlife Research Institute (6/29/2019)
- Florida Department of Environmental Protection (7/9/2019)
- Florida Keys National Marine Sanctuary (7/22/2019)
- Biscayne Bay National Park (8/14/2019)
- SEFCRI Technical Advisory Committee (10/30/2019)

Feedback from these meetings has been incorporated into the models and maps presented here.

In addition, during Phase 2 the work was presented to the following TNC groups:
- Mapping Ocean Wealth (06/02/2020)
- Florida and Caribbean team (09/03/2020)

6. Future Work

This report documents the work completed in Phase 1 and Phase 2 of this project, and the future focus of the project will be to disseminate the results. This is likely to occur through two mechanisms. The first is publication of the results in scientific journals and presentations at conference, and the project team have prepared a draft manuscript focusing on the drivers of fish biomass and how various management actions (reducing fishing, coral restoration, and increasing structure artificially) affect fish biomass. It is anticipated that this paper will be submitted for publication in the fall of 2020.

The second mechanism is by publicizing data layers on the Mapping Ocean Wealth data portal to allow users to explore the products presented here. If paired with corresponding communication efforts, having the products online can increase awareness of the work, and increase their use in conservation planning. It is also possible that resource managers will request additional products to help with their specific needs. We aim to meet these requests to the fullest extent possible given the capacities of the project team. It may also be necessary to form a protocol for sharing the raw data layers (i.e. the original GIS layers): we encourage their use for research and management purposes, but need to ensure TNC receive appropriate credit for the products.

Additional funding could also increase the scope of the work in the future. For example, additional research could include:

- Modelling coral cover and rugosity across the reef tract to improve the fish biomass estimates
- Linking fishing impact to actual fishing pressure through use of data sets such as the State Reef Fish Surveys
- Examining the links between fish standing stocks and fish productivity
- Looking at other management scenarios, and the returns on investment of each one

7. Potential use of map products in marine management

The maps presented in this report are the first spatially explicit, continuous maps of fishing impact and current and potential biomass in south Florida, and provide a visually appealing overview of the current state of fishes and fishing in the region that can be used in a range of education and outreach exercises with multiple stakeholders. The maps also provide a baseline for future comparisons. Finally, the maps of fishing impact and fish biomass implicitly represent aspects of ocean value, as they represent protein that has been, or could be, harvested. Such stocks therefore represent critical ‘natural capital’ and provide important insight into its distribution. As such, these maps may have multiple uses for conservation and management. They could be used to identify priority sites for new reserves should managers wish to establish them. While many spatial planning exercises are limited by data availability (Pittman and Brown 2011), and data are rarely available on fishing and fish stock during the planning process despite being critical inputs, these maps fill that data gap for the Florida reef tract. The maps highlight areas with relatively low fishing impact (limited conflicts with fishers), high potential increases in fish biomass, or particularly high potential stocks that could lead to significant larval production to supply fished reefs. Alternatively, reefs that already have a high biomass and a low potential for improvement may be good choices for protected areas because they are already making important contributions to achieving ecological and social objectives (e.g. biodiversity protection and tourism and recreation). The maps could also be used to provide information when considering other types of fishery regulations, such as bag limits or minimum catch sizes. However, with all planning exercises and consideration of additional regulations, the benefits of management action must be contemplated in the context of trade-offs with a wide range of other ecological and socio-economic considerations (e.g., Seeteram et al. 2019).

Finally, while the results of reducing fishing to zero as would occur in a no-take reserve have been presented here, the models also provide the future opportunity to run additional scenarios for different management techniques that might affect any significant variable in our models. Furthermore, if the cost of each action was known, this work could provide information on return on investments of different activities.

References

Abesamis, R. A., A. L. Green, G. R. Russ, and C. R. L. Jadloc. 2014. The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. Reviews In Fish Biology And Fisheries **24**:1033-1063.

Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society B-Biological Sciences **276**:3019-3025.

Arkema, K. K., G. M. Verutes, S. A. Wood, C. Clarke-Samuels, S. Rosado, M. Canto, A. Rosenthal, M. Ruckelshaus, G. Guannel, J. Toft, J. Faries, J. M. Silver, R. Griffin, and A. D. Guerry. 2015. Embedding ecosystem services in coastal planning leads to better outcomes for people and nature. Proceedings of the National Academy of Sciences of the United States of America **112**:7390-7395.

Ault, J. S., J. A. Bohnsack, and G. A. Meester. 1998. A retrospective (1979-1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fishery Bulletin **96**:395-414.

Ault, J. S., J. A. Bohnsack, S. G. Smith, and J. G. Luo. 2005. Towards sustainable multispecies fisheries in the Florida, USA, coral reef ecosystem. Bulletin of Marine Science **76**:595-622.

Ault, J. S., S. G. Smith, J. A. Bohnsack, J. G. Luo, N. Zurcher, D. B. McClellan, T. A. Ziegler, D. E. Hallac, M. Patterson, M. W. Feeley, B. I. Ruttenberg, J. Hunt, D. Kimball, and B. Causey. 2013. Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. Fisheries Research **144**:28-37.

Baine, M. 2001. Artificial reefs: a review of their design, application, management and performance. Ocean & Coastal Management **44**:241-259.

Bell, J. D., and R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series **15**:265-274.

Blair, S. M., T. L. McIntosh, and B. J. Mostkoff. 1994. Impacts of Hurricane Andrew on the offshore reef systems of central and northern Dade County, Florida. Bulletin of Marine Science **54**:961-973.

Bohnsack, J. A. 2011. Impacts of Florida coastal protected areas on recreational world records for spotted seatrout, red drum, black drum, and common snook. Bulletin of Marine Science **87**:939-970.

Bohnsack, J. A., D. E. Harper, and D. B. McClellan. 2007. Coral reef fish response to FKNMS management zone: the first ten years (1997-2007). Progress Report to the Florida Keys National Marine sanctuary. PRBD 08/09-10.

Bozec, Y. M., L. Yakob, S. Bejarano, and P. J. Mumby. 2013. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. Oikos **122**:428-440.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist **11**:99-118.

Chiappone, M., D. W. Swanson, S. L. Miller, and S. G. Smith. 2002. Large-scale surveys on the Florida Reef Tract indicate poor recovery of the long-spined sea urchin *Diadema antillarum*. Coral Reefs **21**:155-159.

Chollett, I., S. W. J. Canty, S. J. Box, and P. J. Mumby. 2014. Adapting to the impacts of global change on an artisanal coral reef fishery. Ecological Economics **102**:118-125.

Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. Coral Reefs **31**:493-503.

Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. Limnology and Oceanography **57**:1233-1244.

Cinner, J. E., N. A. J. Graham, C. Huchery, and M. A. MacNeil. 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. Conservation Biology **27**:453-458.

Cinner, J. E., C. Huchery, M. A. MacNeil, N. A. J. Graham, T. R. McClanahan, J. Maina, E. Maire, J. N. Kittinger, C. C. Hicks, C. Mora, E. H. Allison, S. D'Agata, A. Hoey, D. A. Feary, L. Crowder, I. D. Williams, M. Kulbicki, L. Vigliola, L. Wantiez, G. Edgar, R. D. Stuart-Smith, S. A. Sandin, A. L. Green, M. J. Hardt, M. Beger, A. Friedlander, S. J. Campbell, K. E. Holmes, S. K. Wilson, E. Brokovich, A. J. Brooks, J. J. Cruz-Motta, D. J. Booth, P. Chabanet, C. Gough, M. Tupper, S. C. A. Ferse, U. R. Sumaila, and D. Mouillot. 2016. Bright spots among the world's coral reefs. Nature **535**:416-419.

Coker, D. J., S. K. Wilson, and M. S. Pratchett. 2014. Importance of live coral habitat for reef fishes. Reviews In Fish Biology And Fisheries **24**:89-126.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science **311**:522-527.

Dames, V., A. Bernard, C. Floros, B. Mann, C. Speed, J. Maggs, S. Laing, M. Meekan, and J. Olbers. 2020. Zonation and reef size significantly influence fish population structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. Ocean & Coastal Management **185**:105040.

Davis, G. E. 1977. Anchor damage to a coral reef on the coast of Florida. Biological Conservation **11**:29-34.

Dorenbosch, M., M. G. G. Grol, I. Nagelkerken, and G. van der Velde. 2006. Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. Biological Conservation **129**:277-282.

Dustan, P. 2000. The Florida Keys. Pages 405-414 *in* C. R. C. Sheppard, editor. Seas at The Millennium: An environmental evaluation. Volume 1. Elsevier Science, Amsterdam.

Ekebom, J., P. Laihonen, and T. Suominen. 2003. A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. Estuarine Coastal and Shelf Science **57**:887-898.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology **77**:802-813.

Ferrari, R., M. Gonzalez-Rivero, J. C. Ortiz, and P. J. Mumby. 2012. Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. Coral Reefs **31**:683-692.

Froese, R., and D. Pauly. 2010. FishBase. Retrieved from http://www.fishbase.org.

Fulton, C. J., D. R. Bellwood, and P. C. Wainwright. 2005. Wave energy and swimming performance shape coral reef fish assemblages. Proceedings of the Royal Society B-Biological Sciences **272**:827-832.

Gove, J. M., G. J. Williams, M. A. McManus, S. F. Heron, S. A. Sandin, O. J. Vetter, and D. G. Foley. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. PLoS ONE **8**:e61974.

Graham, N. A. J., N. K. Dulvy, S. Jennings, and N. V. C. Polunin. 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs **24**:118-124.

Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs **32**:315-326.

Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology **66**:650-667.

Guillemot, N., P. Chabanet, M. Kulbicki, L. Vigliola, M. Léopold, I. Jollit, and O. Le Pape. 2014. Effects of fishing on fish assemblages in a coral reef ecosystem: From functional response to potential indicators. Ecological Indicators **43**:227-235.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters **5**:361-366.

Harborne, A. R., A. L. Green, N. A. Peterson, M. Beger, Y. Golbuu, P. Houk, M. D. Spalding, B. M. Taylor, E. Terk, E. A. Treml, S. Victor, L. Vigliola, I. D. Williams, N. H. Wolff, P. S. E. zu Ermgassen, and P. J. Mumby. 2018. Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia. Diversity and Distributions **24**:1729-1743.

Harborne, A. R., P. J. Mumby, F. Micheli, C. T. Perry, C. P. Dahlgren, K. E. Holmes, and D. R. Brumbaugh. 2006a. The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. Advances in Marine Biology **50**:57-189.

Harborne, A. R., P. J. Mumby, K. Żychaluk, J. D. Hedley, and P. G. Blackwell. 2006b. Modeling the beta diversity of coral reefs. Ecology **87**:2871-2881.

Harborne, A. R., I. Nagelkerken, N. H. Wolff, Y.-M. Bozec, M. Dorenbosch, M. G. G. Grol, and P. J. Mumby. 2016. Direct and indirect effects of nursery habitats on coral-reef fish assemblages, grazing pressure and benthic dynamics. Oikos **125**:957-967.

Hixon, M. A. 2011. 60 years of coral reef fish ecology: past, present, future. Bulletin of Marine Science **87**:727-765.

Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecological Monographs **63**:77-101.

Houk, P., K. Rhodes, J. Cuetos-Bueno, S. Lindfield, V. Fread, and J. L. McIlwain. 2012. Commercial coral-reef fisheries across Micronesia: A need for improving management. Coral Reefs **31**:13-26.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science **265**:1547-1551.

Huijbers, C. M., I. Nagelkerken, A. O. Debrot, and E. Jongejans. 2013. Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. Ecology **94**:1859-1870.

Jacquet, C., D. Mouillot, M. Kulbicki, and D. Gravel. 2016. Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. Ecology Letters:doi:10.1111/ele.12716.

Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. Fish and Fisheries **6**:212-232.

Jennings, S., J. D. Reynolds, and N. V. C. Polunin. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conservation Biology **13**:1466-1475.

Johansen, J. L., D. R. Bellwood, and C. J. Fulton. 2008. Coral reef fishes exploit flow refuges in high-flow habitats. Marine Ecology Progress Series **360**:219-226.

Johns, G. M., V. R. Leeworthy, F. W. Bell, and M. A. Bonn. 2001. Socioeconomic Study of Reefs in Southeast Florida. Hazen and Sawyer, Hollywood, FL.

Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America **101**:8251-8253.

Karr, K. A., R. Fujita, B. S. Halpern, C. V. Kappel, L. Crowder, K. A. Selkoe, P. M. Alcolado, and D. Rader. 2015. Thresholds in Caribbean coral reefs: implications for ecosystem-based fishery management. Journal of Applied Ecology **52**:402-412.

Kemp, D. W., M. A. Colella, L. A. Bartlett, R. R. Ruzicka, J. W. Porter, and W. K. Fitt. 2016. Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. Ecosphere **7**:e01373.

Kronen, M., F. Magron, B. McArdle, and A. Vunisea. 2010. Reef finfishing pressure risk model for Pacific Island countries and territories. Fisheries Research **101**:1-10.

Ladd, M. C., D. E. Burkepile, and A. A. Shantz. 2019. Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. Restoration Ecology **27**:1166-1176.

MacNeil, M. A., N. A. J. Graham, J. E. Cinner, S. K. Wilson, I. D. Williams, J. Maina, S. Newman, A. M. Friedlander, S. Jupiter, N. V. C. Polunin, and T. R. McClanahan. 2015. Recovery potential of the world's coral reef fishes. Nature **520**:341-344.

Manzello, D. P. 2015. Rapid recent warming of coral reefs in the Florida Keys. Scientific Reports **5**:16762.

Maynard, J., J. Byrne, K. Kerrigan, D. Tracey, K. Bohnsack, F. Pagan, J. Walczak, and G. J. Williams. 2017. Coral reef resilience to climate change in the Florida Reef Tract. Florida Department of Environmental Protection, Miami, FL.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17**:1055-1067.

McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences of the United States of America **108**:17230-17233.

McClenachan, L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. Conservation Biology **23**:636-643.

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications **14**:1709-1723.

Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. Proceedings of the Royal Society B-Biological Sciences **275**:767-773.

Mora, C., O. Aburto-Oropeza, A. A. Bocos, P. M. Ayotte, S. Banks, A. G. Bauman, M. Beger, S. Bessudo, D. J. Booth, E. Brokovich, A. Brooks, P. Chabanet, J. E. Cinner, J. Cortés, J. J. Cruz-Motta, A. C. Magaña, E. E. DeMartini, G. J. Edgar, D. A. Feary, S. C. A. Ferse, A. M. Friedlander, K. J. Gaston, C. Gough, N. A. J. Graham, A. Green, H. Guzman, M. Hardt, M. Kulbicki, Y. Letourneur, A. López Pérez, M. Loreau, Y.

Loya, C. Martinez, I. Mascareñas-Osorio, T. Morove, M. O. Nadon, Y. Nakamura, G. Paredes, N. V. C. Polunin, M. S. Pratchett, H. Reyes Bonilla, F. Rivera, E. Sala, S. A. Sandin, G. Soler, R. Stuart-Smith, E. Tessier, D. P. Tittensor, M. Tupper, P. Usseglio, L. Vigliola, L. Wantiez, I. Williams, S. K. Wilson, and F. A. Zapata. 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biology **9**:e1000606.

Mosquera, I., I. M. Côté, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation **3**:321-332.

Mumby, P. J. 2006. Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. Biological Conservation **128**:215-222.

Mumby, P. J., S. Bejarano, Y. Golbuu, R. S. Steneck, S. N. Arnold, R. van Woesik, and A. M. Friedlander. 2013. Empirical relationships among resilience indicators on Micronesian reefs. Coral Reefs **32**:213-226.

Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature **427**:533-536.

Mumby, P. J., and A. R. Harborne. 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS ONE:e8657.

O'Toole, A. C., A. J. Danylchuk, T. L. Goldberg, C. D. Suski, D. P. Philipp, E. Brooks, and S. J. Cooke. 2011. Spatial ecology and residency patterns of adult great barracuda (*Sphyraena barracuda*) in coastal waters of The Bahamas. Marine Biology **158**:2227-2237.

Palandro, D. A., S. Andréfouët, C. Hu, P. Hallock, F. E. Müller-Karger, P. Dustan, M. K. Callahan, C. Kranenburg, and C. R. Beaver. 2008. Quantification of two decades of shallow-water coral reef habitat decline in the Florida Keys National Marine Sanctuary using Landsat data (1984-2002). Remote Sensing of Environment **112**:3388-3399.

Pittman, S. J., and K. A. Brown. 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. PLoS ONE **6**:e20583.

Pratchett, M. S., P. L. Munday, S. K. Wilson, N. A. J. Graham, J. E. Cinner, D. R. Bellwood, G. P. Jones, N. V. C. Polunin, and T. R. McClanahan. 2008. Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. Oceanography and Marine Biology: An Annual Review **46**:251-296.

Precht, W. F., B. E. Gintert, M. L. Robbart, R. Fura, and R. van Woesik. 2016. Unprecedented disease-related coral mortality in southeastern Florida. Scientific Reports **6**:31374.

Riegl, B. M., and R. E. Dodge, editors. 2008. Coral Reefs of the USA. Springer, Dordrecht, Netherlands.

Robertson, D. R., and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. Journal of Experimental Marine Biology and Ecology **40**:285-298.

Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. Current Biology **24**:1000-1005.

Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. Pages 421-443 *in* P. F. Sale, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego.

Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138**:622-627.

Russ, G. R., A. J. Cheal, A. M. Dolman, M. J. Emslie, R. D. Evans, I. Miller, H. Sweatman, and D. H. Williamson. 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. Current Biology **18**:R514-R515.

Ruttenberg, B. I., P. J. Schofield, J. L. Akins, A. Acosta, M. W. Feeley, J. Blondeau, S. G. Smith, and J. S. Ault. 2012. Rapid invasion of Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida Keys, USA: evidence from multiple pre- and post-invasion data sets. Bulletin of Marine Science **88**:1051-1059.

Sherman, K. D., C. P. Dahlgren, J. R. Stevens, and C. R. Tyler. 2016. Integrating population biology into conservation management for endangered Nassau grouper *Epinephelus striatus*. Marine Ecology Progress Series **554**:263-280.

Shin, Y.-J., L. J. Shannon, A. Bundy, M. Coll, K. Aydin, N. Bez, J. L. Blanchard, M. d. F. Borges, I. Diallo, E. Diaz, J. J. Heymans, L. Hill, E. Johannesen, D. Jouffre, S. Kifani, P. Labrosse, J. S. Link, S. Mackinson,

H. Masski, C. Möllmann, S. Neira, H. Ojaveer, K. O. M. Abdallahi, I. Perry, D. Thiao, D. Yemane, and P. M. Cury. 2010. Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. ICES Journal of Marine Science **67**:692-716.

Shin, Y. J., M. J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science **62**:384-396.

Shinn, E. A., and B. H. Lidz. 2018. Geology of the Florida Keys. University Press of Florida, Gainesville, FL.

Soykan, C. U., T. Eguchi, S. Kohin, and H. Dewar. 2014. Prediction of fishing effort distributions using boosted regression trees. Ecological Applications **24**:71-83.

Sponaugle, S., C. Paris, K. D. Walter, V. Kourafalou, and E. D'Alessandro. 2012a. Observed and modeled larval settlement of a reef fish to the Florida Keys. Marine Ecology Progress Series **453**:201-212.

Sponaugle, S., K. D. Walter, K. Grorud-Colvert, and M. J. Paddack. 2012b. Influence of marine reserves on reef fish recruitment in the upper Florida Keys. Coral Reefs **31**:641-652.

Stallings, C. D. 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. PLoS ONE **4**:e5333.

Taylor, B. M., P. Houk, G. R. Russ, and J. H. Choat. 2014a. Life histories predict vulnerability to overexploitation in parrotfishes. Coral Reefs **33**:869-878.

Taylor, B. M., S. J. Lindfield, and J. H. Choat. 2014b. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography **37**:001-011. doi: 010.1111/ecog.01093.

Toth, L. T., I. B. Kuffner, A. Stathakopoulos, and E. A. Shinn. 2018. A 3,000-year lag between the geological and ecological shutdown of Florida's coral reefs. Global Change Biology **24**:5471-5483.

Vallès, H., D. Gill, and H. A. Oxenford. 2015. Parrotfish size as a useful indicator of fishing effects in a small Caribbean island. Coral Reefs **34**:789-801.

Vallès, H., and H. A. Oxenford. 2014. Parrotfish size: A simple yet useful alternative indicator of fishing effects on Caribbean reefs? PLoS ONE **9**:e86291.

van Woesik, R., K. Ripple, and S. L. Miller. 2018. Macroalgae reduces survival of nursery-reared *Acropora* corals in the Florida reef tract. Restoration Ecology **26**:563-569.

Walker, B. K., and D. S. Gilliam. 2013. Determining the extent and characterizing coral reef habitats of the northern latitudes of the Florida Reef Tract (Martin County). PLoS ONE **8**:e80439.

Ward-Paige, C. A., M. J. Risk, O. A. Sherwood, and W. C. Jaap. 2005. Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. Marine Pollution Bulletin **51**:570-579.

Williams, I. D., J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, and R. E. Brainard. 2015a. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. PLoS ONE **10**:e0120516.

Williams, S. M., I. Chollett, G. Roff, J. Cortés, C. S. Dryden, and P. J. Mumby. 2015b. Hierarchical spatial patterns in Caribbean reef benthic assemblages. Journal of Biogeography **42**:1327-1335.

Wolff, N., R. Grober-Dunsmore, C. S. Rogers, and J. Beets. 1999. Management implications of fish trap effectiveness in adjacent coral reef and gorgonian habitats. Environmental Biology of Fishes **55**:81-90.

Appendix 1. List of fish species (and species groups) included in fish survey data used for this project.

Scientific Name	**Common Name**	**Family**		**Tropic group**[1]	**Species groups**[2,3,4]
Engraulidae species	Anchovy Species	Anchovies	Engraulidae		✓
Anchoa lyolepsis	Dusky Anchovy	Anchovies	Engraulidae		✓
Holacanthus species	*Holacanthus* angelfish	Angelfishes	Pomacanthidae		
Centropyge aurantonotus	Flameback Angelfish	Angelfishes	Pomacanthidae		
Pomacanthus species	*Pomacanthus* angelfish	Angelfishes	Pomacanthidae	H	
Centropyge argi	Cherubfish	Angelfishes	Pomacanthidae		
Holacanthus bermudensis	Blue Angelfish	Angelfishes	Pomacanthidae		ML
Holacanthus ciliaris	Queen Angelfish	Angelfishes	Pomacanthidae		ML
Holacanthus tricolor	Rock Beauty	Angelfishes	Pomacanthidae		
Pomacanthus arcuatus	Gray Angelfish	Angelfishes	Pomacanthidae		ML
Pomacanthus paru	French Angelfish	Angelfishes	Pomacanthidae		ML
Holocanthus townsendi	Townsend Angelfish	Angelfishes	Pomacanthidae		ML
Antennarius ocellatus	Ocellated Frogfish	Anglerfishes	Antennariidae	P	ML
Sphyraena barracuda	Great Barracuda	Barracudas	Sphyraenidae	P	✓
Sphyraena guachancho	Guaguanche	Barracudas	Sphyraenidae	P	
Sphyraena picudilla	Southern Sennet	Barracudas	Sphyraenidae	P	
Gramma loreto	Fairy Basslet	Basslets	Grammatidae		ML
Ogcocephalus nasutus	Shortnose Batfish	Batfishes	Ogcocephalidae		ML
Ogcocephalus sp.	Batfish species	Batfishes	Ogcocephalidae		ML
Priacanthus arenatus	Bigeye	Bigeyes	Pricanthidae		
Heteropriacanthus cruentatus	Glasseye Snapper	Bigeyes	Pricanthidae		
Albula vulpes	Bonefish	Bonefishes	Albulidae		✓
Lactophrys species	Trunkfish species	Boxfishes	Ostraciidae		
Lactophrys bicaudalis	Spotted Trunkfish	Boxfishes	Ostraciidae		ML
Acanthostracion polygonia	Honeycomb Cowfish	Boxfishes	Ostraciidae		ML
Acanthostracion quadricornis	Scrawled Cowfish	Boxfishes	Ostraciidae		ML
Lactophrys trigonus	Trunkfish	Boxfishes	Ostraciidae		ML
Lactophrys triqueter	Smooth Trunkfish	Boxfishes	Ostraciidae		ML
Peprilus triacanthus	American Butterfish	Butterfishes	Stromateidae		✓
Stromateidae species	Butterfish species	Butterfishes	Stromateidae		
Prognathodes aya	Bank Butterflyfish	Butterflyfishes	Chaetodontidae		
Chaetodon capistratus	Foureye Butterflyfish	Butterflyfishes	Chaetodontidae		ML
Chaetodon ocellatus	Spotfin Butterflyfish	Butterflyfishes	Chaetodontidae		ML
Chaetodon sedentarius	Reef Butterflyfish	Butterflyfishes	Chaetodontidae		ML
Chaetodon striatus	Banded Butterflyfish	Butterflyfishes	Chaetodontidae		ML

Prognathodes aculeatus	Longsnout Butterflyfish	Butterflyfishes	Chaetodontidae		ML
Astrapogon puncticulatus	Blackfin Cardinalfish	Cardinalfishes	Apogonidae		ML
Phaeoptyx xenus	Sponge Cardinalfish	Cardinalfishes	Apogonidae		ML
Apogon phenax	Mimic Cardinalfish	Cardinalfishes	Apogonidae		ML
Apogon lachneri	Whitestar Cardinalfish	Cardinalfishes	Apogonidae		
Apogon species	Cardinalfish Species	Cardinalfishes	Apogonidae		
Apogon binotatus	Barred Cardinalfish	Cardinalfishes	Apogonidae		ML
Apogon pseudomaculatus	Twospot Cardinalfish	Cardinalfishes	Apogonidae		ML
Apogon maculatus	Flamefish	Cardinalfishes	Apogonidae		
Apogon quadrisquamatus	Sawcheek Cardinalfish	Cardinalfishes	Apogonidae		ML
Astrapogon stellatus	Conchfish	Cardinalfishes	Apogonidae		
Apogon aurolineatus	Bridle Cardinalfish	Cardinalfishes	Apogonidae		ML
Apogon townsendi	Belted Cardinalfish	Cardinalfishes	Apogonidae		ML
Astrapogon sp.	Cardinalfish species	Cardinalfishes	Apogonidae		ML
Rachycentron canadum	Cobia	Cobia	Rachycentridae		✓
Entomacrodus nigricans	Pearl Blenny	Combtooth Blennies	Blenniidae	H	
Hypleurochilus bermudensis	Barred Blenny	Combtooth Blennies	Blenniidae		ML
Ophioblennius macclurei	Redlip Blenny	Combtooth Blennies	Blenniidae	H	ML
Scartella cristata	Molly Miller	Combtooth Blennies	Blenniidae	H	
Parablennius marmoreus	Seaweed Blenny	Combtooth Blennies	Blenniidae		ML
blenny species	Blenny species	Combtooth Blennies	Blenniidae		ML
Ariosoma balearicum	Bandtooth Conger	Conger Eels	Congridae		
Conger triporiceps	Manytooth Conger	Conger Eels	Congridae	P	
Heteroconger longissimus	Brown Garden Eel	Conger Eels	Congridae		
Fistularia tabacaria	Bluespotted Cornetfish	Cornetfishes	Fistulariidae	P	ML
Brotula barbata	Atlantic Bearded Brotula	Cusk-eels	Ophidiidae		
Abudefduf taurus	Night Sergeant	Damselfishes	Pomacentridae	H	
Abudefduf saxatilis	Sergeant Major	Damselfishes	Pomacentridae		
Chromis cyanea	Blue Chromis	Damselfishes	Pomacentridae		
Chromis enchrysura	Yellowtail Reeffish	Damselfishes	Pomacentridae		
Chromis insolata	Sunshinefish	Damselfishes	Pomacentridae		
Chromis multilineata	Brown Chromis	Damselfishes	Pomacentridae		
Chromis scotti	Purple Reeffish	Damselfishes	Pomacentridae		
Microspathodon chrysurus	Yellowtail Damselfish	Damselfishes	Pomacentridae	H	ML
Stegastes diencaeus	Longfin Damselfish	Damselfishes	Pomacentridae	H	ML
Stegastes adustus	Dusky Damselfish	Damselfishes	Pomacentridae	H	ML
Stegastes leucostictus	Beaugregory	Damselfishes	Pomacentridae		
Stegastes partitus	Bicolor Damselfish	Damselfishes	Pomacentridae	H	ML
Stegastes planifrons	Threespot Damselfish	Damselfishes	Pomacentridae		ML
Stegastes variabilis	Cocoa Damselfish	Damselfishes	Pomacentridae	H	ML

damselfish species	Damselfish species	Damselfishes	Pomacentridae		ML
Ptereleotris calliura	Blue Dartfish	Dartfishes	Microdesmidae		
Ptereleotris helenae	Hovering Dartfish	Dartfishes	Microdesmidae		
Callionymus bairdi	Lancer Dragonet	Dragonets	Callionymidae		
Umbrina coroides	Sand Drum	Drums and Croakers	Sciaenidae		✓
drum species	Drum species	Drums and Croakers	Sciaenidae		✓
Pareques acuminatus	High-Hat	Drums and Croakers	Sciaenidae	H	ML
Equetus lanceolatus	Jackknife-Fish	Drums and Croakers	Sciaenidae		ML
Equetus punctatus	Spotted Drum	Drums and Croakers	Sciaenidae		ML
Pareques umbrosus	Cubbyu	Drums and Croakers	Sciaenidae		ML
Odontoscion dentex	Reef Croaker	Drums and Croakers	Sciaenidae		ML
Stephanolepis setifer	Pygmy Filefish	Filefishes	Monacanthidae	H	ML
Monacanthus ciliatus	Fringed Filefish	Filefishes	Monacanthidae	H	ML
Aluterus schoepfii	Orange Filefish	Filefishes	Monacanthidae		ML
Aluterus scriptus	Scrawled Filefish	Filefishes	Monacanthidae		ML
Cantherhines macrocerus	Whitespotted Filefish	Filefishes	Monacanthidae		ML
Cantherhines pullus	Orangespotted Filefish	Filefishes	Monacanthidae		ML
Stephanolepis hispidus	Planehead Filefish	Filefishes	Monacanthidae		ML
Monacanthus tuckeri	Slender Filefish	Filefishes	Monacanthidae		ML
Aluterus monoceros	Unicorn Filefish	Filefishes	Monacanthidae		
Aluterus sp.	*Aluterus* filefish	Filefishes	Monacanthidae		ML
Mocanthus species	*Mocanthus* filefish	Filefishes	Monocanthidae		ML
Dactylopterus volitans	Flying Gurnard	Flying gurnards	Dactylopteridae		
Upeneus parvus	Dwarf Goatfish	Goatfishes	Mullidae		
Mulloidichthys martinicus	Yellow Goatfish	Goatfishes	Mullidae		
Pseudupeneus maculatus	Spotted Goatfish	Goatfishes	Mullidae		
Coryphopterus tortugae	Patch-Reef Goby	Gobies	Gobiidae		
Coryphopterus venezuelae	Sand-Canyon Goby	Gobies	Gobiidae		
Ctenogobius stigmaticus	Marked Goby	Gobies	Gobiidae		
Elacatinus chancei	Shortstripe Goby	Gobies	Gobiidae		
Elacatinus louisae	Spotlight Goby	Gobies	Gobiidae		
Elacatinus multifasciatus	Greenbanded Goby	Gobies	Gobiidae		
Elacatinus prochilos	Broadstripe Goby	Gobies	Gobiidae		
Gobiosoma grosvenori	Rockcut Goby	Gobies	Gobiidae		
Microgobius signatus	Dashback Goby	Gobies	Gobiidae		
Microgobius species	Microgobius gobies	Gobies	Gobiidae	H	
Risor ruber	Tusked Goby	Gobies	Gobiidae		
Syngnathus dawsoni	Dashback Goby	Gobies	Gobiidae	H	
Coryphopterus dicrus	Colon Goby	Gobies	Gobiidae		ML
Coryphopterus eidolon	Pallid Goby	Gobies	Gobiidae	H	ML

Coryphopterus glaucofraenum	Bridled Goby	Gobies	Gobiidae		ML
Coryphopterus personatus	Masked Goby	Gobies	Gobiidae		ML
Gnatholepis thompsoni	Goldspot Goby	Gobies	Gobiidae	H	ML
Elacatinus evelynae	Sharknose Goby	Gobies	Gobiidae		ML
Elacatinus macrodon	Tiger Goby	Gobies	Gobiidae		ML
Elacatinus oceanops	Neon Goby	Gobies	Gobiidae		ML
Microgobius carri	Seminole Goby	Gobies	Gobiidae	H	ML
Microgobius microlepis	Banner Goby	Gobies	Gobiidae		ML
Oxyurichthys stigmalophius	Spotfin Goby	Gobies	Gobiidae		ML
Nes longus	Orangespotted Goby	Gobies	Gobiidae	H	ML
Priolepis hipoliti	Rusty Goby	Gobies	Gobiidae		ML
Elacatinus xanthiprora	Yellowprow Goby	Gobies	Gobiidae		ML
Coryphopterus punctipectophorus	Spotted Goby	Gobies	Gobiidae		ML
Ctenogobius saepepallens	Dash Goby	Gobies	Gobiidae		ML
Elacatinus horsti	Yellowline Goby	Gobies	Gobiidae		ML
Coryphopterus lipernes	Peppermint Goby	Gobies	Gobiidae		ML
Elacatinus saucrum	Leopard Goby	Gobies	Gobiidae		ML
Coryphopterus sp.	*Coryphopterus* gobies	Gobies	Gobiidae		ML
goby species	Goby species	Gobies	Gobiidae		ML
Elacatinus randalli	Yellownose Goby	Gobies	Gobiidae		ML
Elacatinus dilepis	Orangeside Goby	Gobies	Gobiidae		ML
Bollmannia boqueronensis	White-Eye Goby	Gobies	Gobiidae	H	ML
Lophogobius cyprinoides	Crested Goby	Gobies	Gobiidae	H	
Bathygobious soporator	Frillfin Goby	Gobies	Gobiidae		
Emmelichthyops atlanticus	Bonnetmouth	Grunts	Haemulidae	P	
Inermia vittata	Boga	Grunts	Haemulidae		
Anisotremus surinamensis	Black Margate	Grunts	Haemulidae		✓
Anisotremus virginicus	Porkfish	Grunts	Haemulidae		✓, ML
Haemulon album	Margate	Grunts	Haemulidae		SG
Haemulon aurolineatum	Tomtate	Grunts	Haemulidae		SG
Haemulon carbonarium	Caesar Grunt	Grunts	Haemulidae		✓
Haemulon chrysargyreum	Smallmouth Grunt	Grunts	Haemulidae		✓
Haemulon flavolineatum	French Grunt	Grunts	Haemulidae		✓
Haemulon macrostomum	Spanish Grunt	Grunts	Haemulidae		✓
Haemulon melanurum	Cottonwick	Grunts	Haemulidae		SG
Haemulon parra	Sailor's Choice	Grunts	Haemulidae		SG
Haemulon plumierii	White Grunt	Grunts	Haemulidae		SG
Haemulon sciurus	Bluestriped Grunt	Grunts	Haemulidae		✓
Haemulon striatum	Striped Grunt	Grunts	Haemulidae		✓
Orthopristis chrysoptera	Pigfish	Grunts	Haemulidae		✓

Haemulon sp.	Grunt species	Grunts	Haemulidae		✓
Hemiramphus brasiliensis	Ballyhoo	Halfbeaks	Hemiramphidae		✓
Chriodorus atherinoides	Hardhead Halfbeak	Halfbeaks	Hemiramphidae		
Amblycirrhitus pinos	Redspotted Hawkfish	Hawkfishes	Cirrhitidae		ML
Clupeidae species	Herring species	Herrings	Clupeidae		✓
Harengula jaguana	Scaled Sardine	Herrings	Clupeidae		✓
Sardinella aurita	Spanish Sardine	Herrings	Clupeidae		✓
Harengula humeralis	Redear Sardine	Herrings	Clupeidae		✓
Jenkinsia sp.	Herring Species	Herrings	Clupeidae		✓
Trachinotus goodei	Palometa	Jacks	Carangidae	P	✓
Chloroscombus chrysurus	Atlantic Bumper	Jacks	Carangidae		
Seriola zonata	Banded Rudderfish	Jacks	Carangidae		SG
Trachurus lathami	Rough Scad	Jacks	Carangidae		✓
Decapterus sp.	Scad species	Jacks	Carangidae		✓
Selar crumenophthalmus	Bigeye Scad	Jacks	Carangidae	P	✓
Alectis ciliaris	African Pompano	Jacks	Carangidae	P	✓
Carangoides bartholomaei	Yellow Jack	Jacks	Carangidae	P	✓
Caranx crysos	Blue Runner	Jacks	Carangidae	P	✓
Caranx hippos	Crevalle Jack	Jacks	Carangidae	P	✓
Caranx latus	Horse-Eye Jack	Jacks	Carangidae	P	✓
Caranx ruber	Bar Jack	Jacks	Carangidae	P	SG
Decapterus macarellus	Mackerel Scad	Jacks	Carangidae		✓
Decapterus punctatus	Round Scad	Jacks	Carangidae		✓
Elagatis bipinnulata	Rainbow Runner	Jacks	Carangidae		✓
Seriola dumerili	Greater Amberjack	Jacks	Carangidae	P	SG
Trachinotus falcatus	Permit	Jacks	Carangidae	P	✓
Selene vomer	Lookdown	Jacks	Carangidae		✓
Seriola rivoliana	Almaco Jack	Jacks	Carangidae	P	SG
Oligoplites saurus	Leatherjack	Jacks	Carangidae		✓
Caranx lugubris	Black Jack	Jacks	Carangidae	P	✓
Caranx sp.	Jack Species	Jacks	Carangidae		✓
Lonchopisthus micrognathus	Swordtail Jawfish	Jawfishes	Opistognathidae	P	
Opistognathus maxillosus	Mottled Jawfish	Jawfishes	Opistognathidae		
Opistognathus aurifrons	Yellowhead Jawfish	Jawfishes	Opistognathidae		ML
Opistognathus whitehursti	Dusky Jawfish	Jawfishes	Opistognathidae	P	ML
Opistognathus macrognathus	Banded Jawfish	Jawfishes	Opistognathidae	P	ML
Opistognathus sp.	Jawfish species	Jawfishes	Opistognathidae		ML
Labrisomus nigricinctus	Spotcheek Blenny	Labrisomid Blennies	Labrisomidae		ML
Labrisomus kalisherae	Downy Blenny	Labrisomid Blennies	Labrisomidae		ML
Malacoctenus boehlkei	Diamond Blenny	Labrisomid Blennies	Labrisomidae		

Malacoctenus species	Blenny Species	Labrisomid Blennies	Labrisomidae		
Malacoctenus gilli	Dusky Blenny	Labrisomid Blennies	Labrisomidae		ML
Malacoctenus versicolor	Barfin Blenny	Labrisomid Blennies	Labrisomidae		ML
Labrisomus gobio	Palehead Blenny	Labrisomid Blennies	Labrisomidae		ML
Labrisomus nuchipinnis	Hairy Blenny	Labrisomid Blennies	Labrisomidae		ML
Malacoctenus macropus	Rosy Blenny	Labrisomid Blennies	Labrisomidae		ML
Malacoctenus triangulatus	Saddled Blenny	Labrisomid Blennies	Labrisomidae		ML
Paraclinus marmoratus	Marbled Blenny	Labrisomid Blennies	Labrisomidae		ML
Paraclinus nigripinnis	Blackfin Blenny	Labrisomid Blennies	Labrisomidae		ML
Labrisomus filamentosus	Quillfin Blenny	Labrisomid Blennies	Labrisomidae		ML
Labrisomus bucciferus	Puffcheek Blenny	Labrisomid Blennies	Labrisomidae		ML
Malacoctenus aurolineatus	Goldline Blenny	Labrisomid Blennies	Labrisomidae		ML
Syacium micrurum	Channel Flounder	Large-tooth Flounders	Paralichthyidae	P	✓
Syacium species	Sand Flounder Species	Large-tooth Flounders	Paralichthyidae		✓
Paralichthys albigutta	Gulf Flounder	Large-tooth Flounders	Paralichthyidae		✓
Bothus lunatus	Peacock Flounder	Lefteye Flounders	Bothidae	P	✓
Bothus ocellatus	Eyed Flounder	Lefteye Flounders	Bothidae	P	✓
Bothus species	Lefteye Flounders	Lefteye Flounders	Bothidae		✓
Synodus synodus	Red Lizardfish	Lizardfishes	Synodontidae		
Synodus saurus	Bluestriped Lizardfish	Lizardfishes	Synodontidae	P	
Synodus foetens	Inshore Lizardfish	Lizardfishes	Synodontidae	P	
Synodus intermedius	Sand Diver	Lizardfishes	Synodontidae	P	
Acanthocybium solandri	Wahoo	Mackerels, Tunas, Bonitos	Scombridae		✓
Sarda sarda	Atlantic Bonito	Mackerels, Tunas, Bonitos	Scombridae	P	✓
Scomberomorus cavalla	King Mackerel	Mackerels, Tunas, Bonitos	Scombridae	P	✓
Scomberomorus maculatus	Spanish Mackerel	Mackerels, Tunas, Bonitos	Scombridae	P	
Scomberomorus regalis	Cero	Mackerels, Tunas, Bonitos	Scombridae	P	✓
Euthynnus alletteratus	Little Tunny	Mackerels, Tunas, Bonitos	Scombridae	P	✓
Eucinostomus lefroyi	Mottled Mojarra	Mojarras	Gerreidae		
Gerres sp.	Mojarra species	Mojarras	Gerreidae		
Eucinostomus melanopterus	Flagfin Mojarra	Mojarras	Gerreidae		
Eucinostomus argenteus	Spotfin Mojarra	Mojarras	Gerreidae		✓
Gerres cinereus	Yellowfin Mojarra	Mojarras	Gerreidae		✓
Eucinostomus gula	Silver Jenny	Mojarras	Gerreidae		✓
Eucinostomus jonesii	Slender Mojarra	Mojarras	Gerreidae		
Gymnothorax nigromarginatus	Blackedge Moray	Morays	Muraenidae		ML
Enchelycore carychroa	Chestnut Moray	Morays	Muraenidae		

Echidna catenata	Chain Moray	Morays	Muraenidae		
Gymnothorax species	Gymnothorax eels	Morays	Muraenidae	P	
Muraenidae species	Moray species	Morays	Muraenidae		
Gymnothorax miliaris	Goldentail Moray	Morays	Muraenidae		ML
Gymnothorax funebris	Green Moray	Morays	Muraenidae	P	ML
Gymnothorax moringa	Spotted Moray	Morays	Muraenidae	P	ML
Gymnothorax vicinus	Purplemouth Moray	Morays	Muraenidae	P	ML
Gymnothorax saxicola	Honeycomb Moray	Morays	Muraenidae		ML
Muraena retifera	Reticulate Moray	Morays	Muraenidae		ML
Enchelycore nigricans	Viper Moray	Morays	Muraenidae	P	ML
Mugil cephalus	Striped Mullet	Mullets	Mugilidae	H	✓
needlefish species	Needlefish species	Needlefishes	Belonidae		
Ablennes hians	Flat Needlefish	Needlefishes	Belonidae	P	
Platybelone argalus argalus	Keeltail Needlefish	Needlefishes	Belonidae	P	
Strongylura timucu	Timucu	Needlefishes	Belonidae		
Tylosurus crocodilus	Houndfish	Needlefishes	Belonidae		
Strongylura notata	Redfin Needlefish	Needlefishes	Belonidae		
Narcine bancroftii	Lesser Electric Ray	Numbfishes	Narcinidae		
Atherinomorus species	Silverside species	Old World Silversides	Atherinidae		
Atherinomorus stipes	Hardhead Silverside	Old World Silversides	Atherinidae		
Hypoatherina harringtonensis	Reef Silverside	Old World Silversides	Atherinidae		
Cryptotomus roseus	Bluelip Parrotfish	Parrotfishes	Scaridae	H	ML
Nicholsina usta	Emerald Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus coelestinus	Midnight Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus coeruleus	Blue Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus iseri	Striped Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus guacamaia	Rainbow Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus taeniopterus	Princess Parrotfish	Parrotfishes	Scaridae	H	ML
Scarus vetula	Queen Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma atomarium	Greenblotch Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma aurofrenatum	Redband Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma chrysopterum	Redtail Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma radians	Bucktooth Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma rubripinne	Yellowtail Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma viride	Stoplight Parrotfish	Parrotfishes	Scaridae	H	ML
Sparisoma sp.	*Sparisoma* parrotfishes	Parrotfishes	Scaridae	H	ML
Scarus sp.	*Scarus* parrotfishes	Parrotfishes	Scaridae	H	ML
Amphelikturus dendritica	Pipehorse	Pipefishes and Seahorses	Syngnathidae		
Syngnathus scovelli	Gulf Pipefish	Pipefishes and Seahorses	Syngnathidae		ML

Hippocampus reidi	Longsnout Seahorse	Pipefishes and Seahorses	Syngnathidae		ML
Hippocampus erectus	Lined Seahorse	Pipefishes and Seahorses	Syngnathidae		ML
Syngnathus sp.	Pipefish Species	Pipefishes and Seahorses	Syngnathidae		
Cosmocampus elucens	Shortfin Pipefish	Pipefishes and Seahorses	Syngnathidae		
Hippocampus species	Seahorse/Pipefish Species	Pipefishes and Seahorses	Syngnathidae		
Chilomycterus atinga	Spotted Burrfish	Porcupinefishes	Diodontidae		
Chilomycterus antennatus	Bridled Burrfish	Porcupinefishes	Diodontidae		ML
Diodon holocanthus	Balloonfish	Porcupinefishes	Diodontidae		ML
Diodon hystrix	Porcupinefish	Porcupinefishes	Diodontidae		ML
Chilomycterus schoepfii	Striped Burrfish	Porcupinefishes	Diodontidae		ML
puffer species	Puffer species	Porcupinefishes	Diodontidae		ML
Calamus leucosteus	Whitebone Porgy	Porgies	Sparidae		SG
Calamus pennatula	Pluma Porgy	Porgies	Sparidae		✓
Archosargus rhomboidalis	Sea Bream	Porgies	Sparidae	H	✓
Calamus bajonado	Jolthead Porgy	Porgies	Sparidae		SG
Calamus calamus	Saucereye Porgy	Porgies	Sparidae		SG
Calamus penna	Sheepshead Porgy	Porgies	Sparidae		✓
Calamus proridens	Littlehead Porgy	Porgies	Sparidae		✓
Diplodus holbrookii	Spottail Pinfish	Porgies	Sparidae		✓
Archosargus probatocephalus	Sheepshead	Porgies	Sparidae		✓
Diplodus argenteus	Silver Porgy	Porgies	Sparidae		✓
Lagodon rhomboides	Pinfish	Porgies	Sparidae		✓
Pagrus pagrus	Red Porgy	Porgies	Sparidae		SG
Calamus nodosus	Knobbed Porgy	Porgies	Sparidae		SG
porgy species	Porgy species	Porgies	Sparidae		✓
Sphoeroides nephelus	Southern Puffer	Pufferfishes	Tetraodontidae		
Canthigaster jamestyleri	Goldface Toby	Pufferfishes	Tetraodontidae		
Canthigaster species	Puffers	Pufferfishes	Tetraodontidae		
Canthigaster rostrata	Sharpnose Puffer	Pufferfishes	Tetraodontidae		ML
Sphoeroides spengleri	Bandtail Puffer	Pufferfishes	Tetraodontidae		
Sphoeroides testudineus	Checkered Puffer	Pufferfishes	Tetraodontidae		
Echeneis naucrates	Sharksucker	Remoras	Echeneidae		
Remora remora	Remora	Remoras	Echeneidae		
Echeneis neucratoides	Whitefin Sharksucker	Remoras	Echeneidae		
Istiophorus platypterus	Sailfish	Sailfishes and Marlins	Istiophoridae		✓
Scorpaena species	Scorpionfish Species	Scorpionfishes	Scorpaenidae		
Scorpaena plumieri	Spotted Scorpionfish	Scorpionfishes	Scorpaenidae	P	

Scorpaenodes caribbaeus	Reef Scorpionfish	Scorpionfishes	Scorpaenidae	P	
Pterois volitans	Red Lionfish	Scorpionfishes	Scorpaenidae	P	✓
Serranus species	Seabass species	Sea Basses and Groupers	Serranidae	P	✓
Serranus phoebe	Tattler	Sea Basses and Groupers	Serranidae		
Epinephelus drummondhayi	Speckled Hind	Sea Basses and Groupers	Serranidae		✓
Epinephelus niveatus	Snowy Grouper	Sea Basses and Groupers	Serranidae	P	SG
Mycteroperca acutirostris	Western Comb Grouper	Sea Basses and Groupers	Serranidae	P	✓
Liopropoma mowbrayi	Cave Basslet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus gummigutta	Golden Hamlet	Sea Basses and Groupers	Serranidae		ML
Centropristis striata	Black Sea Bass	Sea Basses and Groupers	Serranidae		SG, ML
Centropristis ocyurus	Bank Sea Bass	Sea Basses and Groupers	Serranidae		SG, ML
Rypticus bistrispinus	Freckled Soapfish	Sea Basses and Groupers	Serranidae		
Diplectrum bivittatum	Dwarf Sand Perch	Sea Basses and Groupers	Serranidae	P	
Hypoplectrus aberrans	Yellowbelly Hamlet	Sea Basses and Groupers	Serranidae		
Parasphyraenops incisus	Splitfin Bass	Sea Basses and Groupers	Serranidae		
Serranus flaviventris	Twinspot Bass	Sea Basses and Groupers	Serranidae	P	
Serraniculus pumilio	Pygmy Sea Bass	Sea Basses and Groupers	Serranidae	P	
Mycteroperca species	Grouper species	Sea Basses and Groupers	Serranidae		✓
Diplectrum formosum	Sand Perch	Sea Basses and Groupers	Serranidae	P	
Epinephelus adscensionis	Rock Hind	Sea Basses and Groupers	Serranidae	P	SG
Cephalopholis cruentata	Graysby	Sea Basses and Groupers	Serranidae	P	SG
Cephalopholis fulva	Coney	Sea Basses and Groupers	Serranidae	P	SG
Epinephelus guttatus	Red Hind	Sea Basses and Groupers	Serranidae	P	SG
Epinephelus morio	Red Grouper	Sea Basses and Groupers	Serranidae	P	SG
Epinephelus striatus	Nassau Grouper	Sea Basses and Groupers	Serranidae	P	✓
Hypoplectrus chlorurus	Yellowtail Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus gemma	Blue Hamlet	Sea Basses and Groupers	Serranidae		ML

Hypoplectrus guttavarius	Shy Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus hybrid	Hybrid Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus indigo	Indigo Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus nigricans	Black Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus puella	Barred Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus tann	Tan Hamlet	Sea Basses and Groupers	Serranidae		ML
Hypoplectrus unicolor	Butter Hamlet	Sea Basses and Groupers	Serranidae		ML
Liopropoma eukrines	Wrasse Basslet	Sea Basses and Groupers	Serranidae		ML
Mycteroperca bonaci	Black Grouper	Sea Basses and Groupers	Serranidae	P	SG
Mycteroperca interstitialis	Yellowmouth Grouper	Sea Basses and Groupers	Serranidae	P	SG
Mycteroperca microlepis	Gag	Sea Basses and Groupers	Serranidae	P	SG
Mycteroperca phenax	Scamp	Sea Basses and Groupers	Serranidae	P	SG
Mycteroperca venenosa	Yellowfin Grouper	Sea Basses and Groupers	Serranidae	P	SG
Paranthias furcifer	Atlantic Creolefish	Sea Basses and Groupers	Serranidae		
Rypticus saponaceus	Greater Soapfish	Sea Basses and Groupers	Serranidae		
Serranus baldwini	Lantern Bass	Sea Basses and Groupers	Serranidae	P	
Serranus tabacarius	Tobaccofish	Sea Basses and Groupers	Serranidae	P	
Serranus tigrinus	Harlequin Bass	Sea Basses and Groupers	Serranidae		
Serranus tortugarum	Chalk Bass	Sea Basses and Groupers	Serranidae		
Epinephelus itajara	Goliath Grouper	Sea Basses and Groupers	Serranidae	P	✓
Mycteroperca tigris	Tiger Grouper	Sea Basses and Groupers	Serranidae	P	✓
Serranus annularis	Orangeback Bass	Sea Basses and Groupers	Serranidae	P	
Dermatolepis inermis	Marbled Grouper	Sea Basses and Groupers	Serranidae	P	✓
Epinephelus flavolimbatus	Yellowedge Grouper	Sea Basses and Groupers	Serranidae	P	SG
Alphestes afer	Mutton Hamlet	Sea Basses and Groupers	Serranidae	P	ML
Liopropoma rubre	Peppermint Basslet	Sea Basses and Groupers	Serranidae	P	ML
Serranus subligarius	Belted Sandfish	Sea Basses and Groupers	Serranidae		

Schultzea beta	School Bass	Sea Basses and Groupers	Serranidae		
Rypticus maculatus	Whitespotted Soapfish	Sea Basses and Groupers	Serranidae		
grouper-sea bass species	Grouper-Sea Bass species	Sea Basses and Groupers	Serranidae		✓
Hypoplectrus sp.	Hamlet species	Sea Basses and Groupers	Serranidae		ML
Kyphosus sectatrix	Bermuda Chub	Sea Chubs	Kyphosidae		
Prionotus rubio	Blackwing Searobin	Searobins	Triglidae		
Triglidae species	Sea Robin species	Searobins	Triglidae		
Prionotus ophryas	Bandtail Searobin	Searobins	Triglidae		
Menidia sp.	Silverside species	Silversides	Atherinopsidae		
Myrichthys breviceps	Sharptail Eel	Snake Eels	Ophichthidae		ML
Myrichthys ocellatus	Goldspotted Eel	Snake Eels	Ophichthidae		ML
Myrichthys species	Myrichthys eels	Snake Eels	Ophichthidae		
Ophichthus ophis	Spotted Snake Eel	Snake Eels	Ophichthidae		
Ophichthidae species	Snake Eel Species	Snake Eels	Ophichthidae		
Ahlia egmontis	Key Worm Eel	Snake Eels	Ophichthidae		ML
Lutjanus campechanus	Red Snapper	Snappers	Lutjanidae		SG
Lutjanus analis	Mutton Snapper	Snappers	Lutjanidae	P	SG
Lutjanus apodus	Schoolmaster	Snappers	Lutjanidae	P	
Lutjanus buccanella	Blackfin Snapper	Snappers	Lutjanidae	P	SG
Lutjanus cyanopterus	Cubera Snapper	Snappers	Lutjanidae	P	SG
Lutjanus griseus	Gray Snapper	Snappers	Lutjanidae		SG
Lutjanus jocu	Dog Snapper	Snappers	Lutjanidae	P	✓
Lutjanus mahogoni	Mahogany Snapper	Snappers	Lutjanidae	P	✓
Lutjanus synagris	Lane Snapper	Snappers	Lutjanidae		SG
Ocyurus chrysurus	Yellowtail Snapper	Snappers	Lutjanidae		SG
Rhomboplites aurorubens	Vermilion Snapper	Snappers	Lutjanidae	P	SG
Pristipomoides aquilonaris	Wenchman	Snappers	Lutjanidae	P	✓
snapper species	Snapper species	Snappers	Lutjanidae		
Centropomus undecimalis	Common Snook	Snooks	Centropomidae	P	✓
Platax orbicularis	Orbicular Batfish	Spadefishes	Ephippidae		
Chaetodipterus faber	Atlantic Spadefish	Spadefishes	Ephippidae		SG
Sargocentron bullisi	Deepwater Squirrelfish	Squirrelfishes	Holocentridae		
Holocentrus adscensionis	Squirrelfishes	Squirrelfishes	Holocentridae		
Sargocentron coruscum	Reef Squirrelfish	Squirrelfishes	Holocentridae		
Neoniphon marianus	Longjaw Squirrelfish	Squirrelfishes	Holocentridae		
Holocentrus rufus	Longspine Squirrelfish	Squirrelfishes	Holocentridae		
Sargocentron vexillarium	Dusky Squirrelfish	Squirrelfishes	Holocentridae		
Myripristis jacobus	Blackbar Soldierfish	Squirrelfishes	Holocentridae		ML

squirrelfish species	Squirrelfish Species	Squirrelfishes	Holocentridae		
Astroscopus y-graecum	Southern Stargazer	Stargazers	Uranoscopidae		
Astroscopus guttatus	Northern Stargazer	Stargazers	Uranoscopidae		
Acanthurus bahianus	Ocean Surgeon	Surgeonfishes	Acanthuridae	H	ML
Acanthurus chirurgus	Doctorfish	Surgeonfishes	Acanthuridae	H	
Acanthurus coeruleus	Blue Tang	Surgeonfishes	Acanthuridae	H	ML
Acanthurus sp.	Surgeonfish species	Surgeonfishes	Acanthuridae		ML
Pempheris schomburgkii	Glassy Sweeper	Sweepers	Pempheridae		ML
Megalops atlanticus	Tarpon	Tarpons	Megalopidae	P	✓
Elops saurus	Ladyfish	Tenpounders	Elopidae		✓
Malacanthus plumieri	Sand Tilefish	Tilefishes	Malacanthinae		✓
Opsanus tau	Oyster Toadfish	Toadfishes	Batrachoididae		ML
Xanthichthys ringens	Sargassum Triggerfish	Triggerfishes	Balistidae		
Balistes capriscus	Gray Triggerfish	Triggerfishes	Balistidae		SG
Balistes vetula	Queen Triggerfish	Triggerfishes	Balistidae		✓, ML
Canthidermis sufflamen	Ocean Triggerfish	Triggerfishes	Balistidae		SG
Melichthys niger	Black Durgon	Triggerfishes	Balistidae	H	
Balistes sp.	Triggerfish species	Triggerfishes	Balistidae		✓, ML
Enneanectes altivelis	Lofty Triplefin	Triplefin Blennies	Tripterygiidae		
Enneanectes species	Triplefin species	Triplefin Blennies	Tripterygiidae		✓
Enneanectes boehlkei	Roughhead Triplefin	Triplefin Blennies	Tripterygiidae		
Aulostomus maculatus	Atlantic Trumpetfish	Trumpetfishes	Aulostomidae	P	ML
Acanthemblemaria spinosa	Spinyhead Blenny	Tube Blennies	Chaenopsidae		ML
Emblemariopsis species	*Emblemariopsis* blennies	Tube Blennies	Chaenopsidae		
Acanthemblemaria species	*Acanthemblemaria* blennies	Tube Blennies	Chaenopsidae		
Chaenopsis ocellata	Bluethroat Pikeblenny	Tube Blennies	Chaenopsidae		
Chaenopsis species	Pikeblenny species	Tube Blennies	Chaenopsidae		
Emblemaria species	*Emblemaria* blennies	Tube Blennies	Chaenopsidae		
Emblemariopsis diaphana	Glass Blenny	Tube Blennies	Chaenopsidae		
Acanthemblemaria aspera	Roughhead Blenny	Tube Blennies	Chaenopsidae		ML
Acanthemblemaria chaplini	Papillose Blenny	Tube Blennies	Chaenopsidae		ML
Emblemaria pandionis	Sailfin Blenny	Tube Blennies	Chaenopsidae		ML
Hemiemblemaria simula	Wrasse Blenny	Tube Blennies	Chaenopsidae		ML
Chaenopsis limbaughi	Yellowface Pikeblenny	Tube Blennies	Chaenopsidae		ML
Emblemariopsis bahamensis	Blackhead Blenny	Tube Blennies	Chaenopsidae		ML
Acanthemblemaria maria	Secretary Blenny	Tube Blennies	Chaenopsidae		ML
Stygnobrotula latebricola	Black Brotula	Viviparous Brotulas	Bythitidae		ML
Dasyatis americana	Southern Stingray	Whiptail Stingrays	Dasyatidae		
Halichoeres species	Wrasse species	Wrasses	Labridae		

Halichoeres burekae	Mardi Gras Wrasse	Wrasses	Labridae		
Bodianus rufus	Spanish Hogfish	Wrasses	Labridae		
Clepticus parrae	Creole Wrasse	Wrasses	Labridae		ML
Doratonotus megalepis	Dwarf Wrasse	Wrasses	Labridae		ML
Halichoeres bivittatus	Slippery Dick	Wrasses	Labridae		
Halichoeres garnoti	Yellowhead Wrasse	Wrasses	Labridae		ML
Halichoeres maculipinna	Clown Wrasse	Wrasses	Labridae		ML
Halichoeres pictus	Rainbow Wrasse	Wrasses	Labridae		ML
Halichoeres poeyi	Blackear Wrasse	Wrasses	Labridae		ML
Halichoeres radiatus	Puddingwife	Wrasses	Labridae		
Xyrichtys martinicensis	Rosy Razorfish	Wrasses	Labridae		ML
Xyrichtys novacula	Pearly Razorfish	Wrasses	Labridae		ML
Xyrichtys splendens	Green Razorfish	Wrasses	Labridae		ML
Lachnolaimus maximus	Hogfish	Wrasses	Labridae		SG
Thalassoma bifasciatum	Bluehead	Wrasses	Labridae		
Bodianus pulchellus	Spotfin Hogfish	Wrasses	Labridae		ML
Halichoeres cyanocephalus	Yellowcheek Wrasse	Wrasses	Labridae	P	ML
Halichoeres caudalis	Painted Wrasse	Wrasses	Labridae		ML
razorfish species	Razorfish species	Wrasses	Labridae		ML
Labrisomid sp.	*Labrisomid* blenny species	Wrasses	Labridae		ML

[1] Only 'piscivore' (P) and 'herbivore (H) designations are included. Trophic information was collected from a variety of sources, notably from the NCRMP RVC master species list.

[2] ✓ = Fished species include species commonly landed in commercial and recreational fisheries (including species landed primarily for bait). Several species (Nassau Grouper, Goliath Grouper and Bonefish) that are currently prohibited from take or subject only to catch-and-release fisheries are included as fished species due to prior exploitation and catch-and-release mortality. Species exploited for the aquarium trade (i.e. those taken under commercial or recreational Marine Life permits) are not considered fished species for this project. All species labeled 'SG' are considered to be fished species. Information regarding fishery status of each species was derived from a variety of sources, notably from the NCRMP RVC master species list.

[3] SG = Species in the federally permitted snapper-grouper complex fishery (NOAA 1983).

[4] ML = Species exploited for the aquarium trade (i.e. those taken under commercial or recreational Marine Life permits). See https://myfwc.com/fishing/saltwater/commercial/marine-life/ and https://myfwc.com/fishing/saltwater/recreational/marine-life/

References (Appendix 1)

NOAA National Marine Fisheries Service. 1983. Fishery management plan, regulatory impact review, and final environmental impact statement for the snapper-grouper fishery of the South Atlantic region. Pages 1-89.

Appendix 2. Details of explanatory variables

Area of reef

Biogeographic theory suggests that the area of reef available may affect fish assemblage structure (Jacquet et al. 2016) or concentrate fishing efforts in locations with limited habitat. In addition, recent work has shown reef size to have a significant, positive relationship with abundance and biomass of many fish species (Dames et al. 2019). Therefore, the available area of coral reef and/or pavement habitat close to each reef cell was measured from the Unified Florida Reef Tract habitat map (UFRTM). We calculated this variable at the 20 km and 200 km scale, but the two variables were highly correlated. As such, we included only the 20 km variable in the model, as 20 km represents the approximate high end of larval dispersal estimates for most coral reef fishes (Yeager et al. 2017).

Artificial Reefs

Artificial reefs are known to attract fish, and potentially enhance fish production, thereby increasing biomass in a given area (Seaman 2000, Arena et al. 2007). The presence of an artificial reef may aggregate fish from natural reefs, or they might create habitat and foraging opportunities that increase overall fish biomass (Bohnsack 1989, Grossman et al. 1997). In addition, artificial reefs in Florida are used heavily by fishermen targeting reef fish species, and proximity to these known high biomass artificial reefs may impact fishing pressure on nearby natural reefs by either taking pressure off natural reefs or by increasing fishing on natural reefs nearby heavily targeted artificial reefs (Grossman et al. 1997, Johns et al. 2001). Because these numerous mechanisms effect natural reef biomass differently, predicting the directionality of the relationship between biomass and artificial reefs is difficult, and it is possible that several mechanisms are in operation on the Florida reef tract. The location of artificial reefs in Florida is documented in a Florida Fish and Wildlife Conservation Commission (FWC) GIS shapefile. We calculated the number of artificial reefs within 1 km of each natural reef pixel using the Point Statistics tool in ArcGIS Pro (Rosemond et al. 2018).

Availability of nursery habitat

The availability of nursery habitats, particularly mangroves and seagrass beds, can significantly affect reef fish assemblage structure by increasing survival of juvenile fishes (Mumby et al. 2004, Harborne et al. 2016). Maps of continuous seagrass and mangrove stands adjacent to Florida coral reefs were derived from the UFRTM. Areas of discontinuous or patchy seagrass were not considered as nursery habitat in this project because of their limited functional importance as a nursery (Harborne et al. 2016). Connectivity to mangroves and medium-density and dense seagrass was calculated for all reef cells using a slightly modified version of the algorithm of Mumby (2006). There are few data on how far fish migrate from nursery habitats, but the only Florida and wider Caribbean estimates we are aware of all suggest increased populations up to 10 km (Dorenbosch et al. 2006, Mumby 2006, Huijbers et al. 2013). However, because prime fish habitat on the reef crest in Florida is slightly farther from mangrove nursery habitats, we use 12 km as the maximum distance of nursery influence. The algorithm measures the shortest distance across water between two target pixels and the connectivity metric between a reef site and all the pixels of a particular habitat (e.g. continuous seagrass) is then calculated as:

$$Connectivity_j = \sum_{i=1}^{n} D - c_{ij} \qquad (1)$$

where D is the maximum possible distance between two pixels (10,000 m), i is a nursery habitat pixel from a total of n within the seascape, j is the pixel containing the reef survey site location, and c_{ij} is the shortest across-water distance (m) between the two pixels. Consequently, high connectivity represents a large number of nursery pixels relatively close to the reef site. Only mangrove pixels adjoining fully subtidal habitat were used in order to remove pixels of non-functional mangroves further inland.

Coral cover

Coral cover provides fishes with food (Pratchett et al. 2008), refuge from predators and water flow (Hixon and Beets 1993, Johansen et al. 2008), and nesting sites (Robertson and Sheldon 1979). Consequently, numerous studies have linked coral cover to fish abundance (Bell and Galzin 1984, Jones et al. 2004, Gratwicke and Speight 2005), and it is likely to influence the abundance of many species considered in this project. We used data on coral cover that was estimated *in situ* for a subset of the RVC fish surveys in the Florida Keys. However, coral cover cannot be reliably modelled continuously across the entire reef tract. Therefore, predictions for the continuous maps of fishing impact and biomass were calculated using mean coral cover derived from NCRMP benthic surveys for the fishing impact model and habitat-specific (UFRTM Level 2 classification), regional means derived from NCRMP benthic surveys for the biomass model.

Depth

While rarely affecting fish assemblages directly, depth is a proxy for numerous environmental gradients such as light intensity, temperature, and salinity that may affect fishes. Depth was measured during *in situ* surveys and these values were used in the models. To extrapolate these results to the entire reef tract we used a global depth data layer published by Sbrocco and Barber (2013). This data layer was selected from several bathymetry layers available for the region due to a higher correlation between depths in the global layer (modelled depths) and depths measured by divers during RVC surveys (actual depths).

Distance to deep water

Reef walls represent transitional habitats between forereefs and pelagic environments, and these deeper reefs are important habitats for reef fishes such as planktivores (Harborne et al. 2006a). The approximate distance of each reef cell to these deeper habitats was calculated by measuring the Euclidean distance over water (using the Cost Distance tool in ArcGIS Pro) to the 30-meter bathymetric line as derived from the continuous bathymetric data layer described above (using the Contour List tool in ArcGIS Pro).

Distance to fish spawning aggregation

Only some species migrate to mass spawning sites to reproduce, but these species include many groupers and snappers that represent a significant component of the fishery species considered in this project. This explanatory variable was calculated by measuring the distance over water to the nearest fish spawning aggregation site described by NOAA NMFS (Sherman et al. 2016, Fig. A1). This dataset includes only spawning aggregation sites that have been field-verified by NOAA employees.

Fishing activity

We used several metrics to capture the commercial, charter and recreational fishing activity for each reef pixel considered in the project.

The FWC Marine Fisheries Trip Ticket Program[7] collects information on total volume of each species landed by commercial fisheries in Florida. These data are publicly available by fishing area. The Florida reef tract as defined in this study (Martin County to the Dry Tortugas) encompasses six fishing areas: Fort Pierce, West Palm Beach, Miami, Marathon, Key West, Tortugas, from northeast to southwest. We calculated the average annual pounds landed of all species in the snapper-grouper permit complex using a 10-year mean to capture they differences in fishery landings dynamics over the previous ten years between Southeast Florida and the Florida Keys (Johns et al. 2001). Because these data lack fine spatial resolution, every reef pixel within an FWC fishing area was assigned the same value.

Data on commercial and charter vessel permits in the snapper-grouper fishery are available from NOAA NMFS by the zip code associated with each permit. Though the zip code of reference for a given permit does not necessarily correspond to where the permitted vessel fishes, it is likely (especially for the charter fishery) that fishing occurs on reefs near the zip code of reference. We created GIS layers of the number of commercial and charter snapper-grouper permits, then calculated the number of each of these permits located within 25 km of each reef pixel for charter permits and 50 km for commercial permits. The distance of 25 km for charter vessels was selected to capture the distance travelled for a day trip (e.g. https: www.gulfstreamkeywest.com/faq/), but may not fully capture fishing done on 2-3 day trips leaving from the Keys and going to the Dry Tortugas (McClenachan 2009). Because commercial fishing vessels often travel further to fish, 50 km distance was used for commercial permits. The GIS layer of zip code polygons is a publicly available layer accessed through census.gov.

The environmental and socioeconomic impacts of recreational fishing have gained increasing awareness and attention from the scientific and management communities in recent decades (Lewin et al. 2019). In the state of Florida, where recreational fishing for reef species is economically valuable and socially important for coastal communities, direct and indirect effects of recreational fishing likely play a role in structuring reef fish assemblages (Johns et al. 2001). We used publicly-available data from the state of Florida on recreational fishing licenses. Each recreational license is associated with the zip code of the fisherman. Using these data, and census data describing county-level population in Florida, we calculated the percentage of people in each zip code with a recreational fishing permit. Using these percentages as a multiplier, we converted the population raster layer described below (see the *Human population size* variable) into a raster layer of the number of recreational fishermen within 50 km of each reef pixel to account for the distance that a typical recreational fisherman travels (including travel over land) to reef fish.

Fishing-related tourism is a major industry in Florida (Johns et al. 2001, Ditton et al. 2002). To account for tourism-based recreational coral reef fishing (which was not included in the recreational fishing license-derived metric above), we used statistics from Johns et al. 2001 and a publicly available dataset of hotel units in Florida from the Florida Geographic Data Library. The number of tourist reef fishing days (as estimated in Johns et al. 2001) was distributed across reef pixels relative to the number of hotel units within 50 km of that reef pixel, generating a metric of relative tourist fishing pressure for all reefs considered in the project with the exception of reefs in Martin County where no tourism estimates were available.

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[7] https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/wholesale-retail-dealers/

Finally, metrics of commercial and recreational fishery engagement and fishery reliance were provided by Michael Jepson at NOAA NMFS. Fishery engagement and reliance were calculated as part of a larger effort to develop fishing community social and vulnerability indices in the United States (Jepson and Colburn 2013). The fishing engagement metric relates to the presence of a commercial or recreational fishery in a given community based on landings and permits, and reliance relates to fishing activity relative to the population size of a fishing community. High engagement and/or reliance equates to a community dependent on the fishing industry. Each reef pixel in the project was assigned the commercial engagement and reliance metrics and recreational engagement and reliance metrics corresponding to the nearest fishing community. Because these metrics are derived from some of the same data used to derive the other variables related to commercial, charter and recreational fishing activity, only the variable representing the smallest spatial resolution was retained in each model following a test of inter-variable correlations.

Gravity of markets

In addition to the basic variable capturing population, this project also considered the economic geography concept of 'gravity', as it has been demonstrated to be an important variable in global studies (Cinner et al. 2016). The gravity concept infers that potential interactions increase with population size, but decay exponentially with the effective distance between two points. For this project, we used a dataset of total market gravity within 500 km (the sum of the market gravity of every population center within 500 km) published in Cinner et al. (2018). This follows Cinner et al. (2016) in calculating gravity as the number of people in the population centre divided by the square of the travel time (rather than distance, to account for differences in travel time over different surfaces) between that centre and the reef cell.

Habitat type

The models of both fishing impact and biomass contain a categorical variable for habitat type as described in the Unified Florida Reef Tract habitat map to include any variability that is not contained in the depth, coral cover, and complexity factors. Furthermore, within the fishing impact model this habitat variable may demonstrate differences in fishing pressure among habitat types caused by factors such as trap efficiency (Wolff et al. 1999). We used the UFRTM Level 2 classification which includes the following habitat types: Aggregate Reef, Individual or Aggregated Patch Reef, Spur and Groove, (Coral Reef and Pavement) Ridge, Reef Rubble, Colonized Reef Rubble, Pavement, Colonized Pavement, and Pavement with Sand Channels.

Human population size and population per area reef

The size of local human populations has repeatedly been demonstrated to be an excellent proxy of fishing pressure on reefs (e.g. Mora 2008, Stallings 2009, Mora et al. 2011, Cinner et al. 2013). Therefore, it was anticipated to be a potentially key variable in the model of fishing pressure on Florida coral reefs. Standardised, rasterized, global data sets of human populations are available from Oak Ridge National Laboratory's LandScan dataset[8]. LandScan uses census data in additional to remotely sensed images and multivariate modelling to derive their dataset. Data are highly correlated with population layers from the Socioeconomic Data and Applications Center (SEDAC), but was available for a more recent year (2017).

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[8] https://landscan.ornl.gov/

LandScan estimates population at a resolution of 30 arc-seconds (~1 km). We tested this variable in the model at two scales: the human population size within 20 km and within 50 km to capture both the distance that smaller, private fishing vessels might travel, and that larger charter or commercial fishing vessels might travel (Clark et al. 2002, Gorospe et al. 2018). The 20 km distance likely encompasses the area in which land-based sources of pollution might impact the fish assemblage, though we expect that those effects are better captured by the coral cover variable.

Additionally, the impact of human population sizes on reef fisheries is likely dependent on the reef area available, and we followed other studies in calculating population size per square km of fishable reef (Stallings 2009, Houk et al. 2012, Taylor et al. 2014b, Williams et al. 2015a). Therefore, we divided the population size figure by the area of reef within the same distance, resulting in a metric of human population pressure per km^2.

Latitude and longitude

The reef fishes of the Florida reef tract are recognized as being located within a single biogeographic region in the western Atlantic (Kulbicki et al. 2013). Consequently, biogeography of fishes is unlikely to be as major a confounding factor in the analyses as when working across biogeographic regions. However, there may be small-scale biogeographic patterns (Walker 2012), therefore latitude and longitude were included in initial models of both fishing impact and biomass to account for any variation in fish assemblages and fishing effort across the region. Both latitude and longitude were highly correlated with other covariates in the model (e.g. sea surface temperature), and so were excluded in final models.

Marina slips within 10km

For similar reasons that nearby population density may affect fishing impact, additional metrics of fishery access likely also play a role. We used a dataset developed by FWC and downloaded from the Florida Geographic Data Library[9] that was initially produced for a state-wide report on boating access and marine facilities. The dataset contains location information for every marina and port in Florida, and includes the number of vessel slips at a facility, and the presence and number of launch ramps. From these data we derived a continuous spatial layer of the number of marina slips within 10 km from each reef pixel included in the project to include the area within which most recreational fishermen travel to fish. Only marinas with access to South Atlantic reef habitats were included (e.g. marina slips within 10 km of a reef cell, but that were inland with no ocean access were excluded). We also excluded boat repair facilities, as these were not considered facilities from which fishermen would access reefs. Finally, we only included boat slips that were 45 ft and smaller to exclude large vessels that are not likely being used for reef fishing.

Month

Time of year can affect benthic assemblages and herbivory (Ferrari et al. 2012) and may represent aspects of fish spawning behavior (Sherman et al. 2016). The month that a survey was undertaken was included as an explanatory variable in the model.

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[9] https://www.fgdl.org/metadataexplorer/explorer.jsp

Number of larvae from upstream

The importance of larval supply on the abundance of reef fishes has been a hotly debated topic, leading to a large literature on the relative importance of pre- and post-settlement processes (see Hixon 2011 for an overview of this debate). The debate is now generally less polarized, with the importance of pre- and post-settlement processes apparently varying among species and in space and time. To investigate the importance of larval supply in predicting fish biomass, we used a biophysical model of larval supply throughout the area (see Cowen et al. 2006 for a full description of the model)[10]. Briefly, polygons of reef habitat were identified throughout the Florida reef tract, and then 'virtual larvae' were released monthly within a computer simulation of oceanic conditions (Fig. A2.1). The virtual larvae were given behavioral characteristics (e.g. larval duration, depth preferences) of the bicolor damselfish, *Stegastes partitus*. They were then tracked within the model, and where they 'settle' was recorded (either back to the same reef, to a different reef, or lost into oceanic water). These data generate a connectivity matrix, showing the proportion of larvae moving from each polygon to every other polygon.

This connectivity matrix was used to determine the number of arrivals from upstream sources, following the removal of self-recruiting arrivals at each polygon (arrivals originating and settling at the same patch). This metric was calculated because local-retention patterns tend not to be reliable when extracted from biophysical models because they ignore all local processes (e.g. tides, local-scale eddies, and near-shore turbulence), however our metric was strongly correlated with total arrivals estimated by the model ($p < 0.001$; $R^2 = 0.9995$). The number of larvae arriving was adjusted to account for the amount of coral reef and pavement habitat in each polygon (since virtual larvae may be concentrated on a small patch of reef, so it is important to consider arrivals per unit area of reef). Note that these metrics are not estimates of actual numbers of larvae arriving at each polygon, but are values representing the relative strength of fluxes of larvae among polygons. Note that the larval arrival metrics are the same for every reef pixel within each polygon. Because the connectivity model does not extend to the furthest north reefs (nor does it cover pavement habitat north of the Keys), those cells were assigned no data values.

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[10] Data supplied by Claire Paris, University of Miami

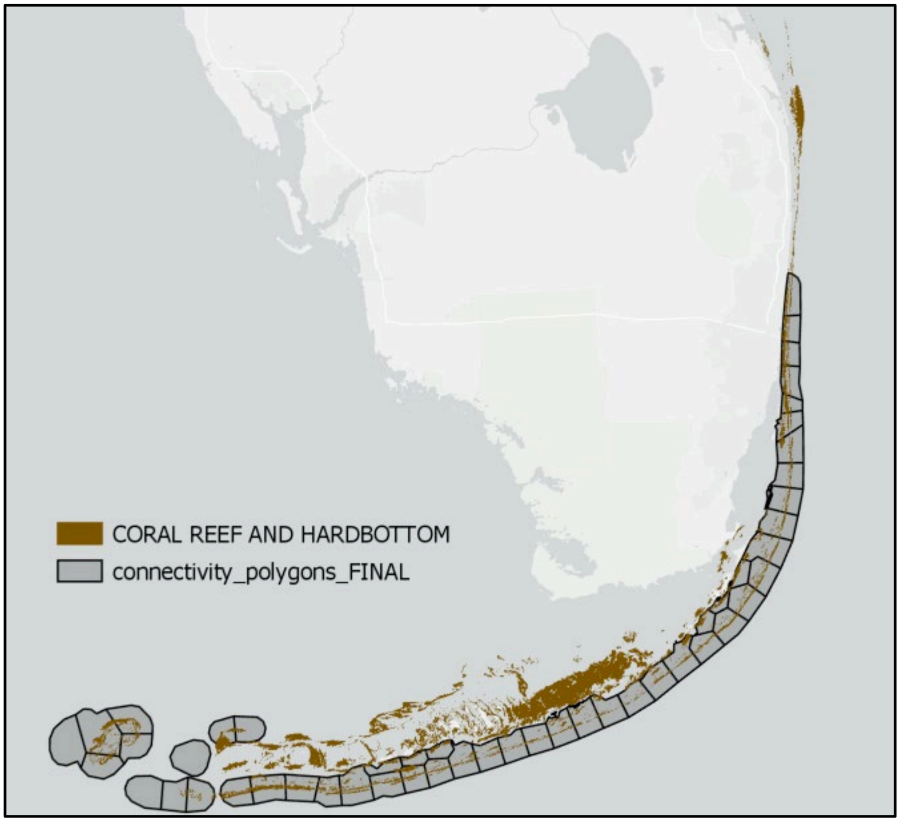

Fig. A2.1. The reef polygons (grey squares) included in the biophysical model of Florida reef tract larval connectivity. Note that connectivity estimates are only available for a subset of coral reef and pavement habitat pixels, and the model does not cover the entire northward extent of the reef tract.

Oceanic net primary productivity

Variations in primary productivity can influence herbivorous fish assemblage structure (Mumby et al. 2013), and the total biomass of reef fishes (Williams et al. 2015a). Therefore, oceanic productivity was included in the models of fishing impact and fish biomass. High-resolution measures of productivity across the entire region are not possible, and the project used remotely sensed data on chlorophyll-*a* as a proxy of primary productivity on reefs. Although these chlorophyll-*a* data do not discriminate small-scale variations in productivity, they do capture larger-scale patterns in productivity across the region (Gove et al. 2013). Mean monthly net primary productivity estimates were obtained from the Oregon State University Ocean Productivity Standard Vertically Generalized Production (VGPM) model (Behrenfeld and Falkowski 1997)[11]. Remotely sensed estimates of productivity over reefs are confounded by bottom reflectance, so only data from pelagic areas around each reef pixel were used. These areas were identified using the protocol described in Gove et al. (2013): productivity data was excluded in cells with a depth of <30 m, and then cells with missing values were populated by interpolating values from surrounding cells (Yeager et al. 2017).

Protected status

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[11] http://www.science.oregonstate.edu/ocean.productivity/index.php

A large literature demonstrates that marine protected areas can effectively reduce fishing pressure and fundamentally change fish assemblages (e.g. Mosquera et al. 2000, Halpern and Warner 2002, Russ 2002). Consequently, whether a fish survey site was inside or outside a protected area was included within the model of reef fishing impact. Although whether fishing is allowed at a given site or not should be captured within the fishing impact data layer, protected status was also included in the model of biomass to account for any differential effects on all fishes compared to all just the recreationally and commercially important species that were included in the fishing impact model (i.e. the fishing impact model only considers fishing of commercially important species, and the effect of marine protection may be clearer in the biomass model that considers all species). NOAA's 2017 Marine Protected Area inventory was merged with a NOAA layer of Sanctuary Preservation Areas (SPAs), Ecological Reserves, and Research Only Areas, all areas that prohibit fishing. We generated two protected area layers. The first layer codes all areas under some form of marine protection by their level of fishing restriction as follows: No restrictions; Commercial fishing restrictions; Commercial and recreational fishing restrictions; Recreational fishing restricted; Commercial fishing prohibited and recreational fishing restricted; Commercial fishing prohibited; All fishing prohibited. Reef pixels not included in the marine protected area layer were considered to have no restrictions. The second layer categorizes a reef pixel as either 'Open to fishing' or 'No take'. Though the SPAs were classified as 'No take' areas, bait fishing is allowed by permit in the SPAs, and catch-and-release trolling is allowed in some of the SPAs. In addition, take of fish for research may occur in the Research Only Areas.

Reef Complexity

Reef complexity provides fishes with refuge from predators and water flow (Hixon and Beets 1993, Johansen et al. 2008), and is a major influence on reef fish assemblages (Graham and Nash 2013). We used data on complexity (maximum vertical hard relief) that was estimated *in situ* during RVC fish surveys. However, complexity cannot be reliably modelled continuously across the entire Florida reef tract. Therefore, predictions for the continuous maps of fishing impact and biomass were calculated using the mean complexity measured for each UFRTM habitat type within each region (SE Florida, Florida Keys, and the Dry Tortugas). Biscayne National Park sites were parameterized with means from the Florida Keys.

Sea surface temperature

Temperature is one of the primary abiotic factors influencing the physiological performance of fish (Brett 1971). Consequently, general patterns of variability in sea surface temperature were included in the models of fishing impact and fish biomass. Sea surface temperature data were obtained online from the Coral Reef Temperature Anomaly Database (CoRTAD)[12] for the years 2012-2016 at a 4 km resolution (Saha et al. 2018). Following Williams et al. (2015a), we calculated the mean temperature from the coldest month of each year (i.e. the lower climatological mean) at each reef location. Interpolation was used to estimate sea surface temperature values for reef pixels where no data were available in the CoRTAD dataset. The final metric was calculated as the mean temperature of the coldest month over the five-year period from 2012-2016.

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[12] https://www.nodc.noaa.gov/SatelliteData/cortad/

Wave exposure

Wave exposure can have significant effects on fish assemblages since the morphologies of some species are better adapted to dealing with high levels of water movement (Fulton et al. 2005), and it can have significant effects on benthic habitat type (Chollett and Mumby 2012). High wave exposure can also limit fishing boat access, reducing fishing pressure (Houk et al. 2012, Chollett et al. 2014, Taylor et al. 2014b).

Exposure was calculated using linear wave theory, which has successfully been used to predict habitat distribution and benthic beta-diversity on reefs (Harborne et al. 2006b, Chollett and Mumby 2012). Full details of the method are described elsewhere (Ekebom et al. 2003), including their application to reefs (Harborne et al. 2006b, Chollett and Mumby 2012, Chollett et al. 2012). Wave exposure was calculated for the Florida reef tract as part of a project to categorize the physical environments of the region (Chollett et al. 2012)[13]. This data layer was used to assign a surface wave exposure to each coral reef and pavement habitat cell along the reef tract.

Year

With the exception of inside marine protected areas, fishing typically increases over time with continually increasing impacts on fish assemblages. Inevitably, the large data set assembled for this project was not collected simultaneously; we use data from fish surveys undertaken from 2005 to 2016. Fish survey data collected in 2010 were excluded from both models due to anomalously cold temperatures and resulting fish kills that were observed to impact survey results in that year. Year of collection was included in the models of both fishing impact and fish biomass to account for any temporal variation in fish assemblages. Where year was a significant variable, values of fishing impact or fish biomass across the region were predicted across the continuous maps using 2016 to provide currently expected values that are most useful for ongoing management planning.

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[13] Data supplied by Iliana Chollett

References (Appendix 2)

Arena, P.T., L.K.B. Jordan, and R.E. Spieler. 2007. Fish assemblages on sunken vessels and natural reefs in southeast Florida, USA. Hydrobiologia 580:157-171.

Bell, J. D., and R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series 15:265-274.

Behrenfeld, M.J., and P.G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42: 1-20.

Bohnsack, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bulletin of Marine Science 44(2): 631-645.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist 11:99-118.

Brewer, T. D., J. E. Cinner, R. Fisher, A. Green, and S. K. Wilson. 2012. Market access, population density, and socioeconomic development explain diversity and functional group biomass of coral reef fish assemblages. Global Environmental Change 22:399-406.

Brewer, T. D., J. E. Cinner, A. Green, and R. L. Pressey. 2013. Effects of human population density and proximity to markets on coral reef fishes vulnerable to extinction by fishing. Conservation Biology 27:443-452.

Clark, B.M., M. Hauck, J.M. Harris, K. Salo, and E. Russell. 2002. Identification of subsistence fishers, fishing areas, resource use and activities along the South African coast. South African Journal of Marine Science 24: 425-437.

Chollett, I., S. W. J. Canty, S. J. Box, and P. J. Mumby. 2014. Adapting to the impacts of global change on an artisanal coral reef fishery. Ecological Economics 102:118-125.

Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. Limnology and Oceanography 57:1233-1244.

Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. Coral Reefs 31:493-503.

Cinner, J. E., N. A. J. Graham, C. Huchery, and M. A. MacNeil. 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. Conservation Biology 27:453-458.

Cinner, J. E. et al. 2016. Bright spots among the world's coral reefs. Nature 535:416-419.

Cinner, J.E. et al. 2018. Gravity of human impacts mediates conservation gains. Proceedings of the National Academy of Sciences 115(27): E6116-E6125.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 311:522-527.

Dames, V., A. Bernard, C. Floros, B. Mann, C. Speed, J. Maggs, S. Laing, M. Meekan, and J. Olbers. 2019. Zonation and reef size significantly influence fish populatino structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. Ocean and Coastal Management 105040.

Ditton, R.B., S.M. Holland, and D.K. Anderson. 2002. Recreational fishing as tourism. Fisheries 23(3): 17-24.

Dorenbosch, M., M. G. G. Grol, I. Nagelkerken, and G. van der Velde. 2006. Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. Biological Conservation 129:277-282.

Ekebom, J., P. Laihonen, and T. Suominen. 2003. A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. Estuarine Coastal and Shelf Science 57:887-898.

Ferrari, R., M. Gonzalez-Rivero, J. C. Ortiz, and P. J. Mumby. 2012. Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. Coral Reefs 31:683-692.

Fulton, C. J., D. R. Bellwood, and P. C. Wainwright. 2005. Wave energy and swimming performance shape coral reef fish assemblages. Proceedings Of The Royal Society B-Biological Sciences 272:827-832.

Gorospe, K.D., M.J. Donahue, A. Heenan, J.M. Gove, I.D. Williams, and R.E. Brainard. 2018. Local biomass baselines and the recovery potential for Hawaiian coral reef fish communities. Frontiers in Marine Science 5: 162.

Gove, J. M., G. J. Williams, M. A. McManus, S. F. Heron, S. A. Sandin, O. J. Vetter, and D. G. Foley. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. PLoS ONE 8:e61974.

Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315-326.

Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650-667.

Grossman, G.D., G.P. Jones, and W.J. Seaman. 1997. Do artificial reefs increase regional fish production? A review of existing data. Fisheries 22(4): 17-23.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361-366.

Harborne, A. R., P. J. Mumby, F. Micheli, C. T. Perry, C. P. Dahlgren, K. E. Holmes, and D. R. Brumbaugh. 2006a. The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. Advances in Marine Biology 50:57-189.

Harborne, A. R., P. J. Mumby, K. Żychaluk, J. D. Hedley, and P. G. Blackwell. 2006b. Modeling the beta diversity of coral reefs. Ecology 87:2871-2881.

Harborne, A. R., I. Nagelkerken, N. H. Wolff, Y.-M. Bozec, M. Dorenbosch, M. G. G. Grol, and P. J. Mumby. 2016. Direct and indirect effects of nursery habitats on coral-reef fish assemblages, grazing pressure and benthic dynamics. Oikos 125:957-967.

Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecological Monographs 63:77-101.

Hixon, M. A. 2011. 60 years of coral reef fish ecology: past, present, future. Bulletin of Marine Science 87:727-765.

Houk, P., K. Rhodes, J. Cuetos-Bueno, S. Lindfield, V. Fread, and J. L. McIlwain. 2012. Commercial coral-reef fisheries across Micronesia: A need for improving management. Coral Reefs 31:13-26.

Huijbers, C. M., I. Nagelkerken, A. O. Debrot, and E. Jongejans. 2013. Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. Ecology 94:1859-1870.

Jacquet, C., D. Mouillot, M. Kulbicki, and D. Gravel. 2016. Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. Ecology Letters doi:10.1111/ele.12716.

Jepson, M., and L.L Colburn. 2013. Development of social indicators of fishing community vulnerability and resilience in the U.S. Southeast and Gulf regions. U.S. Department of Commerce, NOAA Technical Memorandum: NMFS-F/SPO-129, 64 p.

Johansen, J. L., D. R. Bellwood, and C. J. Fulton. 2008. Coral reef fishes exploit flow refuges in high-flow habitats. Marine Ecology Progress Series 360:219-226.

Johns, G.M., Leeworthy, V.R., Bell, F.W., and Bonn, M.A.. 2001. Socioeconomic study of reefs in Southeast Florida. National Oceanic and Atmospheric Administration.

Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101:8251-8253.

Kulbicki, M., V. Parravicini, D.R. Bellwood, E. Arias-Gonzalez, P. Chabanet, S.R. Floeter, A. Friedlander, J. McPherson, R.E. Myers, L. Vigliola, and D. Mouillot. 2013. Global biogeography of reef fishes: a hierarchical quantitative delineation of regions. PLoS One 8(12): e81847.

Lefcheck, J.S., B.B. Hughes, A.J. Johnson, B.W. Pfirman, D.B. Rasher, A.R. Smyth, B.L Williams, M.W. Beck, and R.J. Orth. 2019. Are coastal habitats important nurseries? A meta-analysis. Conservation Letters e12645.

Lewin, W-C., M.S. Weltersbach, K. Ferter, K. Hyder, E. Mugerza, R. Prellezo, Z. Radford, L. Zarauz, and H.V. Strehlow. 2018. Potential environmental impacts of recreational fishing on marine fish stocks and ecosystems. Reviews and Fisheries Science and Aquaculture, DOI: 10.1080/23308249.2019.1586829.

Lindeman, K.C., R. Pugliese, G.T. Waugh, and J.S. Ault. 2000. Development patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bulletin of Marine Science 66(3):929-956.

Mbaru, E. K., N. A. J. Graham, T. R. McClanahan, J. E. Cinner. 2019. Functional traits illuminate the selective impacts of different fishing gears on coral reefs. Journal of Applied Ecology.

McClenachan, L. 2009. Documenting loss of large trophy fish from the Florida Keys with historical photographs. Conservation Biology 23(3): 636-643.

Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. Proceedings Of The Royal Society B-Biological Sciences 275:767-773.

Mora, C., et al. 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biology 9: e1000606.

Mosquera, I., I. M. Côté, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation 3:321-332.

Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533-536.

Mumby, P. J. 2006. Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. Biological Conservation 128:215-222.

Mumby, P. J., S. Bejarano, Y. Golbuu, R. S. Steneck, S. N. Arnold, R. van Woesik, and A. M. Friedlander. 2013. Empirical relationships among resilience indicators on Micronesian reefs. Coral Reefs 32:213-226.

Pratchett, M. S., P. L. Munday, S. K. Wilson, N. A. J. Graham, J. E. Cinner, D. R. Bellwood, G. P. Jones, N. V. C. Polunin, and T. R. McClanahan. 2008. Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. Oceanography and Marine Biology: An Annual Review 46:251-296.

Robertson, D. R., and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. Journal of Experimental Marine Biology and Ecology 40:285-298.

Rosemond, R.C., A.B. Paxton, H.R. Lemoine, S.R. Fegley, C.H. Peterson. 2018. Fish use of reef structures and adjacent sand flats: implications for selecting minimum buffer zones between artificial reefs and existing reefs. Marine Ecology Progress Series 587: 187-199.

Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. Pages 421-443 *in* P. F. Sale, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego.

Saha, K., X. Zhao, H. Zhang, K.S. Casey, B. Dexin, Sheekela, K.A. Kilpatrick, R.H. Evans, T. Ryan, J.M. Relph. 2018. AVHRR Pathfinder Version 5.3 Level 3 Collated (L3C) Global 4km sea surface temperature for 1981-Present. NOAA National Centers for Environmental Information. Dataset. doi: 10.7289/V52J68XX.

Sbrocco, E.J., and P.H. Barber. 2013. MARSPEC: ocean climate layers for marine spatial ecology. Ecology 94(4):979.

Seaman, W. 2000. Artificial reef evaluation with application to natural marine habitats. CRC Press. Boca Raton, FL.

Sherman, K. D., C. P. Dahlgren, J. R. Stevens, and C. R. Tyler. 2016. Integrating population biology into conservation management for endangered Nassau grouper *Epinephelus striatus*. Marine Ecology Progress Series 554:263-280.

Shideler, G.S., R.J. Araujo, B.K. Walker, J. Blondeau and J.E. Serafy. 2017. Non-linear thresholds characterize the relationship between reef fishes and mangrove habitat. Ecosphere 8(9): e01943.

Stallings, C. D. 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. PLoS ONE 4: e5333.

Taylor, B. M., S. J. Lindfield, and J. H. Choat. 2014. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography 37:001-011. doi: 010.1111/ecog.01093.

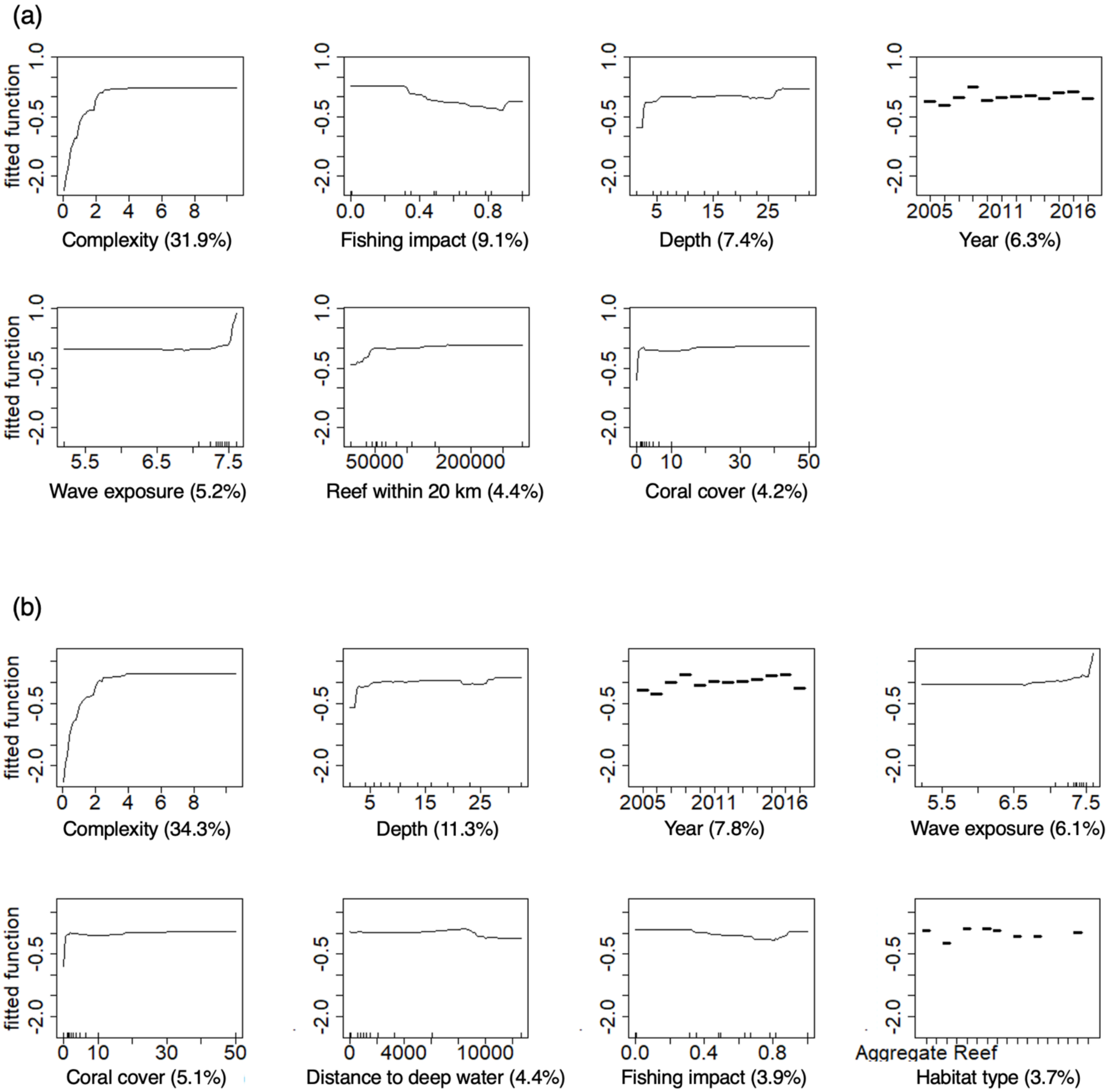
Walker, B. K. 2012. Spatial analyses of benthic habitats to define coral reef ecosystem regions and potential biogeographic boundaries along a latitudinal gradient. PLOS ONE 7(1):e30466.

Williams, I. D., J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, and R. E. Brainard. 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. PLoS ONE 10: e0120516. doi:10.1371/journal.pone.0120516.

Wolff, N., R. Grober-Dunsmore, C. S. Rogers, and J. Beets. 1999. Management implications of fish trap effectiveness in adjacent coral reef and gorgonian habitats. Environmental Biology of Fishes 55:81-90.

Yeager, L.A., P. Marchard, D.A. Gill, J.K. Baum, and J.M. McPherson. 2017. Marine socio-environmental co-variates: queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. Ecology 98(7):1976.

Appendix 3. Additional fish biomass model results



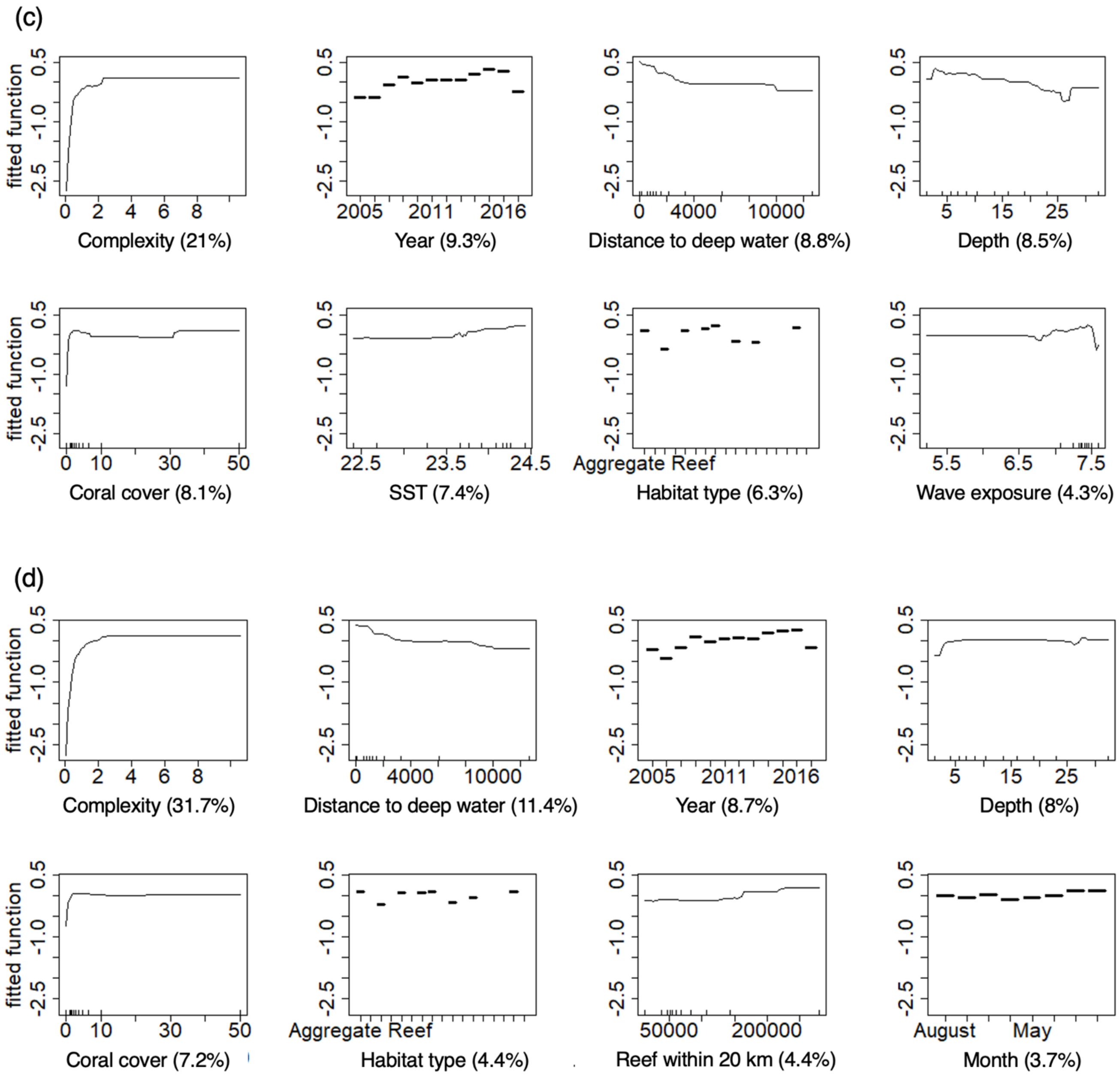
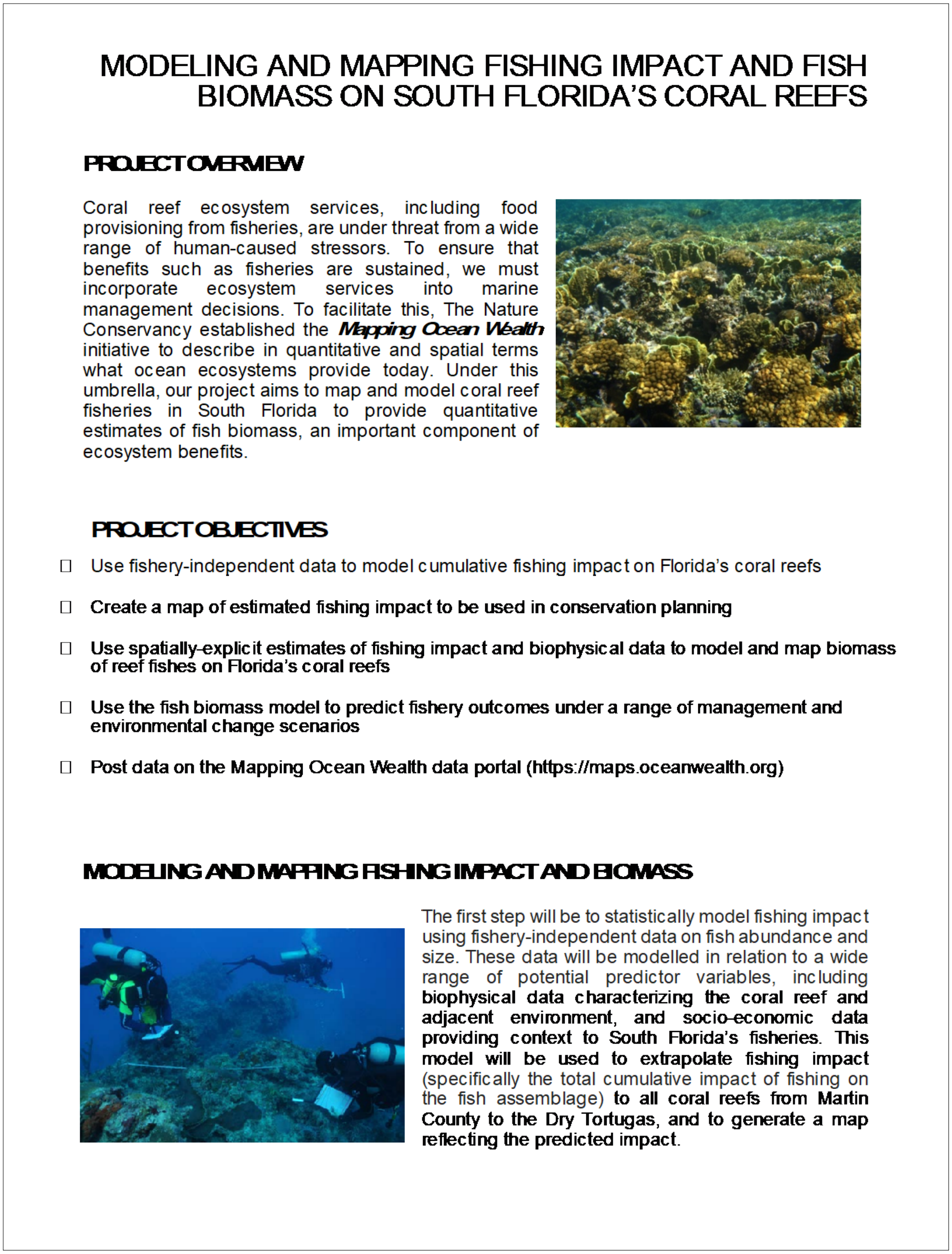


Fig. A3.1. Relationships between the top eight significant variables and the biomass of (a) all fished species; (b) all reef-fish, i.e. total biomass; (c) herbivores; and (d) marine life species as modelled by boosted regression trees. Values of log fish biomass on the y-axis are normalised as opposed to showing actual biomass values. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable.

Appendix 4. Two-page introductory handout for the project



MODELING AND MAPPING FISHING IMPACT AND FISH BIOMASS ON SOUTH FLORIDA'S CORAL REEFS

PROJECT OVERVIEW

Coral reef ecosystem services, including food provisioning from fisheries, are under threat from a wide range of human-caused stressors. To ensure that benefits such as fisheries are sustained, we must incorporate ecosystem services into marine management decisions. To facilitate this, The Nature Conservancy established the ***Mapping Ocean Wealth*** initiative to describe in quantitative and spatial terms what ocean ecosystems provide today. Under this umbrella, our project aims to map and model coral reef fisheries in South Florida to provide quantitative estimates of fish biomass, an important component of ecosystem benefits.

PROJECT OBJECTIVES

- ☐ Use fishery-independent data to model cumulative fishing impact on Florida's coral reefs
- ☐ Create a map of estimated fishing impact to be used in conservation planning
- ☐ Use spatially-explicit estimates of fishing impact and biophysical data to model and map biomass of reef fishes on Florida's coral reefs
- ☐ Use the fish biomass model to predict fishery outcomes under a range of management and environmental change scenarios
- ☐ Post data on the Mapping Ocean Wealth data portal (https://maps.oceanwealth.org)

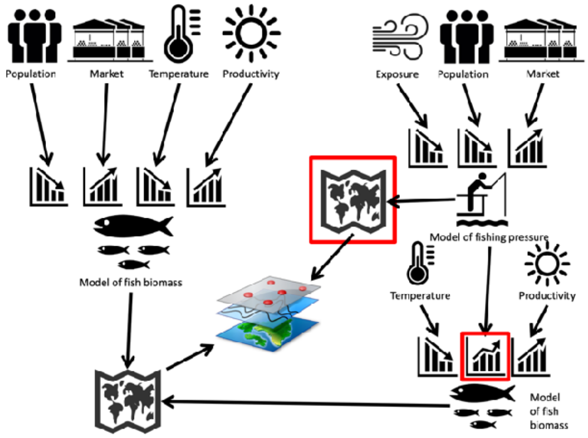
MODELING AND MAPPING FISHING IMPACT AND BIOMASS

The first step will be to statistically model fishing impact using fishery-independent data on fish abundance and size. These data will be modelled in relation to a wide range of potential predictor variables, including biophysical data characterizing the coral reef and adjacent environment, and socio-economic data providing context to South Florida's fisheries. This model will be used to extrapolate fishing impact (specifically the total cumulative impact of fishing on the fish assemblage) to all coral reefs from Martin County to the Dry Tortugas, and to generate a map reflecting the predicted impact.

With this spatial data on fishing impact, we will then model current fish biomass at an independent set of sites where fish survey data are available. Fishing impact will be a key predictor variable. This model will generate a functional relationship between fishing and fish biomass for the region, while accounting for a range of environmental variables, such as sea surface temperate, that may impact biomass. This model will then be used to extrapolate estimates of current biomass to generate a continuous map that will be made available to fishery and marine managers.

ANTICIPATED OUTCOMES

The modeled fish biomass and resultant maps will be useful tools for exploring fishery outcomes under a range of management options (e.g. area-based fishing regulations) and environmental change (e.g. a change in coral cover) scenarios. This new 'Ocean Wealth' information can be used to help set realistic expectations for area-based management outcomes, aid in restoration decision-making, and provide managers information relating to fishery use for areas where few data currently exist. We aim to provide information to managers and stakeholders to improve understanding of ecological trade-offs and potential benefits that are predicted under different management and ocean use scenarios.



PROJECT TEAM

This project is a collaboration between Alastair Harborne's Tropical Fish Ecology Lab at Florida International University and The Nature Conservancy (TNC). The work supports the Mapping Ocean Wealth initiative, which aims to generate high quality, spatially-explicit data to reveal the economic and social benefits of coastal ecosystems, such as coral reefs, around the world.

For more on the *Mapping Ocean Wealth* initiative, visit https://oceanwealth.org/. For questions or to speak with someone about this project, please reach out:

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