MODELLING AND MAPPING FISHING IMPACT AND THE CURRENT AND POTENTIAL STANDING STOCK OF CORAL-REEF FISHES IN THE BAHAMAS

SUPPORTING MARINE RESERVE DESIGN

Final technical report prepared by:

Alastair R. Harborne
Florida International University

Tropical Fish Ecology Lab, Department of Biological Sciences - Marine Sciences Program, Biscayne Bay Campus, 3000 NE 151 Street, North Miami, Florida 33181, USA

Tel: +1 (305) 919 4232
email: aharborn@fiu.edu

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Contents

Summary

To assist the process of extending The Bahamas National Protected Area System, The Nature Conservancy (TNC) contracted Alastair Harborne at Florida International University (FIU) to map coral-reef fisheries at a national scale. The key aims of this work were to model and map fishing impact, model and map the current fish standing stock, and assess the potential benefit of conservation and management measures, such as the potential standing stock on a reef following the cessation of fishing.

Through the generous provision of fish survey data from a range of sources, the project had access to 335 fish surveys from forereefs across the Bahamian archipelago. A major component of this data set used the Atlantic and Gulf Rapid Reef Assessment (AGRRA) survey protocol, which collects data only on ecologically and economically important fish species. Therefore, observations of other species were removed from the other data sets. The data set was then split, and fish data from 165 sites were to statistically model fishing impact. This fishery-independent data set was used to derive the biomass, at each site, of species considered important to fisheries by AGRRA. These biomass data were modelled in relation to 24 potential predictor variables, such as the distance and size of nearby fish markets (market gravity), oceanic temperature, and connectivity to seagrass and mangrove nursery habitats. These analyses demonstrated that biophysical gradients were important factors affecting the biomass of fishery species, particularly the depth, coral cover, and rugosity of the site, along with connectivity to nursery habitats, temperature regime, and distance to a spawning aggregation site. The human influence on fish populations, assumed to be through fishing, was best predicted by total market gravity and the gravity of the nearest market, with fish biomass generally decreasing as market gravity increased. Using the market gravity variables alone (i.e. ignoring biophysical influences), the model was then used to extrapolate relative fishing impact (specifically the total cumulative impact of fishing on the fish assemblage) to all forereef sites across the country, and generate a continuous map at a resolution of 4 ha reef cells.

Estimates of fishing impact were then used as a key data layer, along with 21 other potential environmental variables, to model the current standing stock of all the AGRRA species using the remaining 170 sites where additional survey fish data were available. The model demonstrated that standing stock decreased with increasing fishing impact, and was also affected by depth, coral cover and rugosity of the site, connectivity to nursery habitats, larval supply, and net primary productivity. As for fishing impact, this model was then used to extrapolate estimates of current standing stock across the country to generate a previously unavailable map of fish biomass. To extrapolate the results across the two major habitats found on Bahamian forereefs (*Orbicella*-dominated reefs and gorgonian plains) the project developed a statistical model of the distribution of each habitat type based on exposure and distance to deep water. This model allowed each forereef cell to be assigned to one of the two habitats, which was critical as key variables such as coral cover and rugosity vary significantly between these habitats and consequently *Orbicella* reefs have higher abundances of fishes.

Finally, the model of current standing stock was adjusted to represent a potential management scenario (fishing impact reduced to zero to simulate the establishment of a no-take reserve or other fisheries management tool) and allow the production of a map estimating patterns of potential standing stock across the region. Using the maps of predicted current and potential standing stock, the project generated maps of the expected absolute and percentage gain in biomass following the cessation of fishing in each 4 ha cell, the ratio of current to potential standing stocks, and the predicted time of recovery following the cessation of fishing.

The maps generated by this project represent the first spatially explicit, continuous maps of fishing impact and current and potential standing stock for The Bahamas. They provide baseline estimates of each metric, which can be further refined as additional data become available. However, they also provide important data layers for use in the imminent Marxan analysis to identify key locations for new marine reserves. While such an analysis must address multiple considerations, fishing impact and estimates of current and potential standing stock allow conservation planners to highlight potential reefs for protection if they represent low levels of conflict with fisherfolk (low fishing impact), a large potential for increased fish biomass following the cessation of fishing, or relatively intact fish assemblages that could be protected from any increases in fishing impact.

1. Introduction

1.1. Marine Reserve Planning in The Bahamas

Since 2008 The Bahamas has been a participant in The Caribbean Challenge Initiative (CCI) (Knowles et al. 2015). The goals of the CCI include identifying and facilitating the designation of protected areas, garnering strong political support to enforce declarations, and assembling a funding mechanism to ensure continual preservation of these critical spaces. The Bahamas is committed to effectively conserve and manage at least 20 percent of its marine and coastal environment by 2020. On August 31st, 2015, The Bahamas National Protected Area System (BNPAS) increased to more than 13 million acres when the Government declared 15 new and three expanded MPAs across a dozen islands within the Bahamas archipelago. With 10% of the country's nearshore marine environment now under protection, The Nature Conservancy (TNC), The Bahamas National Trust, Bahamas Reef Environmental Educational Foundation and other partners have begun the process of determining the next priority areas for inclusion into the system. A critical component of identifying new areas to add to the national protected area system is updating the Ecological Gap Analysis which will ultimately identify priority areas for protection based on the best available science.

With generous support from Oceans 5 several entities, including TNC, are working together to realize the 2020 Goal of 20% protection. In February 2016, a preliminary workshop was held to review the major goals and objectives of the "Realizing The 2020 Goal" project and review the draft work plan. Since February, scientists on the "Realizing The 2020 Goal" project have been gathering, generating and improving upon spatial information from various sources. The National Biodiversity Committee is also refining the BNPAS objectives, confirming the planning area and providing advice on the types of MPAs the network design process should focus on.

This report details work led by Alastair Harborne (Florida International University), under a contract from TNC, to model and map fishing impact, fish standing stocks, and potential standing stocks in the absence of fishing across The Bahamas. This project is analogous to work conducted by Alastair Harborne and TNC in Micronesia as part of the Mapping Ocean Wealth Project (Harborne 2016). It is anticipated that the data layers generated by the Bahamas project will be used to support the conservation planning process in the archipelago.

1.2. Project aims

The aims of the Bahamas mapping project were to create:
- A model and map of each of the following:
    - Fishing impact
    - Current standing stock
    - Potential standing stock
    - Potential benefits of expanded management
    - Likely recovery rates to reef carrying capacities
- Options for using these maps for reef conservation and management (e.g. marine spatial planning).

2. Methods and data used in the project

2.1. Methodological overview

The major products of the project, namely the models and maps of fishing impact and current and potential standing stocks throughout The Bahamas, utilised a range of data inputs and are interlinked (Fig. 1). 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 density) variables. Modelling fishing impact used data that were independent of the data used to model standing stock in order to ensure robust statistical models (i.e. the same data were not used to derive fishing impact and then fishing impact used to model standing stock in that data set). 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.
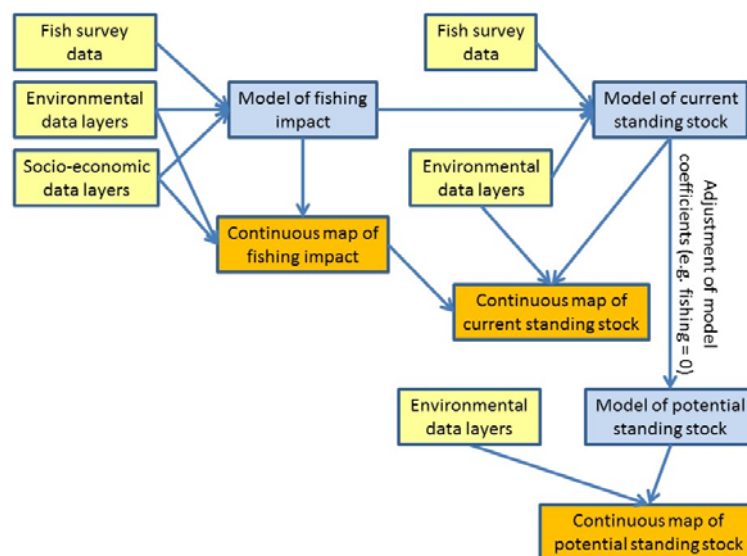
Fig. 1. Overview of the methodology for modelling and mapping the fishing impact and fish standing stocks in The Bahamas. Yellow boxes represent input data, blue boxes represent output models, and orange boxes represent output maps.

The predicted values of fishing impact were then a key input into the model of current standing stock. Predicted fishing impact was combined with environmental data (e.g. sea surface temperature) to model the biomass of the fish assemblage as recorded during fish surveys. As for fishing impact, the model was combined with the continuous data layers of fishing impact and environmental variables to extrapolate values of current standing stock throughout The Bahamas and derive a continuous map. Finally, the coefficients of the model of current standing stock can be adjusted to estimate potential standing stock under different conservation and management initiatives. This includes perhaps the most obvious conservation scenario, namely with fishing impact hypothetically reduced to zero, simulating the effects of a no-take reserve or other fisheries management tool. However, other approaches could

potentially be modelled, such as increasing coral cover, or the models could be used to simulate some of the potential effects of climate change (increasing sea surface temperatures). This adjusted model or models can then be combined with all significant environmental data layers to generate a continuous map of potential standing stock under different management scenarios. This report includes the results of adjusting the model to reflect the potential increases in fish biomass following the cessation of fishing (fishing impact set to 0).

2.2. Approach to modelling fishing impact

Researchers typically use fishery-dependent (e.g. catch data) or fishery-independent (e.g. underwater fish censuses) to assess fishing impact. While some catch data are available from The Bahamas, they lack the spatial resolution, widespread coverage, and species-level detail required for the models and maps produced by this project. Furthermore, there are widespread concerns about the reliability of many fisheries-dependent data sets, which often underestimate catches and may not even give reliable trends in catches (Pauly and Zeller 2014). Consequently, this project focused on using fishery-independent data derived from surveys of fish assemblages at sites in The Bahamas. Where survey data are available there are myriad 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 (Vallès and Oxenford 2014, Vallès et al. 2015), and mean length, trophic level and density of large fishes (Guillemot et al. 2014). This report provides models and maps of fishing impact based on the total biomass of fishes identified by the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program as having at least some commercial value to fisheries in the country (e.g. groupers and snappers). However, future analyses could also examine length-based metrics from the major fishery target species (Ault et al. 1998, Ault et al. 2005, Ault et al. 2008, Ault et al. 2014) or parrotfishes (Vallès and Oxenford 2014, Vallès et al. 2015).

Critically, the maps of fishing impact generated by the Phase 1 project represent relative, unitless patterns of estimated total exploitation <u>impact</u>, as opposed to absolute fishing rates as measured by metrics such as catch per unit effort. This distinction is important because the project highlights areas that have been heavily impacted by fishing (e.g. low biomass of groupers and snappers), rather than identifying areas that are currently being heavily fished. Highly impacted sites may also be currently heavily fished, but equally these sites may be lightly fished because catches are limited and fisherfolk have moved to more profitable locations. However, light fishing impact may be sufficient to limit any recovery of heavily impacted sites. Equally, some sites may currently be heavily fished, but have little evidence of fishing impact (e.g. large biomass of groupers and snappers) because the site has only recently been targeted by fisherfolk. Furthermore, the metric of fishing impact used in this report is scaled from 0-1 based on maximum and minimum values predicted within The Bahamas. 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). Consequently, it is important to recognise that references to high fishing impact are high <u>for The Bahamas</u>, but may be modest <u>when considering the Caribbean as a whole</u>.

2.3. Fish survey data sets

The derivation of the maps and models produced by the project was entirely parameterised using existing fish survey data. Thanks to the generosity of researchers, we have obtained data from numerous sites across The Bahamas to parameterise the fishing impact and current standing stock models (Table 1, Fig. 2). The data sets vary in geographical location, date of collection, survey technique, and taxonomic resolution (Table 1, Fig. 2). However, all the data are comparable (underwater visual censuses using defined belt transects) and were split to provide a wide geographical range of data for both the fishing impact and standing stock models.

Table 1. Summary of fish survey data sets available to the project.

| Source	Dates	Technique	Species	Number of sites	Fishing impact model	Standing stock model
AGRRA	2011-2016	UVC 30x2m belt transects, point intercept benthic transects	Target list of species within 5 or 10cm size classes.	151	80	71
BBP	2002-2011	UVC 30x2, 30x4 or 50x4m belt transects, benthic video quadrats	All non-cryptic species, to nearest cm.	85	29	56
Craig Dahlgren	2001-2015	UVC 30x2m belt transects, point intercept benthic transects	All non-cryptic species, to nearest cm.	99	56	43
Total				**335**	**165**	**170**

(a)

(b)
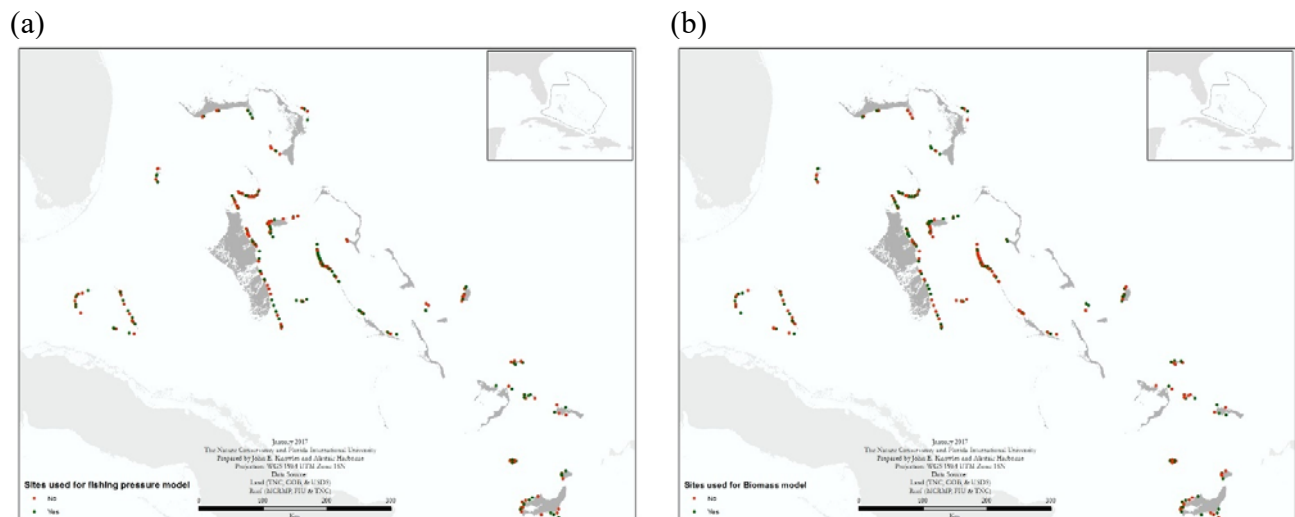
Fig 2. Location of survey sites to be used in the (a) fishing impact and (b) standing stock models.

Briefly, the AGRRA data[1] were collected to assess reef health across the region, and focuses on a sub-set of fish species that are particularly ecologically or economically important. Surveyors count these species along a series of belt transects and size them to the nearest 5 cm. At each site, benthic cover (e.g. cover of live coral) is measured using point intercept transects and rugosity is measured by repeated assessments of the maximum vertical relief of the substrate. The Bahamas Biocomplexity Project (BBP) data set was collected to examine various questions concerning patterns of biodiversity and the effectiveness of marine reserves in The Bahamas. Three surveyors collected the fish data along belt transects of varying size (30 x 2 m for small site-attached species like damselfish, 30 x 4 for larger reef-associated species such as parrotfish, and 50 x 4 for wider ranging predators such as snapper and grouper). Fishes were counted and sized to the nearest cm. At each site, replicate video quadrats were used to assess benthic cover, and within each quadrat rugosity was measured as the maximum vertical relief of the substrate. Data provided by Craig Dahlgren was collected using the AGRRA technique, but was extended to all fish species and benthic data were not always available. Where coral cover or rugosity data were not available, these sites were included in the models but with missing values.

All data were converted into standardised Microsoft Access databases to aid data analysis. To ensure consistency among data sets, the BBP and Dahlgren fish surveys were reduced to only those species recorded by AGRRA surveyors and fish length data were modified to the same 5 cm size classes as the AGRRA data. 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). Data for fishery species (fishing impact model) and all species recorded by AGRRA (standing stock model) were extracted for every site as g m^{-2}. A list of the fishery species, and all the species used in the standing stock model, are listed in Appendix 1, but in summary the fishery species include the groupers, snappers and grunts that are a major component of Caribbean fisheries (Ault et al. 1998), popular species for recreational species such as barracuda (O'Toole et al. 2011), and species such as parrotfishes that are either targeted by traps or are caught as by-catch (Rakitin and Kramer 1996).

2.4. Modelling current standing stock

In order to model standing stock consistently across The Bahamas, the project reduced all data sets to the species list used by AGRRA. This list is all species in the families of angelfish, butterflyfish, grunts, parrotfish, groupers, snappers, surgeonfish, triggerfish, morays, plus hogfish, puddingwife, slippery dick, spanish hogfish, yellowhead wrasse, orangespotted filefish, scrawled filefish, whitespotted filefish, balloonfish, porcupinefish, jolthead porgy, pluma porgy, saucereye porgy, sheepshead porgy, bandtail pufferfish, bar jack, chubs, great barracuda, permit, spotted trunkfish, threespot damselfish, yellowtail damselfish, and lionfish (Appendix 1). It is important to note that because of the use of a shortened list of species, the final models and maps of current standing stock produced by the project only predict standing stock of those species, not total standing stock. However, the species used represent a good proxy of total standing biomass and the resulting maps indicate predicted patterns of variability in total standing stock in The Bahamas.

2.5. Mapping Bahamian reefs

Establishing the extent of reef areas within The Bahamas was critical for the project, and the project used the maps generated by the Millennium Coral Reef Mapping (MCRM) Project (Fig. 3a). The

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[1] http://www.agrra.org/

MCRM Project utilised a global compilation of Landsat 7 ETM+ images to produce consistent map products to assist local, regional, and global research and management applications (Andréfouët et al. 2006). The MCRM project uses a thematically rich habitat classification scheme, and level 4 of this scheme was appropriate for differentiating habitats for the project. Firstly, habitats that would be included in the modelling and mapping work were identified. Only habitats that were well represented in the fish survey data sets could be reliably modelled, which were forereef slopes (Fig. 3b). The project models cannot be reliably extended into other habitats because of the potential for significant inter-habitat variations in how fish assemblages respond to fishing and environmental gradients. For example, since the data were predominantly from forereef slopes, the resulting models cannot be used to predict fishing impact or standing stock on reef crests or patch reefs.

The MCRM Project maps are vector coverages, with habitats represented by polygons of varying size. However, to accurately model the reefs of The Bahamas, the project required a raster (grid) coverage of identically sized cells. Rasterising 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 lagoonal 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 parameterised because of the limitations of the explanatory data sets. Experimentation indicated that 200 x 200 m (4 hectare) cells represented an appropriate grid size that retains habitat detail, but is computationally tractable (~300,000 cells). Consequently, all maps products from the project are at a 4 ha resolution.

Other habitats not considered by the project, such as lagoons or patch reefs, may have significant fish stocks and be heavily exploited by fisherfolk. Rather than being unimportant, their exclusion in this project is a function of a lack of data to parameterise the models adequately. However, the modelling and mapping techniques described in this report could be extended to other habitats, at national or sub-national scales if additional data were available.
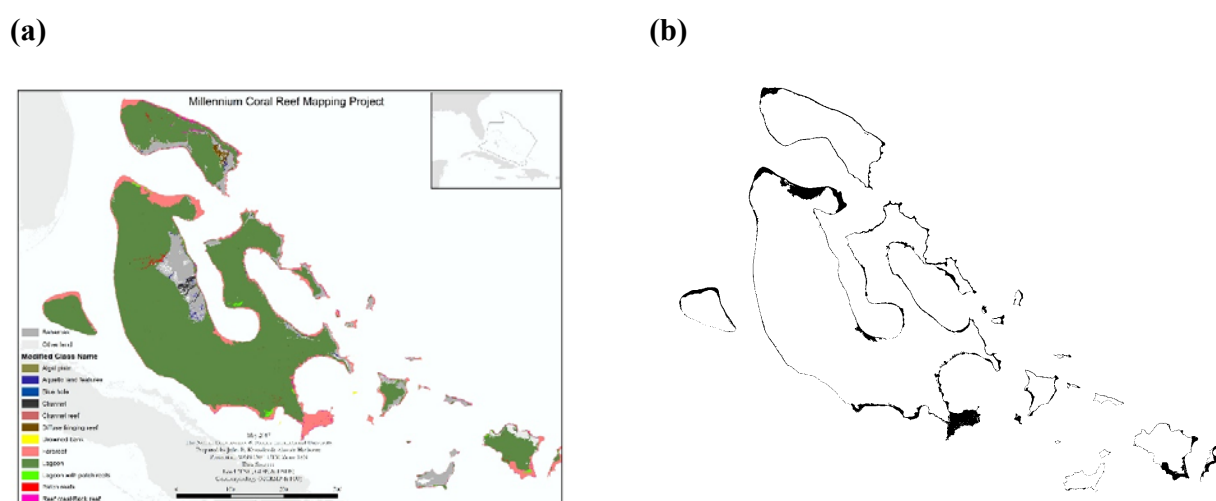
(a)   **(b)**

Fig. 3. (a) The MCRM Project map of The Bahamas and (b) the forereef areas considered in this project.

2.6. Classification of coral reefs and gorgonian-dominated hardgrounds

Caribbean forereefs can typically be classified into two major benthic habitat classes: coral-dominated and gorgonian-dominated (Mumby and Harborne 1999). These habitats, subsequently referred to as *Orbicella* reefs (the visually dominant coral complex) and gorgonian plains, represent very different benthic and fish assemblages, and are driven by different abiotic and biological processes (Mumby 2016). *Orbicella* reefs have much higher abundances of fishes, higher biodiversity, and respond more clearly to protection from fishing (Harborne et al. 2008, Mumby et al. 2008, Mumby 2016). Consequently, it was important to distinguish these habitats otherwise predictions of standing and potential fish biomass could be highly erroneous (i.e. predicting fish biomass typical of an *Orbicella* reef to a forereef cell that was actually characterised by gorgonian plain would significantly over-estimate fish biomass at that location).

Orbicella reefs and gorgonians plains can be separated by high-resolution remotely sensed imagery (Mumby 2016), but such imagery was not available for the entire archipelago. Therefore, the distribution of the two habitats was predicted using a modelling approach based on environmental gradients (Chollett and Mumby 2012). Firstly, a data set of 324 sites where habitat type and depth had been recorded (a subset of the survey sites described in Table 1, see Fig. 4) was compiled, and each record was associated with the estimated wave exposure and distance from the reef wall (see Section 2.7 for a description of the derivation of these data layers). Although the distance from the reef wall was not advocated as a predictive variable by Chollet and Mumby (2012), *Orbicella* reefs are often found along the top of the wall (*pers. obs.*) and it potentially represents a more effective explanatory variable than absolute depth.
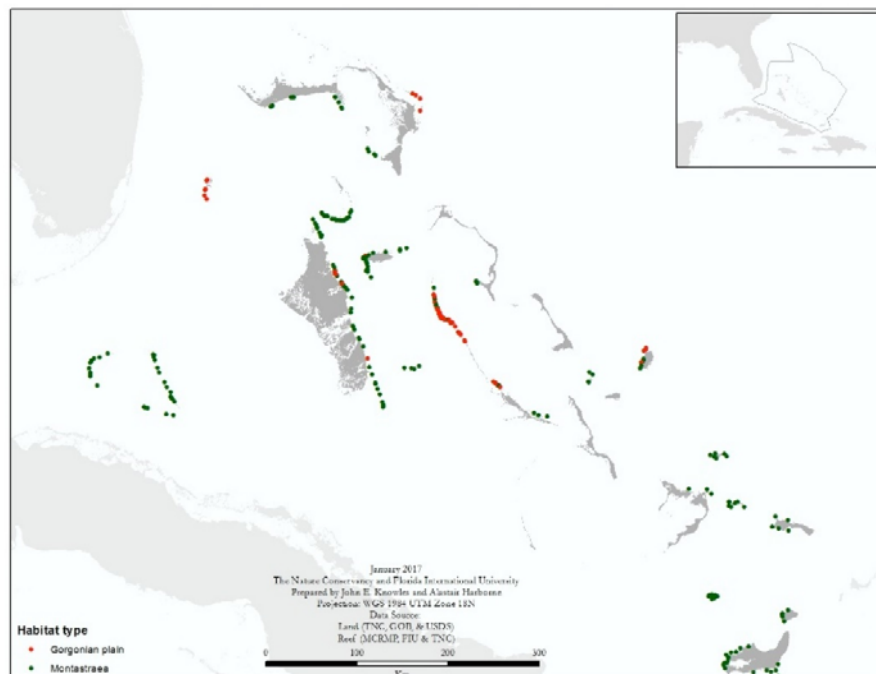

Fig. 4. Location of survey sites to be used in predictive model of *Orbicella* reefs and gorgonians plains.

Firstly, the data set was tested to ensure that the habitat labels used by the surveyors *in situ* were characteristic of two distinct habitat types, using data on depth, rugosity, and coral and macroalgal cover. The analysis was achieved in the PRIMER software by non-metric multidimensional scaling, which is based on a similarity matrix between each pair of sites and displays similar sites close together in a two dimensional plot, and one-way ANOSIM (Clarke 1993). ANOSIM returns a statistic R, which is a measure of separation among groups where 0 indicates complete mixing and 1 represents full clustering in which all samples within groups are more similar to one another than to any sample in another group. The presence or absence of *Orbicella* reef at each site was then modelled as a binomial distributed variable with depth, exposure, and distance from wall, plus an interaction between exposure and distance from wall, as explanatory variables. Since initial investigation of the data set suggested that the relationships were curvilinear, the model was built within a Generalized Additive Model (GAM) framework with binomial error structures and used the mgcv package within R (Wood 2011, R Core Team 2014).

2.7. *Derivation of explanatory variables*

The response variables at each fish survey site (biomass of fished species for fishing impact model and all AGRRA species for current standing stock model) were 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 standing stock across the entire country. Consequently, the project required continuous data layers of numerous potentially important explanatory variables (Table 2 and 3, Fig. 5). Note that two explanatory variables (coral cover and rugosity) were available from the *in situ* fish surveys, and were included in models of fishing impact and standing stock, but cannot be mapped continuously in The Bahamas. For example, deriving a continuous data layer for coral cover requires information on a complex range of variables including recruitment, grazing pressure, wave exposure, and the frequency of cyclones and bleaching events (Williams et al. 2015b). These data, and an understanding of how they interact to affect coral cover and the resilience of reefs, are not available. Therefore, coral cover and rugosity were modelled to assess whether they are important factors, but during the mapping extrapolation across unsurveyed cells this parameter was represented by the mean values for *Orbicella* reefs and gorgonian plains from all the fish survey sites (i.e. only habitat-scale spatial variability). A full description of the derivation of each variable, and a justification for its inclusion, is provided in Appendix 2.

Table 2. Variables used to model fishing impact at each survey site, including brief details of their derivation.

Variable	Description	Derivation
Area of reef within 20 km	Area of forereef within 20 km of reef cell	MCRM
Area of reef within 200 km	Area of forereef within 200 km of reef cell	MCRM
Availability of nursery habitat	Reef connectivity to mangroves and medium-density and dense seagrass beds	Use of algorithm (Mumby 2006) in combination with habitat maps
Coral cover	Coral cover at survey site	From fish survey data set
Data source	AGRRA, BBP or Dahlgren data	Origin of each fish survey
Depth	Depth of data collection	From fish survey data set
Distance to deep water	Perpendicular distance to edge of forereef ('reef wall')	From MCRM forereef layer
Distance to fish spawning aggregation	Distance to nearest known grouper spawning aggregation	Distance to sites described in The Bahamas (Sherman et al. 2016)
Distance to port	Distance to nearest major port	Major potential fish landing ports were Nassau, Freeport, West End, Coopers Town, Marsh Harbour, Freetown, Spanish Wells
Gravity of all potential fish markets	Market gravity defined as population size divided by square of distance	MCRM
Gravity of nearest potential fish market	Market gravity defined as population size divided by square of distance	MCRM
Habitat type	*Orbicella* reef or gorgonian plain	Habitat type assigned during fish surveys, then extrapolated using predictions based on MCRM
Human population pressure within 20 km	Number of people within 20 km divided by area of fishable reef	Online data on human populations and MCRM
Island geomorphology	Geomorphology at location (e.g. atoll, reef around island)	MCRM
Latitude	Latitude of survey site	From fish survey data set
Longitude	Longitude of survey site	From fish survey data set
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2010-2014	Satellite data
Protected status	Whether site is in a well- or partially enforced no-take reserve, or has no protection	Database of marine reserves and expert knowledge
Rugosity	Reef complexity	From fish survey data set
Sea surface temperature (SST)	Mean temperature of the coldest month	Satellite data
Season	Whether data was collected during the dry (Dec-Apr) or wet (May-Nov) season	From fish survey data set
Wave exposure	Wave exposure based on fetch and mean wind data	Provided by I. Chollet (see Chollett et al. 2012)
Year	Year of data collection	From data set

Table 3. Variables used to model total biomass of all the AGRRA species at each survey site, including brief details of their derivation.

Variable	Description	Derivation
Area of reef within 20 km	Area of forereef within 20 km of reef cell	MCRM
Area of reef within 200 km	Area of forereef within 200 km of reef cell	MCRM
Availability of nursery habitat	Reef connectivity to mangroves and medium-density and dense seagrass beds	Use of algorithm (Mumby 2006) in combination with habitat maps
Coral cover	Coral cover at survey site	From fish survey data set
Data source	AGRRA, BBP or Dahlgren data	Origin of each fish survey
Depth	Depth of data collection	From fish survey data set
Distance to deep water	Distance to the nearest reef wall	From MCRM forereef layer
Distance to fish spawning aggregation	Distance to nearest known grouper spawning aggregation	Distance to sites described in The Bahamas (Sherman et al. 2016)
Distance to reef wall	Perpendicular distance to edge of forereef ('reef wall')	MCRM
Fishing impact	Predicted fishing impact on 0-1 scale	From project model
Habitat type	*Orbicella* reef or gorgonian plain	Habitat type assigned during fish surveys, then extrapolated using predictions based on MCRM
Island geomorphology	Geomorphology at location (e.g. atoll, reef around island)	MCRM
Latitude	Latitude of survey site	From fish survey data set
Longitude	Longitude of survey site	From fish survey data set
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents
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Year	Year of data collection	From data set

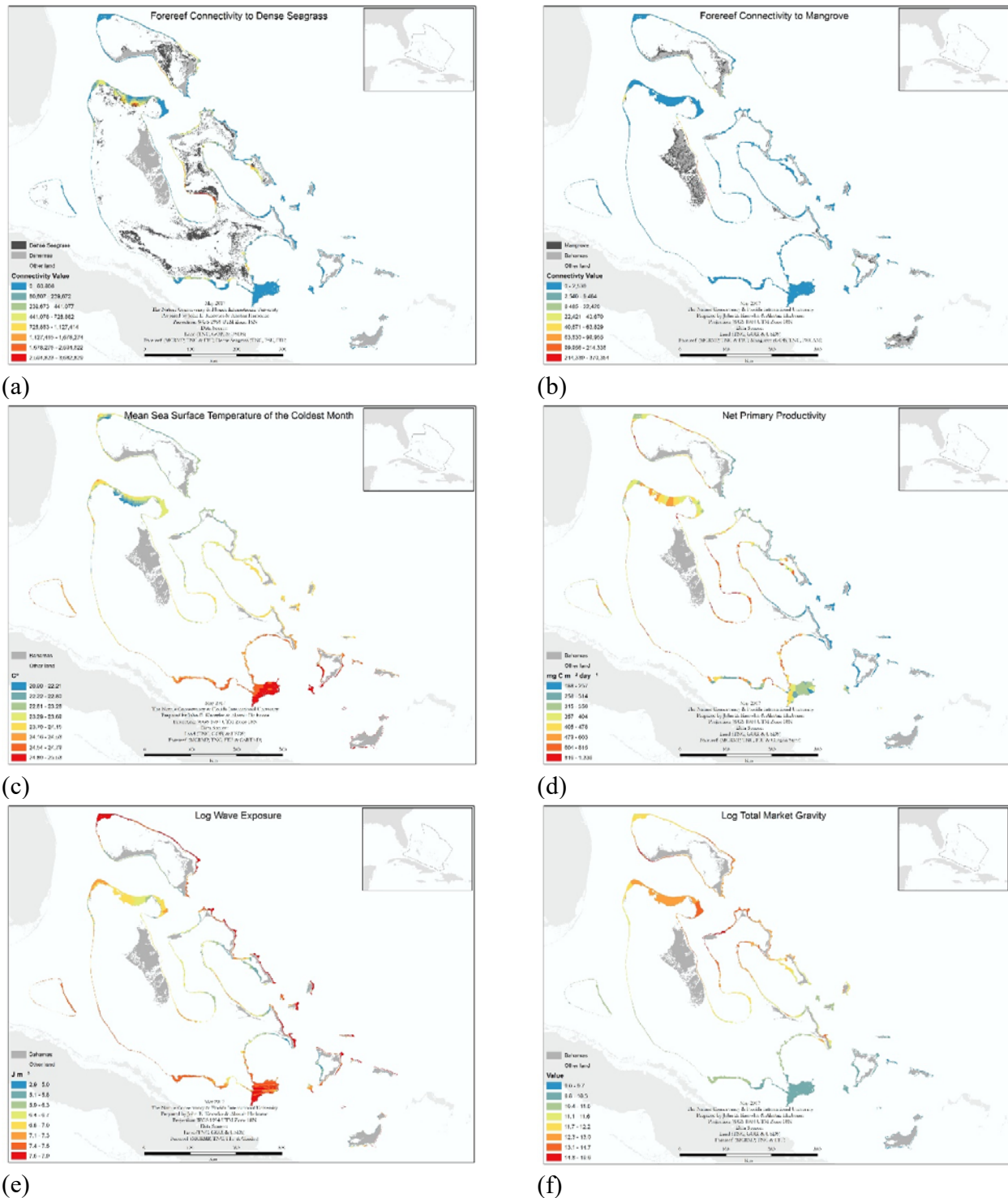**Fig. 5.** Examples of some of the data layers generated for constructing and extrapolating the fishing impact and standing stock models. (a) connectivity to dense seagrass habitats, (b) connectivity to mangrove habitats, (c) mean sea surface temperature of the coldest month (^{o}C), (d) net primary productivity (mg C m^{-2} day^{-1}), (e) log wave exposure (J m^{-3}), and (f) log total market gravity.

2.8. Additional considerations for modelling potential standing stock

As described previously, the map and model of potential standing stock represents a hypothetical data layer of the potential standing stock of fish at any location with no fishing. The map of potential standing stock 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 a sufficiently long time has elapsed to allow fish abundances to recover. However, there are myriad factors that will alter the carrying capacity, such as habitat quality that may be altered by disturbances (Abesamis et al. 2014), and this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors. As for the current standing stock data layers, note that the results show the potential standing stock of the AGRRA species, not the entire assemblage. However, the potential standing stock of these target species is a good proxy of total potential standing stock.

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 the project provides broad spatial estimates of when standing stock might recover using estimates of the ratio of current to potential standing stock and recent, generic insights into the recovery of reef fishes. A global analysis of reef fish stock has provided an estimated relationship between the ratio of current to potential biomass and time to "recovery", defined as reaching 90% of potential biomass (Fig. 6) (MacNeil et al. 2015). The project used this relationship to estimate the time it would take each 4 ha cell to reach this threshold of 0.9 of potential biomass. The project also calculated, and mapped, of the ratio of current to potential standing stock as this metric has been suggested as providing some insights into the status of the fishery and some ecological processes (McClanahan et al. 2011, Karr et al. 2015).
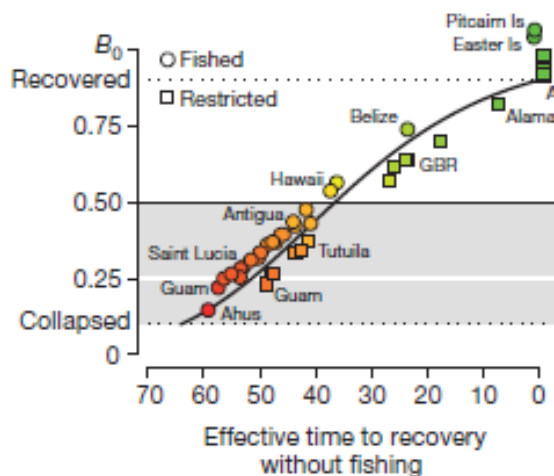

Fig. 6. The relationship between time to recovery (90% of potential biomass) following cessation of fishing and current fishery status. Points highlight reef sites used to parameterise the relationship.

From MacNeil et al. (2015)

2.9. Statistical analyses

For models of both fishing impact and standing stock, the final data set consists of univariate response variables (e.g. biomass of fished species or biomass of all AGRRA species), and a large number of categorical and continuous explanatory variables. Furthermore, the relationships among explanatory and response variables may be curvilinear and include significant interactions that are difficult to predict *a priori*. Consequently, the project used 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, BRT relates a response variable to explanatory variables by recursive binary splits (e.g. sites with high and low human populations) using an adaptive algorithm. BRT essentially creates an additive regression model and the relationships between the variables are visualised in a series of intuitively obvious graphs. Critically, BRTs have many advantages that were 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 national maps of fishing impact and standing stock.

BRTs are generally insensitive to collinearity among explanatory variables (Soykan et al. 2014), but the variables (Tables 2 and 3) were first be tested for correlations (variables removed so that there were no inter-variable correlations >0.8). The remaining variables were then included within the BRT, along with a variable comprising of random numbers. This variable will be included as a guide to which variables were most 'significant' (Soykan et al. 2014): variables which had less explanatory power than this random number 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 model 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. Predicting the distribution of Orbicella reefs

The data set used for building a predictive model of the distribution of *Orbicella* reefs contained 295 sites that had recorded data on at least two of: coral cover, depth, macroalgal cover, and rugosity. These sites allowed for checking that the data set did represent two distinct habitat types. This analysis was undertaken using non-metric multi-dimensional scaling in the PRIMER software, following normalisation of each variable. The resulting nMDS, and associated ANOSIM results (R=0.247, P=0.001), clearly demonstrated that the habitat classes assigned by the surveyors did correspond to two distinct habitat types (complex, coral-rich *Orbicella* reefs and gorgonian plains, Fig. 7). Although there is some limited overlap of benthic characteristics (i.e. some gorgonian plain sites are similar to some *Orbicella* reef sites), these results justify using the data set to build a statistical model of the distribution of each habitat.
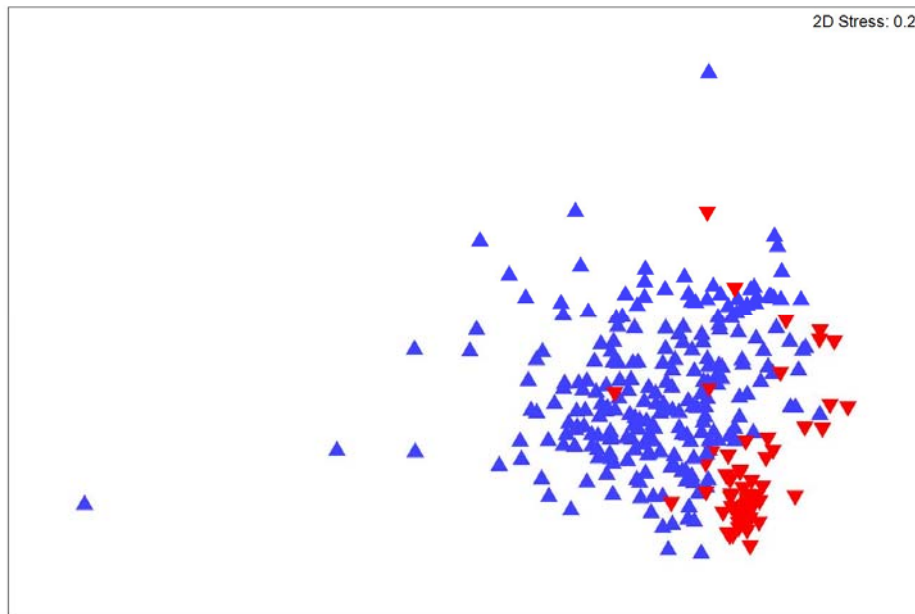
Fig. 7. Non-metric multi-dimensional scaling of the depth and benthic characteristics (rugosity and coral and macroalgal cover) of 295 sites categorised as *Orbicella* reef (blue) or gorgonian plains (red). Sites close together are similar to each other, sites further apart are more different.

The GAM results for the model relating the presence or absence of an *Orbicella* reef to depth, distance from deep water (wall at the edge of the forereef), and wave exposure resulted in significant terms for exposure and an interaction between exposure and distance from deep water. The distance from deep water term was not significant, but it remained in the model because it featured in a significant interaction (Fig. 8). The probability of finding an *Orbicella* reef generally decreased with increased distance from the wall to a distance of ~2 km (gorgonian plains more common), and further inshore reefs were always predicted to be *Orbicella* reefs. Higher exposure generally increased the probability of finding an *Orbicella* reef. However, very close to the wall gorgonian plains were more common at very low exposures, perhaps because there was insufficient water movement for coral growth. Furthermore, gorgonian plains were more common close to the wall at high exposures, as seen in previous studies (Chollett and Mumby 2012). Far from the wall (typically close to shore inside bays), the probability of finding an *Orbicella* reef was high and independent of exposure. Depth was non-significant. The final model explained 33.4% of the deviance in the response variable.

This final model was then used to predict the probability of finding an *Orbicella* reef in each forereef cell. Mapping these results relies on determining a threshold probability to separate *Orbicella* reefs and gorgonian plains (Chollett and Mumby 2012), and this was achieved by examining the predicted probabilities for the sites used to build the model (i.e. cells where the habitat identity was known) (Fig. 9). A threshold of 0.9 was selected as few gorgonian plain habitats were predicted to be *Orbicella* reefs at this value (Fig. 9b). A number of *Orbicella* reefs were found below this threshold, but the aim was to be conservative in predicting *Orbicella* reefs because of their importance in conservation planning (Mumby et al. 2008). Using this threshold allowed every 4 ha forereef cell to be classified as either *Orbicella* reef or gorgonian plain (Map 1). Following map creation, contextual editing was used to switch habitats where the predicted classification was judged incorrect by expert knowledge.
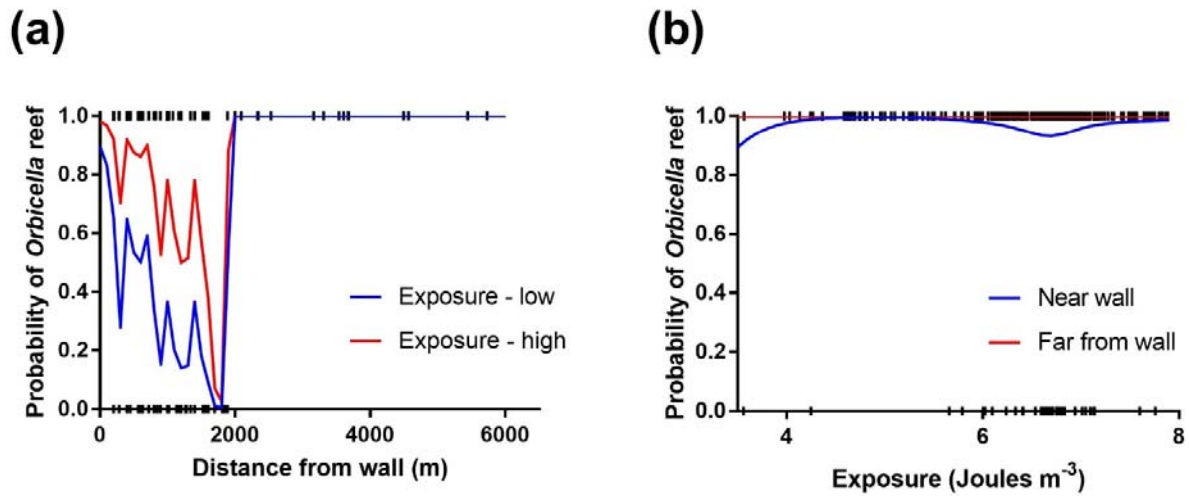
Fig. 8. Interaction plots for the effects of (a) distance from the wall at low and high wave exposures and (b) exposure at different distances from the wall on the probability of finding an *Orbicella* reef. Black marks represent the distribution of the data used to build the model. Low and high exposure = 3.5 and 7.5 J m^{-3} respectively. Near and far from wall = 0 and 5500 m respectively.
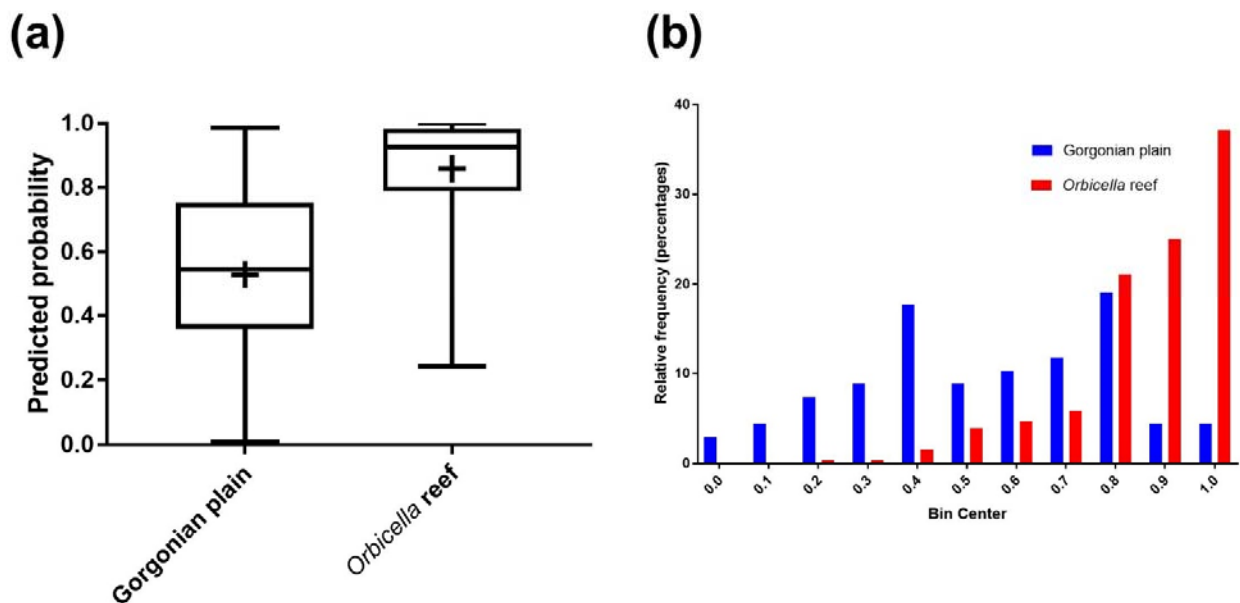
Fig. 9. (a) box and whisker plots of the median, minimum, and maximum values, along with 25th and 75th percentiles and mean (+), of the predicted probabilities of finding gorgonian plains or *Orbicella* reefs at sites used for building the predictive model, (b) frequency distribution of the percentage of reef sites used for building the predictive model within each predicted probability bin (0.1 bin sizes).
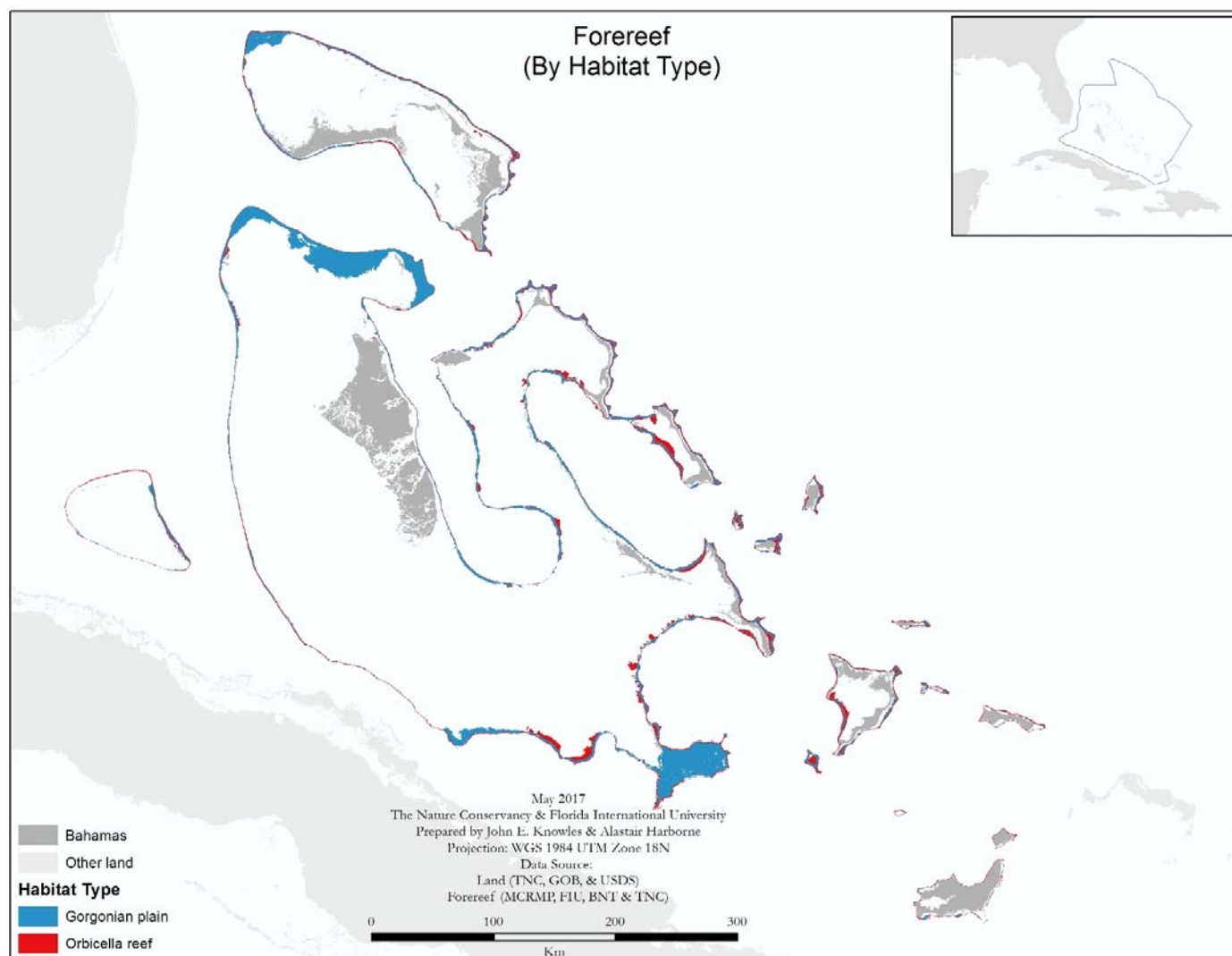
Map 1. Predicted spatial distribution of *Orbicella* reefs and gorgonians plains across The Bahamas.

3.2. Fishing impact model

Correlations of the range of variables proposed for inclusion (Table 2) revealed that latitude was highly correlated with sea surface temperature, and so latitude was removed from the model. Distance to port was highly correlated to many of the market gravity metrics, but the latter were retained because they are likely to be more insightful variables (Cinner et al. 2016). However, many of the market gravity variables were also correlated to each other, so the list of six variables was reduced to two: the total market gravity of all 15 Bahamian settlements and the market gravity of the nearest settlement including the 15 Bahamian settlements and the two settlements in the Turks and Caicos Islands. The larval supply variables were also highly correlated, and only the supply parameterised for *Sparisoma viride* was retained for testing. Finally, reef area within 200 km was also correlated with other variables, and since it didn't have a clear theoretical basis justifying its inclusion it was dropped from the model. The biomass of fished species was log transformed to improve normality of residuals prior to inclusion in the model, and the connectivity metrics and market gravity metrics were log transformed to highlight thresholds among low values.

The model of fished species resulted in a boosted regression tree analysis that provided a series of partial dependency plots that can be interpreted similarly to a regression line on a traditional scatterplot (Fig. 10). This model was then used to predict fishing impact in every 4 ha cell considered by the project. Predictions were made from the model by classifying the significant variables (Fig. 10) into two categories. Firstly, the two market gravity variables were considered to relate entirely to fishing impact (generally higher fishing impact where market gravity is highest). Predictive values unique to each 4 ha cell were used for each of these variables. In contrast, the remaining variables were considered as environmental drivers of fish abundance (e.g. there are more fished species in complex, high coral-cover reefs with high connectivity to dense seagrass). The values of these variables in every 4 ha cell were set to their mean. This ensured that the predictions only represented the effects of fishing on fished species, and not environmental gradients, as required for the map of fishing impact. Actual values of each variable in each cell would have been used if the aim was to predict actual biomass of species: but here the project only wanted to investigate the effect of fishing on fish biomass.

It is important to note that fishing impact was not adjusted for habitat type (*Orbicella* reef or gorgonian plain). There is little data on how fishing effort is partitioned across these habitats, and indeed gear such as fish traps may be more effective on gorgonian plains (Wolff et al. 1999). In the absence of the necessary data, both habitats equally close to urban areas (same market gravity) are considered to be equally impacted by fishing. However, underline actual catches are likely to vary between habitats because of the higher abundance of fish in *Orbicella* reefs (i.e. in a gorgonian plain a fishing impact of 0.5 will result in lower catches than in an *Orbicella* reef). These habitat differences in fish biomass are accounted for in the maps of current and potential standing stocks.

The fishing impact model explained 63% of the variability in the data set, and the correlation between observed and predicted values was 0.463. This exploratory power is considered acceptable given the challenges of the project: combining multiple data sets across a large geographic area and using a relatively crude fishery-independent metric of fishing impact.

Following predictions of human influences on the biomass of fished species in each 4 ha cell, the predicted values were back transformed and then rescaled to range from 0 (lowest fishing impact in the

country) to 1 (highest fishing impact in the region) and plotted (Map 2). As stated previously, it is important that these values are considered to reflect cumulative fishing impact rather than necessarily a measure of current fishing effort. Furthermore, the values are relative to The Bahamas, and are likely to be lower than other countries in the Caribbean region (Kramer 2003).
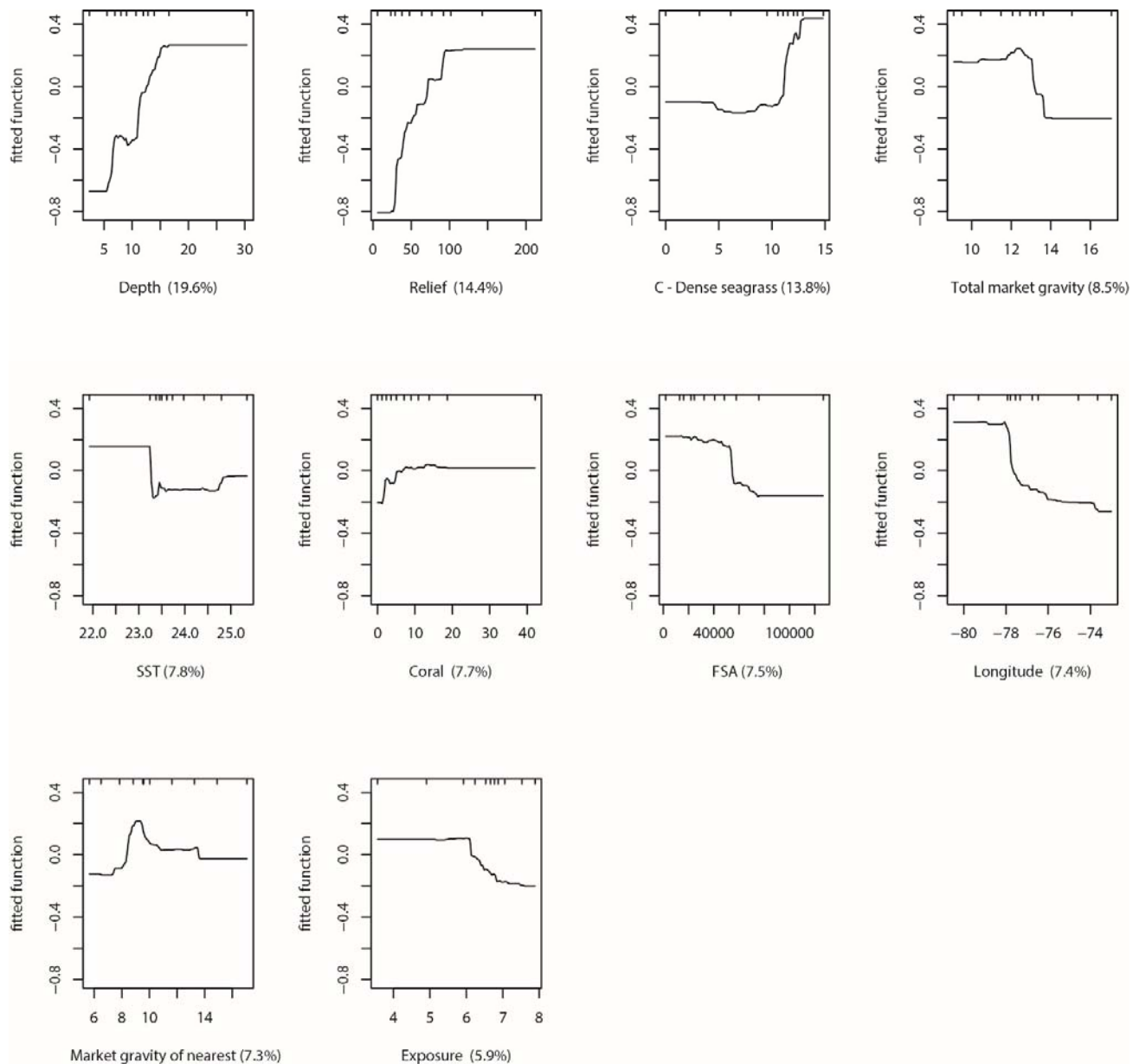
Fig. 10. Relationships between each significant variable and the biomass of fished species (increasing values on y axis, which is equal to decreasing fishing impact) as modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass of fished species on the y axis are normalised. Relief = reef rugosity; C = connectivity; SST = sea surface temperature; FSA = distance to fish spawning aggregation site; nearest = nearest settlement.
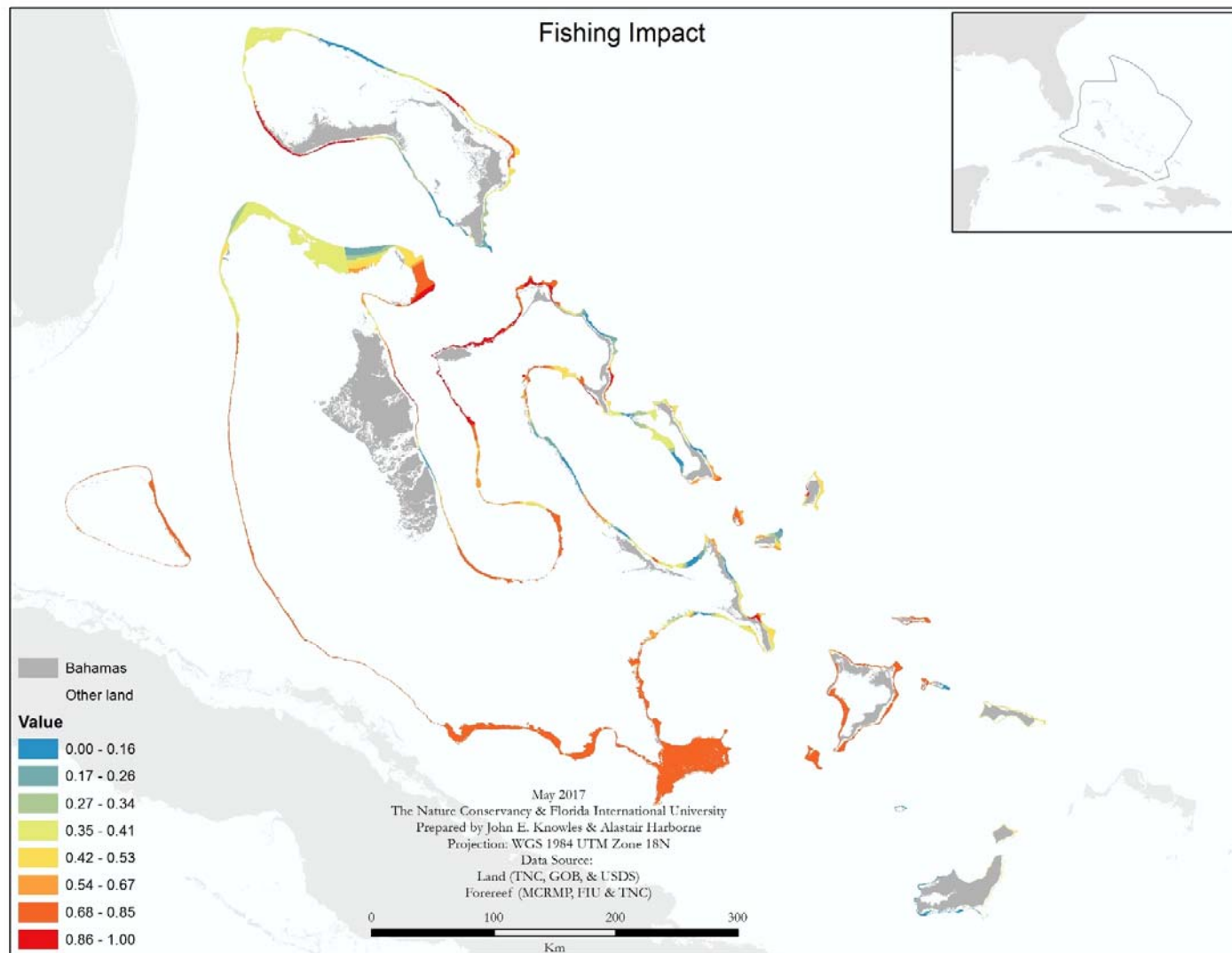
Map 2. Spatial distribution of predicted relative fishing impact (0 = low fishing impact) across The Bahamas.

3.3. Interpretation of the fishing impact model

The model for fishing impact (Fig. 10) shows that the biomass of fished species typically decreased with increasing total market gravity, which is consistent with (e.g. Cinner et al. 2013, Cinner et al. 2016). There also appeared to be a threshold of total market gravity (~13), beyond which human populations had a significant effect on fished species. Above and below this threshold, changes in market gravity had modest effects. The effect of the gravity of the nearest market was less clear, with the biomass of fished species declining as market gravity increased from ~8, but biomasses were also low at low market gravities. This may be caused by illegal fishing by non-Bahamians on remote reefs, small populations focusing on fishing in the absence of a range of other livelihoods, or possibly remote reefs having a higher biomass of apex predators that reduce the abundance of meso-predators that dominate the fished species category. In contrast to the metrics using market gravity, population size within 20 km appeared to be a poor predictor of fishing impact, but it has been shown to be important across larger gradients of population size (Cinner et al. 2013).

The biomass of fished species was also affected by environmental gradients, and tended to be higher on deeper reefs with medium to high coral cover and higher rugosity. These are likely to be predominantly *Orbicella* reefs that are well established to have richer fish assemblages compared to gorgonian plains (Harborne et al. 2008, Mumby et al. 2008, Mumby 2016), and reflect the well-established effect of structure on fish assemblages (Graham and Nash 2013). The importance of complex reefs for supporting fisheries underscores the importance of maintaining positive carbonate budgets for providing ecosystem services (Rogers et al. 2014), and reflects widespread concern about the loss of complexity on Caribbean reefs (Alvarez-Filip et al. 2009). The abundance of fished species was also significantly affected by connectivity to dense seagrass, which is increasingly being recognised as a critical nursery habitat for many species (Harborne et al. 2016). Mangroves are more commonly recognised as important nurseries (Mumby et al. 2004), but dense seagrass beds and mangrove stands often co-occur along sheltered coasts (Brown et al. 2016).

The impact of temperature on fish size is attracting increasing research attention because of the potential impacts of climate change, and there is now a relatively well-established expectation that fish size will decrease with increasing temperature because of changes in distribution and physiological stress (Daufresne et al. 2009, Sheridan and Bickford 2011, Cheung et al. 2013). This is consistent with the project model, which highlights a decrease in fished species above minimum temperatures of ~23°C. The inclusion of distance to nearest fish spawning aggregation in the final model was unexpected, and possibly reflects a poorly known influence on fish assemblage structure. Much of the research on spawning sites has considered their protection or larval export, but the project model suggests that being relatively close to an aggregation site can enrich fish assemblages throughout the year. This may be driven by increased larval settlement close spawning sites and / or adult fish preferring to be relatively close to spawning sites. The decrease in fish biomass to the east of the archipelago is difficult to explain, but may be linked to biogeography or illegal fishing of relatively remote reefs around islands with low populations. The final significant variable was exposure, with biomass decreasing on exposed reefs. This may be a function of these reefs being characterised by gorgonian plains (Chollett and Mumby 2012) or many species being ill-adapted for living on exposed reefs (Fulton et al. 2005). If the effect of exposure was on fishing impact, it would be expected that fish biomass would increase on exposed, difficult to reach reefs (Chollett et al. 2014).

Note that although marine reserve status was not included in the final model, this does not mean that reserves are not locally effective in the region. Rather, their effects were not clear at a national scale because of factors such as the large biophysical gradients and the varying age and enforcement of reserves. Marine reserves have repeatedly been demonstrated to be effective for increasing fish biomass compared to nearby fished reefs, and the local benefits of the Exuma Cays Land and Sea Park are unequivocal (Chiappone and Sullivan Sealey 2000, Mumby et al. 2006, Mumby et al. 2007, Harborne et al. 2008, Mumby and Harborne 2010). The source of the data did not significantly affect the model, suggesting that pooling the three databases is justified.

3.4. Current standing stock model

As for the model of fishing impact, correlations of the variables intended for inclusion in the standing stock model (Table 3) demonstrated that latitude was correlated with temperature and was dropped, only larval supply for *Sparisoma viride* was retained, and reef area within 200 km was not included because of correlations with other variables. The response variable of biomass of all AGRRA species was log transformed to improve normality of residuals prior to inclusion in the model, and the connectivity metrics were log transformed to highlight thresholds among low values.

The model of total biomass of the AGRRA species list (current standing stock) generated a boosted regression tree analysis that provided a series of partial dependency plots that can be interpreted in exactly the same way as a regression line on a traditional scatterplot (Fig. 11). This model was then used to predict the biomass of the current standing stock of these species in every 4 ha cell considered by the project (Map 3). Values specific to each reef cell were used for every variable, except for mean values of coral cover and rugosity (which varied between *Orbicella* reefs and gorgonian plains, Appendix 2) because of the lack of national data layers of these variables. Predicted distributions of each habitat (Section 3.1) were used to determine which mean values were appropriate for each forereef cell.

The standing stock model explained 53% of the variability in the data set, and the correlation between observed and predicted values was 0.534. This exploratory power is considered acceptable given the challenges of the project: combining multiple data sets across a large geographic area.
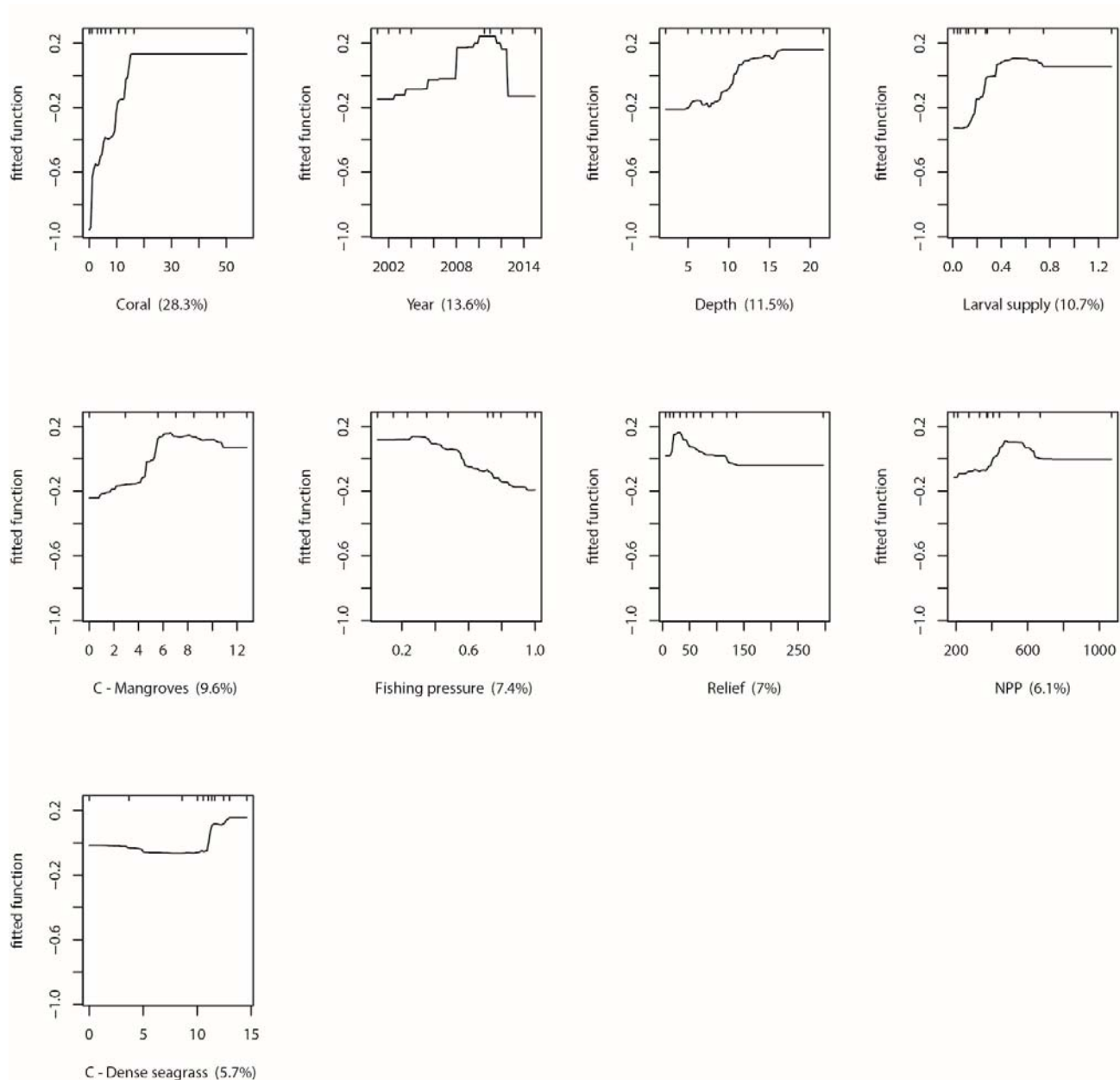
Fig. 11. Relationships between each significant variable and total biomass of the AGRRA species (y axis) modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass on the y axis are normalised. C = connectivity; Relief = reef rugosity; NPP = net primary productivity.
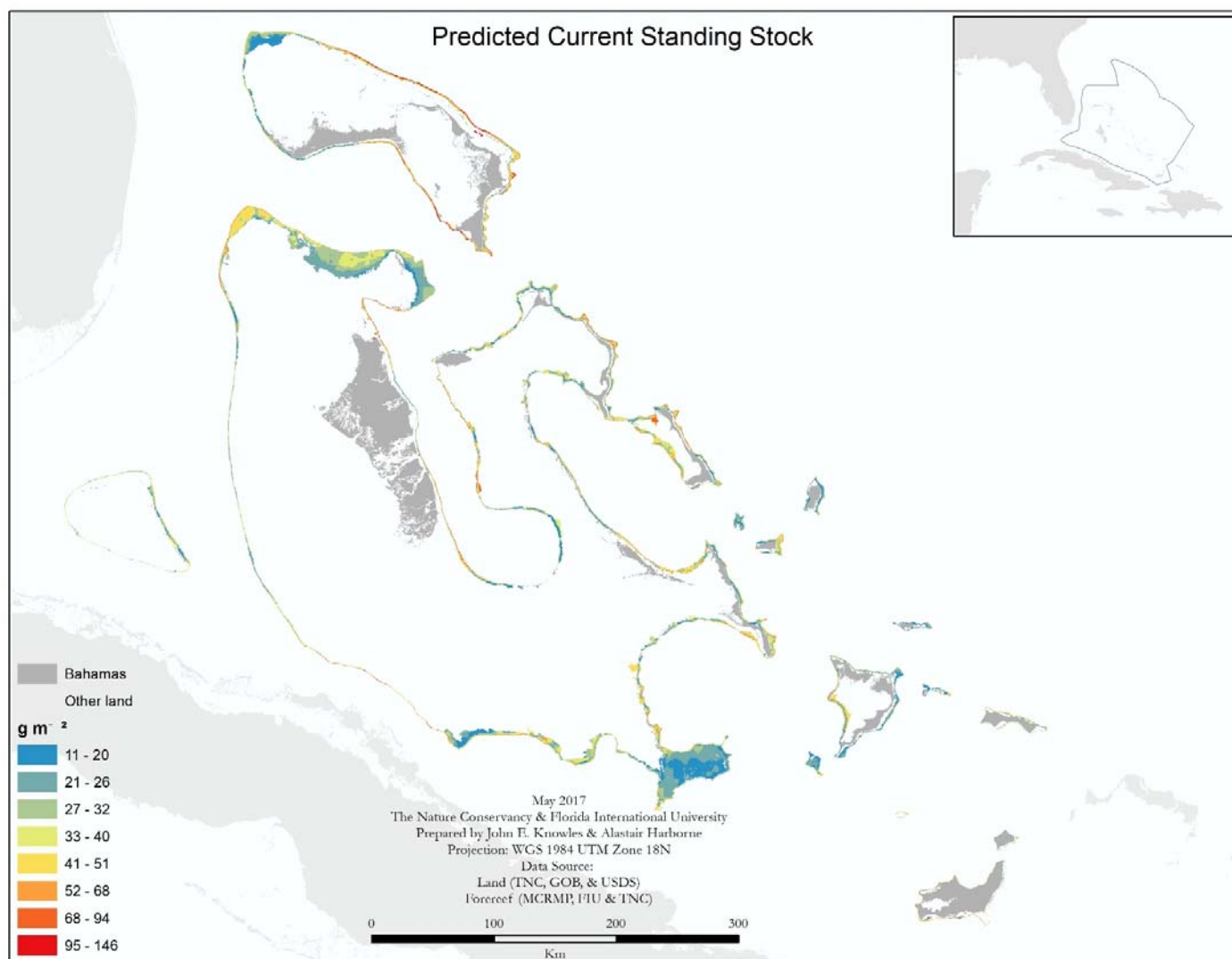
Map 3. Spatial distribution of predicted current standing stock of all AGRRA species (g m^{-2}) across The Bahamas.

3.5. Interpretation of the standing stock impact model

The metric of fishing impact derived by the project appeared to capture important properties of variability in fishing across The Bahamas: when used to predict fish biomass in an independent data set it showed declining fish biomass with increasing fishing impact (Fig.11). Furthermore, changes in fishing impact <~0.3 did not appear to affect fish biomass, but then biomass decreased approximately linearly above that threshold. The inclusion of year as a significant variable within the model is likely to reflect the recent surveying of more remote sites (e.g. Cay Sal, Great Inagua) rather than any change in fishing impact over time.

As for the fishing impact model, fish biomass in the standing stock model increased on deeper, coral-rich forereefs, which are likely to be *Orbicella*-dominated. This result matches expectations of the richer fish assemblage on *Orbicella* reefs compared to gorgonian plains (Mumby et al. 2008, Mumby 2016). The relationship between fish biomass and reef rugosity is less clear than in the fishing impact model, but fish biomass increases from very low values on gorgonian plains to high levels on *Orbicella* reefs. The reason for the decrease of biomass with increasing rugosity is unclear, but may be a function of many of the surveys in the Craig Dahlgren data set not having rugosity data, which limits the explanatory power of the model.

Fish biomass was also increased by a greater supply of larvae from upstream sources, which suggests a potential, assemblage-scale role of increasing larval supply on fish abundances. There has been much debate about the role of larval supply on fish demographics (Hixon 2011), but the data from The Bahamas support species-scale studies that demonstrate higher adult abundances at sites with high larval supply (consistent with the importance of pre-recruitment processes, Doherty and Fowler 1994). Furthermore, the relationship between larval supply and biomass is consistent with expectations that biomass will increase linearly with increasing larval supply at relatively low levels, but then will asymptote when larval supply increases to high levels as density-dependent processes regulate population sizes (Hixon 2011). The role of self-recruitment in determining fish biomass was difficult to assess in this study because of the limitations of the biophysical model, but has been demonstrated in other studies to be an important source of recruits, and is a particularly critical consideration in protected area network planning (Harrison et al. 2012).

Fish biomass tended to be highest in more productive waters. This is consistent with ecological theory that higher primary productivity enriches food webs at higher trophic levels, and has previously been reported as a strong driver of fish biomass across the Pacific (Williams et al. 2015a). Finally, similarly to the fishing impact model, fish biomass increased when reefs were highly connected to the key nursery habitats of mangroves and dense seagrass that can significantly affect fish assemblage structure (Mumby et al. 2004, Harborne et al. 2016).

3.6. Generating a map of potential standing stock

The map of potential standing stock (Map 4) represents a hypothetical data layer of the potential standing stock of fish at any location with no fishing impact. It was created by predicting the standing stock in each 4 ha cell with fishing impact set to 0 (as opposed to the value actually predicted by the fishing impact model). The map of potential standing stock represents a carrying capacity that might be reached within a well-enforced no-take reserve. However, equivalent layers could be created by

predicting standing stock with increased coral cover or sea surface temperature (e.g. the impacts of climate change). Because of the complex ecological processes on reefs, this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors. Note that, as for the current standing stock data layers, the map only shows the potential standing stock of the species surveyed by AGRRA, not the entire assemblage.

The difference between the values for current and potential standing stock were calculated for every 4 ha cell in order to produce an estimated potential gain in absolute biomass if fishing impact was reduced to 0 (Map 5). These values were then used to map the percentage increase in biomass that might occur across the country following the cessation of fishing (Map 6).

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

Previous studies have suggested that the ratio of current to potential fish biomass provides some insights into the status of the fishery and some ecological processes (McClanahan et al. 2011, Karr et al. 2015). For example, when this ratio falls below 0.5 it is possible that the reef is approaching an unsustainable fishery and potentially some thresholds of ecosystem processes. Conversely, reefs where this ratio is >0.9 are considered to be virtually intact and with effectively no impacts on reef functioning (MacNeil et al. 2015). Although the majority of reefs in The Bahamas appear to be above the 0.5 threshold (Map 7), this should be interpreted with caution because whether these thresholds are similar throughout the world is not clear. Consequently, impacts on reef functions may occur when current stocks are at higher proportions of potential biomass.

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 (MacNeil et al. 2015). The project used this relationship to estimate the time it would take each 4 ha cell to reach this threshold of 0.9 of potential biomass (Map 8). For many reefs in the region, reefs may not recover following the cessation of fishing for decades (maximum was ~30 years), underscoring the need to expand fisheries management initiatives as soon as possible.
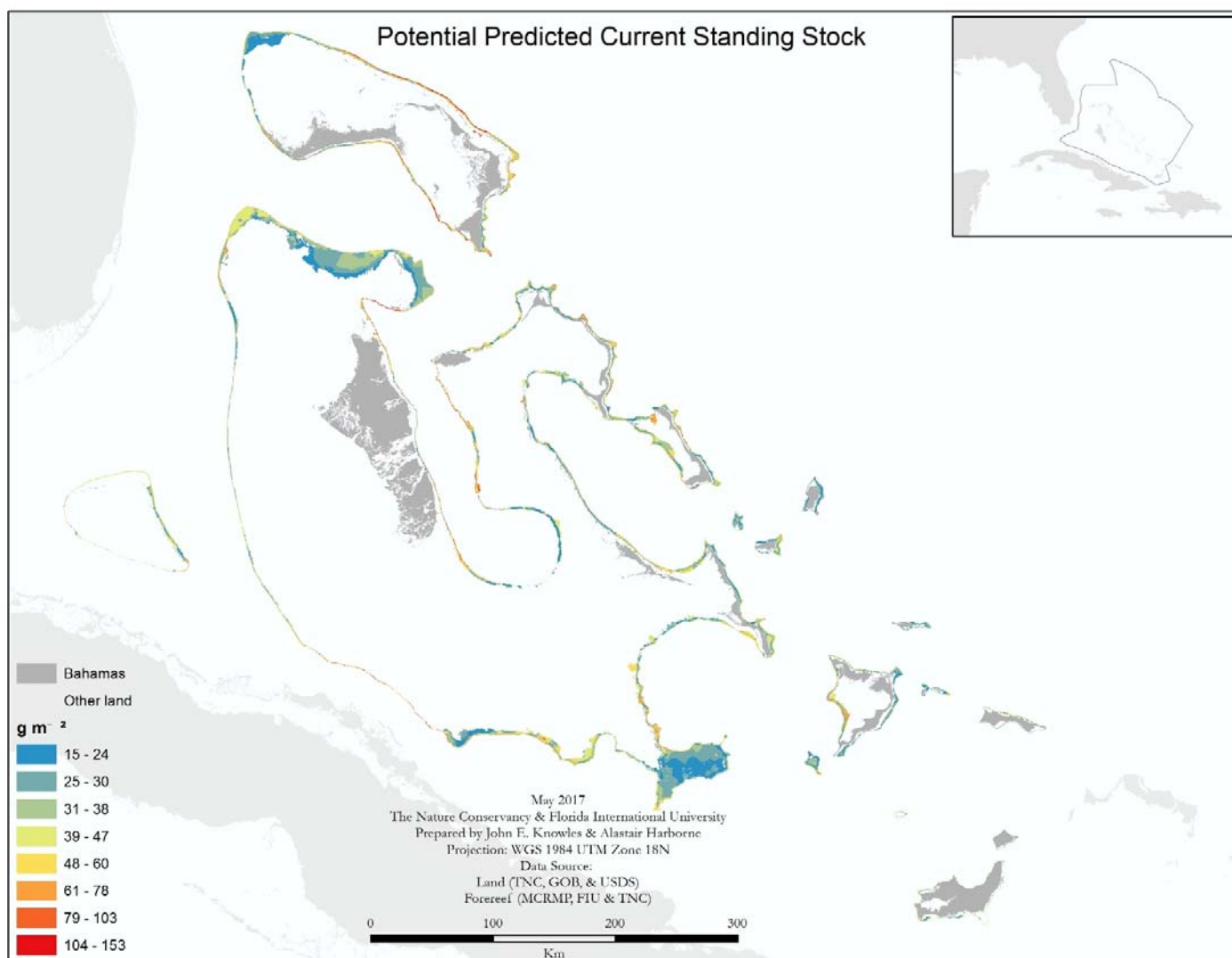
Map 4. Spatial distribution of predicted potential standing stock of all AGRRA species in the absence of fishing (g m^{-2}) across The Bahamas.
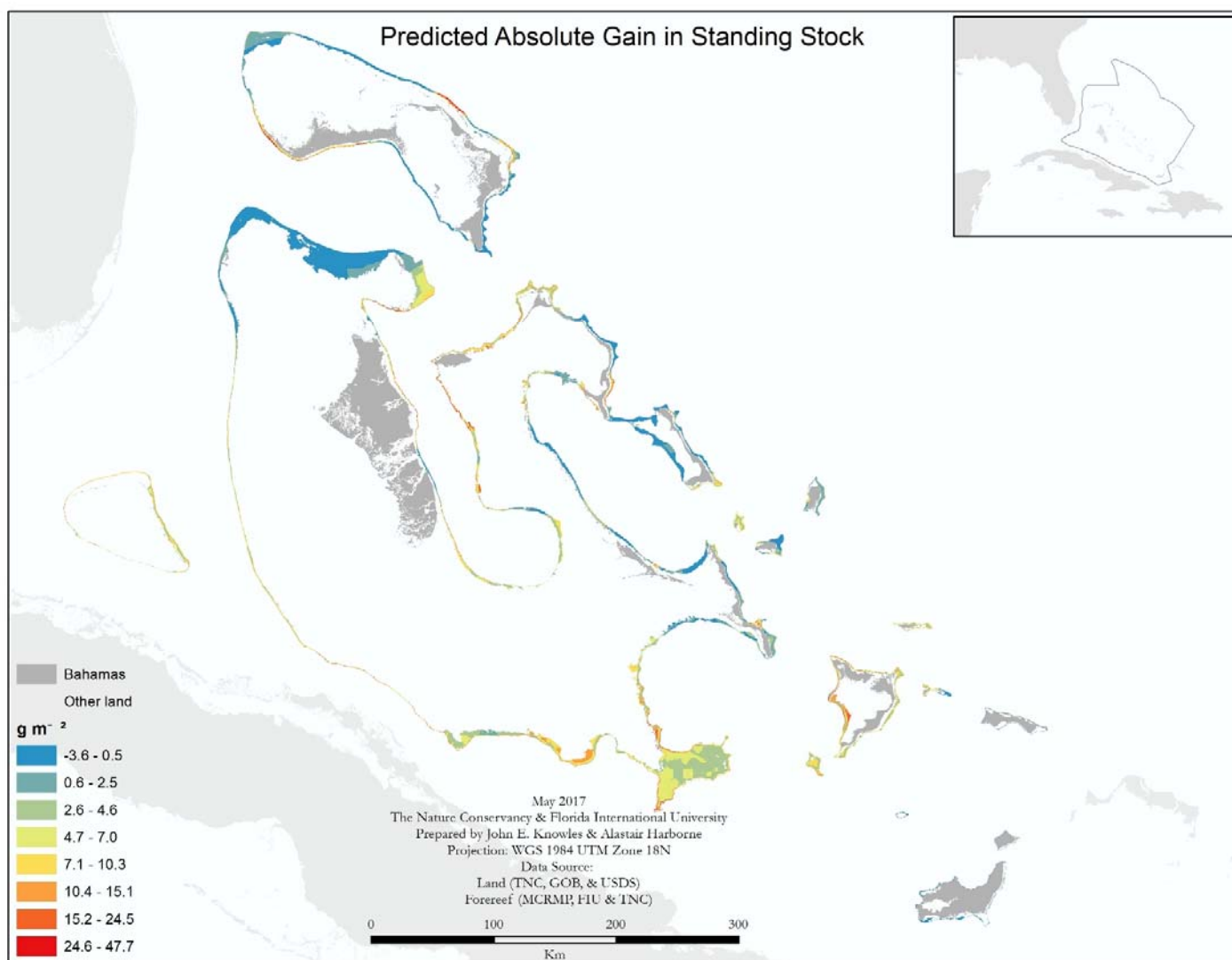
Map 5. Spatial distribution of predicted absolute gain in standing stock of all AGRRA species in the absence of fishing (g m^{-2}) across The Bahamas.
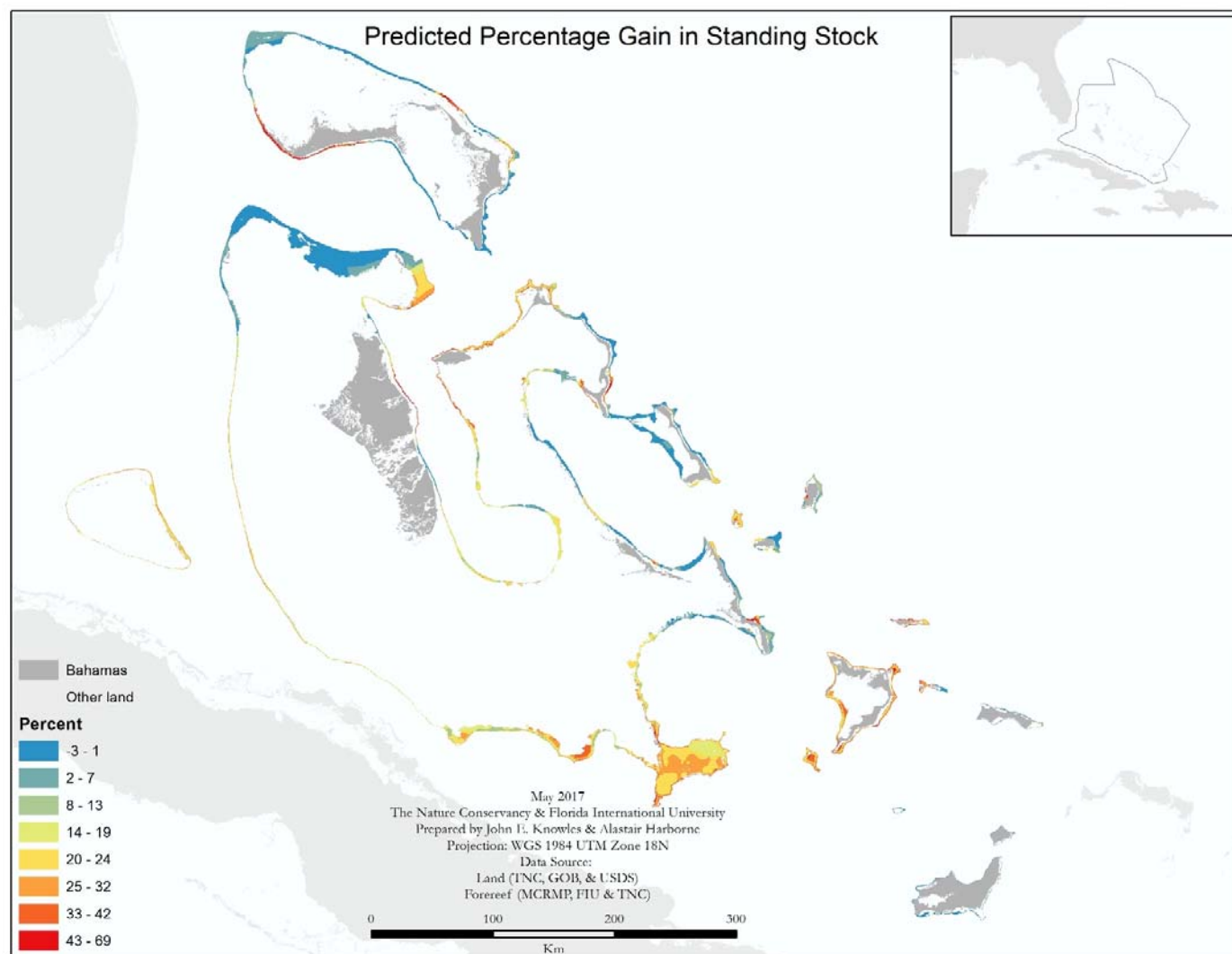
Map 6. Spatial distribution of predicted percentage gain in standing stock of all AGRRA species in the absence of fishing across The Bahamas.
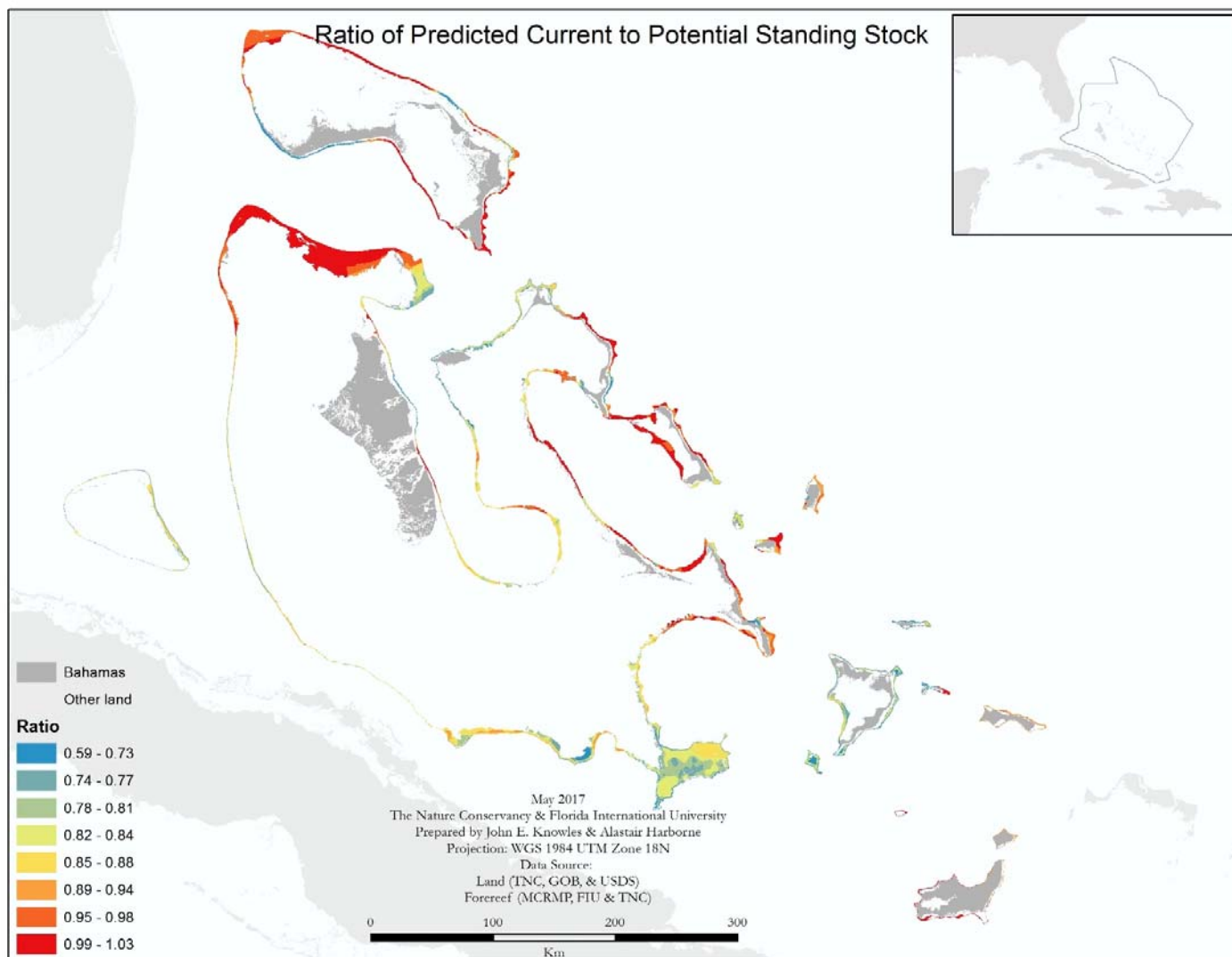
Map 7. Spatial distribution of the ratio of predicted current to potential standing stock of all AGRRA species across The Bahamas.
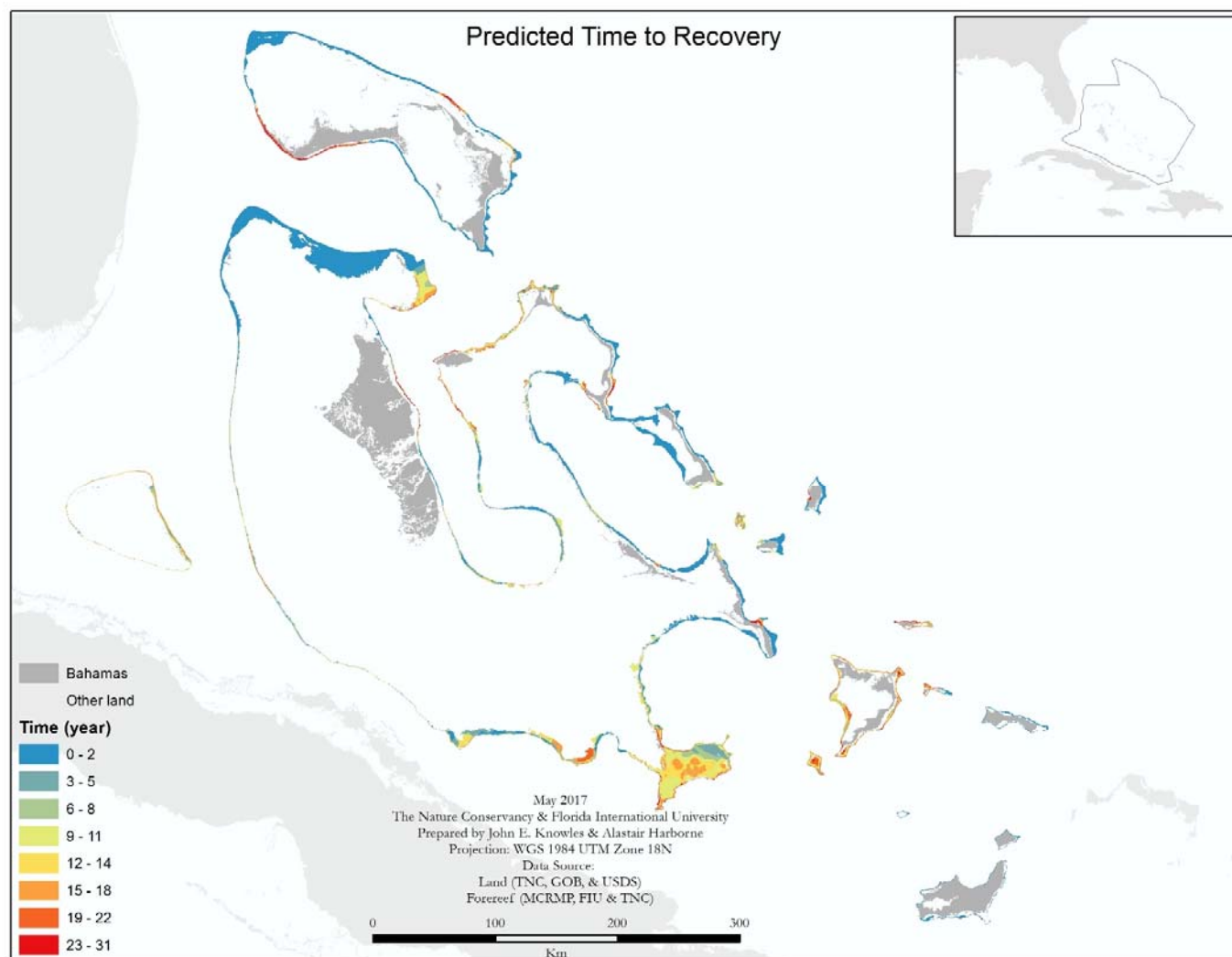
Map 8. Spatial distribution of the predicted time to recovery (90% of predicted potential standing stock of all AGRRA species, measured in years) following the cessation of fishing across The Bahamas.

4. Summary of patterns highlighted in the maps

The maps of fishing impact and standing stock (Maps 2 and 3) highlight the expected patterns of high fishing impact around major population centres such as Nassau and Freeport. In contrast, fishing impact is relatively close to the remote islands in the south-east of the archipelago. The relatively high fishing impact along the south-west edge of Grand Bahama Bank and Cay Sal was more unexpected, and may reflect illegal fishing of these remote reefs by boats from outside The Bahamas. High fishing impact decreased current standing stocks, but the biomass of fishes was also affected by complex interactions of other factors including depth, larval supply, primary productivity, and connectivity to nursery habitats. Consequently, the patterns of fish stocks around The Bahamas highlight significant heterogeneity at a range of spatial scales. The predicted potential biomass of fishes on reefs in the country, following the hypothetical cessation of fishing, also exhibited this complex heterogeneity (Map 4). Since the spatial patterns are complex, a summary of the number of cells in different categories of fishing impact or standing stock was calculated (Fig. 12a)

Following the hypothetical removal of fishing from across The Bahamas, the biomass of fish was predicted to increase by up to 70% (Maps 5 and 6, Fig. 12a). Such increases are relatively modest compared to changes of some families documented inside and outside the Exuma Cays Land and Sea Park (e.g. Mumby et al. 2006, Harborne et al. 2008), but national scale assessments are less sensitive to changes in fishing impact because of the large-scale biophysical gradients that are also included in the predictive model. Furthermore, the national scale assessment does not account for any other changes associated with marine conservation, such as improved habitat quality or protection of nursery areas, that will further increase fish populations in the absence of fishing. Finally, the strength of the national-scale analysis is that it highlights areas that are likely to benefit most from protection from fishing, and smaller-scale studies focused on the local effects of marine reserves will provide more accurate estimates of recovery potential.

The Bahamas is considered to have relatively low fishing impact (Kramer 2003), and this is supported by the generally high ratios of predicted current stocks to potential stocks (Map 7, Fig. 12b). This suggests that many reef functions may be more intact than other reefs in the region (Karr et al. 2015). Consequently, many reefs would take a relatively short time to recover to 90% of their potential maximum biomass (Map 8, Fig 12c). However, it is clear that the cessation of fishing in The Bahamas can significantly increase the resilience of reefs (Mumby and Harborne 2010), and conservation measures should not be delayed until there is clear evidence that reef functions are being severely impacted.
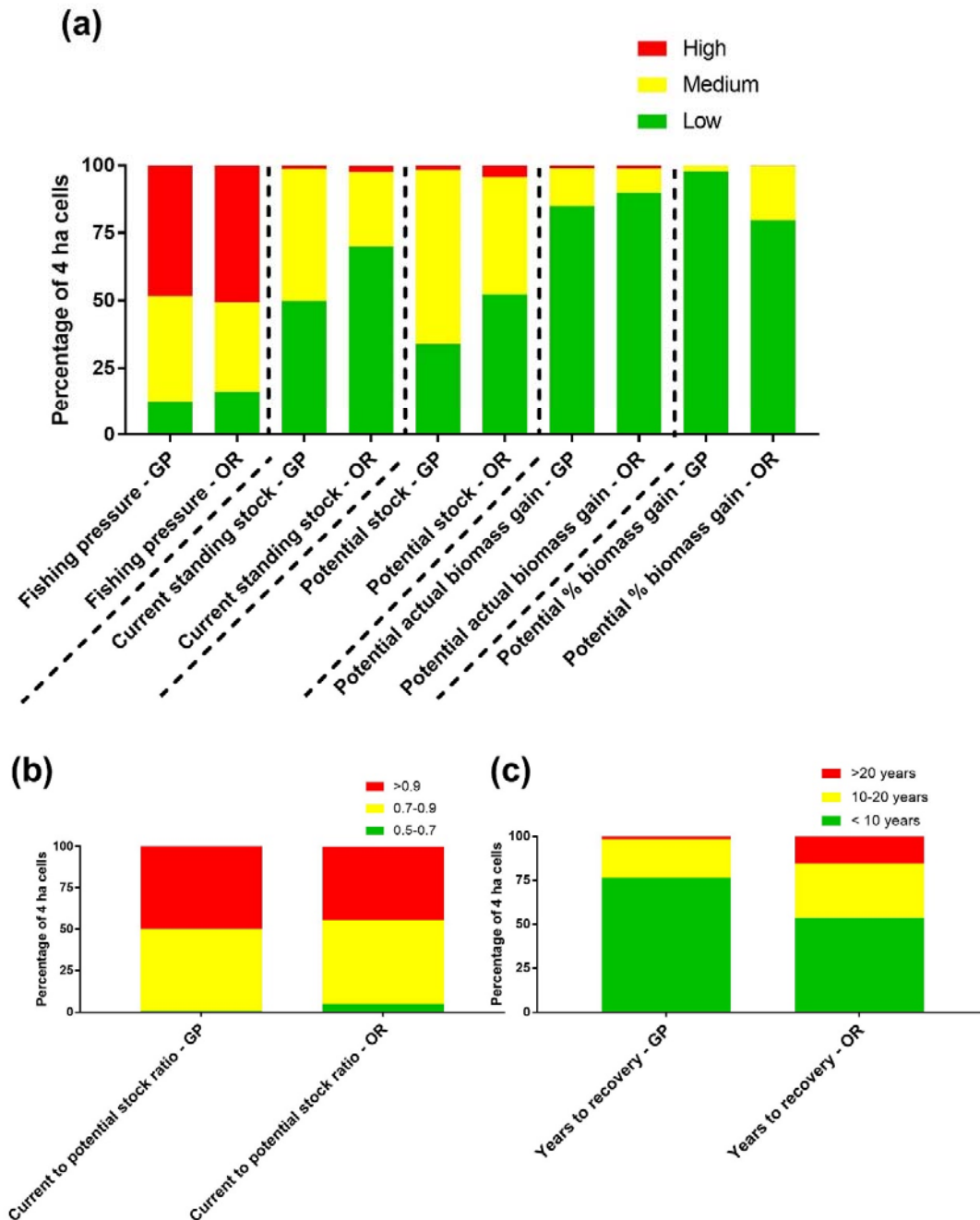
Fig. 12. Summary plots of proportion of Bahamian forereef cells that are within major classes of the main project output metrics. Data are segregated by habitat type (*Orbicella* reef and gorgonian plain). (a) Fishing impact (low = <0.33, medium = 0.33-0.67, high = > 0.67), current and potential standing stock (low = <25, medium = 25-50, high = >50 g m^{-2} [gorgonian plain] and <50, 50-100, >100 [*Orbicella* reef]), potential biomass gain (low = <5, medium = 5-10, high = >10 g m^{-2} [gorgonian plain] and <15, 15-30, >30 [*Orbicella* reef]), and potential percentage gain (low = <33, medium = 33-67, high = >67%). (b) Ratio of current to potential stock. (c) Time to recovery (90% of potential standing stock).

5. Potential use of map products in marine spatial planning

The maps presented in this report are the first spatially explicit, continuous maps of fishing impact and current and potential standing stock in The Bahamas. Consequently, these maps represent products that can be further tested and improved, and provide a baseline for future comparisons. Furthermore, in combination with the summary statistics (Fig. 12) the 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 with multiple stakeholders.

More pertinently to the Caribbean Challenge Initiative, the maps of fishing impact and fish standing stock implicitly represent aspects of ocean value, as they represent protein that has been, or could be, harvested. Therefore, these maps may also have multiple uses for conservation and management. For example, we anticipate that they will form core layers in the Marxan analysis (Ball et al. 2009) to identify priority sites for new reserves within the imminent marine spatial planning project in The Bahamas. Many Marxan analysis are limited by data availability (Pittman and Brown 2011), and rarely are data on fishing and fish stock available during the planning process, despite potentially very important. For example, the maps may be useful to highlight areas with relatively low fishing (low potential for conflicts with local fisherfolk), 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 standing stock and a low potential for improvement may be good choices for protected areas because they are already making important contributions to achieving many ecological and social objectives (e.g. biodiversity protection, fisheries management, cultural heritage and tourism and recreation), and increased fishing will erode these existing ecosystem services. However, as with all planning exercises, these benefits must be traded off against a wide range of other ecological and socio-economic considerations.

Finally, the results of reducing fishing to zero, as would occur in a no-take reserve, have been presented here, the models also provide the opportunity to run scenarios for different management techniques. For example, the models could be used to simulate a scenario where other fisheries management tools (e.g. gear, species or size restrictions) reduce fishing impact by 30% across the entire area, by reducing fishing impact to 70% of its current value in all of the cells. Similarly, management may increase coral cover by improving water quality or increase nursery connectivity by replanting mangroves. Both these actions would be expected to increase fish biomass even in the absence of changes in fishing impact, and the models would facilitate examination of the scale and spatial variations in these increases.

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Appendix 1. List of fish species considered in this project, and those considered as fishery species

Scientific name	Common name	Family		Fishery species?
Acanthurus chirurgus	Doctorfish	Surgeonfishes	Acanthuridae	✓
Acanthurus coeruleus	Blue Tang	Surgeonfishes	Acanthuridae	✓
Acanthurus tractus	Ocean Surgeonfish	Surgeonfishes	Acanthuridae	✓
Balistes vetula	Queen Triggerfish	Triggerfishes	Balistidae	✓
Canthidermis sufflamen	Ocean Triggerfish	Triggerfishes	Balistidae	✓
Melichthys niger	Black Durgon	Triggerfishes	Balistidae	✓
Xanthichthys ringens	Sargassum Triggerfish	Triggerfishes	Balistidae	
Caranx ruber	Bar Jack	Jacks	Carangidae	✓
Trachinotus falcatus	Permit	Jacks	Carangidae	✓
Chaetodon capistratus	Foureye Butterflyfish	Butterflyfishes	Chaetodontidae	
Chaetodon ocellatus	Spotfin Butterflyfish	Butterflyfishes	Chaetodontidae	
Chaetodon sedentarius	Reef Butterflyfish	Butterflyfishes	Chaetodontidae	
Chaetodon striatus	Banded Butterflyfish	Butterflyfishes	Chaetodontidae	
Prognathodes aculeatus	Longsnout Butterflyfish	Butterflyfishes	Chaetodontidae	
Diodon holocanthus	Balloonfish	Porcupinefishes	Diodontidae	✓
Diodon hystrix	Porcupinefish	Porcupinefishes	Diodontidae	✓
Cephalopholis cruentata	Graysby	Groupers	Epinephelidae	✓
Cephalopholis fulva	Coney	Groupers	Epinephelidae	✓
Epinephelus adscensionis	Rock Hind	Groupers	Epinephelidae	✓
Epinephelus guttatus	Red Hind	Groupers	Epinephelidae	✓
Epinephelus itajara	Jewfish/Goliath Grouper	Groupers	Epinephelidae	✓
Epinephelus morio	Red Grouper	Groupers	Epinephelidae	✓
Epinephelus striatus	Nassau Grouper	Groupers	Epinephelidae	✓
Mycteroperca acutirostris	Comb Grouper	Groupers	Epinephelidae	✓
Mycteroperca bonaci	Black Grouper	Groupers	Epinephelidae	✓
Mycteroperca interstitialis	Yellowmouth Grouper	Groupers	Epinephelidae	✓
Mycteroperca microlepis	Gag	Groupers	Epinephelidae	✓
Mycteroperca phenax	Scamp	Groupers	Epinephelidae	✓
Mycteroperca tigris	Tiger Grouper	Groupers	Epinephelidae	✓
Mycteroperca venenosa	Yellowfin Grouper	Groupers	Epinephelidae	✓
Anisotremus surinamensis	Black Margate	Grunts	Haemulidae	✓

Anisotremus virginicus	Porkfish	Grunts	Haemulidae	✓
Haemulon / Anisotremus	Juvenile Grunt	Grunts	Haemulidae	
Haemulon album	White Margate	Grunts	Haemulidae	✓
Haemulon aurolineatum	Tomtate	Grunts	Haemulidae	✓
Haemulon carbonarium	Caesar Grunt	Grunts	Haemulidae	✓
Haemulon chrysargyreum	Smallmouth Grunt	Grunts	Haemulidae	✓
Haemulon flavolineatum	French Grunt	Grunts	Haemulidae	✓
Haemulon macrostomum	Spanish Grunt	Grunts	Haemulidae	✓
Haemulon melanurum	Cottonwick	Grunts	Haemulidae	✓
Haemulon parra	Sailors Choice	Grunts	Haemulidae	✓
Haemulon plumierii	White Grunt	Grunts	Haemulidae	✓
Haemulon sciurus	Bluestriped Grunt	Grunts	Haemulidae	✓
Haemulon steindachneri	Latin Grunt	Grunts	Haemulidae	✓
Haemulon striatum	Striped Grunt	Grunts	Haemulidae	✓
Kyphosus spp.	Chub	Chubs	Kyphosidae	✓
Bodianus rufus	Spanish Hogfish	Wrasses	Labridae	✓
Halichoeres bivittatus	Slippery Dick	Wrasses	Labridae	
Halichoeres garnoti	Yellowhead Wrasse	Wrasses	Labridae	
Halichoeres radiatus	Puddingwife	Wrasses	Labridae	✓
Lachnolaimus maximus	Hogfish	Wrasses	Labridae	✓
Lutjanus analis	Mutton Snapper	Snappers	Lutjanidae	✓
Lutjanus apodus	Schoolmaster	Snappers	Lutjanidae	✓
Lutjanus buccanella	Blackfin Snapper	Snappers	Lutjanidae	✓
Lutjanus cyanopterus	Cubera Snapper	Snappers	Lutjanidae	✓
Lutjanus griseus	Gray Snapper	Snappers	Lutjanidae	✓
Lutjanus jocu	Dog Snapper	Snappers	Lutjanidae	✓
Lutjanus mahogoni	Mahogany Snapper	Snappers	Lutjanidae	✓
Lutjanus synagris	Lane Snapper	Snappers	Lutjanidae	✓
Ocyurus chrysurus	Yellowtail Snapper	Snappers	Lutjanidae	✓
Aluterus scriptus	Scrawled Filefish	Filefishes	Monacanthidae	
Cantherhines macrocerus	Whitespotted Filefish	Filefishes	Monacanthidae	
Cantherhines pullus	Orangespotted Filefish	Filefishes	Monacanthidae	
Monacanthus tuckeri	Slender Filefish	Filefishes	Monacanthidae	
Gymnothorax funebris	Green Moray	Morays	Muraenidae	
Gymnothorax miliaris	Goldentail Moray	Morays	Muraenidae	
Gymnothorax moringa	Spotted Moray	Morays	Muraenidae	
Lactophrys bicaudalis	Spotted Trunkfish	Boxfishes	Ostraciidae	
Centropyge argi	Cherubfish	Angelfishes	Pomacanthidae	
Holacanthus	Blue Angelfish	Angelfishes	Pomacanthidae	

bermudensis				
Holacanthus ciliaris	Queen Angelfish	Angelfishes	Pomacanthidae	✓
Holacanthus tricolor	Rock Beauty	Angelfishes	Pomacanthidae	✓
Pomacanthus arcuatus	Gray Angelfish	Angelfishes	Pomacanthidae	✓
Pomacanthus paru	French Angelfish	Angelfishes	Pomacanthidae	✓
Microspathodon chrysurus	Yellowtail Damselfish	Damselfishes	Pomacentridae	
Stegastes planifrons	Threespot Damselfish	Damselfishes	Pomacentridae	
Cryptotomus roseus	Bluelip Parrotfish	Parrotfishes	Scaridae	
Scarus / Sparisoma	Juvenile Parrotfish	Parrotfishes	Scaridae	
Scarus coelestinus	Midnight Parrotfish	Parrotfishes	Scaridae	✓
Scarus coeruleus	Blue Parrotfish	Parrotfishes	Scaridae	✓
Scarus guacamaia	Rainbow Parrotfish	Parrotfishes	Scaridae	✓
Scarus iseri	Striped Parrotfish	Parrotfishes	Scaridae	✓
Scarus taeniopterus	Princess Parrotfish	Parrotfishes	Scaridae	✓
Scarus vetula	Queen Parrotfish	Parrotfishes	Scaridae	✓
Sparisoma atomarium	Greenblotch Parrotfish	Parrotfishes	Scaridae	
Sparisoma aurofrenatum	Redband Parrotfish	Parrotfishes	Scaridae	✓
Sparisoma chrysopterum	Redtail Parrotfish	Parrotfishes	Scaridae	✓
Sparisoma radians	Bucktooth Parrotfish	Parrotfishes	Scaridae	
Sparisoma rubripinne	Yellowtail Parrotfish	Parrotfishes	Scaridae	✓
Sparisoma viride	Stoplight Parrotfish	Parrotfishes	Scaridae	✓
Pterois volitans	Lionfish	Scorpionfishes	Scorpaenidae	
Calamus bajonado	Jolthead Porgy	Porgies	Sparidae	✓
Calamus calamus	Saucereye Porgy	Porgies	Sparidae	✓
Calamus penna	Sheepshead Porgy	Porgies	Sparidae	✓
Calamus pennatula	Pluma Porgy	Porgies	Sparidae	✓
Sphyraena barracuda	Great Barracuda	Barracudas	Sphyraenidae	✓
Sphoeroides spengleri	Bandtail Pufferfish	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. Therefore, the available area of forereef close to each reef cell was measured from the MCRM. There was no clear theoretical basis for the scale of deriving this variable, so it was calculated at both 20 and 200 km scales.

Availability of nursery habitat

The availability of Caribbean 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 sparse, medium-density, and dense seagrass and mangrove stands throughout The Bahamas were available through an earlier TNC project. The map for sparse seagrass was not used because it has a limited functional importance as a nursery (Harborne et al. 2016). These maps were used to calculate connectivity for a sub-set of reef cells because running the algorithm for all cells was not computationally tractable. Values for the remaining reef cells were calculated by interpolation. Connectivity to mangroves and medium-density and dense seagrass was calculated 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 Caribbean estimates we are aware of all suggest increased populations up to 10 km (Dorenbosch et al. 2006, Mumby 2006, Huijbers et al. 2013), and this was the maximum distance used. 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. dense seagrass) is then calculated as:

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

where D is the maximum possible distance between two pixels (10,000 m), i is a nursery habitat pixel from a total of n within the seascape, j is the pixel containing the forereef 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 forereef site. Only mangrove pixels adjoining water 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. Coral cover was estimated *in situ* during all fish surveys. However, coral cover cannot be reliably modelled continuously across the entire Bahamas. Therefore, predictions for the continuous maps of fishing impact and standing stocks were calculated using mean coral cover

for sites used in the fishing impact model (8.7%) or for survey sites in *Orbicella* reefs (9.9%) or gorgonian plains (0.5%) as appropriate within the standing stock model.

Data source

All fish surveys were conducted by experienced surveyors using analogous methods, but it was possible that the source of the data could affect fish biomass (e.g. some surveyors over-estimating fish size). Therefore, the origin of the data (which of the three databases it was drawn from) was included as a categorical variable in the models.

Depth

While rarely affecting fish assemblages directly, depth is a proxy for numerous environmental gradients such as light intensity, temperature, and salinity that may affect fishes. Depth was measured during *in situ* surveys and these values were used in the models. In order to extrapolate these results to the entire archipelago it was necessary to develop a continuous bathymetric data layer. This was achieved by merging data from a TNC digitising project led by Steve Schill, data from General Bathymetric Chart of the Oceans (GEBCO)[2], and data provided by Sam Purkis (Purkis et al. 2014).

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 distance of each reef cell to this reef edge was calculated by measuring the perpendicular distance to the edge of the forereef habitat as delineated on the MCRM.

Distance to fish spawning aggregation

Only some species migrate to mass spawning sites to reproduce, but these species include many groupers and snappers that represent a significant component of the fishery species considered in this project. This explanatory variable was calculated by measuring the distance, not across land, to the nearest fish spawning aggregation site described in a recent review for The Bahamas (Sherman et al. 2016, Fig. A1).

Distance to port

The distance from a reef to the nearest market for selling and processing fish can be an important determinant of fishing pressure at local and global scales, particularly among reefs with low local population densities (Brewer et al. 2012, Brewer et al. 2013, Cinner et al. 2013). Distance to market may even have a curvilinear relationship to fish biomass, with biomass increasing exponentially at distances over 14 km from a market (Cinner et al. 2013). This response variable was estimated as the Euclidean distance between each reef cell and the nearest major Bahamian population centre (> approximately 4000 people: Nassau, Freeport, West End, Coopers Town, Marsh Harbour, Freetown, plus Spanish Wells because of its importance for fishing boats).
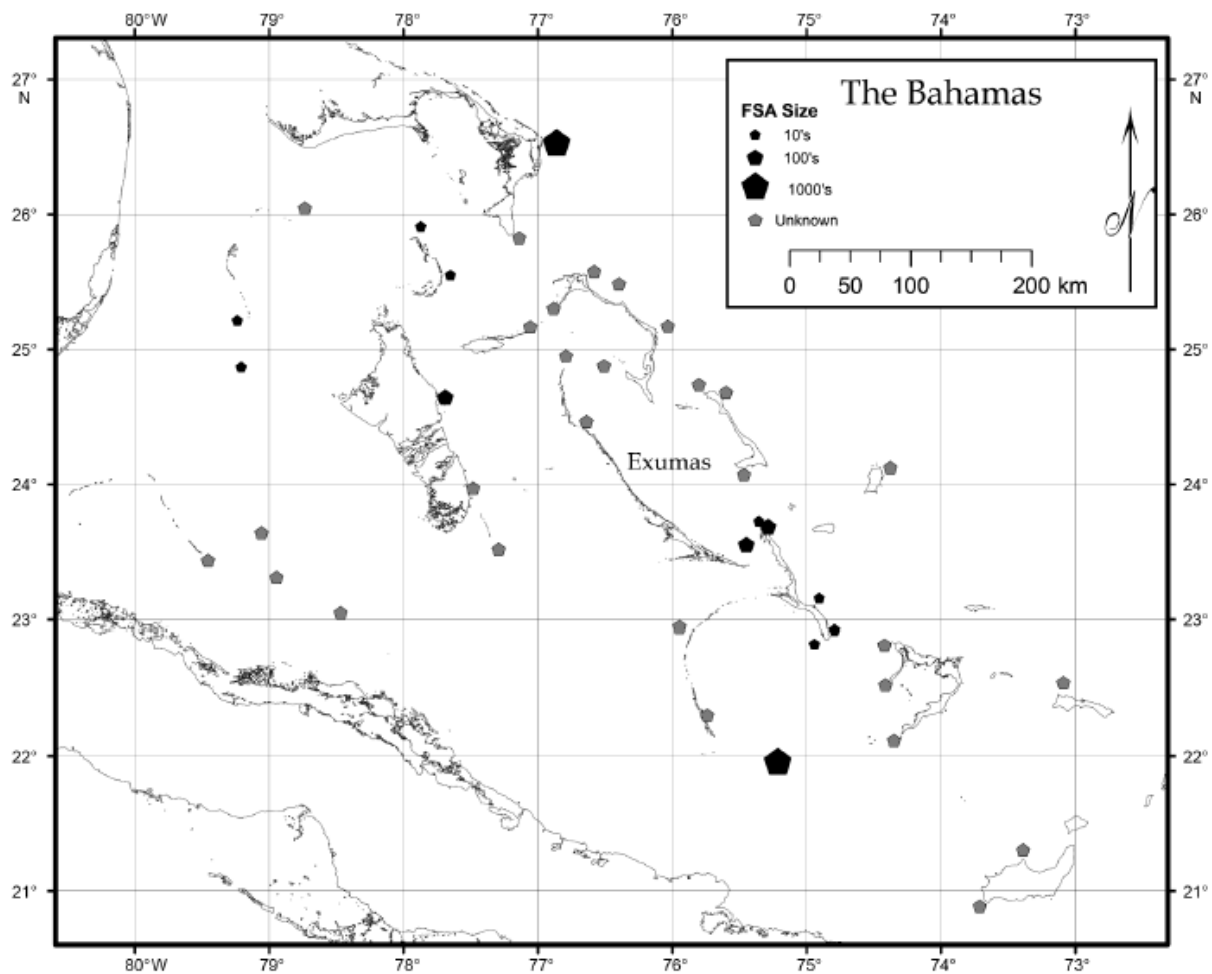
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[2] www.gebco.net/

Fig. A1. Approximate locations of known and anecdotal Nassau grouper *Epinephelus striatus* fish spawning aggregations (FSAs) in the Bahamian archipelago. Spawning aggregation sites are denoted by black pentagons of various sizes corresponding to recent estimates of Nassau grouper abundance. Source: Sherman et al. (2016).

Gravity of markets

In addition to the basic distance to port, this project also considered the economic geography concept of 'gravity' to examine social drivers on fish populations, 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. In this project, we followed Cinner et al. (2016) and calculated gravity as the number of people size in the population centre divided by the square of the distance between that centre and the reef cell. We examined the importance of both the total market gravity (sum of the market gravity of every population centre) and the gravity of the nearest population centre. The total and nearest gravities were calculated for all settlements of >approximately 1000 people in The Bahamas[3] (Andros Town, Arthurs

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[3] https://en.wikipedia.org/wiki/List_of_cities_in_the_Bahamas

Town, Clarence Town, Cockburn Town, Coopers Town, Dunsmore Town, Freeport, Freetown, George Town, High Rock, Marsh Harbor, Nassau, Rock Sound, Spanish Wells and West End), all 15 Bahamian settlements plus Cockburn Town and Providenciales in the Turks and Caicos Islands which may have an influence on Bahamian fisheries, and the six largest Bahamian settlements plus Spanish Wells (Nassau, Freeport, West End, Coopers Town, Marsh Harbour, Freetown, and Spanish Wells). This generated a total of six different variables.

Habitat type

The models of both fishing impact and standing stock contain a categorical variable for habitat type (*Orbicella* reef or gorgonian plain) in order to include any variability not contained in the depth, coral cover, and rugosity factors. Furthermore, within the fishing impact model this habitat variable may demonstrate differences in fishing impact among habitat types caused by factors such as trap efficiency (Wolff et al. 1999).

Human population pressure within 20 km

The size of local human populations has repeatedly been demonstrated to be an excellent proxy of fishing pressure on reefs (e.g. Mora 2008, Stallings 2009, Mora et al. 2011, Cinner et al. 2013). Therefore, it was anticipated to be a potentially key variable in the model of fishing impact in The Bahamas. Standardised, rasterized, global data sets of human populations are available online, and the Phase 1 project used data from SEDAC, the Socioeconomic Data and Applications Center (SEDAC), which part of the Earth Observing System Data and Information System (EOSDIS) of NASA[4]. The project used the Global Rural-Urban Mapping Project (GRUMP) 2000 data layer, which provides estimated population sizes within at a resolution of 30 arc-seconds (~1km). Full details of the derivation of this data layer is provided in Balk et al. (2010), but it is generated using population counts and night-time light intensities.

The impact of human population sizes on reef fisheries is dependent on the reef area available, and the project followed other studies in calculating population size per square km of fishable reef (Stallings 2009, Houk et al. 2012, Taylor et al. 2014, Williams et al. 2015). Defining the area included in assessing human populations affecting a survey site was informed by previous studies that have estimated populations within 5 km^2 (Stallings 2009, Cinner et al. 2013), a radius of 15 km (Williams et al. 2008), and a radius of 25 km (Halpern et al. 2008, Mora et al. 2011). Furthermore, interviews with fisherfolk suggest that on average they travel ~20 km to fish (Harborne et al. 2008). Therefore, the project considered human populations within 20 km of each fish survey site, and divided this figure by the area of reef within the same distance, resulting in a metric of human population pressure per km^2. Investigation of variables at larger scales, such as within 200 km as in Williams et al. (2015), demonstrated that they were unlikely to be informative because they included large population centres within Cuba, Florida, and Haiti, and there is little evidence that these populations have a widespread influence on fishing pressure in The Bahamas.

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[4] http://sedac.ciesin.columbia.edu/

Island geomorphology

Geomorphology may be an important driver of total fish biomass at global scales (Cinner et al. 2013) and can influence finfish catches (Kronen et al. 2010). Geomorphology for each island was derived from levels 2 and 3 of the MCRM project classification scheme (Andréfouët et al. 2006), but there is limited variability with most areas of The Bahamas categorised as 'oceanic island', and only one atoll (Goldberg 2016).

Latitude and longitude

The reef fishes of The Bahamas are recognised as being located within a single biogeographic region in the western Atlantic (Kulbicki et al. 2013). Consequently, biogeography of fishes is unlikely to be a major confounding factor in the analyses, as it might be when working across biogeographic regions. However, there may be some small-scale biogeographic patterns, and latitude and longitude may also be a significant factor in models of finfish catches (Kronen et al. 2010). For example, illegal fishing in Bahamian waters may occur in remote areas near Cuba or Haiti. Therefore, latitude and longitude were included in the models of both fishing impact and standing stock to account for any variation in fish assemblages and fishing effort across the region.

Number of larvae from upstream

The importance of larval supply on the abundance of reef fishes has been a hotly debated topic, leading to a large literature on the relative importance of pre- and post-settlement processes (see Hixon 2011 for an overview of this debate). The debate is now generally less polarised, with the importance of pre- and post-settlement processes apparently varying among species and in space and time. To investigate the importance of larval supply in predicting fish standing stocks, we used a biophysical model of larval supply throughout the area (see Cowen et al. 2006 for a full description of the model)[5]. Briefly, polygons of reef habitat were identified throughout The Bahamas and surrounding areas that might provide larvae (e.g. Cuba and Florida, Fig. A2), and then 'virtual larvae' were released monthly within a computer simulation of oceanic conditions. Virtual larvae had the biological characteristics of either the yellowtail snapper (*Ocyurus chrysurus*), stoplight parrotfish (*Sparisoma viride*), or bluehead wrasse (*Thalassoma bifasciatum*), so they had different pelagic larval durations and depth preferences. These virtual larvae were tracked within the model, and where they 'settle' was recorded (either back to the same reef, to a different reef, or lost into oceanic water). These data generate a connectivity matrix, showing the proportion of larvae moving from each patch to every other patch.

This connectivity matrix was used to determine the number of arrivals from upstream sources, following the removal of self-recruiting arrivals at each patch (arrivals originating and settling at the same patch). This metric was calculated because local-retention patterns tend not to be reliable when extracted from biophysical models because they ignore all local processes (e.g. tides, local-scale eddies, and near-shore turbulence). The number of larvae arriving was adjusted to account for the amount of forereef in each polygon (i.e. virtual larvae may be concentrated on a small patch of reef, so it is important to consider arrivals per unit area of reef). Note that these metrics are not estimates of actual numbers of larvae arriving at each patch, but are values representing the relative strength of

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

fluxes of larvae among patches. Furthermore, the metrics are the same for every location within each patch. Therefore, the larval arrival metrics for each modelled patch were assigned to every reef cell that was located within that patch.
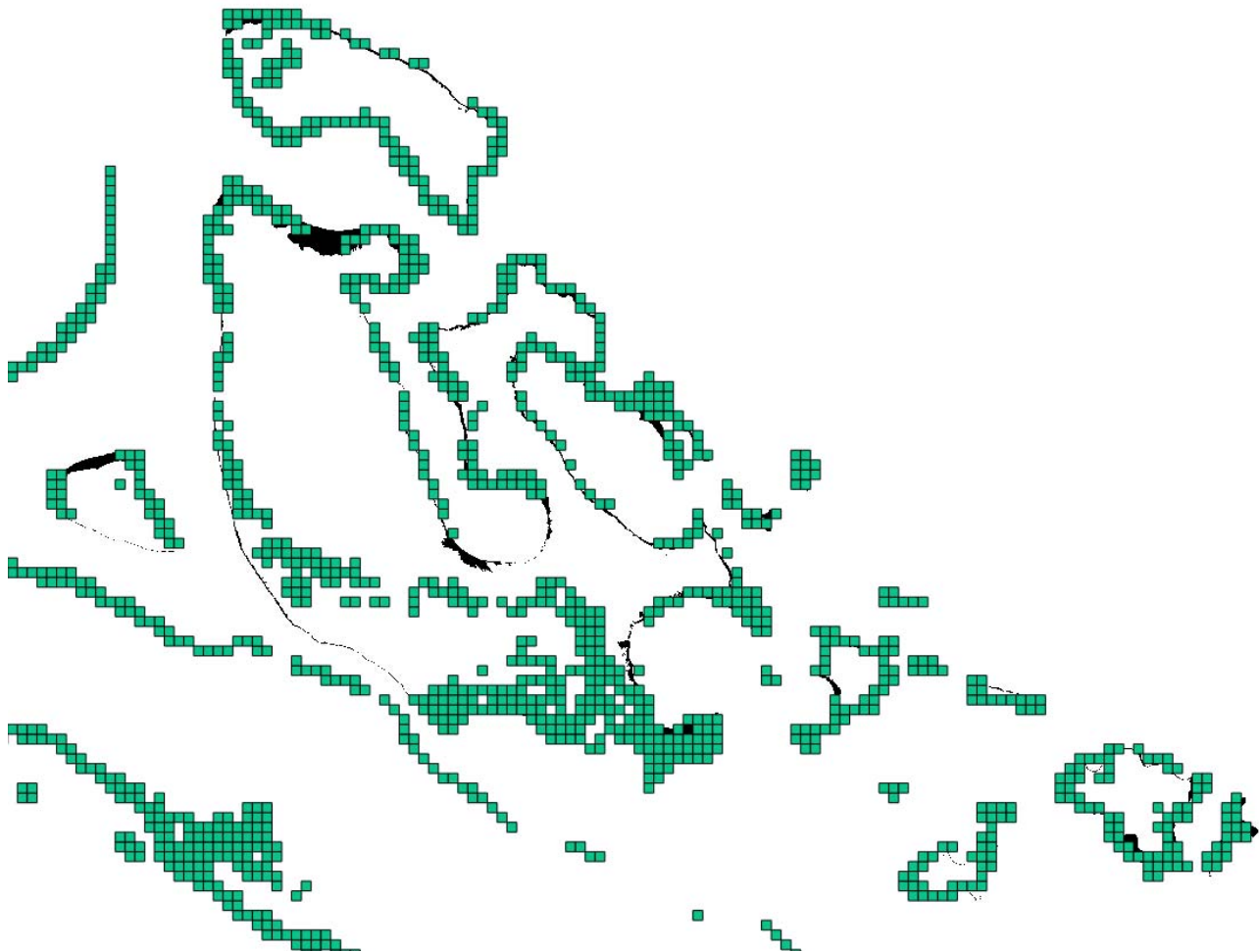

Fig. A2. The reef polygons (green squares) included in the biophysical model of Bahamian larval connectivity. Additional reef polygons that may supply larvae to The Bahamas (e.g. Cuba, Florida) are not shown on this map. Extent of the forereefs considered in this project are shown in black.

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 standing stock. 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 within islands, they do capture larger-scale patterns in productivity across the region (Gove et al. 2013). Mean monthly chlorophyll-*a* data from 2010-2014 at a resolution

of ~350 km^2 was obtained from an online source[6]. Remotely sensed estimate of productivity of over reefs are confounded by bottom reflectance, so only data from pelagic areas around each reef were used. These areas were identified using the protocol described in Gove et al. (2013): productivity data was excluded where they intersected with any polygon delineated by the MCRM, and then the productivity value for each reef cell was derived as the value contained within the nearest, entirely pelagic data cell.

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 protected area was included within the model of reef fishing impact. Although whether fishing is allowed at a given site or not should be captured within the fishing impact data layer, protected status was also included in the model of standing stock to account for any differential effects on all fishes compared to all AGRRA species (i.e. the fishing impact model only considers fishing of commercially important species, and the effect may be clearer in the standing stock model that considers all AGRRA species). A national-scale data layer of the extent of marine protected areas was available. This layer was refined through expert opinion to classify no-take reserves or areas with some enforcement of regulations. The remaining reef cells were considered to have no protection.

Rugosity

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). Rugosity (maximum vertical relief) was estimated *in situ* during fish surveys. However, rugosity cannot be reliably modelled continuously across the entire Bahamas. Therefore, predictions for the continuous maps of fishing impact and standing stocks were calculated using mean coral cover for sites used in the fishing impact model (71.5 cm) or for survey sites in *Orbicella* reefs (86.5 cm) or gorgonian plains (20.4 cm) as appropriate within the standing stock model.

Sea surface temperature

As ectotherms, temperature is the primary abiotic factor 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 standing stock. Sea surface temperature data were obtained online from the Coral Reef Temperature Anomaly Database (CoRTAD)[7], and used data from 2008-2012 at a 4 km resolution. The metric of sea surface temperature followed Williams et al. (2015), namely the mean temperature from the coldest month of each year (i.e. the lower climatological mean) at each reef location. The final metric was calculated as the mean temperature of the coldest month over the five year period from 2008-2012.

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[6] http://www.science.oregonstate.edu/ocean.productivity/index.php
[7] http://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0126774

Season

Season can affect benthic assemblages and herbivory (Ferrari et al. 2012) and may represent aspects of fish spawning behaviour (Sherman et al. 2016). Season was assigned to each fish survey based on the date it was undertaken.

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). Therefore, wave exposure was included in models of both fishing impact and standing stock.

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 Bahamas as part of a project to categorise the physical environments of the region (Chollett et al. 2012)[8]. This data layer was used to assign a surface wave exposure to each forereef cell in The Bahamas.

Year

With the exception of inside marine protected areas, fishing typically increases over time with continually increasing impacts on fish assemblages. Inevitably, the large data set assembled for this project was not collected simultaneously, and some data was collected in 2001. Year of collection was included in the models of both fishing impact and standing stock to account for any temporal variation in fish assemblages. Where year was a significant variable, values of fishing impact or standing stock across the region were predicted across the continuous maps using 2014 to provide currently expected values that are most useful in on-going management planning.

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[8] Data supplied by Iliana Chollett

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