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Identifying correlates of coral-reef fish biomass on Florida's Coral Reef to assess potential management actions

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Abstract

1. Coral reef fish assemblages are threatened globally, underscoring the need for data-driven management to reduce threats and restore populations. Comparing fishery management approaches is aided by a detailed understanding of the key factors controlling species' abundances.
2. The aims of this study were to assess the importance of biophysical factors compared with fishing impacts on the biomass of reef fishes on Florida's Coral Reef and to evaluate the potential effects of common management interventions on fish biomass.
3. Fishing impact was estimated using a fishery-independent modelling approach and the biomass of the snapper–grouper complex as a proxy for the effects of fishing. Using a separate subset of data from underwater fish surveys, estimated fishing impact was then combined with 18 biophysical variables to model the current biomass of all reef fish species, the snapper–grouper complex, grazing species and species collected for aquaria.
4. Models explained between 51 and 64% of the variance in fish biomass for the fish groups. The strongest predictor of biomass in the snapper–grouper complex was fishing impact (accounting for 25.2% of the explained variance), whereas reef complexity was the strongest predictor for all other groups.
5. High-resolution maps were produced from the statistical models, including maps of current fish biomass and maps of potential biomass under several management scenarios: a no-take marine reserve, moderate and extensive coral restoration and the addition of artificial benthic structure. Adding structure had the largest single impact on predicted fish biomass (23–72% increase from current estimated levels). However, beneficial synergies emerged when combining habitat-based management and fishing closures, with some combinations resulting in a reef-wide averaged 89% increase in biomass relative to current estimated levels.
6. The results suggest that conservation strategies aimed at protecting and increasing structural reef complexity should be an important part of fishery management discussions.

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KEYWORDS

coral reef fisheries, coral restoration, Florida fish biomass, management scenarios, snapper and grouper, structural complexity

1 | INTRODUCTION

Coral reef ecosystems and the reef fish populations they support are declining globally in response to local and global stressors (Paddack et al., 2009; Pratchett, Hoey & Wilson, 2014; Hughes et al., 2017; Woodhead et al., 2019). To counter these losses and improve coral reef-associated fisheries, managers look to spatial measures, such as no-take reserves (reviewed by Graham et al., 2011) or non-exclusionary managed zones (Lester & Halpern, 2008; Sciberras et al., 2015), size limits and gear restrictions (MacNeil et al., 2015; Bozec et al., 2016), policies to protect functionally important species (Cox et al., 2013; O'Farrell et al., 2015) and numerous approaches to habitat restoration (NASEM, 2019; Boström-Einarsson et al., 2020; Seraphim et al., 2020). However, funding limitations, political will and stakeholder expectations require managers to assess policy and management options, weigh their probable costs and benefits, and select the approaches most likely to yield positive results (Cinner et al., 2020). Consequently, the best choices for conservation and management actions vary both spatially and temporally across diverse biophysical and socio-economic contexts (Kimball et al., 2015; Rogers et al., 2015; Graham et al., 2020). The absence of data to resolve such variable outcomes of management actions presents a challenge for managers deciding among approaches.

Decision-makers are faced with the particular challenge of discerning the importance of biophysical drivers of fish biomass compared with human-use drivers as they weigh various management options (Jouffray et al., 2019). Overfishing of coral reef species, mediated by factors such as fishing effort, the presence and enforcement of marine reserves, and the species and size preferences of fishers and consumers, is a well-known and widespread threat (McClanahan et al., 2011; Shantz, Ladd & Burkepile, 2019). There are also many anthropogenic threats to coral reef fish assemblages beyond overfishing (Mora, 2008). For example, climate change, decreasing water quality and physical habitat disturbances contribute to declines in reef fish biomass directly (Chabanet et al., 2005; Reopanichkul et al., 2009; Habary et al., 2017) and indirectly by causing coral mortality and reduced structural complexity (Graham & Nash, 2013; Coker, Wilson & Pratchett, 2014). Biophysical features and gradients, such as habitat type, depth, temperature and wave exposure, also play a role in structuring fish assemblages (Alevizon et al., 1985; Hixon & Beets, 1993; Fulton, Bellwood & Wainwright, 2005). Both the human-use threats and biophysical factors vary over time and space and do not influence all species and species groups equally (Cresswell et al., 2019; Jouffray et al., 2019). Therefore, to increase fish populations through local-scale management, it is helpful to understand the factors that influence fish

biomass, the relative importance of these factors in biomass decline, and how these factors differ across the fish assemblage. Without knowledge of these local factors, effectively targeting management actions to increase fish populations at a local scale remains difficult (Ault et al., 2005; Pittman & Brown, 2011; Houk et al., 2015).

Florida's Coral Reef (also known as the Florida reef tract) provides an excellent case of a well-studied reef where major efforts are underway to protect its ecosystem services (Pandolfi et al., 2005; Riegl & Dodge, 2008; Walker & Gilliam, 2013; Lirman et al., 2019). It is threatened by a wide range of stressors (e.g. Ault, Bohnsack & Meester, 1998; Ward-Paige et al., 2005; Manzello, 2015; Precht et al., 2016) and subject to a level of degradation that has created concerns of large-scale loss of coral cover (Palandro et al., 2008) and reef structure (Alvarez-Filip et al., 2009; Toth et al., 2019). In response, managers have enacted spatial management measures (Bohnsack et al., 2009; Bohnsack, 2011; Ault et al., 2013), mandated fish size limits and species-specific bans (Chiappone, Sluka & Sealey, 2000), undertaken reef restoration programmes (van Woesik, Ripple & Miller, 2018) and deployed artificial reefs (Walker, Henderson & Spieler, 2002; Arena, Jordan & Spieler, 2007). These measures have contributed to the reef's ability to continue providing important ecosystem services, albeit at reduced levels. Of particular importance, the reefs support commercial and recreational fishing industries with rich histories in the Florida Keys and Southeast Florida (Ault, Bohnsack & Meester, 1998; McClenachan, 2013; Shivlani, 2014) that provide billions of dollars in economic activity to the state (Johns et al., 2001; Wallmo et al., 2021).

To predict the likely impacts of these and other management measures on coral reef fisheries, this research aimed to clarify our understanding of the factors influencing reef fish biomass along Florida's Coral Reef. Because fishing is predicted to be an important driver of fish biomass, a subset of fish survey data available for the region were initially used to construct a model of fishing impact. This model allowed us to identify the key factors influencing spatial patterns in fishing in this heavily populated area with complex fisheries, and yielded a single fishing variable for comparison with biophysical variables in a subsequent model of reef fish biomass (Harborne et al., 2018). From there, model-derived relationships between fish biomass, fishing and biophysical correlates were used to predict current fish biomass across the entire reef tract. Finally, the models were used to predict the potential reef tract-scale benefits of management scenarios including spatial fishing closures, various levels of restoration, addition of artificial structure and combinations of these approaches. We hypothesized that anthropogenic impacts, particularly fishing and the loss of coral reef structure, are key controls of fish biomass, and thus that both reef restoration and the expansion of no-take zones are optimal management strategies. This

research provides a data-driven approach to the comparison of coral reef management methods at the fine spatial scale necessary to inform local management actions.

2 | METHODS

2.1 | Florida's coral reefs

This study considers the ~500 km Florida reef tract from the northern border of Martin County in the north east to the Dry Tortugas in the south west (approximately 27.50° to 24.55° N, 80.28° to 83.00° W). The area includes the Florida Keys, a barrier reef that extends ~400 km south west along an island archipelago from Key Biscayne near Miami to the Dry Tortugas region west of Key West. Oceanographic conditions in the region are considered marginal for coral growth, especially areas heavily influenced by water generated in Florida Bay and moving into the Atlantic (Riegl & Dodge, 2008). The reef tract supports ~60 species of coral and over 500 species of fish. It is characterized by forereefs, often with distinct spur and groove zones, and many patch reefs further inshore (Riegl & Dodge, 2008; Lirman et al., 2019).

Maps generated by the Florida Fish and Wildlife Conservation Commission (FWC; see <https://myfwc.com/research/gis/regional-projects/unified-reef-map/> for metadata and other details) were used to determine the extent of reef (with a current or historical cover of scleractinian corals). Level 2 of the Unified Florida Reef Tract Map classification scheme was appropriate for identifying habitats for this modelling and mapping work (Walker, Rodericks & Costaregni, 2013; FWC, 2016). This classification included habitats labelled: Aggregate Reef, Individual or Aggregated Patch Reef, Spur and Groove, and (Coral Reef) Ridge. Naturally low-relief hardbottom habitats (visually dominated by gorgonians with low coral cover) that are not typically targeted for certain conservation initiatives, such as coral restoration, were excluded from the analysis. Although these areas constitute habitat for reef fish species, they may be controlled by different biophysical processes than the coral reef areas where this work was focused. For a similar reason, along with very shallow sites not being well parameterized by the large-scale biophysical datasets available for the project, habitats in less than 2 m water depth were excluded. Habitat polygons were rasterized at a spatial scale of 1 ha (100 × 100 m) to preserve habitat detail while keeping the study computationally tractable. This process yielded 39,795 1-ha coral reef pixels along the reef tract.

2.2 | Response variables: fish survey data

The National Oceanic and Atmospheric Administration's (NOAA's) Coral Reef Monitoring Program has carried out Florida's Reef Visual Census since 1979, collecting data using a random stratified sampling method on the coral reef fish assemblages and benthic communities

of the Dry Tortugas, Florida Keys and Southeast Florida (Bohnsack & Bannerot, 1986; Ault, Bohnsack & Meester, 1998; Bohnsack et al., 1999; Brandt et al., 2009). Divers conducted point count fish surveys during which they identified all fish within a 7.5 m radius to species level, and enumerated and sized those fish to the nearest centimetre. Fish survey data from 2005 to 2018 were used, excluding data from 2010 owing to potentially anomalous counts following a cold temperature event and subsequent nearshore reef fish kill (Kemp et al., 2016; Santos et al., 2016). The most recently available data were used for sites that had been surveyed in multiple years (76% of surveys used were done between 2012 and 2018). This yielded a total of 2,779 sites in the Dry Tortugas ($n = 623$), Florida Keys ($n = 931$) and Southeast Florida ($n = 1,225$). At each fish survey site, depth, latitude and longitude were recorded, cover of live coral was estimated and reef complexity (as the maximum vertical relief of the substrate) was measured. After excluding sharks (that tend to be transitory, and not well surveyed by visual methods, but large enough to significantly affect biomass estimates when seen) from the dataset, allometric relationships (estimated from data collected in the Caribbean region when possible) were used to convert fish count and size data into biomass estimates (kg ha^{-1}) for each survey site (Bohnsack & Harper, 1988; Froese & Pauly, 2010; Stevens, Smith & Ault, 2019). While other response variables such as fish species diversity or relative abundance are also of clear management interest, fish biomass is the focus of this study. Biomass is typically a primary concern for managers and is the most commonly used metric in the coral reef literature to summarize fish assemblages (e.g. MacNeil et al., 2015).

2.3 | Predictor variables: biophysical and fishing-related data layers

Biomass at each fish survey site was modelled against spatially continuous biophysical and fishing-related predictor variables to assess the factors correlated with fishing impact and biomass variability (Table 1; Appendix S1). Two important habitat-related biophysical variables, coral cover and maximum hard relief (hereafter referred to as reef complexity), were available from the *in situ* fish surveys and used for the models of fish biomass to assess their importance (Gratwicke & Speight, 2005; Graham & Nash, 2013). However, coral cover and reef complexity are not mapped continuously for Florida's Coral Reef. Deriving a continuous data layer for coral cover or reef complexity requires information on a complex range of factors including recruitment, grazing pressure, wave exposure and the frequency of hurricanes and bleaching events which were not available (Williams et al., 2015). Therefore, during the mapping extrapolation across unsurveyed reef pixels using the statistical models, coral cover and reef complexity were represented by the regional (Dry Tortugas, Florida Keys or Southeast Florida) mean values for each habitat type calculated from Reef Visual Census sites surveyed between 2012 and 2018. To account for any intra-habitat variation across the study area that was not captured by

TABLE 1 Biophysical and fishing-related explanatory variables used in the fishing impact and fish biomass models. Variables are quantified with continuous data unless otherwise noted in the Variable column. Owing to inter-variable correlations, not all variables were used in final models. Additional information regarding data sources and variable derivation can be found in Appendix S1.

Variable	Description	Derivation	Model(s)
<i>Biophysical variables</i>			
Area of reef within proximity	Area of coral reef habitat within 20 or 200 km	UFRTM	Impact; biomass
Artificial reefs ^a	Number of artificial reefs within 1 km	Data provided by state and county agencies	Impact; biomass
Availability of nursery habitat	Reef connectivity to mangrove and nursery habitat	Use of algorithm (Mumby, 2006); UFRTM	Impact; biomass
Coral cover	Average percentage coral cover at survey site	From <i>in situ</i> fish surveys	Impact; biomass
Depth	Depth at fish survey site or reef pixel	From <i>in situ</i> fish surveys; Sbrocco & Barber (2013)	Impact; biomass
Distance to deep water habitats	Distance to the 30 m depth contour	Sbrocco & Barber (2013)	Impact; biomass
Distance to fish spawning aggregation	Distance to nearest known snapper or grouper spawning aggregation	NOAA NMFS	Impact; biomass
Ecoregion	The region (Southeast Florida, Florida Keys or the Dry Tortugas)	From <i>in situ</i> fish surveys; GIS	Impact; biomass
Habitat type (categorical)	Level 2 classification of coral reef habitat type	UFRTM	Impact; biomass
Latitude	Latitude of fish survey site or reef pixel	From <i>in situ</i> fish surveys; GIS	Impact; biomass
Longitude	Longitude of fish survey site or reef pixel	From <i>in situ</i> fish surveys; GIS	Impact; biomass
Number of larvae from upstream sources	Relative number of larvae arriving at each reef from upstream sources	Biophysical model of ocean currents provided by Claire Paris (University of Miami)	Impact; biomass
Oceanic net primary productivity	Mean net primary productivity from monthly data (2012–2016)	Oregon State University modelled product derived from satellite data	Impact; biomass
Protected status ^a (categorical)	No take area vs. open to any form of fishing	FWC and NOAA MPA databases	Impact; biomass
Reef complexity	Maximum hard relief at survey site	From <i>in situ</i> fish surveys	Impact; biomass
Sea surface temperature	Mean temperature of the coldest month (2012–2016)	NOAA CoRTAD satellite-based ocean temperature dataset	Impact; biomass
Wave exposure	Wave exposure based on fetch and mean wind data	Chollett et al. (2012)	Impact; biomass
<i>Fishing-related variables</i>			
Fishing impact	Cumulative impact of fishing	Estimated by this project	Biomass
Community fishing engagement and reliance	Metrics of fishing engagement and economic reliance on fishing by NOAA-identified fishing community	Jepson & Colburn (2013)	Impact
Fishery activity: commercial	Number of federal Class 1 snapper–grouper permits within 50 km	NOAA NMFS	Impact
Fishery activity: charter	Number of federal snapper–grouper charter permits assigned to vessels within 25 km	NOAA NMFS	Impact
Fishery activity: Florida-based recreational	Number of marine recreational fishing licence holders within 50 km	FWC	Impact
Fishery activity: tourism-related	Estimated number of tourist reef fishing days per year	Florida Geographic Data Library; Johns et al. (2001)	Impact
Total gravity of fish markets within 500 km	Market gravity defined as population size divided by the square of travel size	Cinner et al. (2018)	Impact

TABLE 1 (Continued)

Variable	Description	Derivation	Model(s)
Human population	Number of people within 20 and 50 km of a reef pixel	LandScan human population data	Impact
Human population per area reef	Number of people within 20 or 50 km divided by the area of fishable reef within 20 or 50 km	LandScan human population data; UFRTM	Impact
Marina slips	Number of marina slips for vessels under 45 ft within 25 km	FWC	Impact
<i>Methodological variables</i>			
Month (categorical)	Month of fish survey	From <i>in situ</i> fish surveys	Impact; biomass
Year	Year of fish survey	From <i>in situ</i> fish surveys	Impact; biomass

Abbreviations: CoRTAD, Coral Reef Temperature Anomaly Database; FWC, Florida Fish and Wildlife Conservation Commission; UFRTM, Unified Florida Reef Tract Map; UM, University of Miami; NMFS, National Marine Fisheries Service.

^aData layers are included as both biophysical and fishing-related variables.

complexity, depth or coral cover variables, models also included an ecoregion variable (Southeast Florida, Florida Keys, or the Dry Tortugas).

Fishing-related predictor variables were compiled to capture the dynamics of recreational, charter and commercial fisheries operating in south Florida. Because commercial and recreational landing data were not available at the spatial resolution necessary for mapping fishing impacts to 1 ha areas of reef, several alternative spatial datasets were used to correlate with the fishery-independent biomass data at each survey site. Spatial layers of the number of fishing permits within 50 km (commercial) or 25 km (charter) of each reef pixel were created using location (i.e. the zip code of reference) data, based on the assumption that fishermen are more likely to fish closer to their zip code of reference (especially for snapper–grouper charter vessels). Similarly, zip code data associated with marine recreational fishing licences were used in conjunction with census data to create a spatial layer describing the number of recreational permits within 50 km of a reef pixel. To account for tourist (non-FL resident) reef fishing, county-level tourism estimates were coupled with data on the number and location of hotel rooms in the region to estimate the number of tourist reef fishing days for each reef in the project (with the exception of reefs in Martin County, where no tourism estimates were available; Johns et al., 2001). To further characterize all recreational reef fishing, spatial layers were developed to represent the number of marina slips and launch ramps near each reef. To encompass both the impacts of fishing and other anthropogenic impacts on coral reef ecosystems and species, human population density and the related variable of human population per area of reef were included, as well as two additional spatial variables: total market gravity (Cinner et al., 2018) and NOAA-developed metrics of commercial and recreational fishing engagement and reliance (Jepson & Colburn, 2013; data provided by M. Jepson). Finally, the protected status of a reef (whether a reef was closed or open to fishing) was included in all models.

2.4 | Modelling and mapping approach

Following methods previously used by Harborne et al. (2018), two distinct statistical models were developed from the underwater fish census data: first a fishing impact model and then fish biomass models (Figure 1). So that fish data used in the fishing impact model were separate from fish data used in the biomass models, survey sites were separated into two groups by latitude, with alternating sites from north to south assigned to the fishing impact ($n = 1,372$) or biomass models ($n = 1,407$). The first model predicted fishing impact: a unitless, relative metric of the cumulative effects of fishing. Fishing impact is based on the understanding that current or historical fishing has led to distinct fish assemblages which are different from the fish assemblages that would exist if fishing was not currently taking place and/or had never taken place (i.e. current fish biomass is lower than might be expected given no fishing and the same biophysical conditions, with the decrease assumed to be proportional to fishing). Fishing impact is related to, but not the same as, fishing effort (or pressure), which typically refers to some measurement of the current amount of fishing.

There is widespread evidence supporting the use of biomass- and sized-based fishery-independent indicators of fishing (Graham et al., 2005; Piet & Jennings, 2005; Shin et al., 2005; Nash & Graham, 2016). For the fishing impact model, a range of such indicators was tested to determine that the biomass of the South Atlantic Fishery Management Council snapper–grouper complex (excluding goliath groupers, *Epinephelus itajara*, that have been illegal to land or possess since 1990) was the most effective metric for this study (i.e. relative to others tested, it yielded a model with high explanatory power that included known fishing-related variables as significant predictors). The snapper–grouper complex includes 59 species of sea basses and groupers (Serranidae), snappers (Lutjanidae), grunts (Haemulidae), porgies (Sparidae), jacks (Carangidae), triggerfishes (Ballistidae) and several additional species (for a full list, see Table S1 or NOAA (1983)). These fishes are among

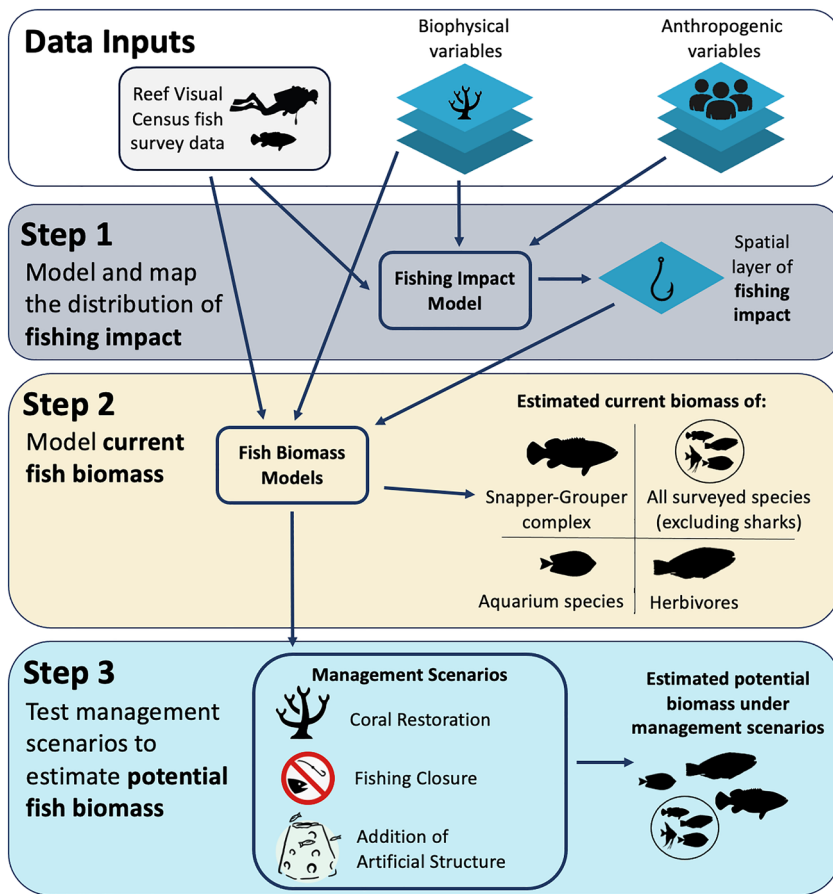


FIGURE 1 A graphical depiction of the modelling approach used in this study.

the most heavily exploited by both commercial and recreational fisheries (Ault, Bohnsack & Meester, 1998; Chiappone, Sluka & Sealey, 2000; O'Toole et al., 2011; Amorim et al., 2019). Many snapper-grouper complex species exhibit life history strategies that put them at high risk of over-exploitation and have been subject to fishing pressure on Florida's reefs for hundreds of years. Consequently, there is substantial evidence of species-, community- and ecosystem-level impacts of fishing from several decades of heavy exploitation (Chiappone, Sluka & Sealey, 2000; Ault et al., 2005; McClenachan, 2009; McClenachan & Kittinger, 2013). Thus, the biomass of the snapper-grouper complex species was extracted from each underwater fish survey, and this metric was modelled against biophysical and anthropogenic variables related to fishing and known or suspected to influence biomass.

The statistical relationships resulting from this model (i.e. the mathematical relationships between fish biomass and each significant predictor variables) were used to isolate the influence of fishing on snapper-grouper biomass in every 1 ha cell along the reef tract while controlling for environmental conditions (e.g. temperature, coral cover and reef complexity). To do this, significant predictor variables in the model were classified into two categories: (1) fishing-related variables; and (2) environmental variables that influence fish biomass. For variables relating to fishing, values unique to each reef pixel in the project were used in a predictive model. In contrast, environmental

variables for every pixel were set to their mean in the predictive model (Harborne et al., 2018). This ensured that the model predicted variation in snapper-grouper biomass as solely depending on fishing-related factors, not environmental gradients, but that emergent relationships with fishing-related factors accounted for biophysical covariates and their interactions with anthropogenic variables. Values of predicted snapper-grouper biomass were then normalized to a scale of 0–1 whereby the highest predicted snapper-grouper biomass translated to the lowest (0) fishing impact along the reef tract and the lowest predicted snapper-grouper biomass translated to the highest (1) fishing impact. All other biomasses converted linearly to values within this range. This model was used to predict fishing impact for all 1 ha reef pixels across Florida's Coral Reef.

A second set of models, using a separate set of fish survey data, were then developed to estimate fish biomass. These models used the same biophysical predictor variables as did the fishing impact model; however, the single metric of 'fishing impact' (as calculated by this study) was used in place of all fishing-related variables. After building the statistical models with data from fish survey sites, current fish biomass was predicted for each of the following species groups for every pixel of coral reef habitat along Florida's Coral Reef: all species (total biomass); snapper-grouper species; grazing species (including parrotfishes which are not a widespread target of commercial or recreational fisheries in Florida; Ault et al., 2006); and species

comprising the Florida Marine Life complex (hereafter referred to as aquarium species, i.e. species landed and sold live for aquaria; see Table S1 for full species lists).

2.5 | Data analysis

The final dataset for the fishing impact model consisted of a univariate response variable (biomass of species in the snapper-grouper fishery complex) and 24 potential covariates of fish biomass. The final dataset for the fish biomass models consisted of univariate response variables, 17 continuous or categorical biophysical variables and the metric of fishing impact calculated by this study. Biomass response variables were $\log(x + 1)$ transformed to improve normality of residuals while preserving zeros in the dataset. Because relationships among predictor and response variables can be curvilinear and include significant interactions that are difficult to predict *a priori*, boosted regression trees were used to generate models (Elith, Leathwick & Hastie, 2008; Pittman & Knudby, 2014). All biophysical and fishing-related predictor variables were tested for collinearity using pairwise comparisons with Pearson's correlation coefficient (Figure S1), and variance inflation factors were calculated to quantify any inflated variance in model results owing to collinearity. A variable trimming threshold of 0.8 pairwise correlation was used to justify dropping the following variables: latitude, longitude, commercial fishing engagement, population-related variables with the exception of population within 50 km (including the distribution of recreational fishing licences) and commercial fishing pounds landed. Following trimming, all variables met the threshold of variance inflation factors <12. Boosted regression trees were constructed and run in R using the 'gbm.step' function in the 'dismo' package (Hijmans et al., 2017; R Core Team, 2019). Optimal model parameters (learning rate 0.01, tree complexity 5 and bag fraction 0.75) were selected by testing each across a range of possible values and selecting the combination of parameters leading to the lowest model deviance (Elith, Leathwick & Hastie, 2008). Moran's *I* was used to assess spatial autocorrelation in the model residuals. The significance of predictor variables was assessed by including a variable of random numbers in the model (Soykan et al., 2014). All variables with less predictive power than the random numbers were excluded from the final, minimal model. Model performance was assessed using the percentage of deviance explained by the model and the correlation between observed and model-predicted biomass values. Bootstrap replication ($n = 1,000$) was used to obtain 95% confidence intervals for partial dependency plots resulting from boosted regression tree models (Jouffray et al., 2019).

2.6 | Management scenarios

By manipulating the values of explanatory variables in the fish biomass models, a series of management scenarios were developed to predict the efficacy of various approaches to increasing fish biomass.

Scenarios simulated realistic management options for Florida, including two variations of coral reef restoration that are currently being planned in the region, the addition of artificial structure, the closure of reefs to fishing and combinations of these approaches (Table 2; Meester et al., 2004; Dupont, 2008; Hunt & Sharp, 2014). For the purposes of this research, the definition of the addition of artificial structure is a management intervention that increases vertical relief and/or structural complexity on a coral reef by adding natural or manmade structures or frames to the benthos on or near a reef (Anthony et al., 2020). This management intervention is separate from coral restoration which has a primary aim to increase live coral cover. While the addition of artificial structure may provide settlement substrate for corals, we envisage it predominantly being used to rebuild structural complexity, particularly for fish. Adding artificial structure is also distinct from building artificial reefs, which are typically built away from natural reefs. Although we are not aware of a large-scale deployment of structure on a natural reef, it could be undertaken by deploying

TABLE 2 Fishery and coral reef management scenarios. The increases in percentage coral cover were informed by Florida's Mission: Iconic Reefs – a restoration programme with an implicit aim of benefiting fish populations. Scenario III was informed by dimensions of artificial structure currently in use on coral reefs (e.g. Reef Balls), and simulates a scenario where sufficient artificial structure is added to a reef to raise maximum hard relief on a section of reef by 1.2 m from current values.

Management scenario	Description
I NOAA reef restoration – phase 1a	Increase all reef pixels to 10% live coral cover with an accompanying 15 cm increase in max hard relief (reef complexity), simulating new coral outplants or artificial substrates used for reef restoration
II NOAA reef restoration – phase 2	Increase all reef pixels to 25% live coral cover with an accompanying 75 cm increase in max hard relief (reef complexity), simulating the presence and growth of both low-relief and rapidly growing branching coral species that add significant structure to a reef (e.g. <i>Acropora palmata</i>).
III Addition of artificial reef structure	1.2 m increase in reef complexity
IV Fishing closure	No-take marine reserve simulated by setting the fishing impact variable in the model to zero. This calculates potential biomass on the reef with no fishing, given the current biophysical conditions on that reef
V Fishing closure + reef restoration	NOAA reef restoration – phase 2 and fishing closure
VI Fishing closure + artificial structure	Scenario III and fishing closure

'Reef Ball'-like modules (<http://www.reefball.com/technicalspecs.htm>). The average height of the five largest Reef Ball designs (~1.2 m) was used for model scenarios.

Biomass predictions under the six management scenarios (Table 2) were estimated using statistical relationships in the previously described models of fish biomass with modified values of coral cover (to simulate coral restoration), reef complexity (to simulate the addition of artificial structure) and/or fishing impact (set to 0 to simulate a fishing closure). Potential biomass under a given management scenario was calculated for each 1 ha reef cell, along with the percentage change in biomass relative to current estimates. These values were averaged across the entire reef tract and by region to generalize likely benefits. However, this analysis is not intended to suggest that a management action would be applied at that scale. Mean benefit values are reported in lieu of specifying particular locations for these potential management actions.

3 | RESULTS

3.1 | Fishing impact model and map

The final impact model explained 56.2% of variation in snapper-grouper biomass with a correlation between observed and predicted values of 0.76. Significant positive spatial autocorrelation was

detected in the model (Moran's I , $P < 0.01$), reflecting the spatial structure in the data for important predictors of fishing. However, as the model product was primarily created to be an explanatory variable in another model, we chose to accept the spatial autocorrelation to allow for inclusion of all sites and a more robust model. There were positive relationships between biomass and several biophysical variables (including reef complexity, depth and net primary productivity) and three fishing-related variables with significant predictive power (Figure 2). The human population within 50 km was the most important fishing-related predictor of snapper-grouper biomass (accounting for ~12% of the variance explained), followed by the number of marina slips within 25 km of a coral reef (a metric of fishing access) and the number of commercial snapper-grouper permits within 50 km. These variables show lower snapper-grouper biomass on reefs in closer proximity to dense human populations, fishing access points and zip codes associated with more commercial fishing permits.

The fishing impact model yielded predictions of the biomass of snapper-grouper species for every coral reef pixel in the project area, based on the three significant fishing-related variables (i.e. holding all biophysical variables constant). Reefs with high fishing impacts were found along Florida's south-east coast, and in several highly populated areas in the Florida Keys (e.g. Key West, Marathon and Islamorada; Figure S2). The lowest levels of fishing impact were found in the Marquesas and Dry Tortugas, removed from human population centres and distant from fishing access points.

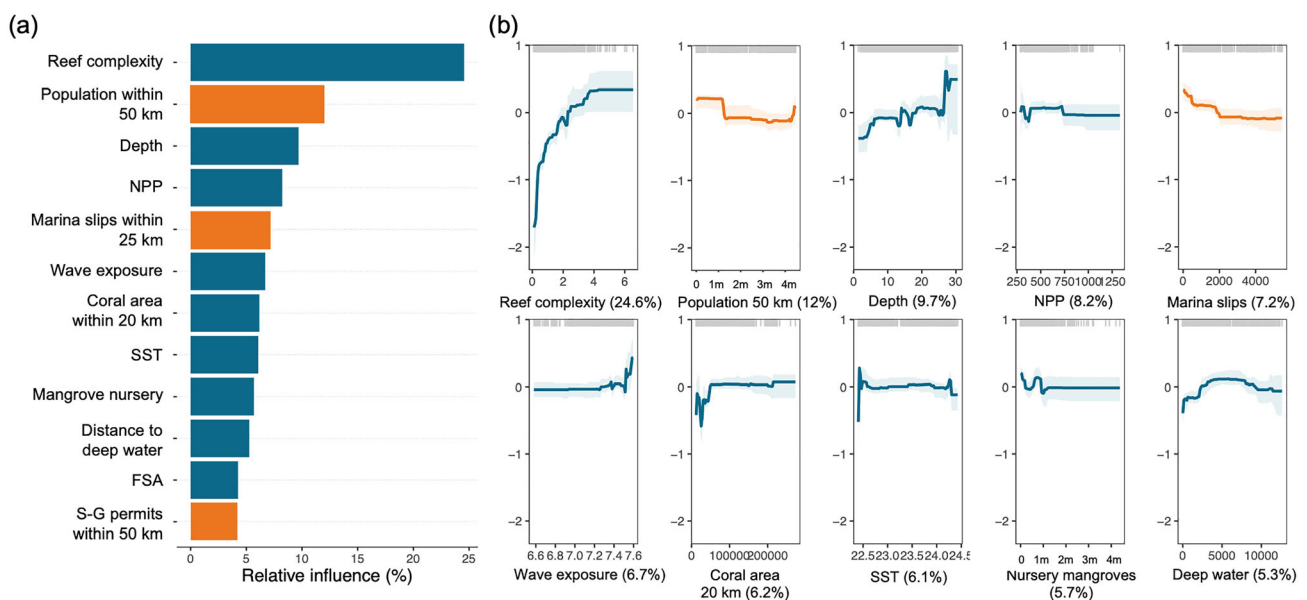


FIGURE 2 (a) Ranked influence of each variable in the fishing impact model (blue = biophysical variables; orange = fishing-related variables); and (b) relationships between the significant variables explaining $\geq 5\%$ of the explained variance and the biomass of species in the snapper-grouper fishery complex. The partial dependency plots represent both the relative importance (values in parentheses) of each significant predictor variable and the directionality of that variable's relationship with snapper-grouper biomass. Shaded areas represent the 95% confidence intervals obtained through bootstrapping. Vertical grey lines on the top of each plot indicate the spread of data points for each variable. Values of $\log(x + 1)$ biomass of snapper-grouper species on the y-axis are normalized. NPP, net primary productivity; SST, sea surface temperature; FSA, fish spawning aggregation.

TABLE 3 Boosted regression tree results for all current biomass models.

Species group	Variance explained	Correlation between observed and predicted values	Top five explanatory variables (and percentage of variance explained)
All species	51.0%	0.73	Reef complexity (37.3%) Wave exposure (13.1%) Depth (12.5%) Reef area within 20 km (10.5%) Net primary productivity (10.2%)
Snapper–grouper complex	51.5%	0.73	Fishing impact (25.2%) Reef complexity (22.1%) Net primary productivity (9.0%) Depth (8.9%) Wave exposure (5.9%)
Grazing species	63.7%	0.81	Reef complexity (17.4%) Sea surface temperature (11.5%) Distance to deep water habitats (9.1%) Depth (9.0%) Net primary productivity (8.8%)
Aquarium species	53.9%	0.75	Reef complexity (28.8%) Distance to deep water habitats (13.1%) Net primary productivity (9.1%) Sea surface temperature (8.8%) Year (7.7%)

3.2 | Fish biomass models and maps

Models of current fish biomass explained between 51.0 and 63.7% of the variability in biomass, with no spatial autocorrelation detected in the models (total biomass – Moran's I , $P = 0.11$; snapper–grouper – Moran's I , $P = 0.50$; grazing species – Moran's I , $P = 0.11$; aquarium species – Moran's I , $P = 0.15$; Table 3). Reef complexity (maximum hard relief) ranked as the most or second most important predictor of biomass across all groups. Additional results place the models into two categories: groups with biomass highly influenced by fishing impact and groups where fishing was less important in influencing biomass. For snapper–grouper species, fishing impact represented ~25% of the variance explained, with biomass declining approximately linearly with increasing fishing impact (Figure 3; a partial dependency plot for the interaction between fishing impact and reef complexity can be found in Figure S3). In addition, the biomass of snapper–grouper species exhibited a significant positive relationship with wave exposure, depth and the area of reef within 20 km, and a negative relationship with net primary productivity. Fishing impact was also a significant predictor variable for all other species groups tested, although it showed less explanatory power for total biomass (all species; ~7%), biomass of grazing species (~8%) and biomass of aquarium species (~7%) (Figure S4). Each of these groups showed lower biomass with increasing fishing impact, especially at high levels. For these groups, reef complexity, net primary productivity, depth and distance to deep water habitats were among the most important correlates of biomass (Table 3). Biomass of grazing and aquarium species showed positive relationships with coral cover with a threshold at approximately 3% cover (Figure S4). These relationships were used to predict current biomass for every 1 ha cell

of coral reef from Martin County to the Dry Tortugas (example of snapper–grouper species in Figure 4). Estimates of current total biomass ranged from ~57 to 2,422 kg ha⁻¹ and of snapper–grouper biomass from ~14 to 980 kg ha⁻¹. Biomass estimates were uniformly low on reefs in Southeast Florida, adjacent to the largest urban areas in the region, and higher throughout the Florida Keys, especially on fore reef areas. Biomass, particularly that of snappers and groupers, was highest in the Dry Tortugas on structurally complex reefs most isolated from human impacts.

3.3 | Management scenarios

Predictive models simulating various management scenarios (Table 2) showed widespread potential for biomass increases, with differences among species groups (Table 4). The impact of a fishing closure varied substantially, with the snapper–grouper complex showing the strongest response (average of 23% increase) and other species groups showing smaller increases (average of 6–14% increase). Regional estimates of snapper–grouper increase ranged from virtually no change in the Dry Tortugas to a 91% increase in biomass on coral reef habitats of Biscayne National Park (Table 4; regional breakdown of results in Table S2). The predictive models also highlighted considerable differences in the ability of various reef restoration approaches to restore fish biomass. All species groups responded to a large increase in reef complexity (management scenario III) with significant biomass increases (all species, 72%; snapper–grouper, 44%; grazing species, 23%; aquarium species, 37%). While still positive, the responses to increased live coral cover paired with a small increase in reef complexity (management scenario I) were more modest, with live

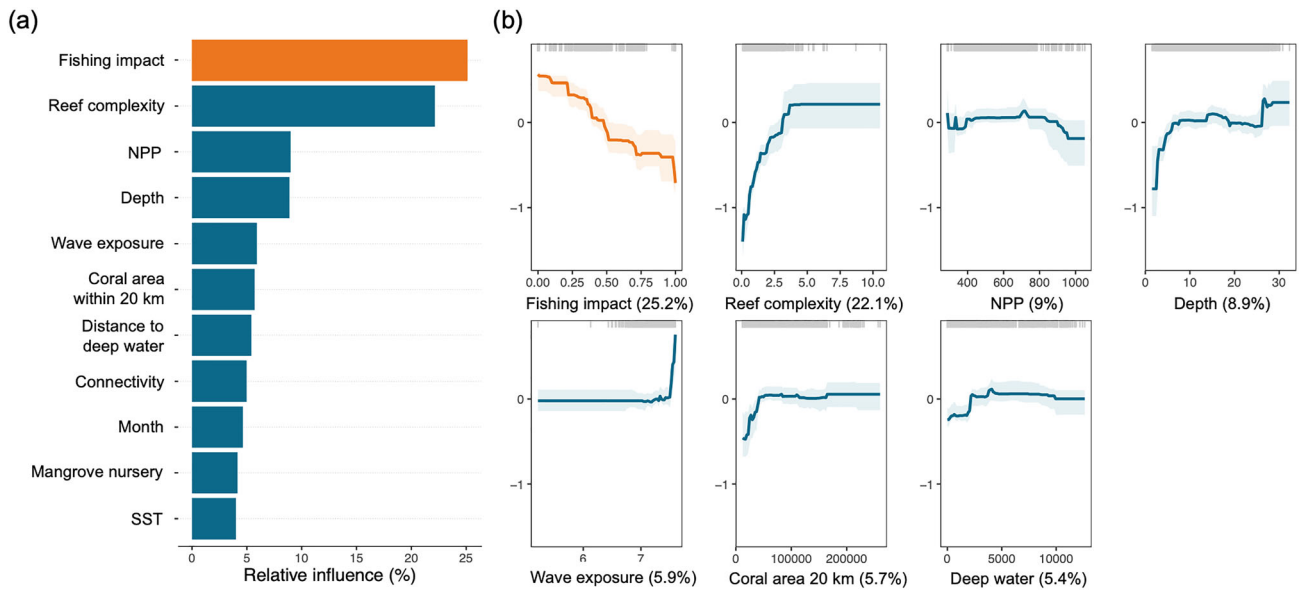


FIGURE 3 (a) Ranked influence of each variable (blue = biophysical variables; orange = fishing-related variables); and (b) relationships between the significant variables explaining $\geq 5\%$ of the explained variance variables and the biomass of species in the snapper–grouper fishery complex. The partial dependency plots represent both the relative importance (values in parentheses) of each significant predictor variable and the directionality of that variable’s relationship with snapper–grouper biomass. Shaded areas represent the 95% confidence intervals obtained through bootstrapping. Vertical grey lines on the top of each plot indicate the spread of data points for each variable. Values of $\log(x + 1)$ biomass of snapper–grouper species on the y-axis are normalized. NPP, net primary productivity; SST, sea surface temperature.

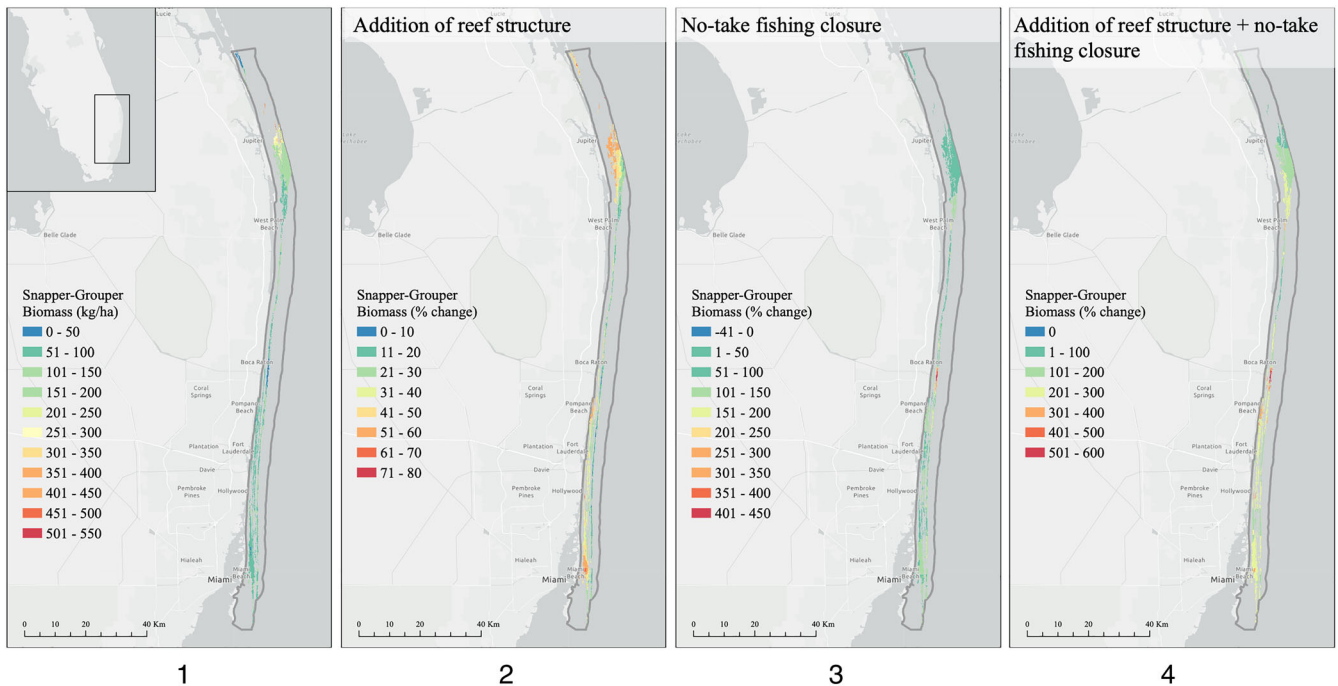


FIGURE 4 Spatial distribution of the estimated current biomass of all species in the snapper–grouper complex (kg ha^{-1} ; panel 1), and the estimated percentage change in the biomass of snapper–grouper species under management scenarios adding reef structure (panel 2), creating a no-take fishing closure (panel 3) and both of these measures combined (panel 4) in Southeast Florida’s Coral Reef Ecosystem Conservation Area.

coral increases most beneficial for snapper–grouper species (Table 4). Finally, management approaches that restore reefs or increase structural complexity while also addressing fishing impact

yielded synergistic results. When simulating an increase in coral cover and a substantial increase in complexity (management scenario II) and separately a fishing closure (management scenario

TABLE 4 The average estimated potential biomass (kg ha^{-1}), standard deviation (SD) and the percentage change in biomass for each species group modelled for management scenarios I–VI (Table 2). The absolute biomass (kg ha^{-1}) represents the average estimated biomass for coral habitats on Florida's Coral Reef; percentage change represents the average percentage change from current estimated biomass values. The results divided by region (Coral ECA, Biscayne National Park, Florida Keys National Marine Sanctuary, Dry Tortugas) can be found in Table S2.

Management scenario	All species		Snapper–grouper		Grazing species		Aquarium species	
	kg ha^{-1} (SD)	% Δ	kg ha^{-1} (SD)	% Δ	kg ha^{-1} (SD)	% Δ	kg ha^{-1} (SD)	% Δ
Current	657 (252)	–	218 (137)	–	98 (35)	–	189 (52)	–
I: Reef restoration – phase 1a	689 (242)	5%	237 (159)	8%	94 (33)	-4%	198 (52)	5%
II: Reef restoration – phase 2	996 (508)	52%	285 (191)	31%	103 (41)	5%	225 (69)	19%
III: Artificial structure	1,132 (482)	72%	314 (208)	44%	121 (42)	23%	258 (70)	37%
IV: Fishing closure	698 (204)	6%	269 (110)	23%	112 (42)	14%	201 (52)	6%
V: Reef restoration + fishing closure	1,094 (520)	67%	369 (150)	69%	117 (48)	19%	240 (72)	27%
VI: Artificial structure + fishing closure	1,241 (477)	89%	411 (160)	89%	136 (49)	39%	274 (73)	45%

IV), models estimated an additive 54% increase in snapper–grouper biomass. However, a management approach that addressed the two together resulted in a 69% increase in snapper–grouper biomass. This synergy is particularly pronounced in Biscayne National Park, where snapper–grouper biomass responds to reef restoration (management scenario II) with a 16% increase, to a fishing closure (management scenario IV) with a 91% increase, and to the two interventions together with a 141% increase (Table S2). Similarly, the addition of artificial structure (management scenario III) along with a fishing closure yielded a synergistic 89% increase in snapper–grouper biomass (while increases from each intervention alone sum to 67%) (Figure 4).

4 | DISCUSSION

Decision-makers frequently struggle to discern the relative influence of different factors known to affect reef fish biomass, which can impede their ability to target local management approaches. In particular, it has long been difficult to isolate the impact of reef fishing. These results put the estimated impact of fishing in Florida in context with well-known biophysical drivers of reef fish biomass (e.g. reef complexity) for four species groups. Notably, fishing was shown to have particular importance for species in the snapper–grouper complex, whereas biophysical factors were more important when considering all reef fish species (i.e. both fished and unfished species) together. Furthermore, the statistical models allowed the parameterization of scenarios that highlight the significant benefits of restoring physical complexity to reefs. The scenarios supported the well-established benefits of no-take closures and coral restoration, albeit with more modest increases in predicted fish biomass than gains from the less traditional approach of adding substantial reef complexity. Importantly, for most species groups, including the heavily exploited snapper–grouper complex, the benefits of individual management actions can build on each other, with synergistic effects of addressing both fishing and habitat-related threats. This information is relevant in light of global

interest in better understanding how habitat management may or may not contribute to fisheries outcomes, biodiversity (species and habitat) and ecosystem goals, and socio-economic objectives, and under what conditions benefits may occur (Cinner et al., 2020). This work could also inform a detailed cost–benefit analyses if the benefits of increased ecosystem goods and services are paired with emerging details of the costs of different management actions (e.g. Bayraktarov et al. (2019) for coral restoration).

4.1 | Management scenarios

Given the underlying models, we expected to see large increases in snapper–grouper biomass resulting from a theoretical fishing closure, a management strategy widely used in tropical marine ecosystem management. It is important to note that although the fishing closure was modelled for the entire reef tract for the purposes of this research, we are not suggesting that entire regions of the reef tract be closed. Rather, the model is meant to predict the potential increase in biomass within a typically sized no-take area on a coral reef. Modest biomass increases seen when modelling all species combined are consistent with monitoring data from the no-take zones within the Florida Keys National Marine Sanctuary (Ault et al., 2013), and could be even greater than predicted given that increasing populations of some snapper and grouper species could work to rebuild spawning aggregations and increase larval production. Interestingly, models predicted a 14% increase in the biomass of grazing species (which are not widely targeted by fisheries). This result could indicate some fishing mortality of parrotfish species (e.g. via indiscriminate spearfishing or trap bycatch) or might result from complex trophic relationships within the wider fish assemblage (Mumby et al., 2006). However, small percentage increases such as this one should be interpreted with caution given the unexplained variance in the model. Taken together, the results provide strong support for adding to or expanding the current network of small (mean size = 0.85 km^2) no-take areas in the Florida Keys National Marine Sanctuary to further rebuild fish stocks, a management action that could also lead to

fishery spillover and other indirect benefits to the well-being of Florida residents (Bhat, 2003; Ault et al., 2005; Bohnsack et al., 2009).

The state of Florida, and coral reef jurisdictions around the world, are investing in various forms of habitat protection and restoration to safeguard ecosystems and ecosystem services, including those provided by fish. The most effective single management measure for increasing predicted fish biomass was found to be a substantial increase in reef complexity, matching theoretical predictions for low-complexity reefs (Rogers et al., 2015). Artificially enhancing the relief or the complexity of a coral reef system at a large scale has rarely been attempted, and the amount of structure suggested here (a 1.2 m structure per 176 m²) clearly represents a significant and costly engineering project. However, reef-enhancing structures for fish could be combined with the increasing interest in rebuilding coastal reefs to provide the significant economic benefits of flood risk reduction in coastal communities (Storlazzi et al., 2019). If properly designed, these flood-mitigation structures could enhance habitat for multiple fish species at different life stages. Substantial research from the artificial reef and eco-engineering fields is available to inform this type of intervention (Hixon & Beets, 1989; Morris et al., 2018). While it is unlikely that artificial structure would fully mimic natural coral reef habitats (and therefore fish assemblages will probably differ from those on natural reefs in both composition and functioning), there is evidence for secondary benefits to the settlement of coral and other benthic organisms. And importantly, artificial structure would not be as vulnerable to the stressors (e.g. heat-related stress) that can jeopardize coral restoration projects. The potential benefits of artificial structure for fish warrant field testing to corroborate our results and further explore the direct and indirect impacts of this approach.

In contrast to the biomass gains with large increases in structural complexity, biomass increases were limited when complexity was increased by only 15 cm as part of a simulated restoration effort, despite significant increases in coral cover. This suggests that for naturally low-relief reefs or reefs that have deteriorated over time and lost significant structure (Palandro et al., 2008), small increases in relief may not yield substantial increases in fish biomass. Coral cover is important to reef fishes (Coker, Wilson & Pratchett, 2014), has a range of other benefits and will lead to functionally important structure for fishes in time. However, the results here suggest that benefits to fishes may be limited in the short term (see also Hein et al., 2020). This finding is consistent with field-based studies showing that while an increase in coral cover does not necessarily translate to population increases for all fish species, benefits may accrue for some (Opel et al., 2017; Ladd, Burkepile & Shantz, 2019). Benefits of increasing live coral cover that were demonstrated, especially for grazing species (e.g. parrotfishes), are perhaps linked to settlement preferences (Tolimieri, 1998) or additional food (Burkepile, 2012). Increases in grazing species and herbivory on restored reefs are particularly important for lowering coral mortality and could positively influence restoration efforts (Frias-Torres et al., 2015; Seraphim et al., 2020). Scenario II (which corresponds to NOAA's Phase 2 reef restoration plans) represents an increase in live

coral cover to 25%, an ambitious and costly goal for coral reefs adjacent to high-population areas and subject to land-based and other anthropogenic stressors. While Scenario II is likely to be more typical of historical coral cover on reefs in the Florida Keys and Dry Tortugas (owing to ecological constraints that limit coral growth in Southeast Florida), these results suggest substantial benefits for fishes, assuming that the restoration technique also leads to increases in reef complexity. If out-planted corals flourish in the long term, increases in complexity will potentially be comparable with an intervention that adds artificial structure, with equivalent benefits to fish biomass. While there were not sufficient data available on fishery recovery times to parameterize models with a time component, the positive impacts outlined here could take years to accrue and will vary by scenario (Bellwood et al., 2012; MacNeil et al., 2015). Therefore, managers need to consider recovery timescales, among many other factors including cost, logistics and future stressors to out-planted corals.

The study of synergies on coral reefs is increasingly recognized as relevant for conservation (Darling & Côté, 2008; Olds et al., 2012; Hopf et al., 2016). In practice, management plans are likely to combine multiple approaches. To explore potential synergies, management scenarios that we expect will be common to protect restored reefs were selected: no-take fishing reserves along with reef restoration (Scenario V in Table 2), and no-take fishing reserves along with the addition of artificial structure (Scenario VI). The results of these scenarios showed a combined positive effect on predicted fish biomass that is greater than the sum of effects from either action alone. The mechanisms for the synergistic effects are unclear, but potential explanations include increases in numbers of larger individuals that are critical for larval production (Marshall et al., 2019) combined with the sensory benefits of live coral to settling fish (Coker, Wilson & Pratchett, 2014), or the provision of complexity that then increases juvenile survival during the post-settlement period when mortality can be particularly high (Almany & Webster, 2006). It could also reflect an increase in the carrying capacity of a reef as structural complexity increases, thus leading to higher biomass than could be achieved with only a marine reserve. Such hybrid management strategies warrant more study to identify synergistic mechanisms and explore stakeholder acceptance. Finally, the process of calculating predictions based on short- to long-term management scenarios is incomplete without considering that global climate change will certainly impact the efficacy of management initiatives. The results presented here set the stage for future work to better understand how increasing sea temperatures, species' range shifts, shifts in hurricane dynamics and other impacts of climate change might influence reef fish recovery potential.

4.2 | Fishing impact metric and the spatial distribution of fishing

The models underpinning these scenarios provided important insights into the correlates of fishing impact and fish biomass in Florida. As

demonstrated by Harborne et al. (2018), using a single variable to represent fishing in biomass models allowed easy visualization and interpretation of the relationship between fishing and fish biomass. The impact metric appeared to capture important properties of variability in fishing across Florida's Coral Reef; when used to predict fish biomass in an independent dataset it showed declining fish biomass with increasing fishing impact. The shape of the relationship between impact and log-transformed total biomass and the biomass of snapper-grouper species also aligns with previous research suggesting non-linear impacts of fishing (Cinner et al., 2013; D'agata et al., 2016). The model of grazing species biomass provided a unique test of the fishing impact metric. Many of the species in this group are not fished (e.g. goby species), and while it is legal to land parrotfishes under 12 cm alive for aquaria, it is not legal to take parrotfish in other recreational or commercial fisheries in the state of Florida (Ault et al., 2006; Florida Administrative Code [Fla. Admin. Code], 1998; Florida Fish and Wildlife Conservation Commission [FWC], 2020). Although significant, as expected the fishing impact variable was not among the most important factors influencing grazer biomass, highlighting the metric's utility. Furthermore, the spatial patterns in fishing impact are similar to the previously described declining fishing impacts from human population centres in Miami and Key Largo to the virtually unpopulated Dry Tortugas region with local peaks in fishing in locations like Marathon and Key West (Ault et al., 2001; Ault et al., 2002).

The fishing impact model made it possible to begin to explore the relative influences of the commercial and recreational sectors, reef fisheries with characteristics and practices that can differ markedly in gears used, spatial distribution and outcomes (Arlinghaus et al., 2019). For the subset of the snapper-grouper complex that lives on the shallow, nearshore reefs mapped here, these results suggest that recreational fishing (as captured by two variables: the population within 50 km and the number of marina slips within 25 km) is more influential than commercial or charter fishing (represented in the model as permit density in those fisheries). In other words, the spatial patterns in recreational fishing-related variables align more closely with spatial patterns in fish biomass than do variables related to other fishery sectors. Although these results rely on two imperfect proxies of recreational fishing pressure, they lend support to several studies that find substantial impacts of recreational fishing on the snapper-grouper assemblage in Florida (Ault et al., 2001; Ault et al., 2013). And while the effects of a particular fishery sector that is part of a complex social-ecological system will never be fully distinguishable (Coleman, 2004; Cooke & Cowx, 2006), these results challenge the sometimes pervasive assumption that commercial fisheries (despite a shrinking commercial reef fishery in Florida, Schittone (2001)) have a much larger impact on reef fish assemblages than recreational fisheries. Multi-species, multi-gear coral reef fisheries are notoriously difficult to manage, and the management of the open-access recreational sector poses unique challenges (Peterman, 2004; Burns & Froeschke, 2012; Hicks & McClanahan, 2012; van Poorten, Cox & Cooper, 2013; Holder et al., 2020). Florida's recreational fisheries provide coastal

communities with an important connection to nature and healthy food, promote well-being among participants, and generate substantial funds for the conservation of species and habitats (Cowx, Arlinghaus & Cooke, 2010; Brownscombe et al., 2019). With these benefits in mind, state and federal management must confront and continue posing solutions to the challenges of managing Florida's recreational fishing sector.

4.3 | Factors influencing fish biomass on Florida's Coral Reef

While areas of high and medium fishing impact showed decreased current biomass estimates, the biomass of fishes was also affected by a complex interaction of factors including reef complexity, depth, net primary productivity and wave exposure. The shape of the relationship between biomass and reef complexity was similar across all species groups tested, with additional relief corresponding to a large biomass increase until the relationship flattened above ~3 m of relief. With the exception of the snapper-grouper species complex, which was notably impacted by fishing, reef complexity was the most important predictor of all species groups, aligning with widely documented evidence on the relationship between physical structure and reef fish abundance and distribution (Graham & Nash, 2013; Darling et al., 2017). This finding underscores the challenge of managing and rebuilding reef fisheries as reefs flatten across the Caribbean (Alvarez-Filip et al., 2009; Rogers, Blanchard & Mumby, 2014), and as negative carbonate budgets are expected to cause long-term loss of reef structure (Toth et al., 2019). Higher estimates of biomass of snapper-grouper species were found at deeper sites, which agree with multiple studies where this correlation was also apparent (Pittman & Brown, 2011; Ames, 2017; McClanahan et al., 2019). This relationship also potentially reflects depth refuges from fishing (Lindfield, McIlwain & Harvey, 2014). However, the relationship between biomass and depth was reversed in the case of grazing species, reflecting the well-established preference of these fishes for relatively shallow, productive reefs (Lewis & Wainwright, 1985; Mumby & Hastings, 2008). The protected status of a reef (i.e. whether the reef was open to fishing of any kind or closed entirely to fishing) was not shown to be a significant predictor of biomass. We do not take this to mean that protected areas in Florida are ineffective, as they have been shown to be effective in this region (Bohnsack, 2011). Rather, locally important effects of marine reserves on fishes can be overwhelmed by large biophysical gradients (Harborne et al., 2018).

While the ability to compare relative fish biomass across a management area is useful, absolute estimates of fish biomass provide key information to managers and the opportunity to compare reef fish assemblages in Florida with those in the wider Caribbean. Florida reefs are in subtropical waters, and sites in the Florida Keys are at the northern range of several grouper species. Thus we expected estimates of fish biomass to be naturally lower than on other well-managed Caribbean reefs (Chiappone, Sluka & Sealey, 2000;

McClanahan et al., 2019). At the high end of biomass estimates for Florida's Coral Reef are sites with over 2,000 kg ha⁻¹ in the Dry Tortugas. For these sites, biomass falls within the range calculated by previous research for healthy coral-dominated reefs, largely absent of fishing (Karr et al., 2015; MacNeil et al., 2015). This high biomass is also consistent with the findings of Valdivia, Cox & Bruno (2017) who showed the protected area of the Dry Tortugas to be one of the few sites in the Caribbean that had predatory reef fish biomass that might be expected at an unfished site. At the lower end of the estimates presented here are sites in south-east Florida at 57 kg ha⁻¹. These estimates situate reefs adjacent to Miami well below the 360 kg ha⁻¹ threshold estimated by Karr et al. (2015) as the value below which widespread community and ecosystem impacts of low fish biomass are likely to occur on Caribbean reefs. This value points to heavy exploitation and suggests that the low level of fish biomass probably contributes to poor ecosystem health and declining function, although some of these sub-tropical reefs may naturally support lower fish biomass than elsewhere in the region. Finally, while we determined that reef fish biomass was the most appropriate metric for this study, future work examining the factors influencing reef fish richness and diversity can provide additional insights into the health of Florida's reefs and the likely efficacy of different management initiatives.

The research presented here represents one of the most detailed and well-parameterized models of fish biomass on any large coral reef area. While data alone will not slow the degradation of coral reefs or the decline in reef fish populations, these products provide realistic estimates for fish biomass recovery following management interventions. The management scenarios provide a starting point for discussions among the many parties with an interest in Florida's fisheries and can assist as decision-makers fine-tune local management plans. When paired with other knowledge sources, these products can help prioritize the management proposals that will most effectively protect coral reefs and their associated fisheries for the continued provision of social, cultural, and economic services.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a Github repository at https://github.com/rachelzuercher/MOW_FL.

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SUPPORTING INFORMATION

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