



Organisation of Eastern Caribbean States



Coral Reef Fish and Fisheries Final Technical Report CARIBBEAN REGIONAL OCEANSCAPE PROJECT (CROP)

Saint Kitts and Nevis, Dominica, Saint Lucia,
Saint Vincent and the Grenadines, Grenada



Photo: Peter Mumby



Photo: The Nature Conservancy

Rachel Zuercher, Melanie Esch, and Alastair R. Harborne

Tropical Fish Ecology Lab, Institute of Environment & Department of Biological
Sciences, Biscayne Bay Campus, 3000 NE 151st Street,
North Miami, FL 33181, USA.
Email: aharborn@fiu.edu

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Mapping Ocean Wealth Caribbean Regional Oceanscape Project kick-off meeting. St. Lucia, May 2019. Photo credit: The Nature Conservancy.

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Executive Summary

Highlights:

- This report describes work done at Florida International University to map fish and fishing as a component of the Caribbean Regional Oceanscape Project (CROP) focusing on St. Kitts and Nevis, Dominica, St. Lucia, St. Vincent and the Grenadines, and Grenada.
- We used fish surveys from across the Lesser Antilles to build statistical models of fishing impact (for reef fishes over key reef zones only) and fish biomass using a range of fishing-related and biophysical variables.
- The major drivers of fishing impact were distance to a fish landing site, the estimated number of small-scale fishers in a country, and the size and proximity ('gravity') of the nearest potential fish market. Fishing impact was negatively correlated with the biomass of snappers and groupers.
- We used the models to build continuous maps (1 ha resolution) across the project region, providing the first spatially explicit maps of fishing impact and fish biomass that can be used for a range of marine spatial planning purposes
- Fishing impact is medium to high on all reefs in the focal CROP countries, and the only areas of low impact in the region are relatively remote reefs away from human populations.
- Statistical models allowed us to simulate the effects of a no-take fishing closure on snappers and groupers and coral restoration on parrotfishes for every 1 ha reef area in the region. These simulations demonstrated, for example, that marine reserves have the potential to increase the biomass of snappers and groupers by up to 113%. However, reserves need to be well-enforced and established for a long time to have this effect, and such reserves are currently rare in the region.
- The results highlight considerable potential to increase fish stocks in the focal countries through management and conservation initiatives such as marine reserves.

The Caribbean Regional Oceanscape Project (CROP) aims to foster a Blue Economy and promote greater consideration of the ecosystem functions and services that the ocean provides for the focal countries of St. Kitts and Nevis, Dominica, St. Lucia and St. Vincent and the Grenadines, and Grenada. Coral reefs within the CROP area provide vital protein and income to fishers, but are threatened by a range of stressors that have impacted the health of reefs and the fish assemblages they support. Within the CROP, a sub-project conducted at Florida International University was established to map fish and fishing throughout the region. The aims of this project were to model and map fishing impact, model and map current fish biomass, and assess the potential benefit of conservation and management measures on reef fisheries.

Using data obtained from a range of organizations and researchers, the project had access to 202 fish surveys from coral reef and pavement (non-accreting hardbottom) habitats across both the focal countries and other nearby islands, which were analyzed to increase the available dataset. The fish survey dataset was haphazardly split into two groups, and fish data from the first group (109 sites) were used to statistically model fishing impact (a unitless metric varying from 0 to 1 representing the cumulative effect of fishing on fish assemblages while controlling for biophysical gradients, such that 0 means the assemblage

in the region closest to its natural state). At each survey site, we used the mean length of parrotfishes (>10 cm), which are known to be susceptible to fishing (i.e. mean length decreases with increasing fishing pressure), as a proxy of fishing impact. The mean length data were modelled in relation to 25 potential predictor variables, such as the distance to nearby fish landing sites and sea surface temperature. These analyses demonstrated that both human-related and biophysical gradients, particularly wave exposure, are important factors affecting mean parrotfish length. The human influence on fish populations, assumed to be through fishing, was best correlated with the distance to a fish landing site (greater distance was associated with higher mean parrotfish length), the estimated number of small-scale fishers in a country (more fishers was associated with lower mean parrotfish length), and the gravity of the nearest potential fish market (very low market gravity was associated with higher mean parrotfish length). 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 on reef fish assemblages to all reef sites across the project region and generate a continuous map at a 1 ha resolution. Our results show medium to high fishing impacts in the CROP countries relative to more remote areas in the Eastern Caribbean. These maps do not apply to pelagic or invertebrate (e.g. lobster) fisheries.

Estimates of fishing impact were then used as a key data layer, along with 19 environmental variables, to model the current biomass of all surveyed reef-fish species, snapper and grouper species, and parrotfishes using the remaining 93 sites (second group) where survey fish biomass data were available. These three models included relationships with biophysical variables that were consistent with the ecology of these species. For example, fish biomass generally increased with increasing depth, decreased with increasing sea-surface temperatures, and parrotfish biomass was positively correlated with the availability of seagrass and mangrove nursery habitats. Fishing impact was a significant variable in the model of snapper and grouper biomass, reflecting that these species are particularly targeted by fishers. However, the relationship was weaker than expected, and was not present in the models of total biomass or parrotfish biomass, perhaps reflecting data limitations, the relatively homogenous fishing pressure across the entire area, or the complexities of modeling fishing across the region where gear types and target species are known to vary in space and time. Marine reserves have repeatedly been demonstrated to increase local fish biomass, but were not important in our models. This is likely due to other large biophysical gradients and because reserves only cover a small area of reefs in the region and hence few data points fell within reserves. Although the models could potentially be improved with further data, they explain a large amount of variability in the dataset and were used to extrapolate estimates of current biomass across the project area to generate previously unavailable maps.

Finally, the model of current biomass was adjusted to represent two potential management scenarios: the cessation of fishing on snapper and grouper species and the effect of coral restoration on parrotfish biomass. The first scenario involved reducing fishing impact to 0 to simulate a reserve (i.e. to estimate the biomass possible on a reef given limited fishing impacts with the current biophysical conditions). To simulate coral restoration, we increased coral cover by 25%. These scenarios allowed the production of maps estimating patterns of potential biomass if these management measures were implemented. The no-

fishing scenario shows that additional, well-enforced, old reserves represent a key tool to increase fish biomass in the CROP countries, but these are currently rare in the region. We also mapped the number of years estimated for snapper and grouper populations to recover under a simulated no-fishing scenario, providing data-based estimates that can be used to inform expectations of population recovery for proposed reserves.

The maps generated by this project represent the first spatially explicit, continuous maps of fishing impact and current and potential biomass for the CROP area. While the maps could certainly be improved with further survey work (data in the region are relatively sparse), current iterations can be provided to management agencies to support reef and fishery-related decisions. For example, decision-makers might use our maps of fishing impact and estimates of current and potential biomass to highlight reefs where there is a high potential for fishery benefits with spatial protection or other strengthened management. Potential protected areas could be designated on reefs with low levels of fishing impact (relatively unfished reefs that could be protected from increases in anthropogenic impact) or on more heavily fished reefs with a large potential for fish biomass increases if fishing was limited. Furthermore, the models can be used by planners to examine a wide range of management scenarios for their effects on fish biomass.

1. Introduction

1.1. The reefs of the Eastern Caribbean

The island arc of the Lesser Antilles spans southeast of the Virgin Islands to the northern coast of Venezuela and forms a barrier between the Caribbean Sea and the Atlantic Ocean (Fig. 1). The majority of islands in the Eastern Caribbean are volcanically formed and typified by steep slopes and a narrow euphotic zone, leaving little habitat for coral reefs (Adey and Burke 1976, Bouchon et al. 2008, Wynne 2013). The islands of the Lesser Antilles are often subdivided into three groups: northern Leeward Islands, the eastern Windward Islands, and southwestern islands along the inner arc (the latter of which are not included in this project) (Hubbard 2010).

This subdivision also characterizes the surrounding reefs. The Windward Islands, centered around Martinique and Saint Lucia, have greater wave exposure and high

hurricane frequency, which limit the growth of branching corals like Acroporids, resulting in a shallow algal ridge with a greater relative abundance of corals in deeper water (Hubbard 2010). The Leeward Islands, a cluster of islands to the southeast of the Virgin Islands, including St. Kitts and Nevis, have relatively less hurricane activity and wave

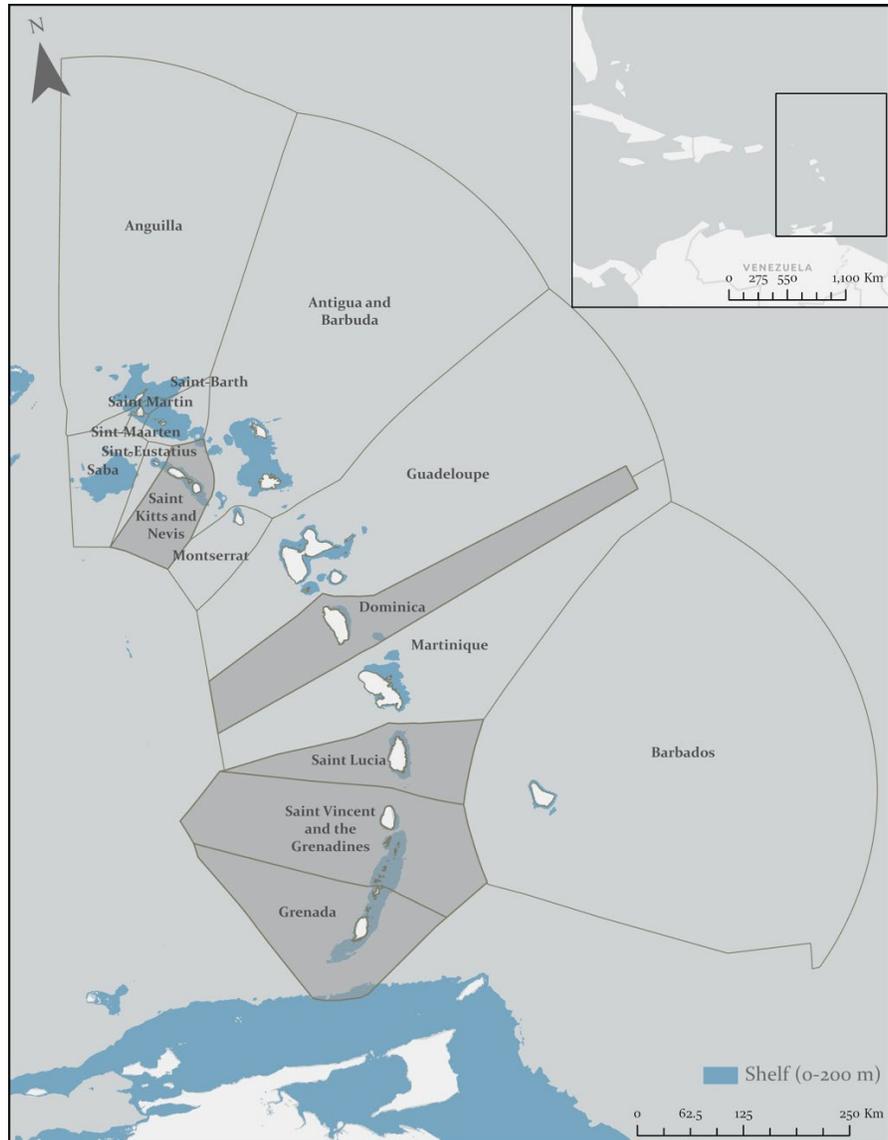


Fig. 1. Map of the Eastern Caribbean and the location relative to other Caribbean islands (inset). Each country's exclusive economic zone is outlined with CROP countries highlighted in dark grey. Blue areas depict the 0-200m bathymetric contour.

exposure which leads to greater diversity of branching corals on shallow reefs (Hubbard 2010). Variations in wave exposure also drive significant differences in patterns of habitat zonation around individual islands (i.e. windward versus leeward sides of each island). Oceanographic conditions in the region are influenced by global equatorial currents that interrupt the connectivity between reefs, affecting larval transport compared to continuous stretches of barrier or fringing reefs (which have not formed extensively in the region; Hubbard 2004). Because sedimentation rates are high on reefs from the adjacent steeply sloped islands, corals do best in locations with some wave activity to clear sediments (Bouchon et al. 2008). The reefs of the Lesser Antilles are relatively understudied compared to other regions of the Caribbean and data remain sparse for many islands (Williams et al. 2017). However, multiple agencies and organizations are working to increase surveys across the region and to make these datasets available.

The reefs of the Eastern Caribbean are a vital resource for island residents, supporting subsistence, artisanal, and small-scale commercial fishing (Bouchon et al. 2008, Gill et al. 2019). Demersal reef fisheries contribute to social well-being by supporting island economies, contributing to food security, and playing a role in the region's cultural identity (McConney et al. 2015). The demersal reef fishery is multi-species and multi-gear, targeting several major finfish groups: snappers, groupers, parrotfish, grunts, jacks, squirrelfish, surgeonfish and triggerfish (Harvey 2019, Mohammed and Lindop 2015a). Traps and hook-and-line (predominately handlines) are the most common gears used for reef fishing along with some use of spears, nets, and vertical and bottom longlines (Gobert 2000, Hawkins and Roberts 2004, Gill et al. 2007, Harvey 2019). Though fishing pressure on reef species is heterogeneous across the region, generally reef fisheries have been heavily fished with populations of snappers and groupers especially depleted (Hawkins and Roberts 2004, Ramdeen et al. 2014, Ruttenberg et al. 2018). In response to this overexploitation, many countries in the Lesser Antilles have shifted substantial fishing effort from reef-dwelling species to pelagic and coastal pelagic species through the use of fish aggregating devices (FADs) and other governmental programs to build the pelagic fleet (Mohammed and Lindop 2015a, 2015b). Despite this shift, many people continue to rely on reef fisheries for food and income, especially as part of broader fishery portfolios that include nearshore invertebrates (e.g. queen conch and spiny lobster) and pelagic species. Recently, there has been an increasing recognition of the high socio-economic vulnerability of reef fisheries in the region to climate change, underscoring the need for prudent management (Forster et al. 2014, Siegel et al. 2019, Pinnegar et al. 2019).

Like reefs around the world, the marine ecosystems of the Lesser Antilles are threatened by myriad stressors in addition to fishing. These include coral bleaching driven by climate change (Wilkinson and Souter 2008), coral diseases (Gladfelter 1982, Van Woesik and Randall 2017), loss of grazing species (Hughes 1994), sedimentation (Steiner 2015), habitat destructive fishing techniques (Munro 1983, Jennings and Polunin 1996), and invasive species such as lionfish (Betancur-R et al. 2011). The stressors interact with natural threats, including damage from hurricanes (Wilkinson and Souter 2008, Turner et al. 2020). This combination of natural and anthropogenic stressors has led to increasing concerns of large-scale loss of coral cover and ultimately the disappearance of the ecosystem goods and services they provide (Jackson et al. 2014).

Efforts to ameliorate threats to reefs in the Eastern Caribbean vary by island nation. The Caribbean Challenge Initiative¹ launched in 2008 with a goal to manage at least 20% of marine and coastal habitats by 2020 to conserve biodiversity and support the social and economic livelihoods of island communities. To achieve this goal, participating countries (including four of the five CROP countries) have established marine protected areas (MPAs) or marine managed areas (MMAs). Dominica is a non-participating country in the Caribbean Challenge Initiative, but also has marine managed areas that protect nearshore resources. However, the total area of no-take reserves in the region remains small, and many management areas lack adequate enforcement due to a lack of resources (Bouchon et al. 2008, Knowles et al. 2015). Those areas that are able to enforce no-take restrictions have reported increases of important fished species such as snapper and grunts (Polunin and Roberts 1993, Criquet et al. 2007), increased catches by artisanal fishers in adjacent fishing areas (Roberts et al. 2001), and improved resilience of coral reefs by increasing the biomass of parrotfishes (Steneck et al. 2018). Increasingly, MPA and MMA planning has been integrated into overarching marine spatial planning efforts in the region that aim to involve diverse stakeholders in the management process (e.g. Montserrat: Flower et al. 2020; Barbuda: Johnson et al. 2020; St. Kitts and Nevis: Agostini et al. 2015). In addition to spatial forms of management, seasonal closures and gear restrictions have been implemented for various fisheries, and ongoing efforts to collect landings data provide information necessary to better understand fishery dynamics and their impacts (Chakalall 1992, Ramdeen et al. 2014, Gumbs et al. 2015). Conservation and management approaches are also underway to limit impacts on coral reef habitats and food webs, including efforts to provide mooring anchorages, remove invasive lionfish and implement small-scale coral restoration (Chamberland et al. 2012) and coastal resilience projects (At The Water's Edge²).

1.2 Caribbean Regional Oceanscape Project (CROP)

Ocean resources in the Caribbean have the potential to make a much greater contribution to poverty reduction and shared prosperity for the region's growing population of 40 million than they do currently, and to increase community resilience to climate change. The Caribbean region has been at the forefront of a movement towards the development of the blue economy (the economics associated with the exploitation and preservation of the marine environment) and is home to a growing number of states that share the Caribbean Sea and have embraced the concept as the centerpiece of future growth strategies (McHale 2018, CANARI 2019). Given the value of the region's marine space and its resources, with support from the Global Environment Facility (GEF), The Organisation of Eastern Caribbean States (OECS) Commission, in partnership with the World Bank, is implementing the Caribbean Regional Oceanscape Project (CROP). CROP aims to improve systems and put relevant structures in place to foster a Blue Economy and to promote greater consideration of the ecosystem functions and services, which the ocean provides for member states. Under the CROP, the OECS Commission has engaged The Nature Conservancy (TNC) to provide consultancy services and deliver novel maps and statistics of ocean assets, focusing on tourism and fisheries, developing and enhancing tools to enable easy access

¹ <https://www.caribbeanchallengeinitiative.org>

² <https://coastalresilience.org/project/grenada-at-the-waters-edge/>

to both visualize and interrogate data and information, providing training, and incorporating stakeholder input and feedback into data and tool development.

CROP products will contribute to the development of marine spatial plans for each of five participating countries: St. Kitts and Nevis, Dominica, St. Lucia, St. Vincent and the Grenadines and Grenada. Consequently, the project intends to strengthen ocean governance and build capacity in the region using available data regarding ocean uses, ecosystem condition, and ecosystem services. As part of this process, TNC is developing ecosystem service models and maps to fill gaps in essential knowledge to inform the spatial planning process. Currently, few data exist on the relative impacts of reef fishing throughout the region, and estimates of fish biomass at a fine spatial scale are not available. This report details a sub-project, conducted at Florida International University, to map demersal reef fish and fishing throughout the region. Our metric of fishing impact, spatially explicit data on reef fishing ecosystem services (as quantified by current and potential fish biomass), and estimates of fish assemblage recovery time following the closure of an area to fishing are intended to fill information gaps for CROP stakeholders and decision-makers.

1.3. Mapping fishing and fish biomass in the Eastern Caribbean

Coral reef ecosystem services, including food provisioning from fisheries, are under threat from a wide range of human-caused stressors, and underscore the need to incorporate these services into marine management decisions (Arkema et al. 2015). To facilitate this goal, TNC established the Mapping Ocean Wealth initiative³ to spatially quantify what ocean ecosystems provide today. Under this umbrella, the work described here in the Eastern Caribbean aims to map and model reef fish and fisheries to provide quantitative estimates of fish biomass, an important component of ecosystem benefits. Though models and maps focus on the five CROP countries, we were able to extend them from Anguilla in the north to Grenada in the south. The work will provide analogous data to projects assisting marine management in Florida (Zuercher et al. 2020), Micronesia (Harborne et al. 2018), and The Bahamas (Harborne 2018). The data will be added to the Mapping Ocean Wealth online data portal.

1.4. Project aims

The aims of the CROP fisheries mapping project were to create:

- A model and map of each of the following:
 - Fishing impact (a unitless metric varying from 0 to 1 representing the cumulative effect of fishing on fish assemblages while controlling for biophysical gradients, such that 0 means the assemblage in the region closest to its natural state)
 - Current standing stock (estimated biomass of fish on the reef)
 - Potential standing stock (estimated biomass of fish possible on the reef in the absence of fishing)

³ <https://oceanwealth.org>

- Potential benefits of additional management (estimates of increased fish biomass given other management actions)
- Likely recovery rates for reef fish assemblages to reef carrying capacities
- 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 10, 2019 and this document represents the final technical report. However, the project will officially conclude on September 30, 2021.

2. Methods and data used for the project

2.1. Methods overview

The major products of the project, namely the models and maps of fishing impact and current and potential biomass for the Eastern Caribbean region, 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. population) 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 in 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.

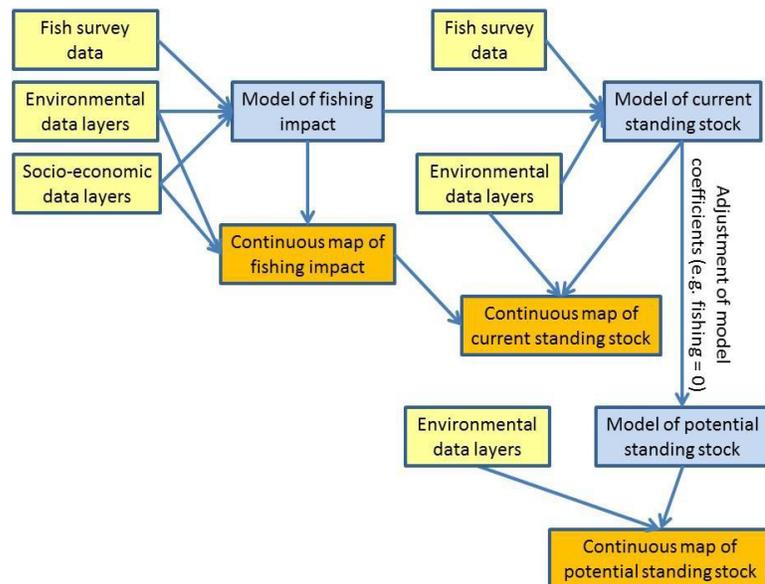


Fig. 2. Overview of the methods for modelling and mapping fishing impact and fish biomass. Yellow boxes represent input data, blue boxes represent output models, and orange boxes represent output maps.

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 data layers for the Eastern Caribbean region to derive a map of current biomass. Finally, the coefficients of the model of current biomass can be 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 marine reserve. It also includes increasing the percentage of hard coral cover to simulate a restoration effort that increases live coral. Indeed, any model outputs that identify additional management-related covariates as significant (e.g. mangrove availability for parrotfishes) can be used to simulate other management approaches, such as restoring mangrove forests or to estimate 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 censuses) data to assess fishing impact. While basic fishing landings data are available for some jurisdictions in the Eastern Caribbean, 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 datasets (Pauly and Zeller 2016). Consequently, this project used fishery-independent data derived from surveys of fish assemblages at sites across the region. 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. 2014), 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 (Valles and Oxenford 2014, Vallès et al. 2015), and mean length, trophic level and density of large fishes (Guillemot et al. 2014). Irrespective of which metric is used, both biophysical variables and fishing-related variables must be used in explanatory models since fish metrics (e.g. biomass or mean size) will be a function of both natural conditions and fishing effects.

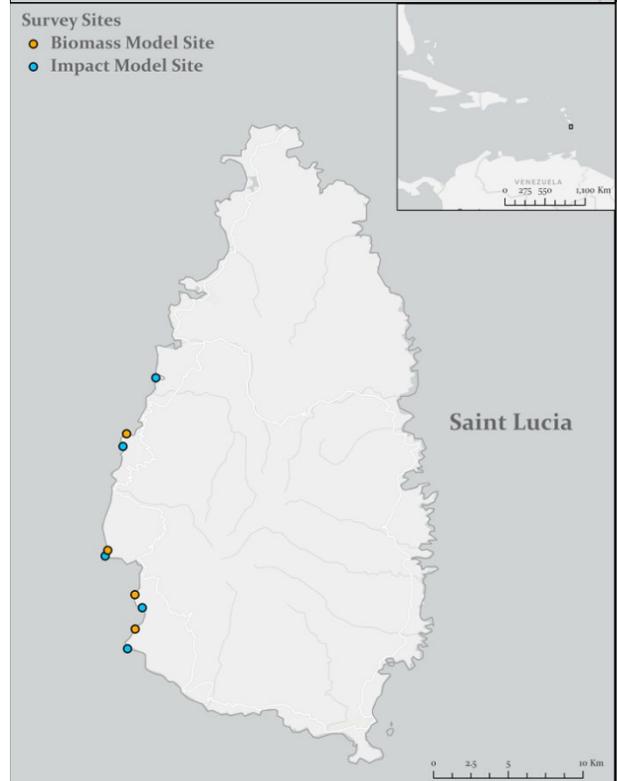
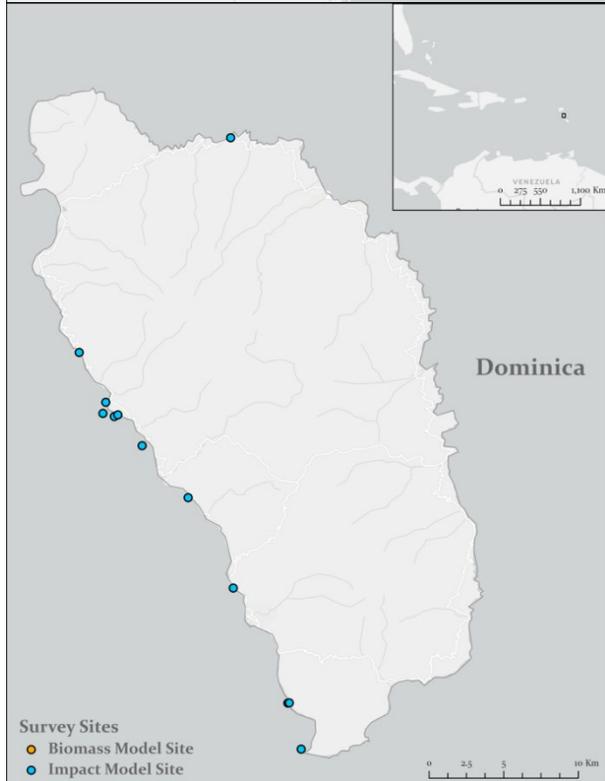
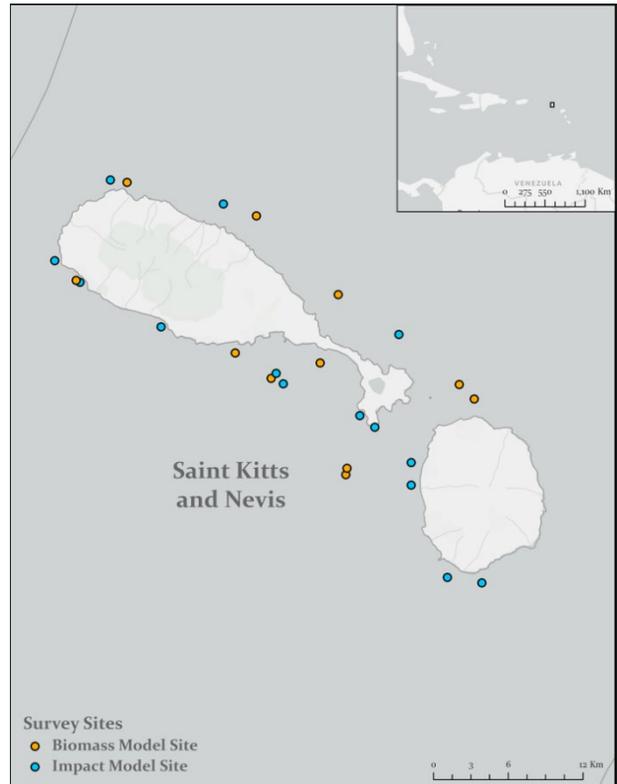
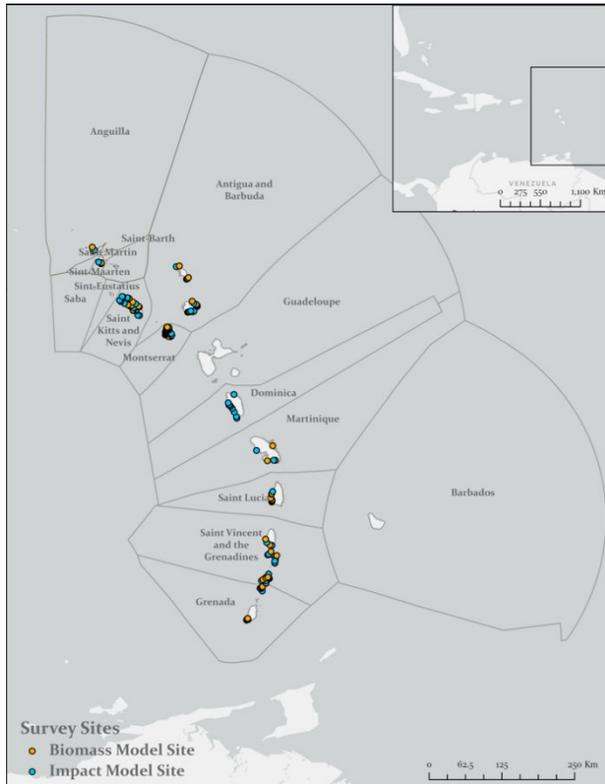
While we have explored several of these indicators, this report provides models and maps of fishing impact based on the mean length of parrotfish species. Recently, there has been a growing interest in the derivation of metrics of fishing pressure from surveys of herbivorous species, particularly parrotfishes. Although parrotfish are typically targeted only after more valuable species, such as grouper, are extirpated (Mumby et al. 2012), parrotfish are increasingly found in catches from reefs and benefit significantly from protection (Mumby et al. 2006). Consequently, large-bodied parrotfishes are often rare on heavily fished reefs, with assemblages shifting towards smaller-bodied species, and these changes in species structure and decreasing mean size have been highlighted as a potential indicator of over-exploitation (Clua and Legendre 2008). Working across the Caribbean, Vallès and Oxenford (2014) demonstrated that mean parrotfish weight, but not density or total biomass, was a better metric of fishing pressure than the biomass of some commercially important species. In subsequent research, average parrotfish weight was

shown to vary linearly with fishing pressure at smaller spatial scales, as required by a good indicator, and to be a preferred metric compared to those derived from other targeted species (Vallès et al. 2015). Parrotfish mean length has also been used to estimate fishing impact in Micronesia (Harborne et al. 2018). A further advantage of using parrotfish-derived metrics is that, unlike groupers, parrotfish are rarely totally absent under very high fishing pressure regimes, thus allowing for mean length or weight to be calculated at all sites. Deriving accurate estimates of mean length from fish surveys is also robust to survey technique and the taxonomic expertise of the observer, as it simply requires counts and sizes of each individual identified as a parrotfish and does not need standardizing to a fixed area. Finally, because of their global functional importance as grazers of macroalgae (e.g. Bellwood et al. 2004), parrotfishes data are usually recorded in surveys, providing a wealth of data for analysis.

Critically, the maps of fishing impact generated by the project represent relative, unitless patterns of estimated total fishing 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 mean length of parrotfishes), 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. Similarly, some sites may currently be heavily fished, but have little evidence of fishing impact (e.g. high mean size of parrotfishes) because the site has only recently been exploited. 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 project. 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 (Mumby et al. 2006). Consequently, it is important to recognize that references to high or low fishing impact are high or low for the Lesser Antilles archipelago. The maps of fishing impact also only apply to demersal reef fishes on hard-bottom habitats, not pelagic (e.g. tuna) or invertebrate (e.g. lobster) fisheries. Additionally, it is important to note that equal values of fishing impact on different habitat types do not signify that an equal number of fishermen have been or are exploiting that site. Instead, it is simply that the cumulative impact on the fish assemblage is equal (e.g. reduction to 50% of what that reef would naturally support).

2.3. Fish survey datasets

The maps and models produced by the project were entirely parameterized using existing fish survey data collected by the Atlantic and Gulf Rapid Reef Assessment (AGRRA), independent researchers Drs. Bob Steneck (University of Maine) and Peter Mumby (University of Queensland), the Waitt Institute, the Institute for Tropical Marine Ecology (ITME), the Observatoire du Milieu Marin Martiniquais (OMMM), and the FORCE project (Dr. Steven Newman, Newcastle University) (Table 1, Fig. 3). Although the focus of the project is on the five CROP countries, because these reefs are not well surveyed we used data from additional islands in the region to increase the database we had to analyze (Fig. 3).



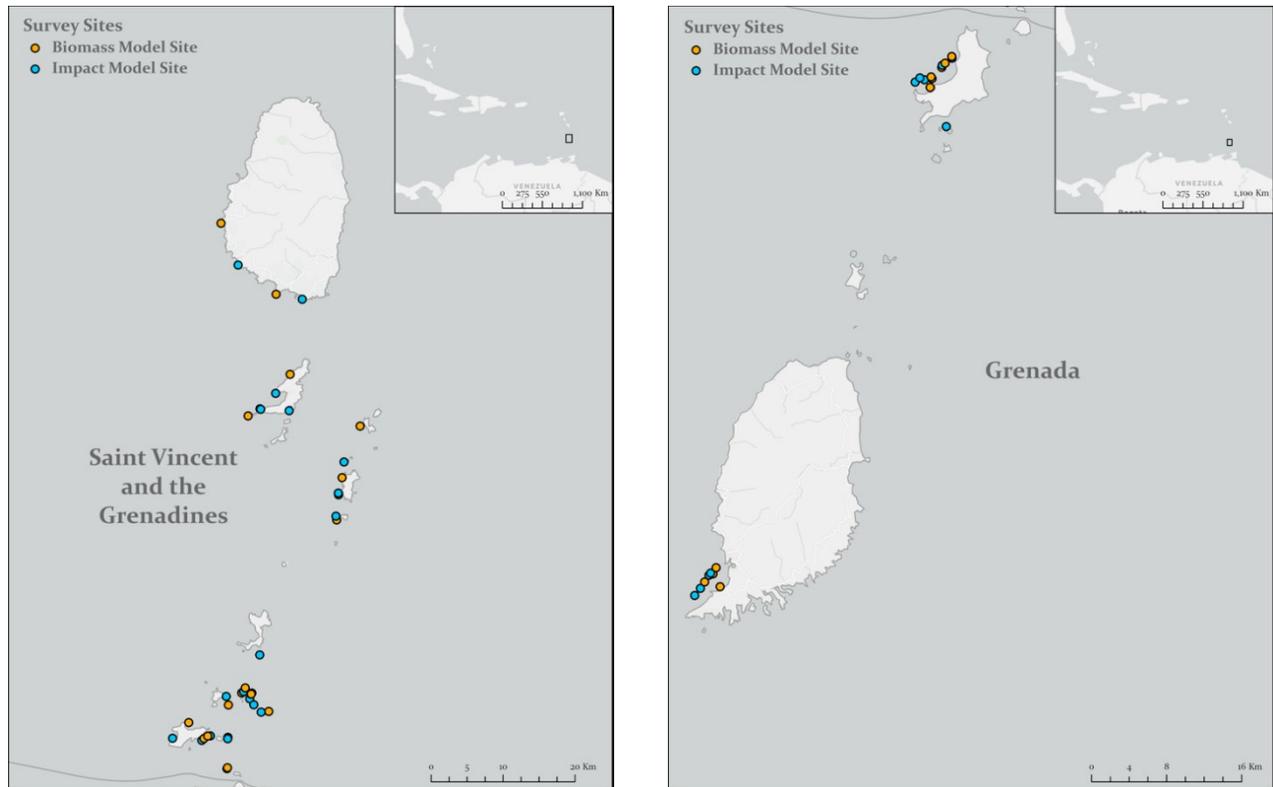


Fig. 3. Location of survey sites used in the fishing impact (blue) and biomass (orange) models. First panel shows all survey sites, and the remaining panels show survey sites for focal islands.

The survey methods used for datasets in the analysis of this project varied by the organization that collected the data and are as follows:

AGRRA: The AGRRA data (Lang et al. 2010) are collected to assess reef health across the region and focus on a subset of fish species that are ecologically important. Surveyors counted these species along 10, 30 x 2m belt transects and sized them to the nearest 5 cm. Rugosity was measured by repeated assessments of the maximum vertical relief of the substrate at 6 intervals along each of the transects. Benthic cover (e.g. cover of live coral) was measured every 10 cm along 6, 10 m long point intercept transects.

Only methods that differ from the AGRRA protocol will be described for the other datasets.

Steneck et al. 2018: A slightly modified AGRRA methodology was used to collect data (Steneck et al, 2018). Rugosity was measured using the ratio of distance covered when following the benthos compared to linear distance. Fish surveyors collected data on all large fishes (excluded blennies, gobies, and small planktivores such as *Chromis*) within the 30 x 4 m belt transects.

Waitt Institute: Methods followed the monitoring guidelines used by GCRMN-Caribbean¹ and were dependent on the skill level of the surveyors. At each site, all fishes were recorded along a single 30 x 4 m belt transect and sized to the nearest centimeter. Surveyors collected benthic measures using a photoquadrat technique. Images of a 90 x 60 cm quadrat placed along the same belt transect every meter, alternating sides of the transect were collected and later analyzed using an image processing software. A photomosaic (methods in Sandin et al. 2016) was used to assess the benthic community at a larger scale (100 m²) and was processed to extract metrics such as coral cover and rugosity. Lower skilled surveyors used AGRRA benthic techniques or a combination of both approaches.

Institute for Tropical Marine Ecology (ITME): Surveys were done with an early (now outdated) AGRRA protocol that recorded only a subset of the species currently included in AGRRA datasets. As such, ITME surveys (Dominica) were not used for biomass estimates but were used to estimate mean parrotfish length at survey sites (i.e. used to parameterize the fishing impact model).

Observatoire du Milieu Marin Martiniquais (OMMM): Fish and benthic surveys were conducted at five permanent monitoring sites. At each site, fish were counted and sized on 3, 50 x 2 m belt transects. Coral cover and rugosity data were collected at the same permanent monitoring sites following GCRMN-Caribbean protocols.

FORCE: Fishes (all species > 10 cm and all groupers and snappers irrespective of size) were identified to species, counted, and total length estimated to the nearest centimeter in eight 30 by 4 m belt transects. Benthic communities were assessed at each site on six randomly placed 10 m transects. Transect lines were set 5m apart and positioned parallel to the coastline. Benthic cover was measured using the point intercept method, with coral, octocoral, sponge and algal species identified and recorded every 10 cm. Reef complexity was estimated using relief height, which was quantified within 1m radius at four locations along the 10 m transect by measuring the highest point above the substrate following the AGRRA protocol.

To ensure consistency among datasets, the Steneck et al. (2018), Waitt Institute, FORCE and OMMM surveys were reduced to only those species recorded by AGRRA surveyors and fish lengths were modified to the same 5 cm size classes as the AGRRA data (0-5 cm, 6-10 cm, 11-20 cm, 21-30 cm, 40+ cm). The biomass of each fish was calculated using a single set of allometric parameters derived from a range of sources, but primarily from FishBase (Froese and Pauly 2010) and Bohnsack and Harper (1988). Data for the biomass of all species recorded by AGRRA, snapper and grouper species, and parrotfish species (for biomass models) were extracted for every site as g m⁻². A list of the species included in the project can be found in Appendix 1.

As recommended in previous studies (Shin et al. 2010, Vallès et al. 2015), mean parrotfish size was calculated after excluding smaller fishes (individuals < 10 cm) to make the analyses robust to inter-observer differences (e.g. some surveys may ignore small juveniles) and variability in recruitment not linked to fishing (e.g. some sites may have large numbers of small individuals because of naturally high recruitment rates or surveys

coinciding with recruitment events). While removing small individuals means that the values are higher than the actual mean length of all parrotfish, the aim was to generate a consistent and robust metric of parrotfish that might be targeted by fishers and this typically does not include small individuals. Consequently, all individuals >10 cm of all parrotfish species surveyed at a given site were pooled and their mean size calculated.

Data used in the models were distributed across six habitat types, with most classified as 'Fringing reef' (Table 2). However, co-ordinates for many survey sites did not appear to be exact (e.g. anchoring location rather than survey location) and therefore some sites may have been misclassified.

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

Country / Jurisdiction	Year(s)	Number of sites	Fishing impact model sites	Biomass Model sites	Source
Anguilla	2013	3	1	2	Steneck et al. 2018
Sint Maarten (Dutch)	2013	3	2	1	Steneck et al. 2018
St. Kitts and Nevis	2011	25	14	11	Lang et al. 2010
Antigua and Barbuda	2013, 2017	33	15	18	Waitt Reports, Steneck et al. 2018
Montserrat	2015	48	24	24	Waitt Reports
Dominica	2005	16	16	0	ITME
Martinique	2019	5	2	3	OMMM
St. Lucia	2013, 2014	9	5	4	Steneck et al. 2018
St. Vincent and the Grenadines	2014 - 2018	40	20	20	Lang et al. 2010, Steneck et al. 2018, Newman et al. 2015
Grenada	2014 - 2018	20	10	10	Lang et al. 2010, Steneck et al. 2018
Total		202	109	93	

Habitat type	Number of sites
Back Reef	3
Reef Crest	6
Fore Reef	4
Fringing Reef	132
Spur and Groove	5
Uncategorized	52
Total	202

Table 2. Habitat types where surveys were conducted. Uncategorized habitat represents surveys with coordinates that neither fell over any of the five mapped reef habitats nor were associated with metadata that distinguished a habitat type.

2.4. Modelling current biomass

We modelled biomass across the Eastern Caribbean for two focal fish groups: snapper and grouper species and parrotfishes, in addition to total biomass which includes all species documented in AGRRA surveys (Appendix 1). Since the AGRRA species span a range of

taxa and functional roles, it is anticipated that this metric of total biomass is a good proxy for total biomass.

2.5. Mapping reefs in the Eastern Caribbean

Establishing the extent of reef areas in the five CROP countries and for all additional areas in the region where fish survey data was available was critical for the project. To do this we used a high-resolution benthic habitat layer developed by TNC (Schill et al. *in prep*) using Planet Lab Inc.'s Dove satellite 4-meter imagery (Li et al. 2019). The layer categorizes shallow benthic habitats across the region, including five coral reef habitat types: Reef Crest, Reef Fringing, Reef Fore, Reef Back, Spur and Groove.

The Dove habitat products are vector coverages, with habitats represented by polygons of varying size. However, to accurately model reef fish in the CROP countries, 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 datasets. Experimentation indicated that 100 x 100 m (1 hectare) cells represented an appropriate grid size that retains habitat detail, but is computationally tractable (~6800 cells). Consequently, all map products from the project are at a 1 ha resolution. The Dove habitat map was rasterized and all coral reef pixels were included in the project. Where possible, in cases where fish surveys (known to have taken place on coral reef habitat) did not intersect with the rasterized coral reef habitat map, a nearby reef habitat type was assigned, taking into consideration any habitat-related metadata associated with the fish survey.

To further capture differences in fishing and fish biomass across habitat types in the models, we also used a higher-resolution habitat layer developed by TNC for the five CROP countries. Habitat class polygons in St. Kitts and Nevis, Dominica, St. Lucia, St. Vincent and the Grenadines and Grenada were standardized across countries to yield the following list of nearshore benthic habitat classes: Boulders and Rocks, Coral *Acropora*, Coral Algal Rim, Coral Framework, Coral *Orbicella* (*Montastraea*) with Gorgonians, Coral Patch Reef, Deep water, Hardground Algal, Hardground Gorgonian, Hardground Turf, Land, Mud and Silt, Rubble, Sand, Sand with Macroalgae, Seagrass Dense, Seagrass Sparse. Each fish survey site that intersected with this layer (i.e. the fish survey sites in the CROP countries) was assigned to a habitat class. The 'CROP Habitat Class' was then used as a biophysical variable in the fishing impact and biomass models.

Other habitats not included in the project, such as seagrass beds, 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.

2.6. Derivation of explanatory variables

The response variable at each fish survey site (e.g. mean parrotfish length or total biomass) was modelled against a range of explanatory variables to assess the significant factors driving their variability. 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 3). Two of the explanatory variables, coral cover and rugosity, were available from the *in situ* fish surveys and/or associated benthic surveys, but cannot be mapped continuously in the Eastern Caribbean region. 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. 2015). 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 rugosity 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 country-specific mean values for each habitat type. A full description of the derivation of each variable, and a justification for its inclusion, is provided in Appendix 2.

Table 3. Biophysical, fishing-related and methodological variables used in the fishing impact and fish biomass models, including brief details of their derivation. Due to inter-variable correlations, not all variables were included in final models. Additional information regarding data sources and variable derivation can be found in Appendix 2.

Variable	Description	Derivation/Source	Model(s)
Biophysical Variables			
Area of reef within proximity	Area of coral reef habitat with 20 km, 200 km	TNC habitat layer ¹	Impact; Biomass
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 TNC habitat layer	Impact; Biomass
Coral cover	Average percent coral cover at survey site	From <i>in situ</i> fish surveys or paired benthic surveys	Impact; Biomass
Depth	Depth at fish survey site or reef pixel	From <i>in situ</i> fish surveys; GEBCO ²	Impact; Biomass
Diadema density (by country)	Average <i>Diadema</i> density (individuals / m ²)	Data compiled by Siegel et al. 2019	Impact; Biomass
Distance to deep water habitats	Distance to the 30 m depth contour	GEBCO	Impact; Biomass
Geomorphology (by country)	Reefs categorized as generally 'fringing' or 'fringing with lagoon'	Google Earth imagery	Impact; Biomass
Habitat Type (categorical)	Habitat type (two variables: OECS Crosswalk classes/CROP	TNC habitat layers	Impact; Biomass

	Habitat Class; Dove habitat classes)		
Latitude	Latitude of fish survey site or reef pixel	From in situ fish surveys; GIS	Impact; Biomass
Longitude	Longitude of fish survey site or reef pixel	From in situ fish surveys; GIS	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 (categorical; also considered a fishing-related variable)	No take area versus an area open to any form of fishing	TNC protected areas layer	Impact; Biomass
Reef complexity (categorical)	Relief at fish survey site (Low, Medium, High)	From in situ fish surveys, paired benthic surveys or TNC Reef Report Cards	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
Fishing-related Variables			
Demography	The first principal component of a range of demographic variables: population density, median age, population growth rate, birth rate, death rate, % urban population, life expectancy, GDP, GDP growth rate, GDP per capita, unemployment rate	Data from a variety of governmental and non-governmental data sources	Impact
Distance to fish landing site	Distance to a fish landing site identified by in-country experts	Data layer created by this project	Impact
Distance to major fish landing site	Distance to a fish landing site identified as 'major' by in-country experts	Data layer created by this project	Impact
Distance to major port	Distance to a port where cruise ships berth or anchor	Data layer created by this project	Impact
Fishing Impact	Cumulative impact of fishing	Estimated by this project	Biomass
Fish landing sites within 5km, 20km	The number of fish landing sites within x km of a reef	Data layer created by this project	Impact
Governance	The average of six governance indicator scores: voice and accountability, political stability, government effectiveness, regulatory quality, rule of law, control of corruption	Worldwide Governance Indicators (WGI) ³ (Kaufman et al. 2010) compiled by Siegel et al. 2019	Impact
Human population	Number of people within 20 km, 50 km, 100 km of a reef pixel	LandScan human population data	Impact
Human population per area reef	Number of people within x km divided by the area of fishable reef within x km	LandScan human population data	Impact
Reef fisheries economy	Estimated proportion of total GDP that is derived from reef fisheries	Data compiled by Siegel et al. 2019	Impact

Small-scale fishing population (by country)	Estimated number of small-scale fishers in each country	Data compiled by Siegel et al. 2019	Impact
Total gravity of fish markets within 500km	Market gravity defined as population size divided by the square of travel time	Cinner et al. 2018	Impact
Gravity of the nearest fish market	Market gravity defined as population size divided by the square of distance, calculated for population centers >1000, >2000 and >5000 residents	Data layer created by this project	Impact
Methodological Variables			
Month (categorical)	Month of fish survey	From in situ fish surveys	Impact; Biomass
Season (categorical)	Season (wet, dry) of fish survey	From in situ fish surveys	Impact; Biomass
Survey method (categorical)	Fish count and sizing methods	From in situ fish surveys	Impact; Biomass
Year	Year of fish survey	From in situ fish surveys	Impact; Biomass

¹ CaribbeanMarineMaps.tnc.org

² GEBCO: General Bathymetric Chart of the Oceans (gebco.net)

³ Detailed documentation of the WGI, interactive tools for exploring the data, and full access to the underlying source data available at www.govindicators.org. The WGI are produced by Daniel Kaufmann (Natural Resource Governance Institute and Brookings Institution) and Aart Kraay (World Bank Development Research Group).

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. 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 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 fish 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. 4) (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.

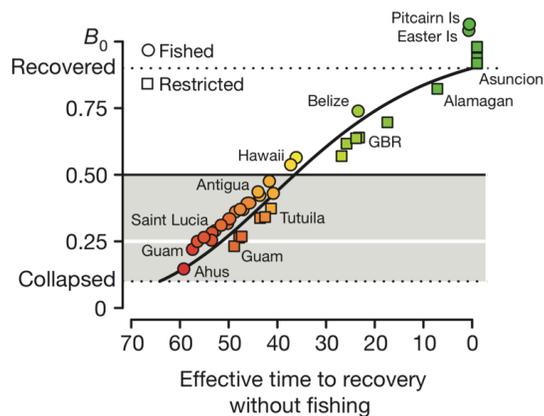


Fig. 4. The relationship between time to recovery (90% of potential biomass) following the cessation of fishing and current fishery status. Points highlight reef sites used to parameterize the relationship. Graph from MacNeil et al. 2015.

2.8. Statistical analyses

For models of both fishing impact and biomass, the final dataset consisted of univariate response variables (e.g. biomass of parrotfish), 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 visualized 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 biophysical and fishing-related predictor variables were tested for collinearity using pairwise comparisons with Pearson's correlation coefficient, and variance inflation factors (VIF) were calculated to quantify any inflated variance in model results due to co-linearity. A variable trimming threshold of 0.8 pairwise correlation and $VIF > 10$ led us to drop the following variables: latitude, longitude, area reef within 200 km, human population within 50 km and 100 km, the variable representing demography, and the reef fisheries economy variable. 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. Project results

3.1. Fishing impact model

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. 5). Three human-related variables, distance to a fish landing site, the estimated number of small-scale fishers in a country, and gravity of the nearest potential market explained significant variation in the mean length of parrotfish (12.1%, 13.5%, and 3.9% of explained variance, respectively). Additionally, several biophysical variables were important for explaining variation in mean length of parrotfish: wave exposure (9.4%), sea surface temperature (6.2%), coral cover (5.6%), and area of reef within 20 km (4.2%). Month of survey was also significant (12.1%), but this is more likely to reflect the timing of surveys at different locations as opposed to time of year affecting fish assemblages, and there was some effect of the methodology used. The fishing impact model explained 48% of the variability in the dataset, and the correlation between observed and predicted values was 0.77. This exploratory power is considered acceptable given the challenges of the project: combining multiple datasets across a large geographic area and using a relatively crude fishery-independent metric of fishing impact.

This model was then used to predict fishing impact in every 1 ha cell along the reef tract considered by the project (Map 1). Predictions were made from the model by classifying the significant variables into two categories. First, distance to a fish landing site, estimated number of small-scale fishers, and gravity of the nearest potential market were considered to relate entirely to fishing impact (generally higher fishing impact closer to landing sites and where there are more fishers). Values unique to each 1 ha cell (i.e. actual values for each cell) were used for these three variables. In contrast, the remaining significant variables were considered to be environmental or temporal drivers of fish abundance. These variables included wave exposure, and while this factor is clearly an important biophysical driver of fish assemblages (e.g. Fulton et al. 2005), it could potentially also impact fishing activity since exposed reefs may be less fished because of the challenges of fishing in high-wave areas. However, discussions with in-country partners suggested that while fishers may not be able to access these reefs on some days, they are adept at accessing exposed reefs and target these areas on calm days. Consequently, we considered wave exposure as a biophysical rather than fishing-related variable. The values of these variables in every 1 ha cell were set to their mean or the most common month of data collection (October). This ensured that the predictions only represented the effects of fishing on mean parrotfish length 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 mean length, but in this step, we only wanted to investigate the effect of fishing on mean parrotfish length, although we control for environmental

variables when building the model. Predicted mean parrotfish lengths were then converted to values from 0 (highest mean length, lowest fishing impact) to 1 (lowest mean length, highest fishing impact).

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 in this region, and whether the efficacy of gear such as fish traps varies among habitats (Wolff et al. 1999). In the absence of the necessary data, all habitat types are considered to be equally impacted by fishing. However, absolute 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.

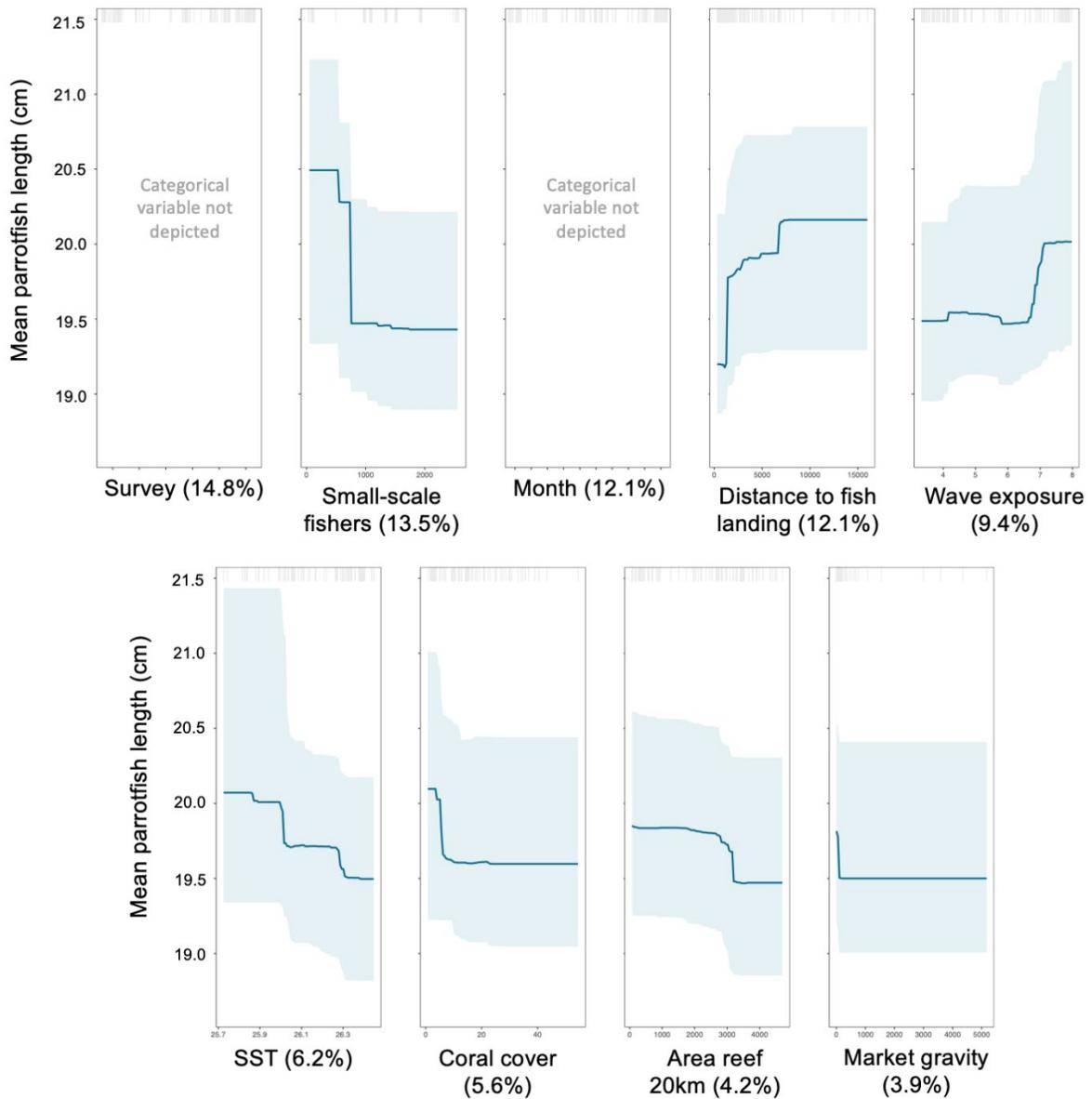
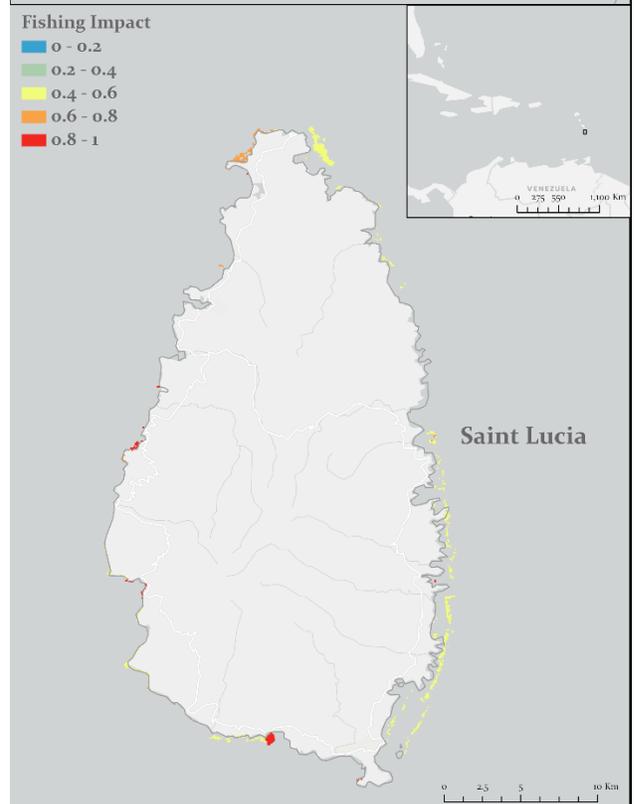
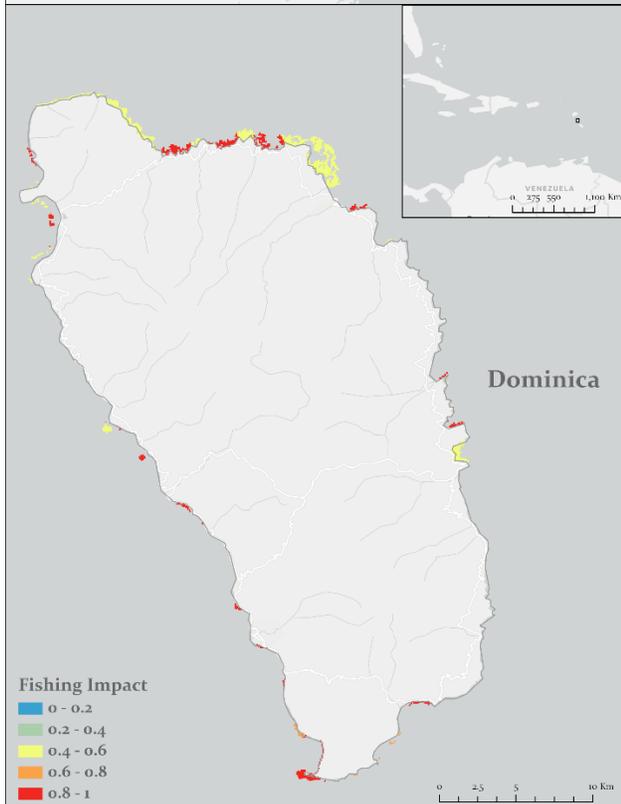
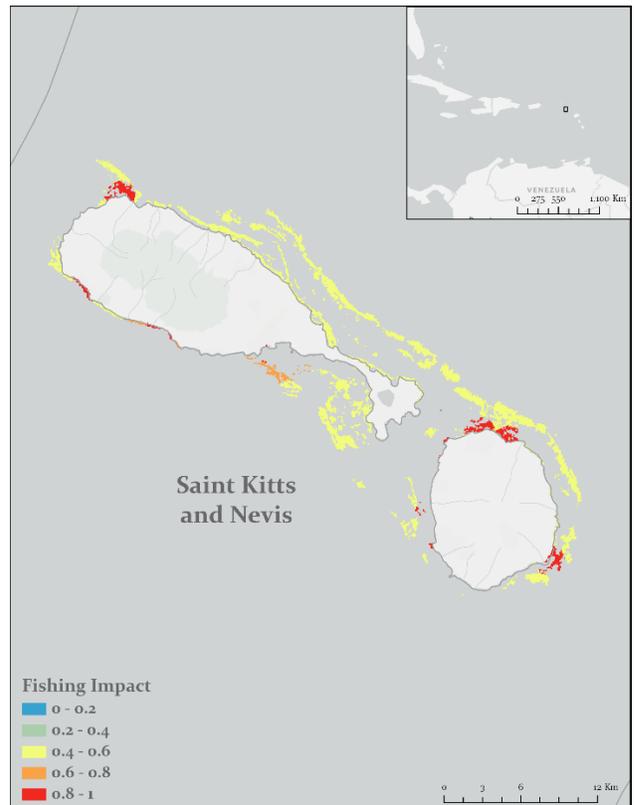
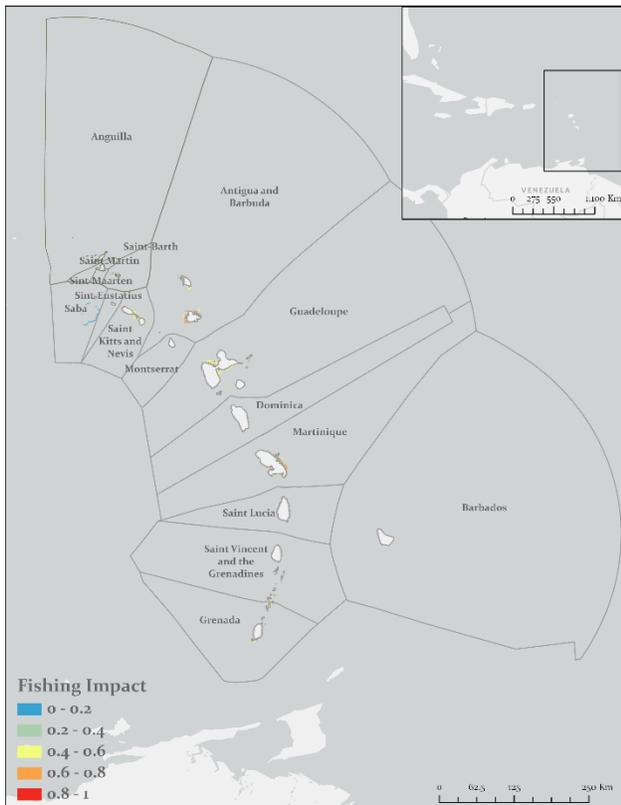
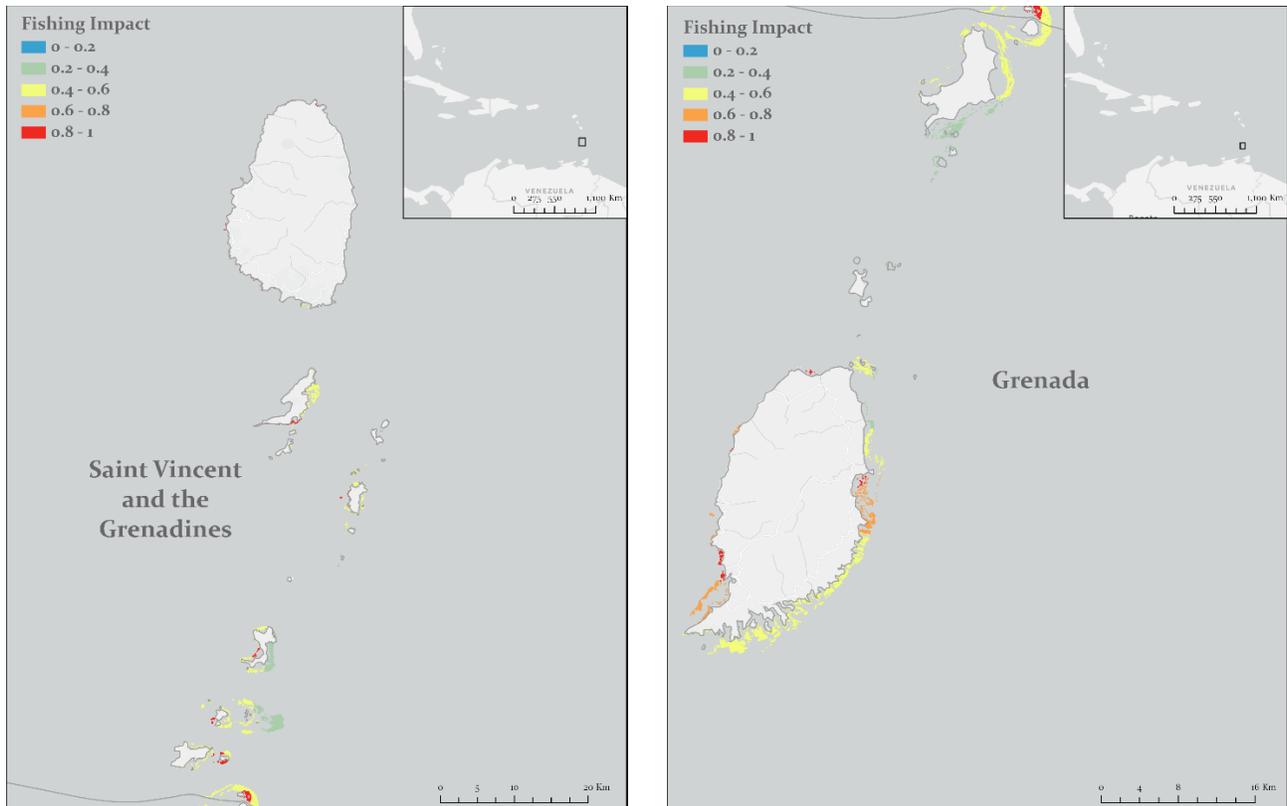


Fig. 5. Relationships between the significant biophysical and fishing-related variables and mean parrotfish length (y-axis) as modelled by boosted regression trees. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable. Shaded areas represent 95% confidence intervals obtained through bootstrapping.





Map 1. Spatial distribution of estimated relative fishing impact (0 = lowest fishing impact) across the Eastern Caribbean.

3.2. Interpretation of the fishing impact model

The fishing impact model captures a series of variables that intuitively might be expected to affect fishing. In particular, fishing impacts (as represented by mean parrotfish size) decrease with increasing distance from fish landing sites and increase with increasing market gravity. These variables reflect the growing recognition of the importance of reefs distant from human populations for maintaining fish stocks (Cinner, et al 2013, Maire et al 2016) and the utility of market gravity as a proxy for fishing impacts (Cinner et al 2018). As expected, an increasing number of small-scale fishers in a country also increases fishing impact, and there appears to be a threshold beyond which fishing impact is significantly higher. Parrotfish mean size is also influenced by biophysical variables, particularly wave exposure that is a proxy for reef primary productivity. Primary production, and thus grazer populations, can be influenced by wave exposure that increases nutrient supply (Mumby et al 2013). These patterns of primary production may be affecting parrotfish size structure, and lead to a larger proportion of larger individuals. The mean size of parrotfish decreased with increasing sea-surface temperature, which is consistent with research examining the effects of climate change that suggests fish may become smaller (Cheung et al. 2013). Our results show a decrease in mean parrotfish length with coral cover above a threshold of approximately 5%. An increase of coral cover may increase the abundance

of small-bodied parrotfishes (reduce mean size) because it provides more shelter from predators.

A summary of the proportion of reef area in each country that has low, medium, or high fishing impact highlights minor differences across the region (Fig. 6). None of the CROP countries have reefs that fall into the low impact category which was restricted to offshore areas more remote from human populations. While Dominica and St. Lucia have ~40% of their reefs categorized as having high fishing impact, fewer areas in Grenada, St. Kitts and Nevis and St. Vincent and the Grenadines fall into this category. The metric of fishing impact used in this project is relative to the reefs surveyed. Thus 'high' fishing impact may not be as high as other locations in the wider Caribbean.

It could be insightful to conduct more detailed comparisons between our fishery-independent estimates of fishing impact and other estimates of fishery-independent and fishery-dependent work in the region (e.g. Gobert 2000, Gill et al. 2019). For example, fishing in Barbados is reported to be concentrated on more sheltered western reefs (Gill et al. 2019), but fishing impact in our maps was high on some sheltered and exposed reefs around each island (Map 1). However, such comparisons are challenging because the relationships between our measure of fishing impact (the cumulative impact of fishing on the current fish assemblage) and fishery-dependent data (the catches of fishers on any given day) are not clear. Studies aiming to establish these relationships would be beneficial for understanding fishing patterns across the study area. Despite only being a relative metric of fishing, the patterns of fishing impact around islands in the CROP countries were generally judged to be a reasonable reflection of expectations among project partners (feedback obtained during workshops). Such patterns are intrinsically useful to assess relatively heavily and lightly fished areas, despite it being difficult to quantify these values in terms of actual catches and judgements of what fishing impacts are too high will be context dependent (e.g. among countries).

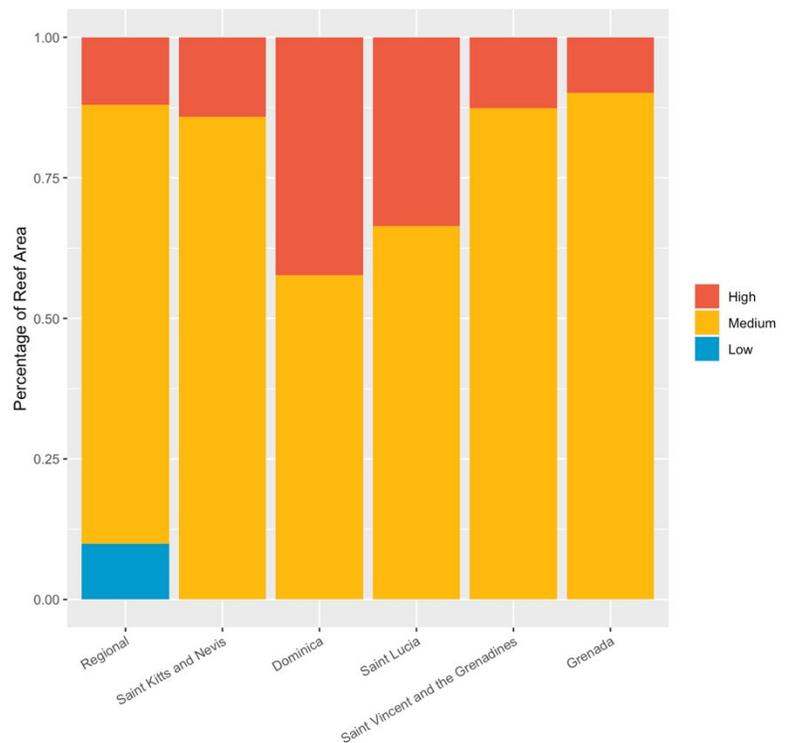
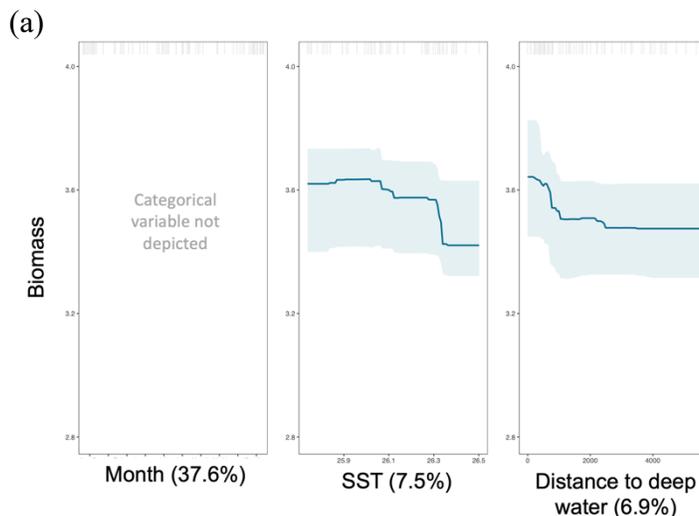


Fig. 6. The proportion of reef cells in the entire study region and in each CROP country assigned to low (0-0.33), medium (0.34-0.67), or high (0.68-1.0) fishing impact. All low impact reefs were outside of the CROP countries.

3.3. Current biomass model

Integrating the newly derived fishing impact data layer with the biophysical variables included in the project (Table 3) allowed us to build statistical models of the biomass of all AGRRA fish species, snapper and grouper species, and parrotfish species (Fig. 7, Table 4). All fish biomass response variables were log transformed to improve normality of residuals. The boosted regression tree analysis provided a series of partial dependency plots, and the models explained reasonable amounts of deviance in the dataset (Table 4). These models included between three and eight significant variables, with month included in all models. Fishing impact was included in the model for snapper and grouper species (4.5% of deviance) showing a negative correlation between fishing and biomass of this highly targeted group. Other important biophysical variables included sea surface temperature that affected both AGRRA fish species and snapper and grouper species and the availability of seagrass and mangrove nursery habitats that was positively correlated with the biomass of parrotfishes. These models were then used to predict the total biomass of all AGRRA 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 was set to October (the most common month for fish surveys in the dataset) and coral cover was set to a mean coral cover value for each country. Maps of current biomass of snapper and grouper species and parrotfishes are in Appendix 3 (Maps 7 and 8).



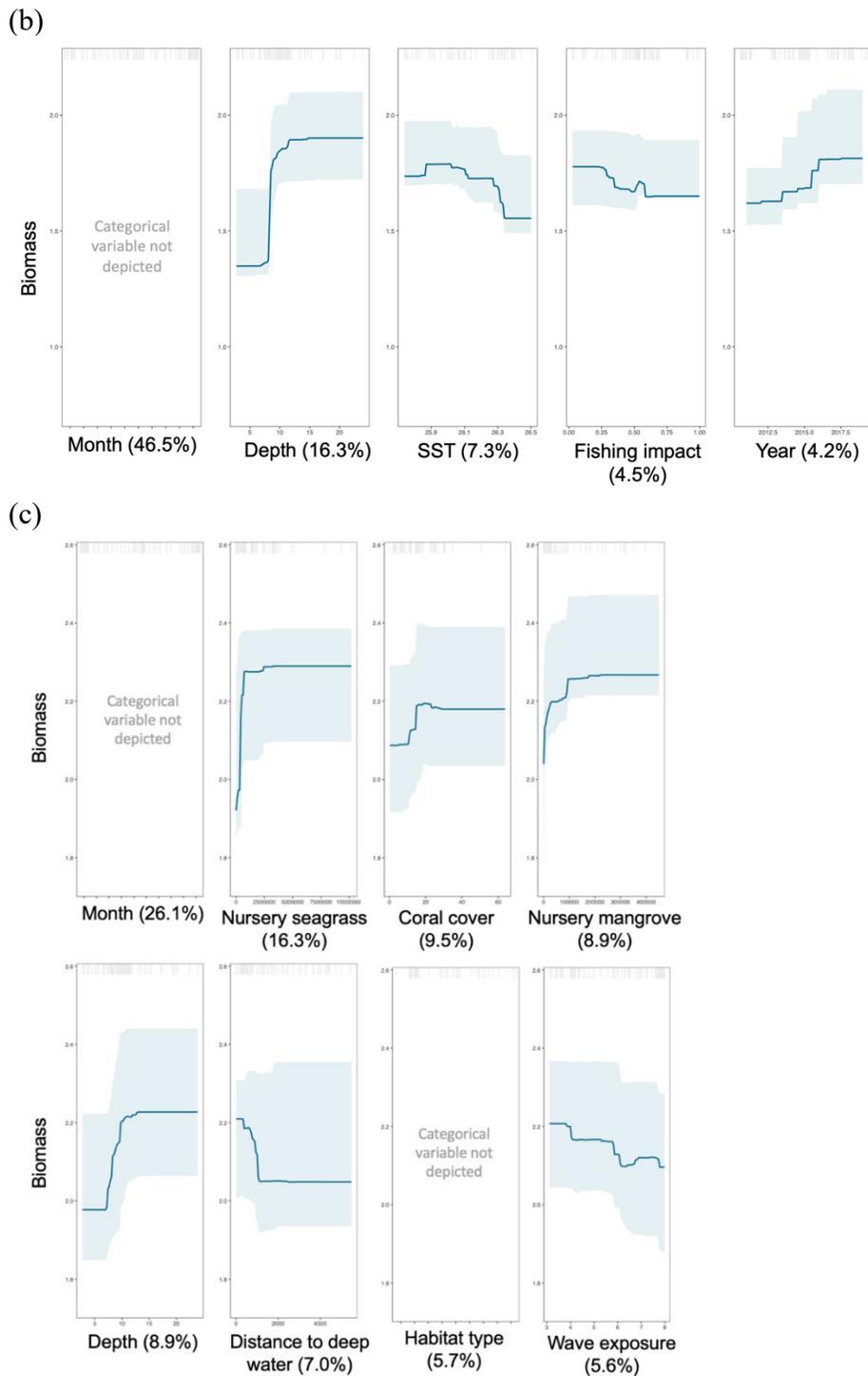
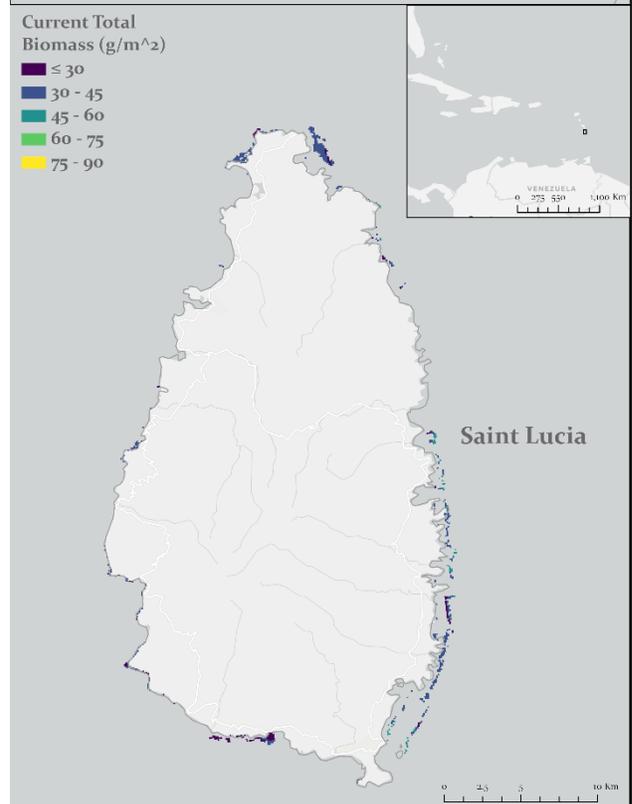
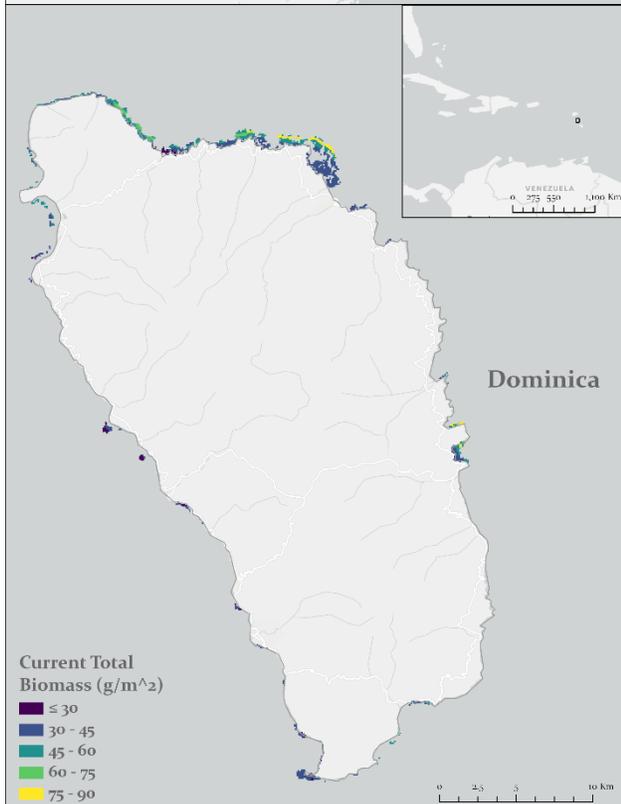
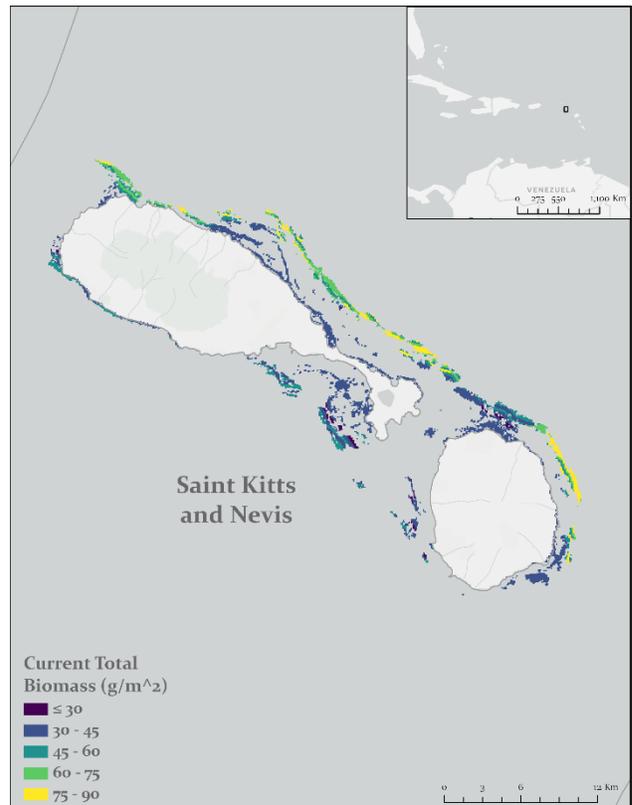
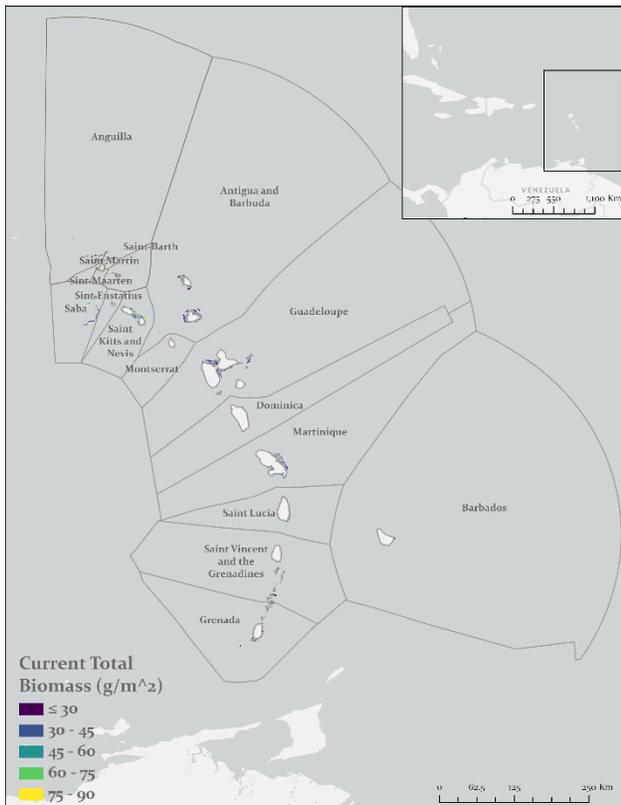
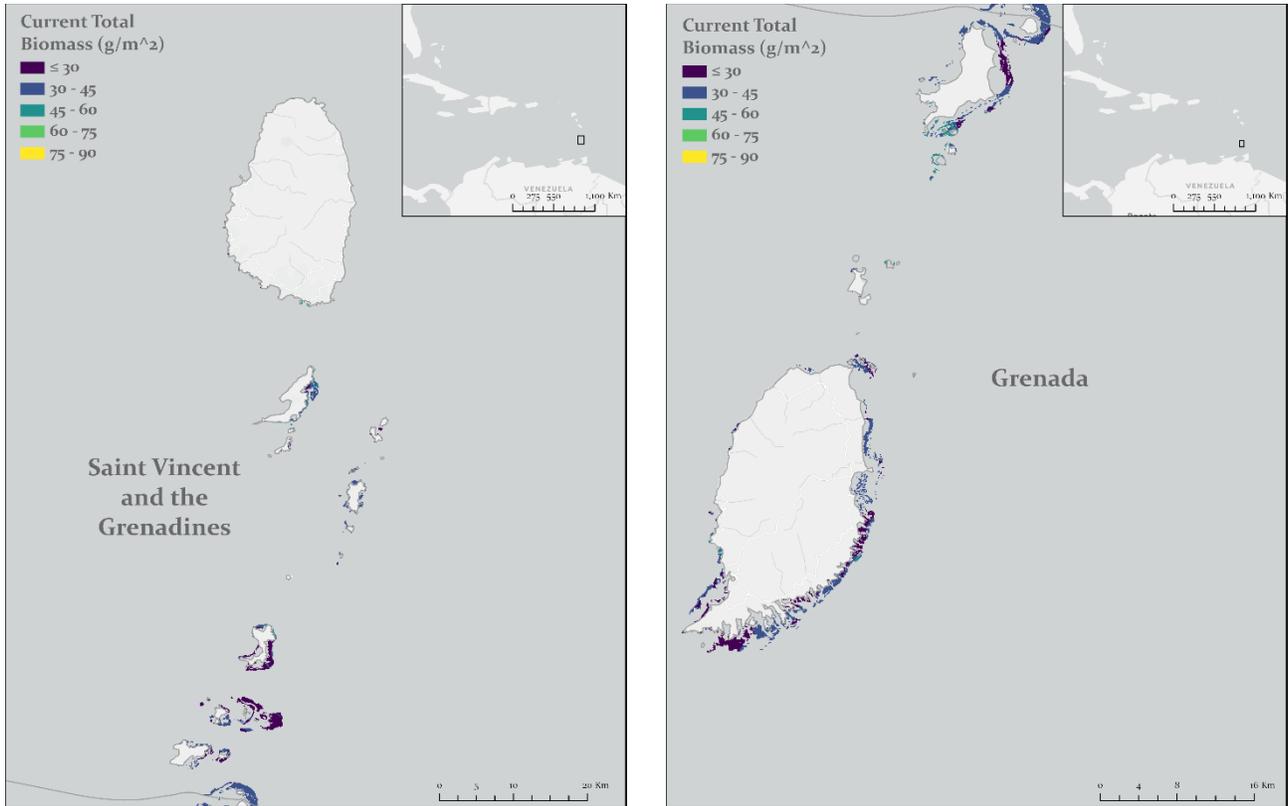


Fig. 7. Relationships between the significant variables and biomass of (a) all AGRRA species; (b) snapper and grouper species; and (c) parrotfish species modelled by boosted regression trees. Values of log fish biomass on the y-axis are normalized rather than showing actual biomass values. Percentage values in the x-axis labels represent the percentage of explained deviance that was explained by that variable. Shaded areas represent 95% confidence intervals obtained through bootstrapping.





Map 2. Spatial distribution of estimated current total biomass (g m⁻²) in the Eastern Caribbean.

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

Species Group	Variance explained	Correlation between observed and predicted values	Significant explanatory variables (and percentage of variance explained)
AGRRA species	70.9%	0.88	Month (37.6%), Sea surface temperature (7.5%), Distance to deep water habitat (6.9%)
Snapper and grouper species	72.7%	0.88	Month (46.5%), Depth (16.3%), Sea surface temperature (7.3%), Fishing impact (4.5%), Year (4.2%)
Parrotfishes	66.8%	0.85	Month (26.1%), Availability of seagrass nursery habitat (16.3%), Coral cover (9.5%), Availability of mangrove nursery habitat (8.9%), Depth (8.9%), Distance to deep water habitat (7.0%), Habitat type (5.7%), Wave exposure (5.6%)

3.4. Interpretation of the current biomass model

The models of current biomass for all AGRRA fish, snapper and grouper species, and parrotfish highlight some expected patterns. In particular, total fish biomass and the biomass of snapper and grouper decreased in warmer waters, potentially reinforcing some concerns about the impact of climate change on fishes (Cheung et al. 2013). The increased total biomass in areas closer to deep water habitats may reflect increased productivity close to areas of upwelling water (Gove et al. 2016) and the use of reef walls by large transient predators. The increase of snappers, groupers, and parrotfishes in deeper water is likely reflecting the challenges of living in shallow areas that have high water movement (Fulton et al. 2005). Although parrotfishes can be abundant on shallow reefs in some areas (e.g. Belize, Mumby and Hastings 2008), many of the reefs in the Lesser Antilles have higher wave energy. Parrotfish biomass increases with increasing coral cover to approximately 20% cover before leveling out, reflecting the importance of both coral cover and structure to these species (Bozec et al. 2013). The increasing biomass of parrotfishes with the availability of nursery habitats is consistent with many of these species using seagrass and mangroves as juveniles before moving to offshore reefs (Mumby et al. 2004, Harborne et al. 2016). Typically, we would expect reef complexity to be important in these models because of its pervasive effect on fish assemblages (Graham and Nash 2013). However, good reef complexity data were not available for many sites, and this inevitably affects the power of the model.

Our derived layer of fishing impact was included in the model of snapper and grouper species, as was expected for these species that are heavily targeted on reefs (Stallings 2009). Although included in the model, its effect is perhaps weaker than anticipated and we might expect this covariate to also be included in the total and parrotfish biomass models. While we are confident that the fishing impact model captures the main gradients of fishing in the area, all reefs are relatively heavily fished and this may make it difficult to detect the link to fish biomass (limited variance among countries). Furthermore, there is a limited amount of data available for the region, which may limit the power of the models. Finally, if fishers use different gear types among islands and at different times, this may affect different fishes within the assemblage more than others (e.g. hook and line will remove groupers and snappers but not parrotfishes, while traps remove a wider range of species). Such heterogeneity of fishing methods may weaken the link between our metric of fishing impact (mean parrotfish length) and the effect on the biomass of fish seen on the reefs. While the relationship to fishing impact within the biomass models may be weak, it is important to recognize that the models explain a relatively high amount of deviance within the dataset and thus the predictions of current biomass are likely to be realistic.

The resulting maps of biomass allow us to quantify variations across the focal islands (Fig. 8). For example, St. Kitts and Nevis has the largest proportion of reef cells with high current biomass of snapper and grouper, perhaps reflecting the relatively low fishing impact for these species in this country. However, these comparisons also reflect variations in biophysical context (e.g. reef depth profiles).

Biomass at a survey site will also be affected by management status (e.g. whether it is inside a marine protected or marine managed area). Although management status was not a significant variable within the models, it is clear that they can increase fish biomass locally and have a range of other benefits (reviewed by Graham et al. 2011). However, while effective, their effects are typically overwhelmed by large-scale biophysical gradients (as seen elsewhere, such as in Micronesia, Harborne et al. 2018). Furthermore, the limited number of no-take reserves in the region, existing reserves being relatively newly established, and the variable levels of enforcement mean that their effects are not well parameterized in the model. Despite not being included in the model, our results do not detract from the critical role that reserves can play in conserving fish biomass in the Eastern Caribbean. For example, our simulations of zero fishing impact (Section 3.5) shows that a well-enforced, old reserve can have significant benefits to grouper and snapper biomass.

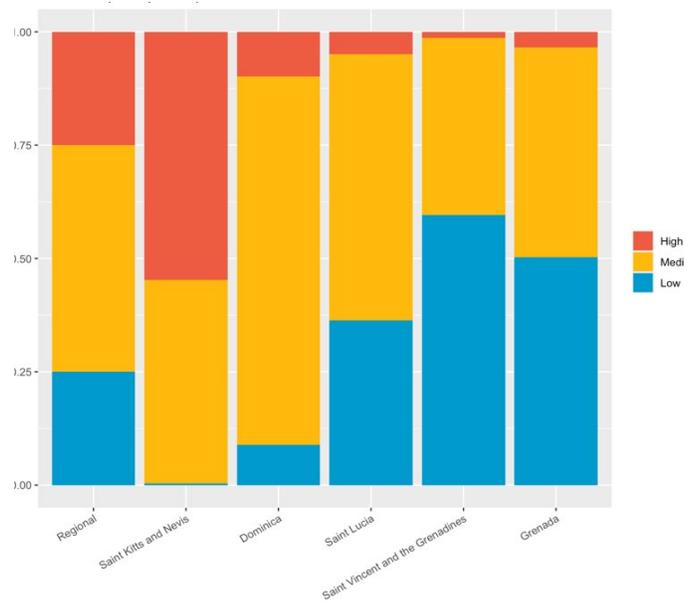
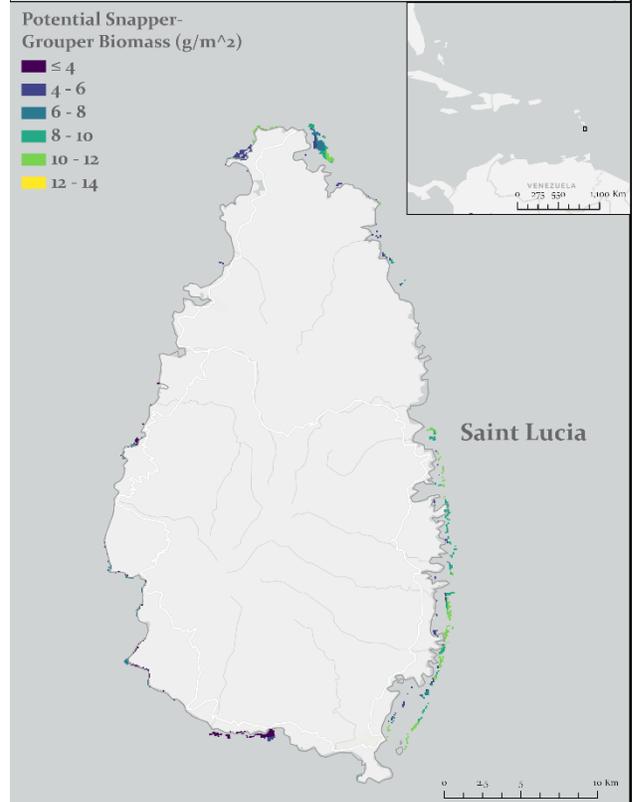
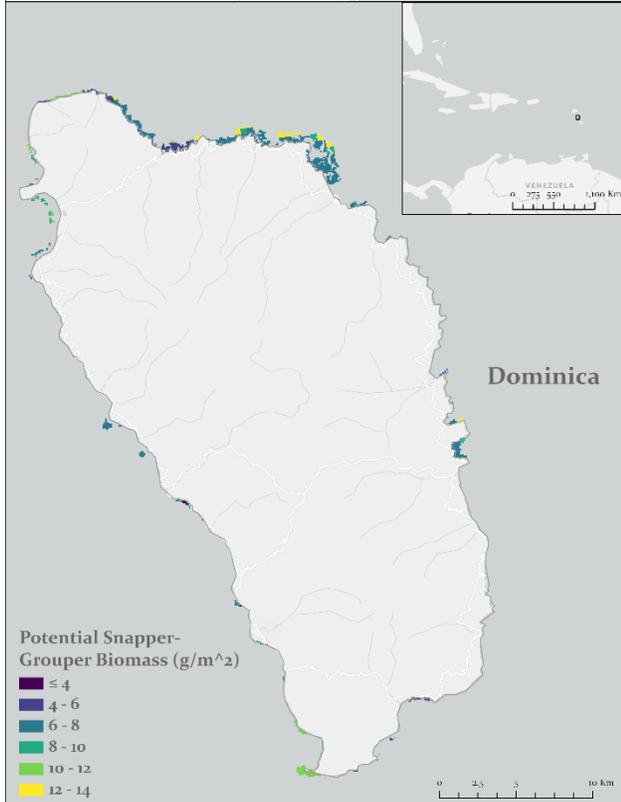
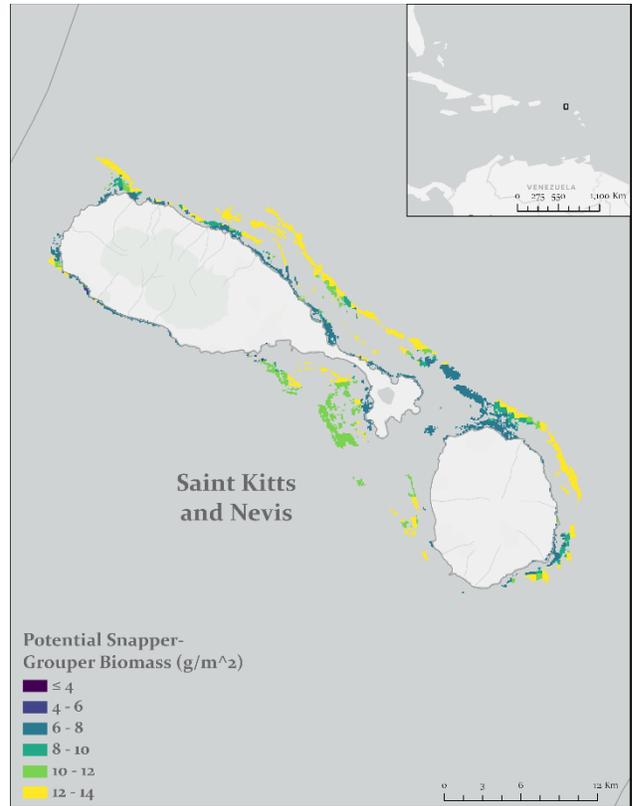
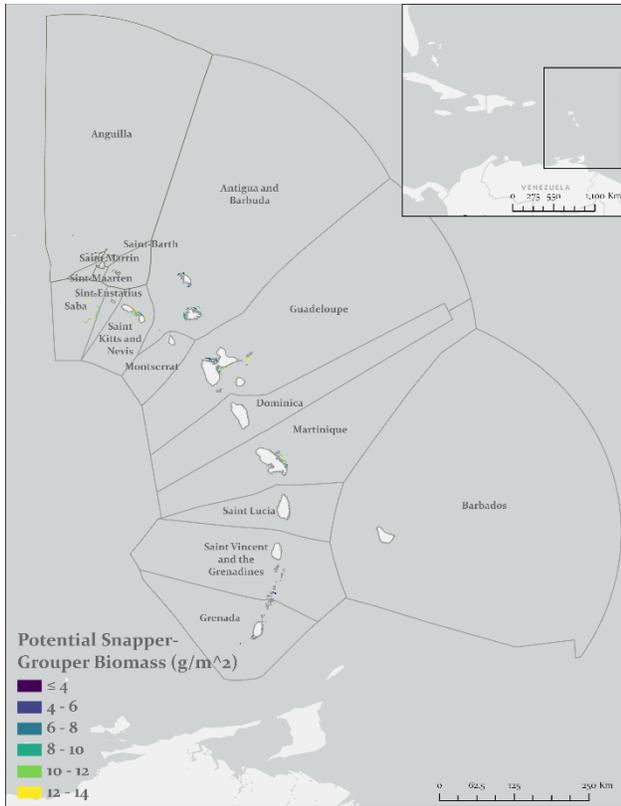
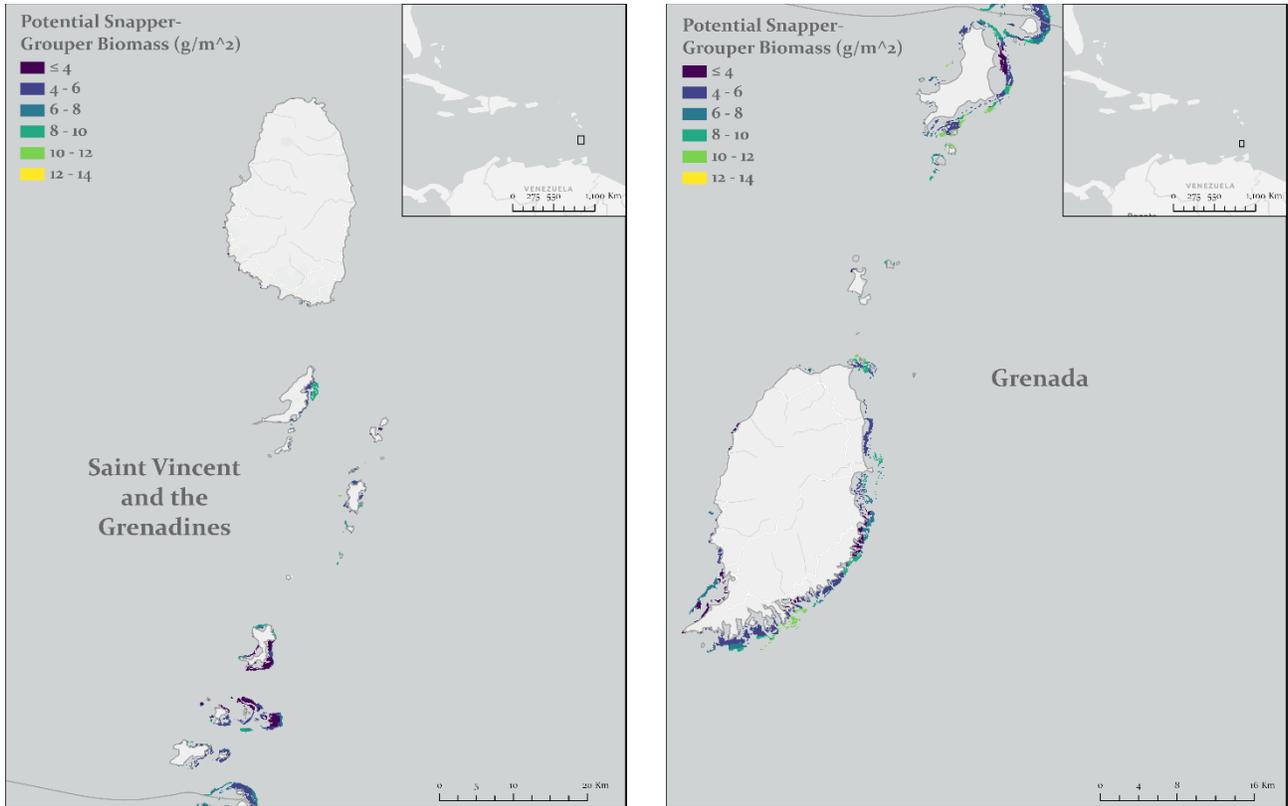


Fig. 8. The proportion of reef cells in each country assigned to low, medium, or high biomass of snapper and grouper species. Categories defined as low = less than 1st quartile, high = greater than 3rd quartile.

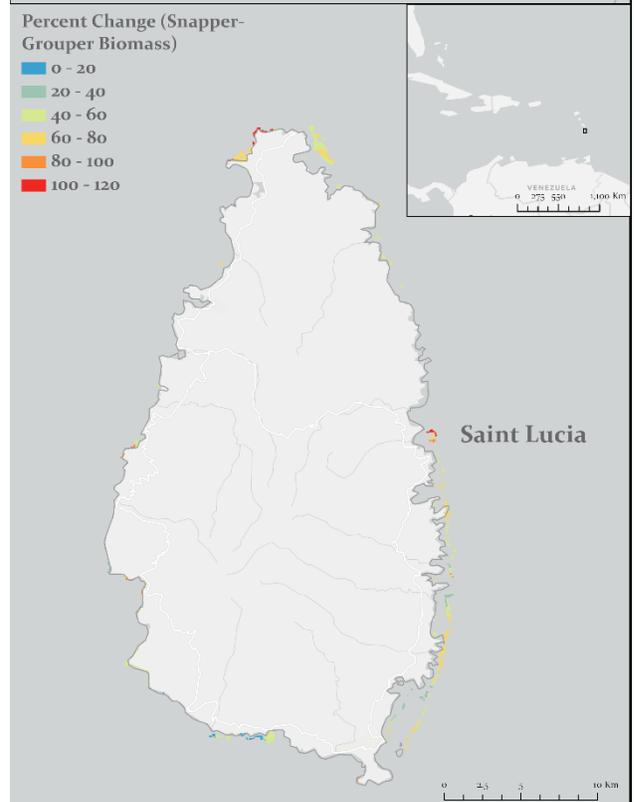
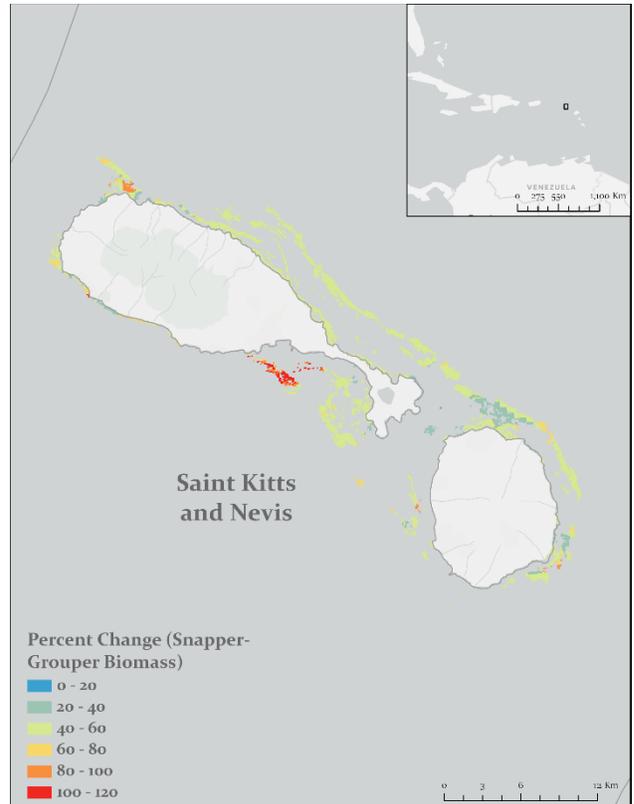
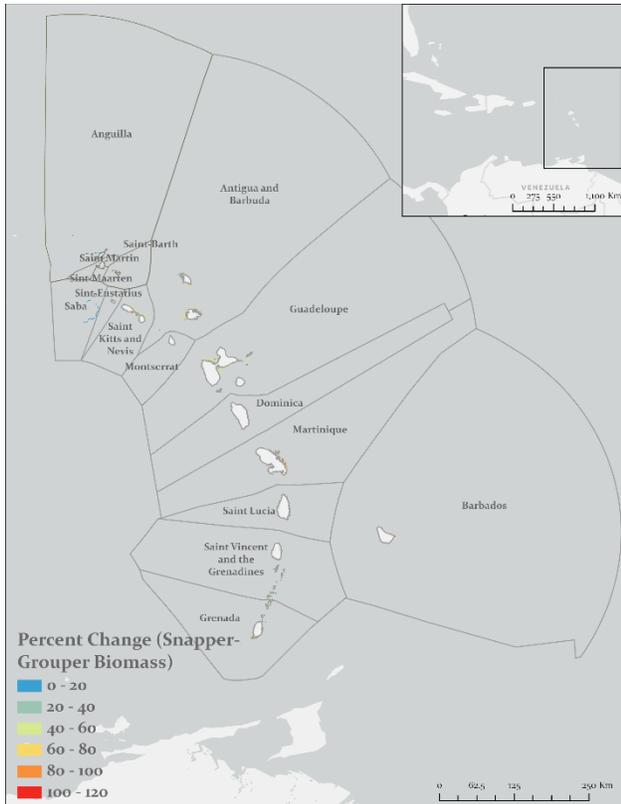
3.5. Generating a map of potential biomass

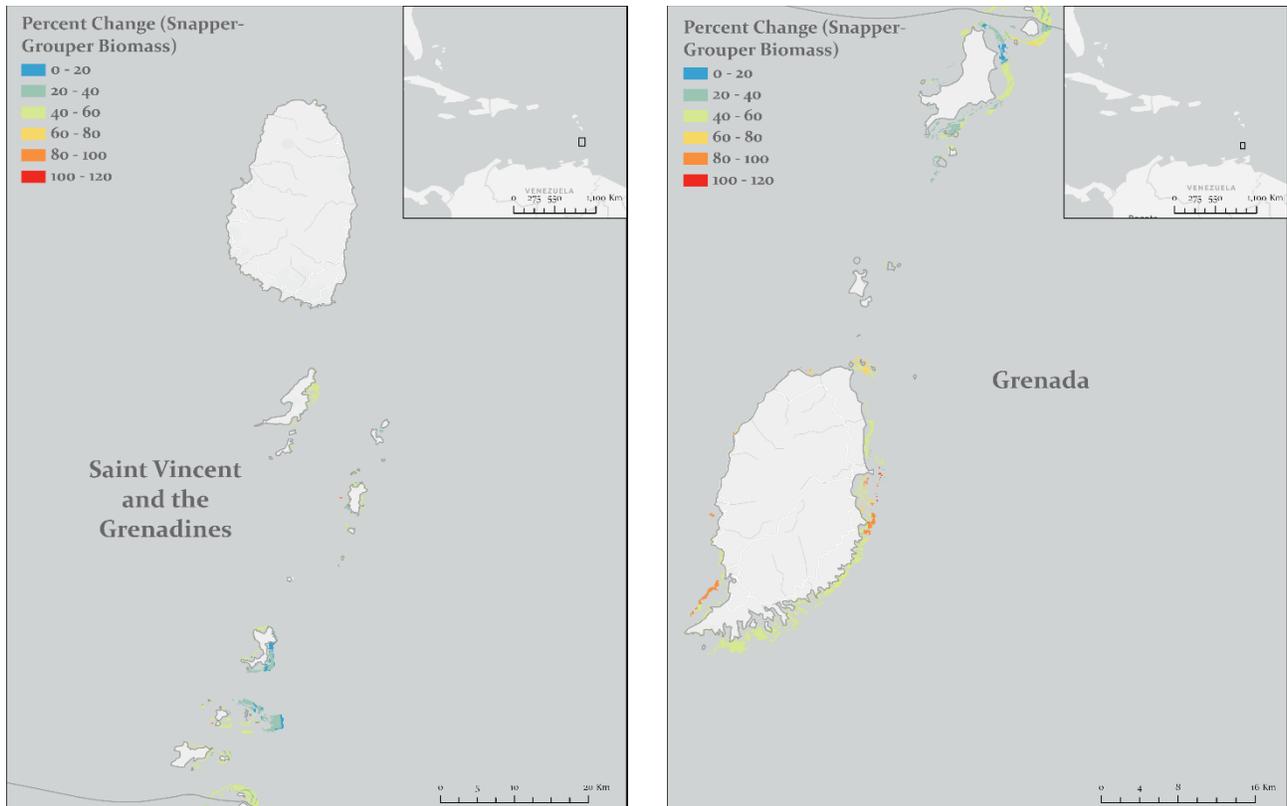
The project methodology builds a single functional relationship between fishing impact and fish biomass, which allows us to examine scenarios with lower fishing impact. Here we provide a map of potential snapper and grouper biomass after reducing fishing impact to 0 to simulate a marine no-take reserve (absolute increase and percentage increase, Maps 3 and 4 respectively). Such a map provides a useful resource in marine spatial planning by showing the likely benefits of excluding fishing from any area. For example, managers may want to target areas for protection that have the potential for significant gains in biomass and is acceptable to local stakeholders. Note that this potential increase in biomass is based on the carrying capacity of each reef under current biophysical conditions, and increases could be higher (or lower) if covariates such as coral cover or availability of nursery habitats change. For example, gains could be higher if reefs recover with increased coral cover or rugosity, or be lower if more coral is lost. Thus, protecting fish biomass by limiting fishing ideally needs to be part of a holistic approach that also addresses other factors including climate change and decreasing water quality to improve general reef health and maximize the effectiveness of no-take reserves.





Map 3. Spatial distribution of estimated potential biomass (g m⁻²) of snapper and grouper species after reducing fishing impact to zero across the Eastern Caribbean.

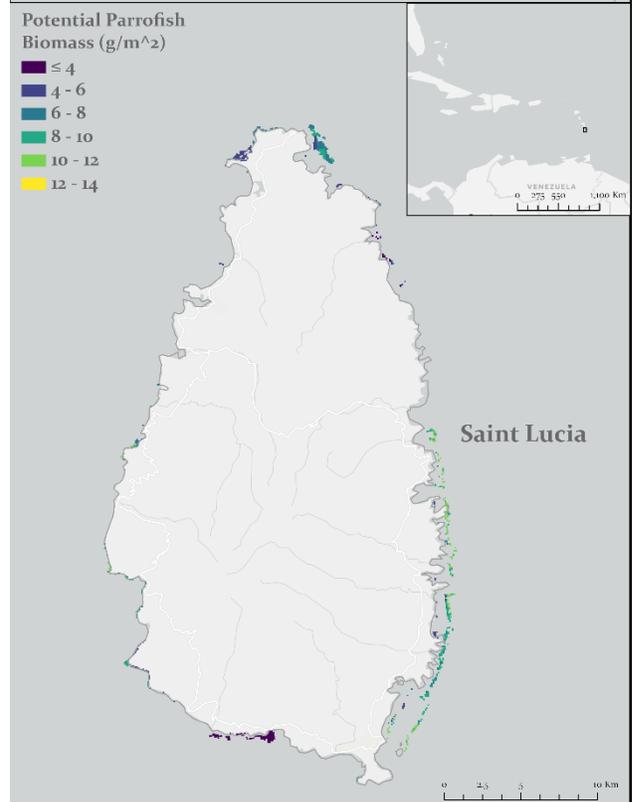
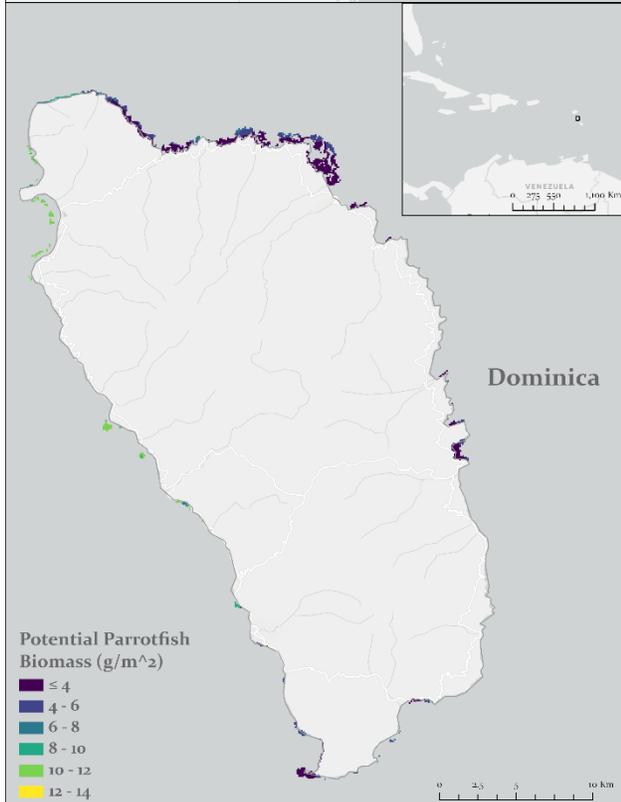
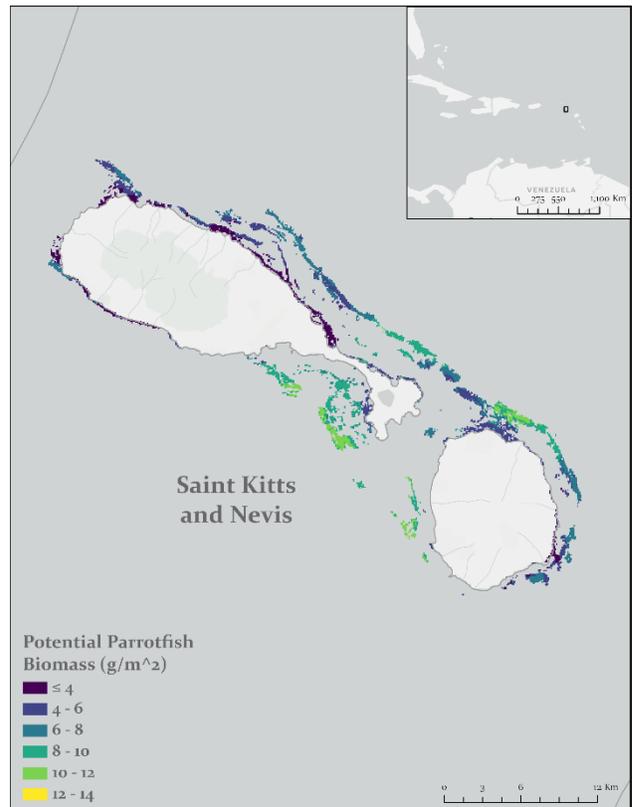
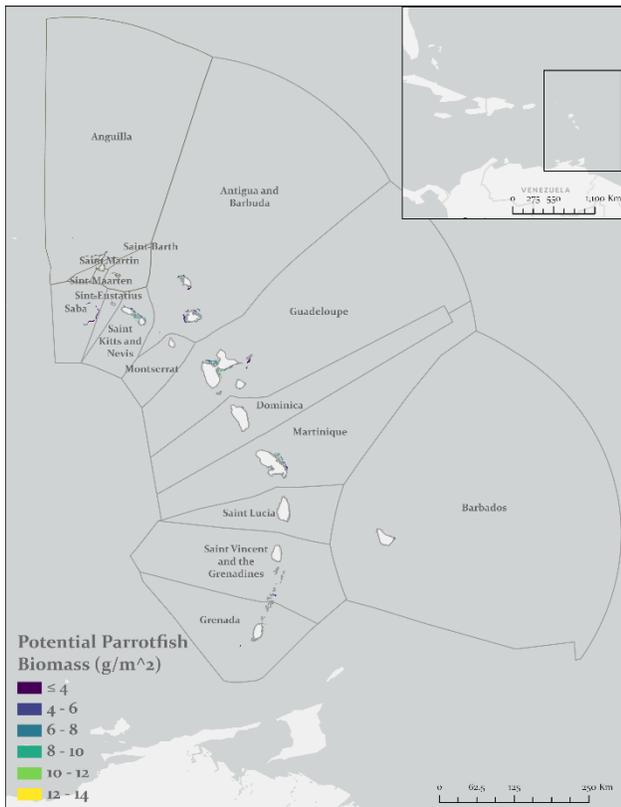


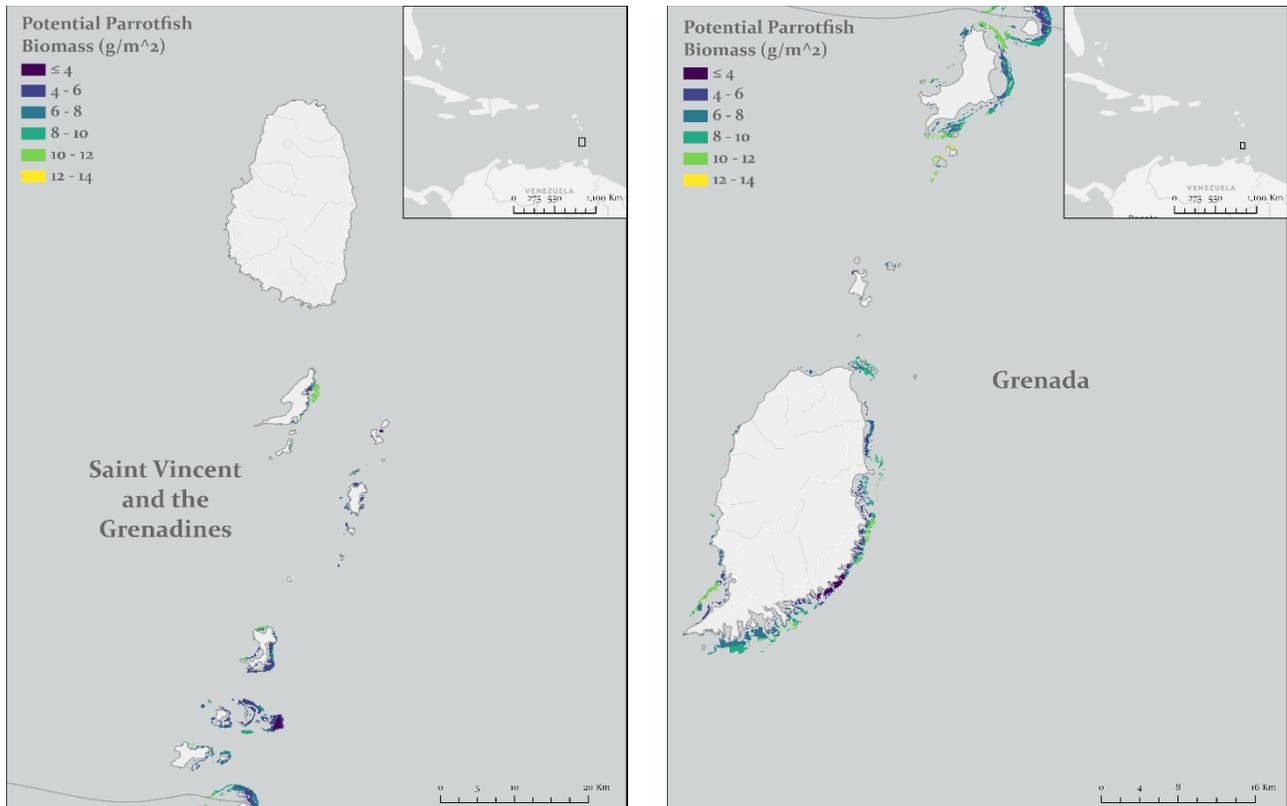


Map 4. Spatial distribution of estimated percent change for snapper and grouper species in the absence of fishing across the Eastern Caribbean.

3.6. Exploring potential benefits of management actions

While reducing fishing is typically the most interesting scenario for end-users, the models in this report can be used to simulate a range of other management scenarios. Such scenarios require a significant relationship between a driver that can be altered by some management action and fish biomass. Here we use the relationship between parrotfish biomass and coral cover to examine potential parrotfish biomass if coral cover increased by 25%, simulating a coral restoration activity (Map 5). Outplanting corals is becoming an increasingly popular management technique for reefs (Bayraktarov et al. 2019), and restoration can have significant impacts on fish assemblages (Seraphim et al. 2020).

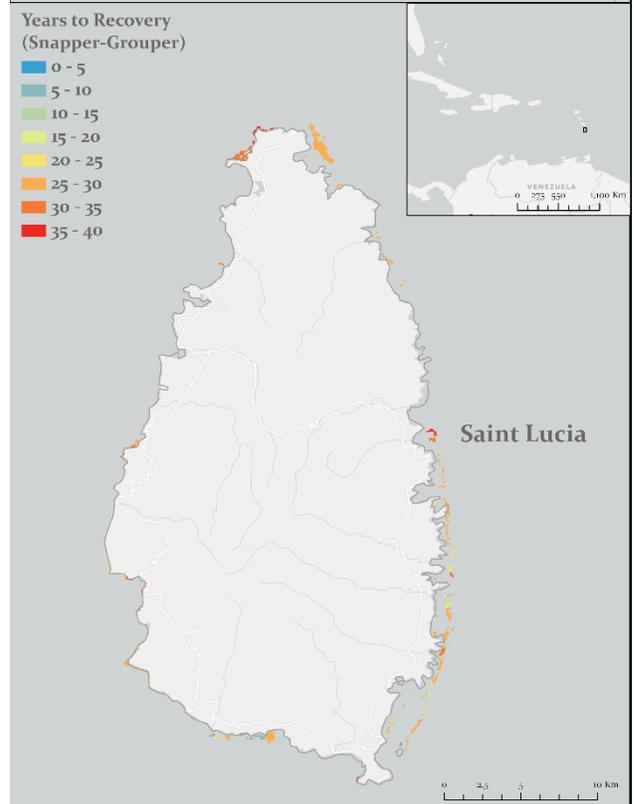
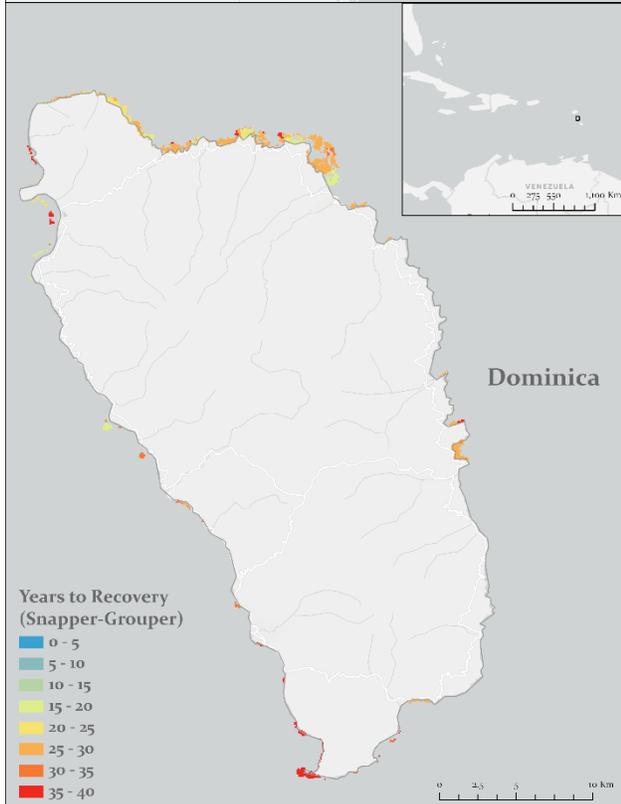
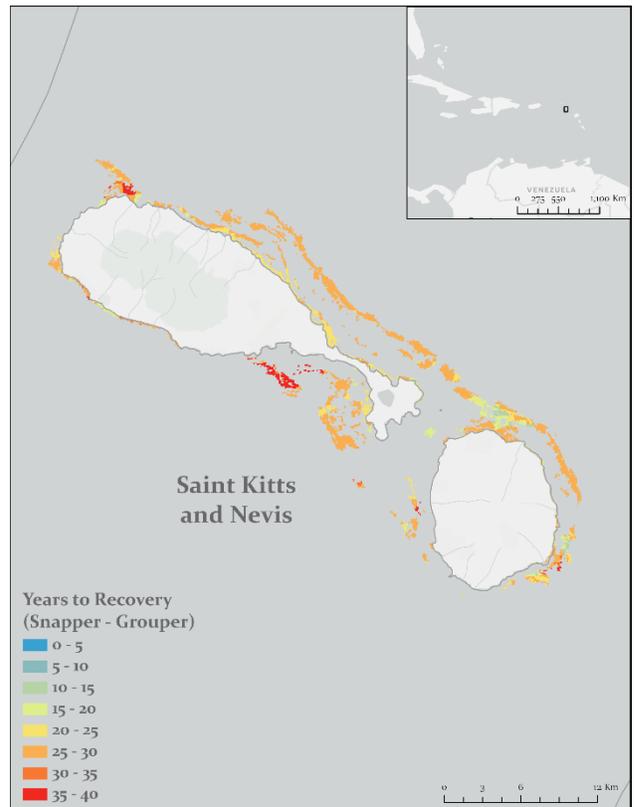
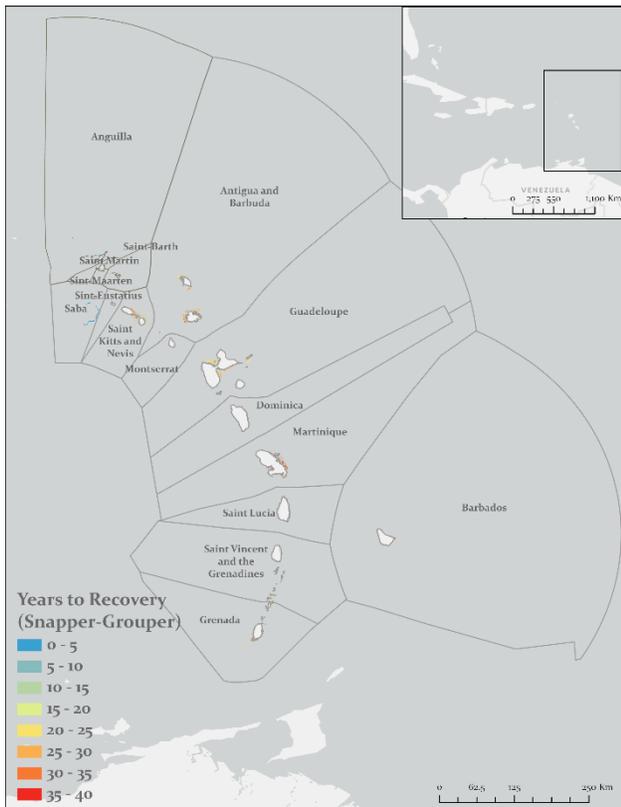


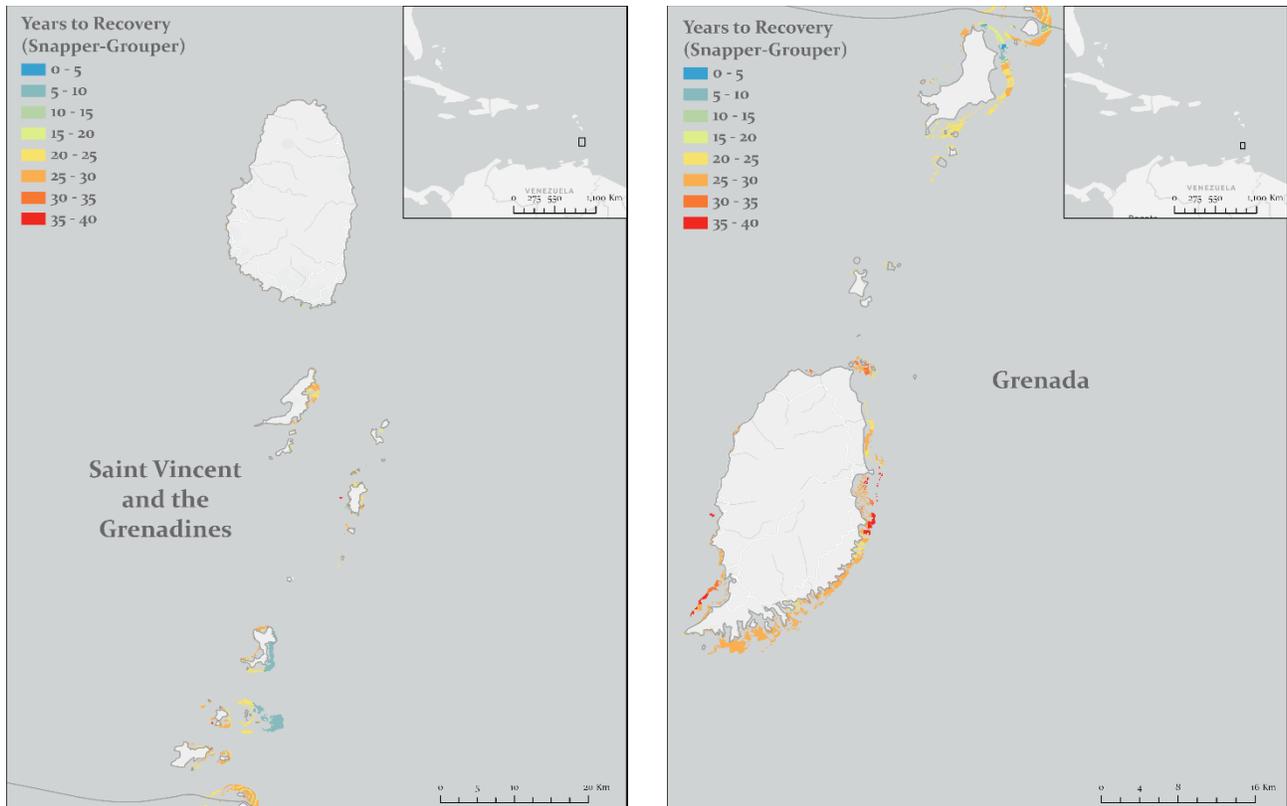


Map 5. Spatial distribution of estimated potential biomass (g m^{-2}) of parrotfish with national mean coral cover values increased by 25%.

3.7. Generating maps of fish assemblage time to recovery

The impacts of a no-take marine reserve or a habitat-based management intervention (e.g. reef restoration to increase coral cover) on fish biomass are not instantaneous and will lag behind the management intervention. While predicting the rate of fish biomass recovery is challenging, an approximate time to recovery can be estimated using the relationship generated by MacNeil et al. (2015) (Section 2.7). Although that relationship was developed for total biomass in the assemblage, here we apply it to the recovery of snapper and grouper after a cessation of fishing (Map 6). This product should be viewed with caution given the challenges of making these predictions and the complex life history of many snapper and groupers (e.g. mass spawning aggregations), but it does show estimated rates of recovery, and that some reefs may not reach carrying capacity for ~ 40 years. Such a result is comparable to the estimate of ~ 50 years for St Lucia (MacNeil et al. 2015), suggesting the approach is reasonable for snapper and grouper. Note that reefs with zero estimated fishing impact will also take 0 years to recover (first legend category in Map 6).





Map 6. Spatial distribution of the estimated time to recovery (90% of predicted potential biomass of snapper and grouper species, measured in years) following the cessation of fishing across the reefs of the Eastern Caribbean.

4. Participation in meetings

Rachel Zuercher participated in the St Lucia meeting to initiate the project in May 2019. The models and maps have been presented to project partners and in-country stakeholders through a virtual workshop on 11/11/2020. Participants felt the maps captured the major known patterns, but this workshop also generated useful feedback to help improve the models. There was also a follow-up meeting between FIU and TNC on 12/2/2020 and a final discussion of the results on 2/24/2021. There have also been a series of ad hoc meetings between FIU, TNC, and in-country partners to finalize aspects of the input data for the models. Unfortunately, Covid-19 has limited travel during 2020, meaning there have been no in-person workshops that could have potentially been useful for getting feedback on the models.

5. Data limitations and future work

Model building for this project was challenging because reef fish survey data for the region are limited. We were able to obtain data from 202 surveyed sites, which is relatively depauperate over such a large region (e.g. analogous work on the Florida reef tract had

access to >4000 surveys). While we feel that the models capture the main drivers of fish and fishing, there were wide confidence intervals for each model-estimated relationship. Support for additional reef fish census work and benthic monitoring in the region would be extremely useful to document the status of these reefs and improve the models presented here.

Another challenge was characterizing habitats and habitat attributes for the models. For example, some of the fish survey sites did not have accurate coordinates, which limited our ability to match them to habitat types on the underlying maps. While it is well established that reef complexity is important for predicting fish biomass, this metric was poorly quantified for many survey sites in this region. Consequently, we are unlikely to have captured all the variation that is occurring across habitat types (e.g. between spur and groove reef and low-relief back reef areas). Thus, while the products shown in this report were not previously available and result from many scientists and groups sharing their data, it would be prudent to use our maps in combination with other information (e.g. fishery-dependent surveys or community-generated maps) where possible.

6. 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 the CROP region. These maps provide a visually appealing overview of the current state of fishes and fishing that can be used in a range of education and outreach exercises and as a baseline for future comparisons. Furthermore, 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. Many spatial planning exercises are limited by data availability (Pittman and Brown 2011), and spatial data are rarely available on fishing and fish stocks during the planning process despite being critical inputs: these maps fill that data gap for the Lesser Antilles. Thus the maps could be used to identify priority sites for new marine reserves or other management measures aiming to increase fish biomass. Despite data-associated caveats, 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. The maps could also be used to provide some information when considering other types of fishery regulations, such as bag limits, species-specific fishing bans, or minimum catch sizes. However, as 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, this work provides the future opportunity to run additional scenarios for management techniques that might affect any significant variable in our models. And if the cost of each management action was known, the models could provide information regarding return on investments for each action. The maps and scenarios could also be

combined with data and maps from other CROP components (e.g. maps of reef-associated tourism) to generate novel insights into interactions among uses of coral reefs for consideration in upcoming marine spatial planning development.

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

Common Name	Scientific Name	Family	
		Common Family	Latin Family
Doctorfish	<i>Acanthurus chirurgus</i>	Surgeonfishes	Acanthuridae
Blue Tang	<i>Acanthurus coeruleus</i>	Surgeonfishes	Acanthuridae
Ocean Surgeonfish	<i>Acanthurus tractus</i>	Surgeonfishes	Acanthuridae
Queen Triggerfish	<i>Balistes vetula</i>	Triggerfishes	Balistidae
Ocean Triggerfish	<i>Canthidermis sufflamen</i>	Triggerfishes	Balistidae
Black Durgon	<i>Melichthys niger</i>	Triggerfishes	Balistidae
Sargassum Triggerfish	<i>Xanthichthys ringens</i>	Triggerfishes	Balistidae
Bar Jack	<i>Caranx ruber</i>	Jacks	Carangidae
Permit	<i>Trachinotus falcatus</i>	Jacks	Carangidae
Foureye Butterflyfish	<i>Chaetodon capistratus</i>	Butterflyfishes	Chaetodontidae
Spotfin Butterflyfish	<i>Chaetodon ocellatus</i>	Butterflyfishes	Chaetodontidae
Reef Butterflyfish	<i>Chaetodon sedentarius</i>	Butterflyfishes	Chaetodontidae
Banded Butterflyfish	<i>Chaetodon striatus</i>	Butterflyfishes	Chaetodontidae
Longsnout Butterflyfish	<i>Prognathodes aculeatus</i>	Butterflyfishes	Chaetodontidae
Balloonfish	<i>Diodon holocanthus</i>	Porcupinefishes	Diodontidae
Porcupinefish	<i>Diodon hystrix</i>	Porcupinefishes	Diodontidae
Graysby	<i>Cephalopholis cruentata</i>	Sea Basses and Groupers	Serranidae
Coney	<i>Cephalopholis fulva</i>	Sea Basses and Groupers	Serranidae
Rock Hind	<i>Epinephelus adscensionis</i>	Sea Basses and Groupers	Serranidae
Red Hind	<i>Epinephelus guttatus</i>	Sea Basses and Groupers	Serranidae
Goliath Grouper	<i>Epinephelus itajara</i>	Sea Basses and Groupers	Serranidae
Red Grouper	<i>Epinephelus morio</i>	Sea Basses and Groupers	Serranidae
Nassau Grouper	<i>Epinephelus striatus</i>	Sea Basses and Groupers	Serranidae
Comb Grouper	<i>Mycteroperca acutirostris</i>	Sea Basses and Groupers	Serranidae
Black Grouper	<i>Mycteroperca bonaci</i>	Sea Basses and Groupers	Serranidae
Yellowmouth Grouper	<i>Mycteroperca interstitialis</i>	Sea Basses and Groupers	Serranidae
Gag	<i>Mycteroperca microlepis</i>	Sea Basses and Groupers	Serranidae
Scamp	<i>Mycteroperca phenax</i>	Sea Basses and Groupers	Serranidae

Tiger Grouper	<i>Mycteroperca tigris</i>	Sea Basses and Groupers	Serranidae
Yellowfin Grouper	<i>Mycteroperca venenosa</i>	Sea Basses and Groupers	Serranidae
Black Margate	<i>Anisotremus surinamensis</i>	Grunts	Haemulidae
Porkfish	<i>Anisotremus virginicus</i>	Grunts	Haemulidae
Juvenile Grunt	<i>Haemulon / Anisotremus</i>	Grunts	Haemulidae
White Margate	<i>Haemulon album</i>	Grunts	Haemulidae
Tomtate	<i>Haemulon aurolineatum</i>	Grunts	Haemulidae
Caesar Grunt	<i>Haemulon carbonarium</i>	Grunts	Haemulidae
Smallmouth Grunt	<i>Haemulon chrysargyreum</i>	Grunts	Haemulidae
French Grunt	<i>Haemulon flavolineatum</i>	Grunts	Haemulidae
Spanish Grunt	<i>Haemulon macrostomum</i>	Grunts	Haemulidae
Cottonwick	<i>Haemulon melanurum</i>	Grunts	Haemulidae
Sailors Choice	<i>Haemulon parra</i>	Grunts	Haemulidae
White Grunt	<i>Haemulon plumierii</i>	Grunts	Haemulidae
Bluestriped Grunt	<i>Haemulon sciurus</i>	Grunts	Haemulidae
Latin Grunt	<i>Haemulon steindachneri</i>	Grunts	Haemulidae
Striped Grunt	<i>Haemulon striatum</i>	Grunts	Haemulidae
Chub	<i>Kyphosus spp.</i>	Sea Chubs	Kyphosidae
Spanish Hogfish	<i>Bodianus rufus</i>	Wrasses	Labridae
Slippery Dick	<i>Halichoeres bivittatus</i>	Wrasses	Labridae
Yellowhead Wrasse	<i>Halichoeres garnoti</i>	Wrasses	Labridae
Puddingwife	<i>Halichoeres radiatus</i>	Wrasses	Labridae
Hogfish	<i>Lachnolaimus maximus</i>	Wrasses	Labridae
Mutton Snapper	<i>Lutjanus analis</i>	Snappers	Lutjanidae
Schoolmaster	<i>Lutjanus apodus</i>	Snappers	Lutjanidae
Blackfin Snapper	<i>Lutjanus buccanella</i>	Snappers	Lutjanidae
Cubera Snapper	<i>Lutjanus cyanopterus</i>	Snappers	Lutjanidae
Gray Snapper	<i>Lutjanus griseus</i>	Snappers	Lutjanidae
Dog Snapper	<i>Lutjanus jocu</i>	Snappers	Lutjanidae
Mahogany Snapper	<i>Lutjanus mahogoni</i>	Snappers	Lutjanidae
Lane Snapper	<i>Lutjanus synagris</i>	Snappers	Lutjanidae
Yellowtail Snapper	<i>Ocyurus chrysurus</i>	Snappers	Lutjanidae
Scrawled Filefish	<i>Aluterus scriptus</i>	Filefishes	Monacanthidae
Whitespotted Filefish	<i>Cantherhines macrocerus</i>	Filefishes	Monacanthidae
Orangespotted Filefish	<i>Cantherhines pullus</i>	Filefishes	Monacanthidae
Slender Filefish	<i>Monacanthus tuckeri</i>	Filefishes	Monacanthidae
Green Moray	<i>Gymnothorax funebris</i>	Morays	Muraenidae
Goldentail Moray	<i>Gymnothorax miliaris</i>	Morays	Muraenidae

Spotted Moray	<i>Gymnothorax moringa</i>	Morays	Muraenidae
Spotted Trunkfish	<i>Lactophrys bicaudalis</i>	Boxfishes	Ostraciidae
Cherubfish	<i>Centropyge argi</i>	Angelfishes	Pomacanthidae
Blue Angelfish	<i>Holacanthus bermudensis</i>	Angelfishes	Pomacanthidae
Queen Angelfish	<i>Holacanthus ciliaris</i>	Angelfishes	Pomacanthidae
Rock Beauty	<i>Holacanthus tricolor</i>	Angelfishes	Pomacanthidae
Gray Angelfish	<i>Pomacanthus arcuatus</i>	Angelfishes	Pomacanthidae
French Angelfish	<i>Pomacanthus paru</i>	Angelfishes	Pomacanthidae
Yellowtail Damselfish	<i>Microspathodon chrysurus</i>	Damselfishes	Pomacentridae
Threespot Damselfish	<i>Stegastes planifrons</i>	Damselfishes	Pomacentridae
Bluelip Parrotfish	<i>Cryptotomus roseus</i>	Parrotfishes	Scaridae
Juvenile Parrotfish	<i>Scarus / Sparisoma</i>	Parrotfishes	Scaridae
Midnight Parrotfish	<i>Scarus coelestinus</i>	Parrotfishes	Scaridae
Blue Parrotfish	<i>Scarus coeruleus</i>	Parrotfishes	Scaridae
Rainbow Parrotfish	<i>Scarus guacamaia</i>	Parrotfishes	Scaridae
Striped Parrotfish	<i>Scarus iseri</i>	Parrotfishes	Scaridae
Princess Parrotfish	<i>Scarus taeniopterus</i>	Parrotfishes	Scaridae
Queen Parrotfish	<i>Scarus vetula</i>	Parrotfishes	Scaridae
Greenblotch Parrotfish	<i>Sparisoma atomarium</i>	Parrotfishes	Scaridae
Redband Parrotfish	<i>Sparisoma aurofrenatum</i>	Parrotfishes	Scaridae
Redtail Parrotfish	<i>Sparisoma chrysopterus</i>	Parrotfishes	Scaridae
Bucktooth Parrotfish	<i>Sparisoma radians</i>	Parrotfishes	Scaridae
Yellowtail Parrotfish	<i>Sparisoma rubripinne</i>	Parrotfishes	Scaridae
Stoplight Parrotfish	<i>Sparisoma viride</i>	Parrotfishes	Scaridae
Lionfish	<i>Pterois volitans</i>	Scorpionfishes	Scorpaenidae
Jolthead Porgy	<i>Calamus bajonado</i>	Porgies	Sparidae
Saucereye Porgy	<i>Calamus calamus</i>	Porgies	Sparidae
Sheepshead Porgy	<i>Calamus penna</i>	Porgies	Sparidae
Pluma Porgy	<i>Calamus pennatula</i>	Porgies	Sparidae
Great Barracuda	<i>Sphyraena barracuda</i>	Barracudas	Sphyraenidae
Bandtail Puffer	<i>Sphoeroides spengleri</i>	Pufferfishes	Tetraodontidae
Surgeonfishes	<i>Acanthuridae</i>	Surgeonfishes	Acanthuridae
Triggerfishes	<i>Balistidae</i>	Triggerfishes	Balistidae
Jacks	<i>Carangidae</i>	Jacks	Carangidae
Butterflyfishes	<i>Chaetodontidae</i>	Butterflyfishes	Chaetodontidae
Porcupinefishes	<i>Diodontidae</i>	Porcupinefishes	Diodontidae
Groupers	<i>Serranidae</i>	Sea Basses and Groupers	Serranidae
Grunts	<i>Haemulidae</i>	Grunts	Haemulidae

Wrasses	<i>Labridae</i>	Wrasses	Labridae
Snappers	<i>Lutjanidae</i>	Snappers	Lutjanidae
Filefishes	<i>Monacanthidae</i>	Filefishes	Monacanthidae
Morays	<i>Muraenidae</i>	Morays	Muraenidae
Boxfishes	<i>Ostraciidae</i>	Boxfishes	Ostraciidae
Angelfishes	<i>Pomacanthidae</i>	Angelfishes	Pomacanthidae
Damselfishes	<i>Pomacentridae</i>	Damselfishes	Pomacentridae
Parrotfishes	<i>Scaridae</i>	Parrotfishes	Scaridae
Scorpionfishes	<i>Scorpaenidae</i>	Scorpionfishes	Scorpaenidae
Porgies	<i>Sparidae</i>	Porgies	Sparidae
Barracudas	<i>Sphyraenidae</i>	Barracudas	Sphyraenidae
Pufferfishes	<i>Tetraodontidae</i>	Pufferfishes	Tetraodontidae

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. 2020). Therefore, the available area of coral reef and/or hardbottom habitat close to each reef cell was measured using the coral reef habitat raster derived from the Dove satellite habitat layer. We calculated this variable at the 20 km and 200 km scale, but due to inter-variable correlations, the 200 km scale variable was not used in the model. The 20 km scale represents the approximate high end of larval dispersal estimates for most coral reef fishes (Yeager et al. 2017).

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 Eastern Caribbean coral reefs were derived from TNC's Dove satellite habitat layer (seagrass) and their 'car_mar_mangrovemosaic_2013' layer (mangrove). 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 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). 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:

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

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 available fish surveys. However, coral cover cannot be reliably modelled continuously across the entire reef tract.

Demography

Socio-economic attributes and dynamics of an island can affect many aspects of fishing activity and outcomes. While a decrease in fishing in areas with higher levels of socio-economic development has been reported in the literature (Brewer et al. 2012), recent research points to complex links among social and economic attributes and fishing activity. Characterizing the socio-economic development and dynamics of an island is beyond the scope of this project, however, we included a range of demographic information in the model of fishing impact to attempt to capture broad variation across the region. Demographic data was compiled at the national level, derived from a variety of online sources, most notably the World Bank Socio-economic Indicators⁴ (Table A1).

Rather than use each variable separately, they were combined into a composite index using principal components analysis (PCA, Fig. A1). This analysis separated the jurisdictions with, for example, Anguilla and Sint Maarten, for example, having a higher life expectancy, per capita GDP, and proportion of their population living in urban areas (positive scores on PC1). The first axis was used as a metric of socio-economic development for fish surveys and reef pixels.

Table A1. National-scale, raw demographic data used in the project.

Country	Pop. density (ppl/km ² land)	Median age (yrs)	Pop. growth rate (%)	Birth rate (per 1000 ppl)	Death rate (per 1000 ppl)	Urban pop. (%)	Life expectancy (yrs)	GDP (PPP, million ECD)	GDP growth rate (%)	GDP per capita (ECD)	Unemployment rate (%)
Anguilla	192	35.1	1.92	12.4	4.7	100	81.6	175.4	-8.5	12200	8
Antigua and Barbuda	208	32.2	1.2	15.6	5.8	24.5	76.9	2398	2.8	26400	11
Barbados	662	38.9	0.26	11.6	8.6	31.2	75.7	5218	-0.2	18600	10.1
Dominica	97	34	0.17	15	7.9	70.8	77.4	783	-4.7	11000	23
Grenada	304	32.1	0.42	15.2	8.2	36.4	74.8	1634	5.1	15100	24
Montserrat	53	33.8	0.43	10.5	6.2	9.1	74.8	167.4	7.4	34000	5.6
St. Kitts and Nevis	200	35.5	0.7	13	7.2	30.8	76.2	1550	2.1	28200	4.5
St. Lucia	266	35.5	0.31	13.1	7.8	18.8	78.1	2542	3	14400	21
St. Maarten	1154	41.2	1.39	13.1	5.4	100	78.5	368.8	3.6	66800	9.9
St. Vincent and the Grenadines	250	34.2	-0.23	13	7.4	52.6	75.8	1265	0.7	11500	18.8

⁴ <https://data.worldbank.org/indicator>

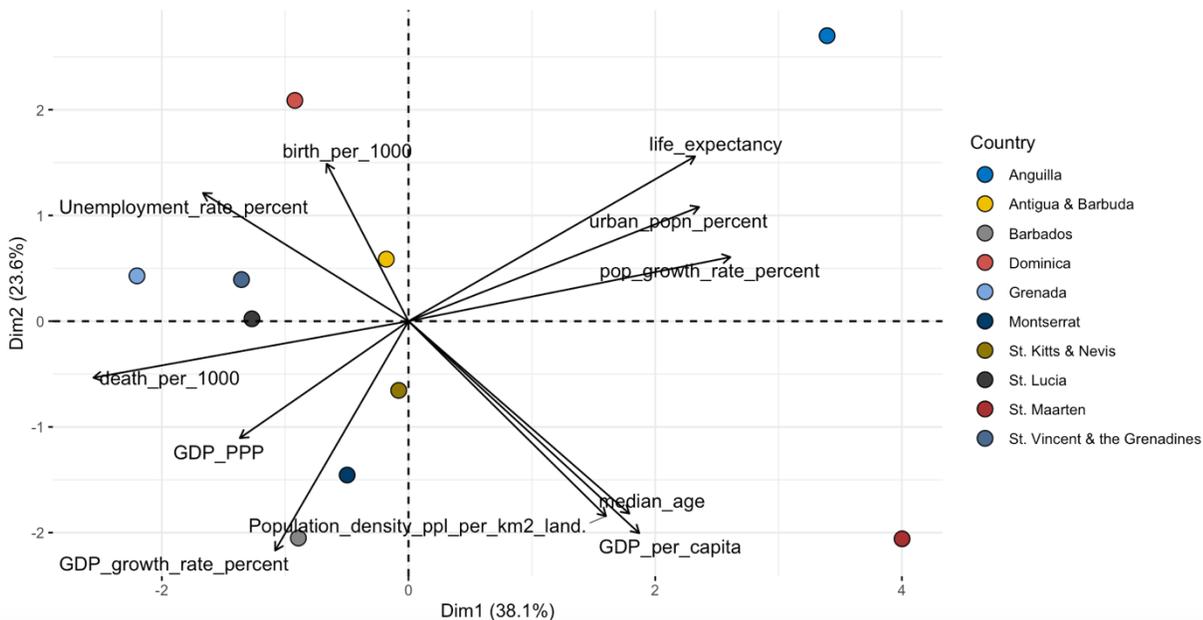


Figure A1. Position of each jurisdiction on the first two axes (PC1 and PC2) of a principal components analysis of demographic data.

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 *in situ* during most of the fish surveys and these values were used in the models. Depth was estimated for surveys where it was not recorded using a distance-from-shore regression. The regression ($Depth = 8.82680 + Distance * 0.00112$) was developed using fish survey sites across the region with *in situ* depth readings. To extrapolate these results to the entire reef tract we used a global depth data layer published by the General Bathymetric Chart of the Oceans (gebco.net). While the resolution of the bathymetry layer is sufficient for nearshore areas with a wide shelf, the GEBCO bathymetry does not perform well for areas in the region with steep, nearshore drop-offs. This led to shallow nearshore reef pixels estimated at depths of greater than 100 m. To improve the depth estimates for these reef pixels, any pixel assigned a GEBCO depth deeper than the maximum depth of a fish survey (23.9 m) was reassigned to 23.9 m. Similarly, any reef pixel that intersected with land in the GEBCO layer (i.e. was assigned an elevation value) was assigned the minimum depth recorded in fish surveys (2.3 m).

Diadema density

The inverse relationship between *Diadema* abundance and the abundance of predatory fishes on Caribbean reefs has been well documented following the mass mortality event in the 1980s (Hay 1984, Hughes 1994). However, when present at functional densities, *Diadema* also change benthic assemblages by reducing macroalgae (Carpenter and

Edmunds 2006) and potentially impact fish populations. *Diadema* may also represent a proxy of reef complexity (Weil et al. 1984). *Diadema* density (individuals / m²) estimates (Fig. A2) were only available at an island scale and obtained from Siegel et al. (2019) which used data from the following sources: Jackson et al. 2014, Reef Check, Wynne 2010, Rémi et al. 2012, Meesters 2010, and PARETO 2012. *Diadema* estimates are as follows: Anguilla (0.065), Antigua and Barbuda (0.219), Barbados (0.004), Dominica (2.754), Grenada (0.030), Guadeloupe (1.520), Martinique (2.870), Montserrat (0.758), Saba (0.00), St. Barthélemy (0.00), St. Eustatius (0.001), St. Kitts and Nevis (0.007), St. Lucia (1.958), St. Maarten (0.004), St. Martin (0.742), St. Vincent and the Grenadines (0.442).

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).

Fish landing sites

Fish landing sites represent foci for fishers and thus fishing is expected to be higher close to these places where boats are moored and fish are delivered. Landing sites were identified for each of the five CROP countries by in-country experts. These sites were cross-referenced with information from the peer-reviewed literature and other sources (e.g. Ramdeen et al. 2014b, Gumbs et al. 2015, VanAnrooy et al. 2018, Harvey 2019, Pinnegar et al. 2019). Landing sites for non-CROP countries were identified using various reports and peer-reviewed articles (e.g. Staskiewicz et al. 2008, Guyader et al. 2013, Ramdeen et al. 2014a, de Graaf et al. 2017, Gumbs et al. 2015, Lindop et al. 2015). Using port and fish landing site location information, five spatial data layers were developed to capture the potential relationship between mean parrotfish length and/or reef fish biomass and ports/landing sites: distance to the nearest fish landing site, distance to the nearest major fish landing site, distance to the nearest major port, the number of fish landing sites within 5 km of a reef, and the number of fish landing sites within 20 km of a reef.

Geomorphology

Island geomorphology in the Lesser Antilles (whether they are steep volcanic islands with narrow shelves or limestone platforms) is an important factor influencing herbivorous fish assemblages and coral communities on surrounding reefs (Adey and Burke 1976, Hubbard 2010). For example, the presence of an extensive lagoonal area may provide critical nursery habitat for some reef fish species (Harborne et al. 2016). For this variable, we assessed the geomorphology of each country using Google Earth imagery and categorized reefs as fringing or fringing with lagoon.

Governance

Governance is the formal and informal institutions through which authority and power are conceived and exercised (Larson and Soto 2008), can have significant impacts on social-ecological interactions in marine ecosystems and direct impacts on the services that it provides (Bundy et al. 2016). Per Seigel et al. (2019), each island was assigned the average score of six Worldwide Governance Indicators (WGI): voice and accountability, political stability, government effectiveness, regulatory quality, rule of law, and control of corruption (Kaufman et al. 2010). WGI scores (2013) are as follows: Anguilla (1.37), Antigua and Barbuda (0.82), Barbados (1.15), Dominica (0.76), St. Eustatius (0.74), Grenada (0.39), St. Kitts and Nevis (0.86), St. Maarten (0.74), Martinique (0.77), Saba (0.74), St. Lucia (0.80), St. Vincent and the Grenadines (0.83).

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 (sum of the market gravity of every population center) published in Cinner et al. (2018) which followed Cinner et al. (2016) and calculated gravity as the number of people in the population center divided by the square of the distance between that center and the reef cell. We also developed data layers for the gravity of the nearest potential market where markets were defined as (1) capital cities; (2) population centers with greater than 1000 people; (3) population centers with greater than 2000 people; and (4) population center with greater than 5000 people. For these layers, we used online sources to estimate the population of cities, towns and villages in the Eastern Caribbean.

Habitat type

The models of both fishing impact and biomass contain a categorical variable for habitat type as described in the Planet Dove satellite 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). Only coral reef habitat types were included in the model, including: Reef Fore, Reef Crest, Reef Back, Reef Fringing and Spur and Groove. In addition, fish survey sites and reef pixels in the five CROP countries were assigned to a habitat type based on TNC 'CROP crosswalk habitat classes'. This categorical variable (included as NA / missing data for non-CROP countries) further characterized habitat differences across the study region known to influence aspects of the fish assemblage.

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 key variable in the model of fishing pressure on Eastern Caribbean coral reefs. Standardised, rasterized, global datasets of human populations are available from Oak Ridge National Laboratory's LandScan dataset. LandScan uses census information in addition 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 were available for a more recent year (2017). LandScan estimates population at a resolution of 30 arc-seconds (~1 km). We tested this variable in the model at several scales: the human population size within 20 km, 50 km and 100km of a reef pixel to capture various distances that fishing vessels might travel or other aspects of fishing activity impacted by population size (Clark et al. 2002, Gorospe et al. 2018). The 20 km distance likely also 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. 2015, Williams et al. 2015). Therefore, we divided the population size figure by the area of coral reef within the same distance, resulting in a metric of human population pressure per km².

Latitude and longitude

Biogeographic patterns of fish likely play a role in determining the composition of fish assemblages across the large Eastern Caribbean region, therefore latitude and longitude were included in initial models of both fishing impact and biomass to account for any variation in fish species and fishing effort across the region. Both latitude and longitude were highly correlated with other covariates in the model (e.g. net primary productivity), and so were excluded in final models.

Month and Season

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. The season (wet, dry) that a survey was undertaken was also included with June-November categorized as wet season and December – May as dry season.

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. 2015). 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). We generated a layer derived from 8-day composite net primary productivity estimates from 2003-2013 generated by NOAA CoastWatch (Behrenfeld and Falkowski 1997)⁵. 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

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 no-take 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 total biomass because the fishing impact metric is based on parrotfish size and no-take areas may have a different impact on the biomass of other fishes in the assemblage. No differentiation could be made about which managed areas were well enforced, but it is anticipated that enforcement varies across protected areas in the region.

Reef fisheries economy

The importance of fish protein as a food source both on and island and as revenue through export is likely to affect fishing pressure among countries. Proportion of GDP from reef fisheries (2010 USD) were compiled in Siegel et al. (2019) as follows: Anguilla (0.056), Antigua and Barbuda (0.006), Barbados (2.54×10^{-4}), Dominica (0.002), Grenada (0.002), Guadeloupe (1.47×10^{-4}), Martinique (0.001), Montserrat (0.001), Saba (0.044), St. Barthélemy (0.003), St. Eustatius (0.009), St. Kitts and Nevis (0.006), St. Lucia (0.001), St. Maarten (4.75×10^{-7}), St. Martin (0.007), St. Vincent and the Grenadines (0.007).

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). Data on rugosity or reef relief that was estimated *in situ* during a subset of available fish surveys, but these data were not collected in a standardized manner across all fish surveys used. As such, reef complexity measurements were binned as 'low', 'medium' or 'high' complexity relative to other sites in the project. However, rugosity cannot be modelled continuously across the entire region.

⁵ <http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdPPbfp28day.graph?productivity>

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)⁶, and used data from 2012-2016 at a 4 km resolution (Saha et al. 2018). Following Williams et al. (2015), we calculated the mean temperature from the coldest month of each year (i.e. the lower climatological mean) at each reef location. Interpolation using the IDW tool in ArcGIS Pro 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.

Small-scale fishing population

As for the proportion of GDP generated from fishing, the number of fishers per island will affect fishing pressure. The total number of small-scale fishers and the proportion of an island's population that works as small-scale fishers was obtained from Siegel et al. (2019); original data sources can be found in Table S8 of that article. Small-scale fishing population (and proportion of the total population) data are as follows: Anguilla 500 (0.0385), Antigua and Barbuda 1521 (0.0174), Barbados 2200 (0.0081), Dominica 1340 (0.0186), Grenada 1931 (0.0188), Guadeloupe 1200 (0.0030), Martinique 2500 (0.0063), Montserrat 101 (0.0202), Saba 50 (0.0325), St. Barthélemy 43 (0.0046), St. Martin 11 (0.0004), St. Eustatius 24 (0.0095), St. Maarten 50 (0.0014), St. Kitts and Nevis 1086 (0.0207), St. Lucia 2556 (0.0141), St. Vincent and the Grenadines 980 (0.0090).

Survey method

The project used data from fish surveys employing five distinct sets of methods. Due to potential variation in the performance of these different survey methods, we included it as a variable in the fishing impact and fish biomass models. Where data source was a significant variable, values of biomass were predicted across the continuous maps as if collected using AGRRA protocol as this was the most common survey in our full dataset.

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. 2014).

⁶ <https://www.nodc.noaa.gov/SatelliteData/cortad/>

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 Eastern Caribbean as part of a project to categorize the physical environments of the region (Chollett et al. 2012)⁷. This data layer was used to assign a surface wave exposure to each coral reef and hardbottom 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 dataset assembled for this project was not collected simultaneously; we use data from fish surveys undertaken from 2011 to 2019 (with the exception of Dominica surveys completed in 2005 and used only for estimates of parrotfish mean length). 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 2018 to provide currently expected values that are most useful for ongoing management planning.

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⁷ Data supplied by Iliana Chollett

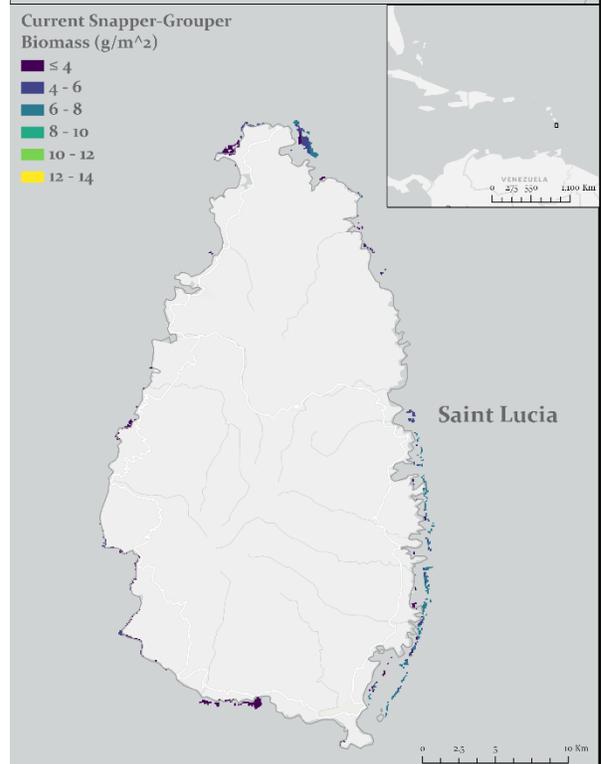
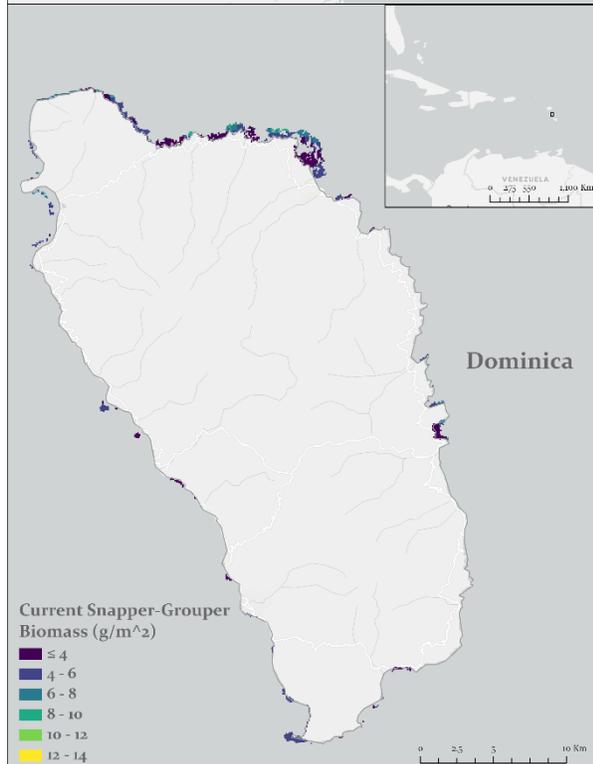
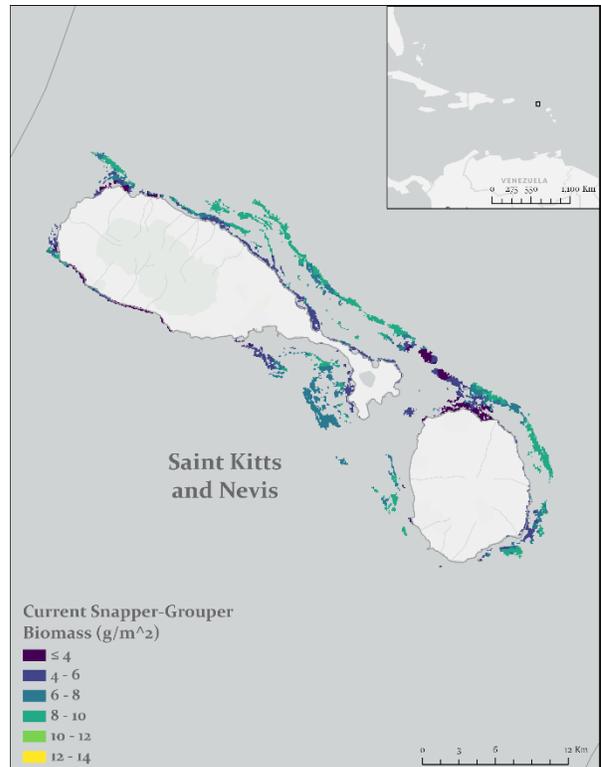
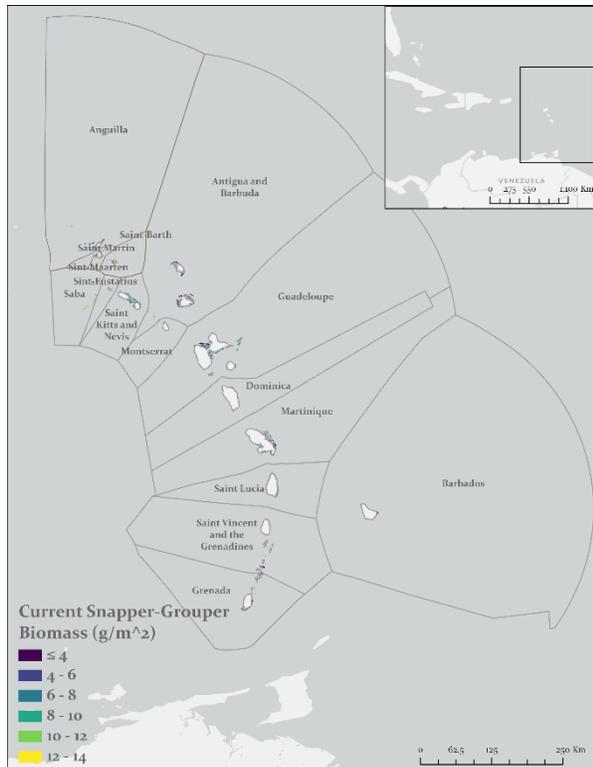
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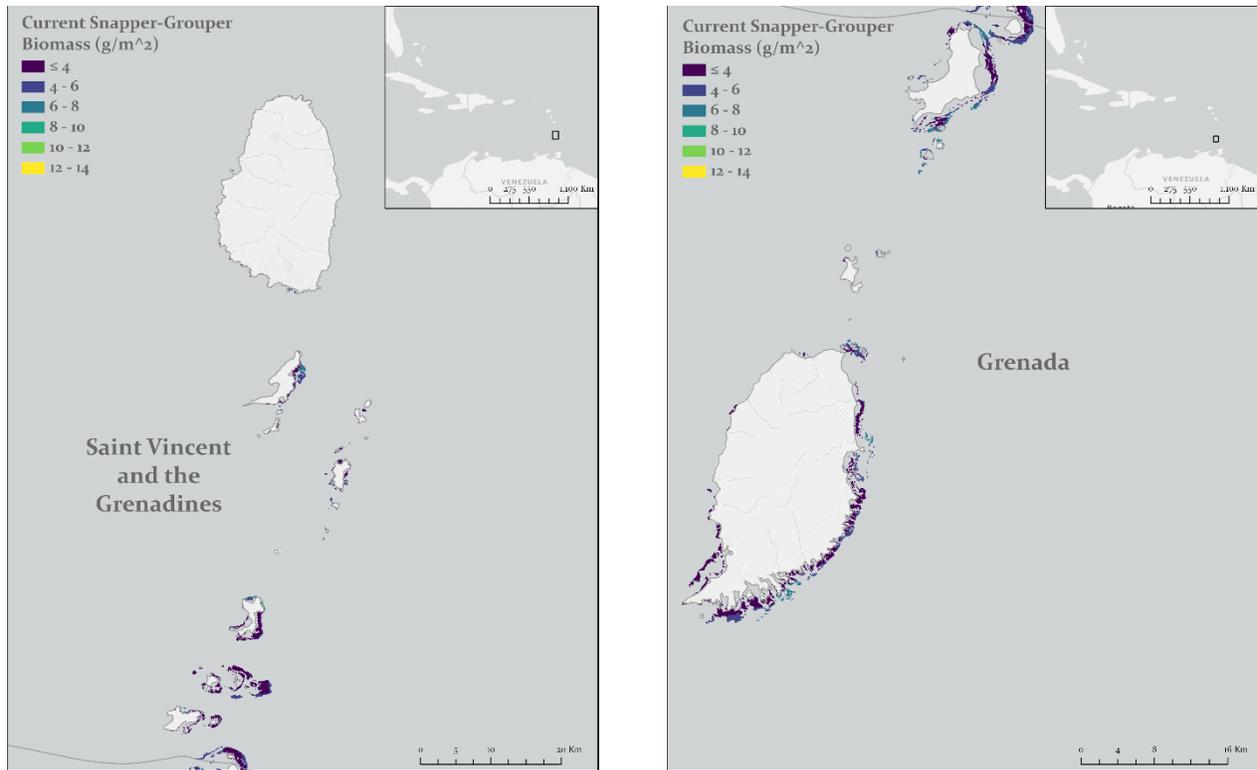
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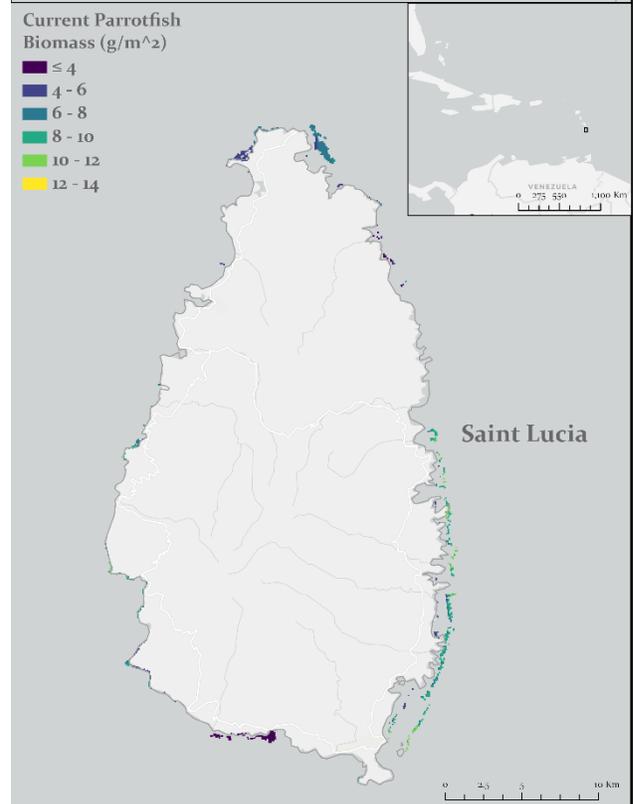
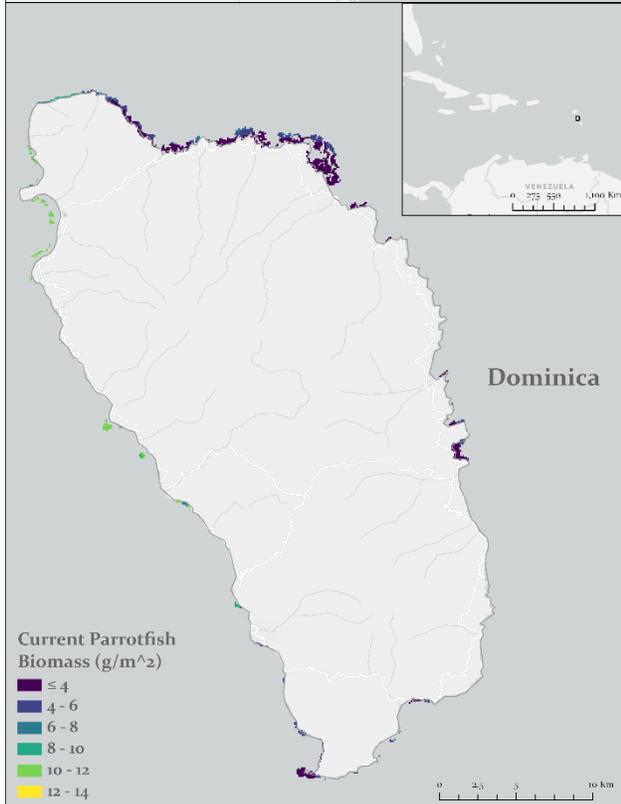
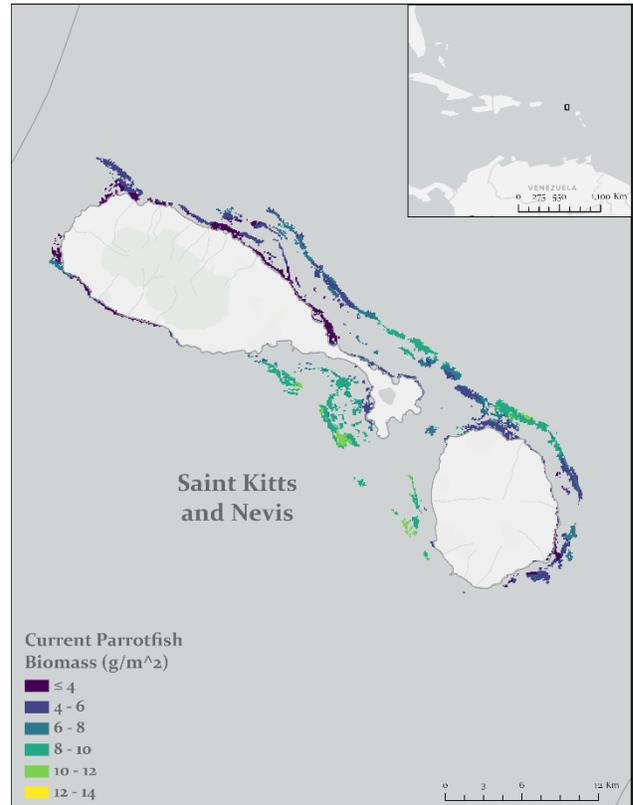
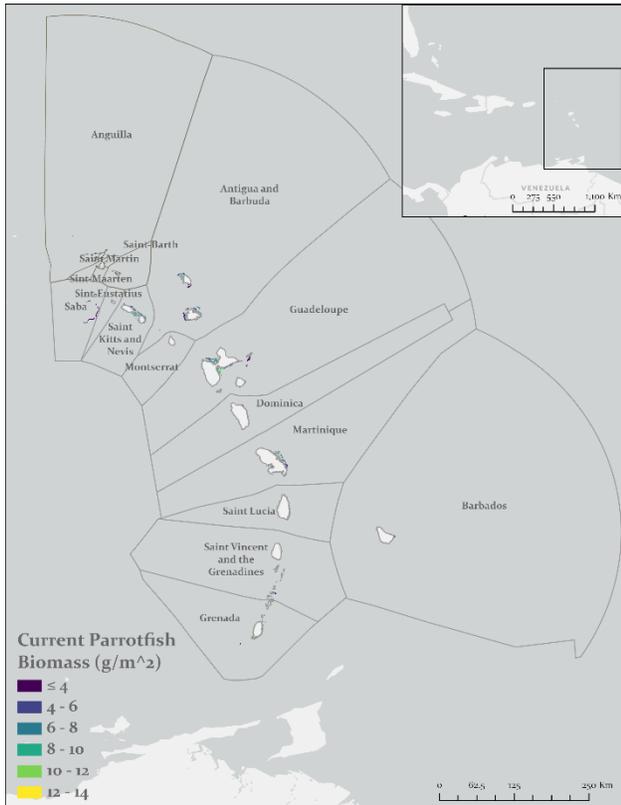
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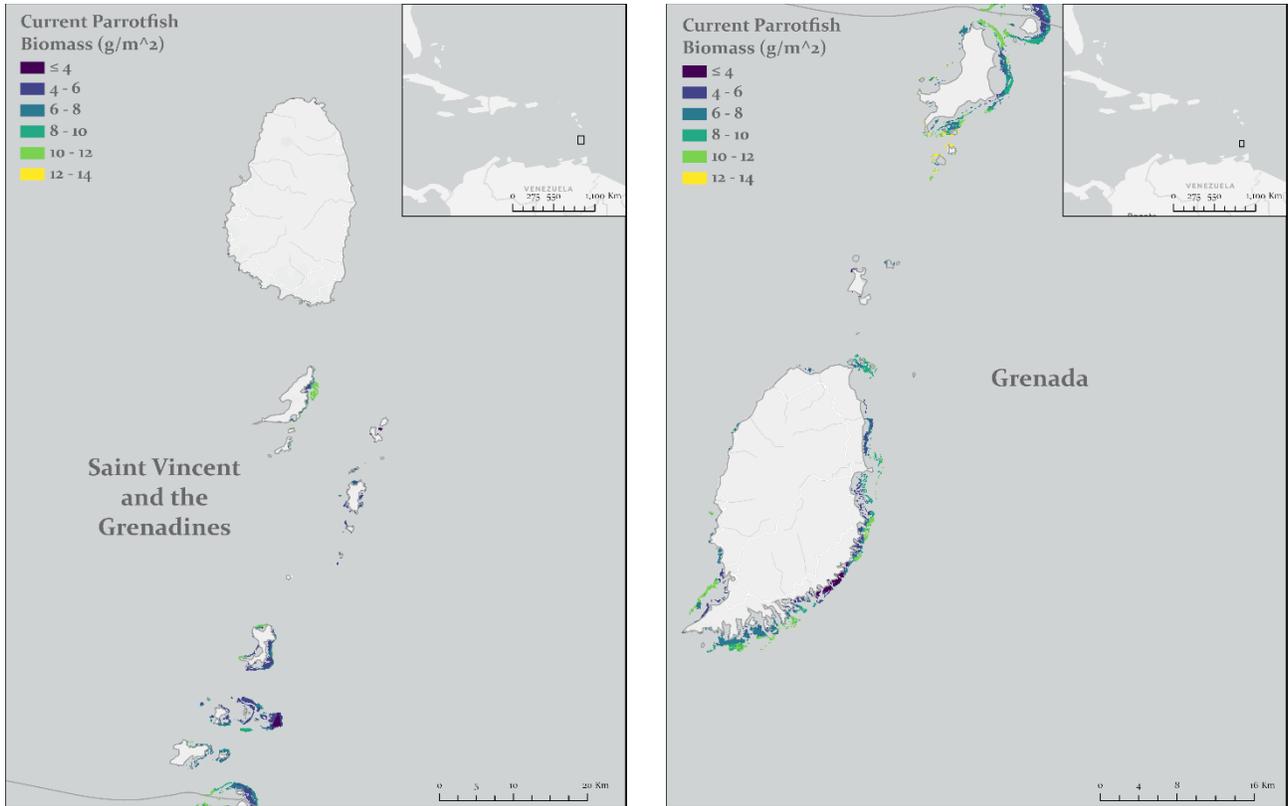
Appendix 3. Maps of current biomass of snapper and grouper species and parrotfishes





Map 7. Spatial distribution of estimated current biomass (g m⁻²) of snapper and grouper species in the Eastern Caribbean.





Map 8. Spatial distribution of estimated current biomass (g m^{-2}) of parrotfish in the Eastern Caribbean.