




# Seascape models reveal places to focus coastal fisheries management

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**Abstract.** To design effective marine reserves and support fisheries, more information on fishing patterns and impacts for targeted species is needed, as well as better understanding of their key habitats. However, fishing impacts vary geographically and are difficult to disentangle from other factors that influence targeted fish distributions. We developed a set of fishing effort and habitat layers at high resolution and employed machine learning techniques to create regional-scale seascape models and predictive maps of biomass and body length of targeted reef fishes for the main Hawaiian Islands. Spatial patterns of fishing effort were shown to be highly variable and seascape models indicated a low threshold beyond which targeted fish assemblages were severely impacted. Topographic complexity, exposure, depth, and wave power were identified as key habitat variables that influenced targeted fish distributions and defined productive habitats for reef fisheries. High targeted reef fish biomass and body length were found in areas not easily accessed by humans, while model predictions when fishing effort was set to zero showed these high values to be more widely dispersed among suitable habitats. By comparing current targeted fish distributions with those predicted when fishing effort was removed, areas with high recovery potential on each island were revealed, with average biomass recovery of 517% and mean body length increases of 59% on Oahu, the most heavily fished island. Spatial protection of these areas would aid recovery of nearshore coral reef fisheries.

**Key words:** coral reefs; essential habitat; fisheries replenishment; fishing effort; Hawaii; LiDAR; marine protected areas; marine reserve design; predictive modeling; recovery potential; spatial planning; species distribution modeling.

## INTRODUCTION

Coastal marine ecosystems are in decline worldwide due to multiple interacting stressors operating from global to local scales (Lotze et al. 2006, Norström et al. 2016). Fishing is one of the most direct of these stressors and removes fish biomass, distorts trophic and size structure, and alters community composition resulting in the loss of ecological functions and ecosystem services (Jackson et al. 2001). These demonstrated impacts point to a need for better management of fisheries worldwide, including the implementation of additional marine reserves to recover fish biomass and restore key ecosystem functions (Edgar et al. 2014). Numerous studies have documented the benefits of spatial protection on exploited fish assemblages, such as increased biodiversity and resilience (Mellin et al. 2016), resistance to invasive species (Giakoumi and Pey 2017), and fisheries enhancement (Weigel et al. 2014). Increases in biomass and size of targeted fish species in marine reserves have been particularly well documented (Lester et al. 2009). Current research includes a focus

on maximizing reserve benefits by incorporating connectivity, the demographic linking of local populations through dispersal of individuals as larvae, juveniles or adults, and habitat quality as explicit considerations in marine reserve design (Almany et al. 2009, Green et al. 2015). As larval export from marine reserves has been shown to replenish stocks in fished areas (Harrison et al. 2012), reserves that support healthy spawning populations which act as larval sources may be key for fisheries recovery. Thus, identifying areas with habitats that have the potential to support reproductive populations of targeted fishes is critical to the design of effective place-based fisheries restoration strategies.

Rarely, however, do studies of coastal marine ecosystems integrate local context and stressors in estimates of recovery potential. Specifically, fishing patterns must be considered to inform effective placement of marine reserves intended to enhance fisheries. Fishing effects vary geographically and are difficult to disentangle from other factors that influence targeted fish distributions, creating a spatially complex challenge for understanding patterns of fishing impacts on these assemblages (Taylor et al. 2015, Nash and Graham 2016). Spatial ecological modeling techniques, where predicted variable distributions are mapped across geographical space, have proven useful to examine spatial trends and fill gaps in

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coverage of empirical data sets (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009). Models can be calibrated using ecological field survey data to establish relationships between fish species and/or assemblage characteristics and remotely sensed habitat and environmental variables. These calibrated models, referred to here as seascape models, can then be used to make spatial predictions of fish, or fishery indicators, across the area of interest (Pittman and Knudby 2014). However, these approaches have yet to incorporate spatially explicit estimates of fishing pressure and are rarely applied to prioritize areas to inform fisheries replenishment strategies in coastal marine ecosystems.

Seascape variables such as seafloor topography, benthic cover, and wave exposure, at varying spatial scales, have been shown to be important predictors of fish assemblages (Friedlander et al. 2003, Bouchet et al. 2015, Galaiduk et al. 2017). Impacts from fishing have been inferred by comparing fish populations in populated vs. remote areas (e.g., Friedlander et al. 2018) and by using proxies such as local human population density and distance to markets (Williams et al. 2008, Cinner et al. 2013). Fishing effects have also been investigated through studies of fish populations along gradients of protection ranging from gear restrictions (Campbell et al. 2017), to rotational closures (Cohen and Foale 2013), to marine protected areas (MPAs) including full no-take marine reserves (Sciberras et al. 2013). Due to increased availability and coverage of empirical and remotely sensed data sets, there is opportunity to build on these studies by using seascape models to better understand fish habitat relationships in the context of fishing impacts and make realistic and spatially explicit estimates of recovery potential.

We address these knowledge and capacity gaps by developing a set of fishing effort map layers at high resolution and employing machine-learning techniques to create regional-scale seascape models and predictive maps of targeted reef fish biomass and body length for the Main Hawaiian Islands (MHI). We use a large and geographically comprehensive database of reef fish surveys and of predictor variables that includes measures of two-dimensional and three-dimensional spatial patterning of the seafloor and the distribution of wave energy. Study objectives were to (1) quantify and map fishing effort and habitat patterns around the MHI, (2) identify and characterize key habitat variables that promote high targeted fish biomass and body length, (3) model and quantify the recovery potential of targeted fish assemblages in the absence of fishing pressure (in terms of mean biomass and body length), and (4) identify areas with the highest recovery potential to prioritize for management actions.

## METHODS

### *Study area*

The Hawaiian Islands are located near the center of the Pacific Ocean and are the most isolated archipelago in the world. The MHI consist of high volcanic mountain peaks, with steep topographic relief to the coastline and fringing reefs accreting on the submerged slopes. There are eight islands that comprise the MHI, six of which were evaluated in this study (from north to south): Kaua'i, Ni'ihau, O'ahu, Moloka'i, Maui, and Hawai'i islands (Fig. 1). The islands of Lāna'i and Kaho'olawe were not included due to the lack of high-resolution bathymetry data.

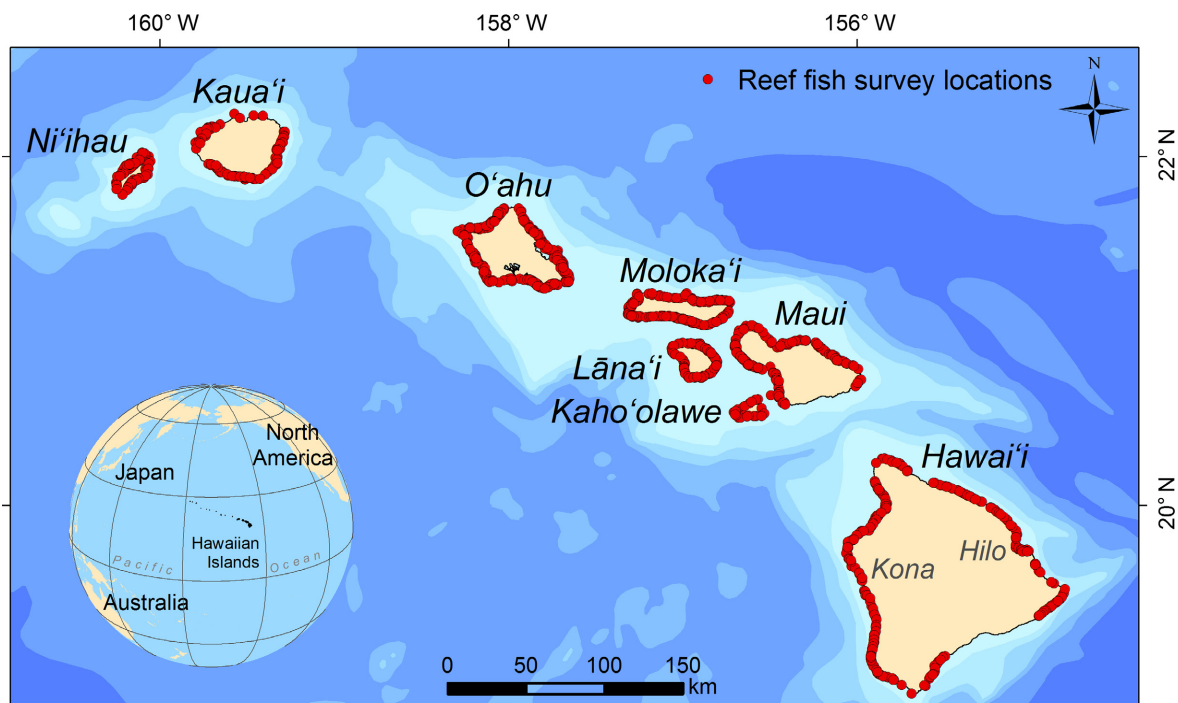


FIG. 1. Main Hawaiian Islands (MHI) study domain with reef fish survey locations used for modeling.

*Reef fish survey data*

A spatially comprehensive data set of reef fish surveys of the MHI conducted between 2010 and 2016 was contributed by the Pacific Islands Fisheries Science Center's Ecosystem Science Division (Heenan et al. 2017). Fish surveys utilized a paired stationary point count (SPC) protocol and were conducted on hard bottom habitat, stratified by reef zone and depth (Heenan et al. 2017). A total of 1,184 independent survey locations across the MHI were used for modeling (Fig. 1). Spatial predictions were generated on a  $60 \times 60$  m resolution grid to account for the dimensions of the survey method and the positional uncertainty of the global positioning systems used to navigate to survey locations.

Targeted species of the MHI nearshore fishery were defined as coral reef fishes having  $\geq 450$  kg of annual recreational or commercial harvest for the past 10 yr (2000–2010), or otherwise recognized as important for recreational, subsistence, or cultural fishing (Hawaii Division of Aquatic Resources 2018). Biomass was estimated using the allometric length–mass conversion  $M = aTL^b$ , where parameters  $a$  and  $b$  are species-specific fitting parameters, TL is total length (cm), and  $M$  is mass (g). Parameters were obtained from a comprehensive assessment of Hawaii length–mass fitting parameters (M. Donovan, unpublished data) and FishBase (Froese and Pauly 2017). Cryptic and soft-bottom species were excluded due to low sampling effectiveness. Planktivores were excluded due to patchy distributions and weak benthic-habitat relationships, as were pelagic species (Appendix S1: Table S1). Targeted species biomass was calculated as the sum biomass of modeled species at each survey location. Targeted species body length was calculated as the average recorded body length of modeled species at each survey location.

*Predictor data*

*Fishing effort.*—We modeled and mapped spatial patterns of fishing effort based on non-commercial island-scale effort estimates (McCoy 2015), following the methods of Lecky (2016) (Wedding et al. 2018). This previous work mapped spatial patterns of catch, though did not incorporate measures of human population in the distribution of shore-based fishing estimates. We did not consider nearshore commercial fishing because it only represents a small fraction of total estimated effort and data quality is questionable (McCoy 2015). Furthermore, commercial fishing data are recorded for large reporting blocks that would obscure fine-scale spatial patterns of fishing effort. Shore and boat fishing were modeled separately by major gear type (line, net, and spear), which were assumed to have different spatial footprints. Despite different magnitudes, patterns of total shore effort hours between gear types were very similar among islands (Appendix S1: Fig. S1) and both shore and boat fishing effort layers were highly correlated among gear types ( $>0.8$  Pearson  $r$ ). Because spear fishing had the largest spatial footprint, highest catch per unit effort, and targets the greatest variety of species, it was used as a proxy of total effort for both shore and boat fishing, respectively.

We used average annual fishing effort (hours per year) for reef fish by island from 10 years of recreational fishery data (2004–2013) compiled by McCoy (2015) and distributed

these values into the nearshore marine area based on weighting factors related to accessibility to fishers. Fishing effort showed a declining trend over time for all islands with the exception of Lāna'i (McCoy 2015), so estimated values were conservative. Marine managed areas where fishing is prohibited were set to zero. For shore fishing, proximity and type of roads along with shoreline steepness were used as proxies for accessibility, and values were weighted by human population within 30 km. To model spear fishing, a logistic decay function was used so effort decreased with depth to a maximum distance of 2 km from shore. The parameters of the function were set based on discussions with fishing experts in Hawai'i and assume the vast majority of spearfishing effort is shallower than 20 m and there is no effort beyond 40 m (Lecky 2016). For boat fishing, accessibility measures were based on distance to boat launch/harbor weighted by human population within 30 km. There was no recreational fishery data available for Ni'ihau (population 170) and, while subsistence fishing does occur, shore-fishing effort was assumed to be zero. To ground-truth the fishing effort maps, estimated shore-based spear fishing effort values were compared to total shore fishing effort values from 12 independent fishing (creel) survey locations across the MHI. Total shore fishing effort values were obtained from Delaney et al. (2017) and compared to derived spear fishing effort maps based on the sum of grid cell values within polygons representing each survey area. Empirical boat based fishing effort estimates were not available for comparison.

*Habitat variables.*—A set of 62 gridded environmental data sets at  $60 \times 60$  m resolution was generated for each island as potential predictor variables used to model reef fish assemblage metrics (Stamoulis et al. 2016). Selection of predictors was based on an extensive literature review and input from experts in Hawaiian reef ecology (Delevaux 2017). There were four types of predictor variables: seafloor topography, benthic habitat composition, geographic, and wave energy.

Seafloor topography variables were included to account for variation in reef fish distributions due to direct and indirect effects of depth and seafloor structure. A gridded synthesis of multibeam sonar and light detection and ranging (LiDAR) bathymetry at 5-m resolution was used as the depth variable and to derive the suite of seafloor topography metrics. For example, the morphometric Slope of slope (a second derivative of bathymetry) measures the maximum rate of change in slope between cells within the specified analytical neighborhood. Slope of slope is a measure of surface topographic complexity, sometimes called terrain roughness, and has been shown to be positively correlated with finer scale in situ measures of rugosity such as chain-tape measurements (Pittman et al. 2009, Pittman and Brown 2011). The modeled area was limited by gaps in the LiDAR bathymetry data. For this reason, the islands of Lāna'i and Kaho'olawe were not modeled, as well as much of the nearshore area around Ni'ihau, and large portions of the north-east and southeast coasts of Hawai'i island.

Benthic habitat composition variables from existing habitat maps (Battista et al. 2007) were included to account for variation in reef fish assemblages arising from the direct and indirect effects of the spatial configuration of benthic habitats. Geographic variables were used to account for variation

in reef fish assemblages arising from spatial location. Wave energy variables were included to account for variation in reef fish assemblages arising from the direct and indirect effects of ocean wave dynamics.

A pairwise correlation analysis was performed on the full set of predictors for the whole study area (MHI). Highly correlated predictors (Spearman  $|\rho| > 0.7$ ) were identified, and those highly correlated with two or more other predictors were removed. In cases where only two predictors were highly correlated, those with greater ecological importance (based on expert opinion and scientific literature) were retained. After the correlation analysis, 25 out of 62 seascape predictors were retained for model development (Table 1; Appendix S1: Table S2).

### Seascape models

Boosted regression trees (BRT) were used to estimate relationships between targeted fish assemblage metrics (biomass and length) and the predictor data sets (De'ath 2007, Elith et al. 2008). These modeled relationships were then used to create spatial predictions of targeted fish biomass and body length. Each metric was modeled independently at the archipelago scale. To make predictions with fishing pressure removed, fishing predictors were set to zero. Statistical models and spatial predictions were generated in R (R Core Team 2014) using the *dismo* (Hijmans et al. 2014) and *raster* (Hijmans 2014) packages. BRT is effective at modeling nonlinearities, discontinuities (threshold effects), and interactions between variables (Breiman 1996, 2001, De'ath and Fabricius 2000).

BRT can accommodate many types of response variables. Since the targeted fish assemblage metrics were continuous variables, they were modeled using a Gaussian (normal) distribution, and appropriate data transformations were applied to improve normality. Targeted fish biomass was fourth-root transformed and targeted fish body length was square-root transformed. Prior to model fitting, reef fish survey data were randomly divided into model training (70%) and test (30%) subsets. The test data set was withheld from model fitting and used only to evaluate predictive performance (map accuracy). Although boosting makes BRT models less prone to overfitting (Friedman 2002, Elith et al. 2008), predictive performance was evaluated using the test data to measure how well the model generalized to new data.

Model fitting and selection was accomplished following the procedures detailed in Elith et al. (2008). To increase parsimony, selected models were then simplified to remove less informative predictor variables. This was accomplished by dropping the least contributing predictor, re-fitting the model, and computing the change in predictive deviance relative to the initial model (Elith et al. 2008). The predictive deviance indicates the amount of variation in the response variable not explained by the model. This process was repeated and the predictive deviance was plotted over the full range of predictors. The final number of predictors was selected at the inflection point in the predictive deviance curve, where change in predictive deviance increased relative to previous values. In general, this resulted in the removal of predictors that explained  $<5\%$  of the variation in the response variable.

Bootstrapping was used to create spatially explicit predictions and calculate prediction precision. The model training data set was repeatedly sampled with replacement to create 20 bootstrap samples. Using the optimal parameter value combination and simplified set of predictor variables, a BRT model was fit to each bootstrap sample and used to make predictions to a spatially explicit gridded map using the values of the predictor variables at each grid cell. This resulted in a total of 20 spatial prediction grids that were used to calculate the mean and coefficient of variation (CV) in each grid cell (Leathwick et al. 2006), where low CV values indicate high precision. Prediction means and CVs were plotted against each other to visualize the relationship between the magnitude and precision of predictions. The mean of the bootstrapped predictions was used for interpretation and further analysis.

Model performance was evaluated using the cross-validation percent deviance explained (PDE) and test PDE. The cross-validation PDE is the 10-fold cross-validation estimate of the percent deviance explained for the best model (as described above). Similarly, the test PDE was determined by calculating the percent deviance explained by the model when evaluated using the model test data set. Both metrics indicate overall model fit, but the test PDE also provides a measure of model performance when predicting data that were independent of model fitting. To better understand the relationship between measured and predicted values, average measured values by island were compared with predicted

TABLE 1. Final predictor data sets used in model development.

Predictor data set types	Data sets	Description
Fishing (2)	boat-fishing spear, shore-fishing spear	boat and shore based fishing effort represented by spearing effort
Seafloor topography (12)	depth, slope, slope of slope, aspect, planar and profile curvature, bathymetric position index (BPI)	seafloor topography and exposure metrics derived from LiDAR bathymetry; slope, slope of slope, and BPI were calculated at two scales
Benthic habitat composition (7)	percent cover of coral, crustose coralline algae, macroalgae, turf, and soft bottom, proximity index, Shannon's diversity index	percent benthic cover of major cover types, seascape fragmentation/patch isolation, habitat diversity
Geographic (3)	latitude, longitude, distance to shore	geographic location and distance from shore
Wave energy (1)	wave power	wave height $\times$ wave period

*Notes:* The number of individual data sets of each type is indicated in parenthesis. A pairwise correlation analysis was performed on the full set of predictors for the whole study area (Main Hawaiian Islands [MHI]). Highly correlated predictors (Spearman  $|\rho| > 0.7$ ) were identified and those highly correlated with two or more other predictors were removed. See Appendix S1: Table S2 for more details.

values under current fishing levels and with fishing pressure removed. Finally, the relative importance of predictor variables for each model was evaluated and partial dependence plots were generated for each predictor variable to interpret their individual effects on the response variables (De'ath 2007, Elith et al. 2008).

#### *Recovery potential in the absence of fishing*

Final BRT models were used to generate gridded predictions of targeted fish biomass and body length across the MHI study area ( $60 \times 60$  m resolution) under current fishing levels and with fishing pressure removed. Values from these layers were used to create distribution curves of predicted biomass and body length under each fishing scenario for each island. Differences were assessed visually and tested using a two-sample Kolmogorov-Smirnov test. Overall change in spatial patterns of high predicted targeted fish biomass and body length were assessed using maps of predicted values. Finally, means and percent change between predicted values across all modeled habitats for present conditions and with fishing effort set to zero were calculated by island to estimate recovery potential at the island scale.

#### *Spatial prioritization for management*

To identify places that could be prioritized for management actions that would support fisheries restoration, we evaluated spatial differences between predictions of targeted fish biomass and body length under current fishing levels and predictions with fishing effort set to zero. We assumed that areas with the greatest differences have the highest potential for fisheries replenishment if fishing pressure were limited or removed through management actions. To identify areas where predictions differed significantly between models, we applied the methodology of Januchowski et al. (2010) using the SigDiff function in the R package SDMTools (VanDerWal et al. 2014). We computed the significance of the pairwise differences (for each grid cell) for the response variables (biomass and length) relative to the mean and variance of all differences for each island. The resulting probability values represent the area under the curve of a Gaussian distribution defined by the mean and variance across all cells for that island. The spatial grids representing the individual significance values were reclassified to indicate cells where predictions with fishing pressure removed were significantly higher than present predictions ( $P < 0.10$ ). Mean absolute difference and mean percent change relative to modeled values under current fishing pressure were calculated for cells showing significant increase by island. Finally, the spatial grids representing regions of significant increase for biomass and body length were combined into a single map for interpretation.

## RESULTS

### *Fishing and habitat patterns*

Modeled shore-spearfishing effort values under-estimated total shore effort from creel surveys by a factor of two. However, there was a strong positive relationship ( $r^2 = 0.7$ )

across all sites, indicating that this measure of shore spearfishing effort provides a reliable proxy for overall shore fishing effort (Fig. 2). The highest intensity of shore fishing effort was estimated to be near the highly populated areas of Hawai'i Island near Hilo and Kona, followed by the south and southeast shores of O'ahu and near the populated areas around Kahului and Kihei on Maui (Fig. 3a). Boat fishing effort for reef fish was generally much lower than shore fishing effort (Fig. 3b). The highest values for boat fishing effort were found offshore of south O'ahu. Moderate boat fishing effort was found along the southwest shore of Kaua'i, south Moloka'i, northwest Maui, and near Kona and Hilo on Hawai'i Island (Fig. 3b).

While a more complete description of marine habitat patterns in the MHI is outside the scope of this study, here we focus on several key variables shown to be important determinants of targeted fish biomass and body length. Seafloor topographic complexity (slope of slope) was highly variable within islands. Generally, areas with low values (indicating flat bottom) encompassed the greatest area, while high values (indicating complex structure) were few and widely dispersed. Islands with more shallow water habitat such as O'ahu tended to have more flat bottom. Sine aspect represents the east-west exposure of benthic habitats. The highest values were located on east-facing shores and the lowest values on west-facing shores. Eastern exposures are most exposed to the predominate trade winds and associated short-period swells. Wave power was highest on the north shores of all islands, with the exception of Hawai'i Island, and generally decreased among islands from north to south. Depth increased with distance from shore on all islands, and the largest shallow water areas were found on O'ahu and the south shore of Moloka'i.

### *Seascape models*

The final BRT model for targeted fish biomass had nine predictors. Cross-validation PDE was 37.5%, and test PDE was 35.3%. The final BRT model for targeted fish body length had nine predictors, a cross-validation PDE of 21.2%,

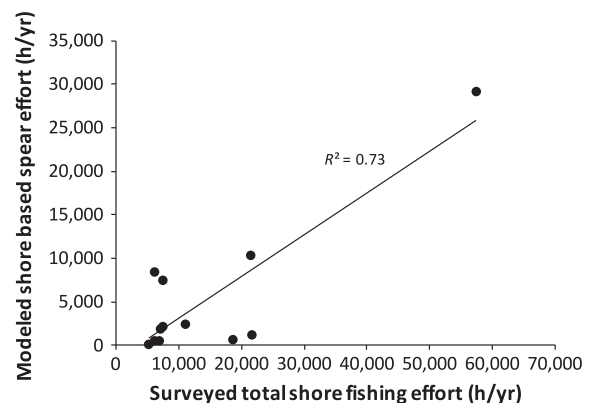


FIG. 2. Comparison of modeled shore fishing effort with empirical fishing survey values from 12 sites across the MHI (Hawai'i, 4; Maui, 2; O'ahu, 5; Kaua'i, 1). Total fishing effort values were obtained from Delaney et al. (2017) and compared to derived spearfishing effort maps based on the sum of grid cell values within polygons representing each survey area. The equation of the fitted line is  $y = 0.48x - 1660$ .

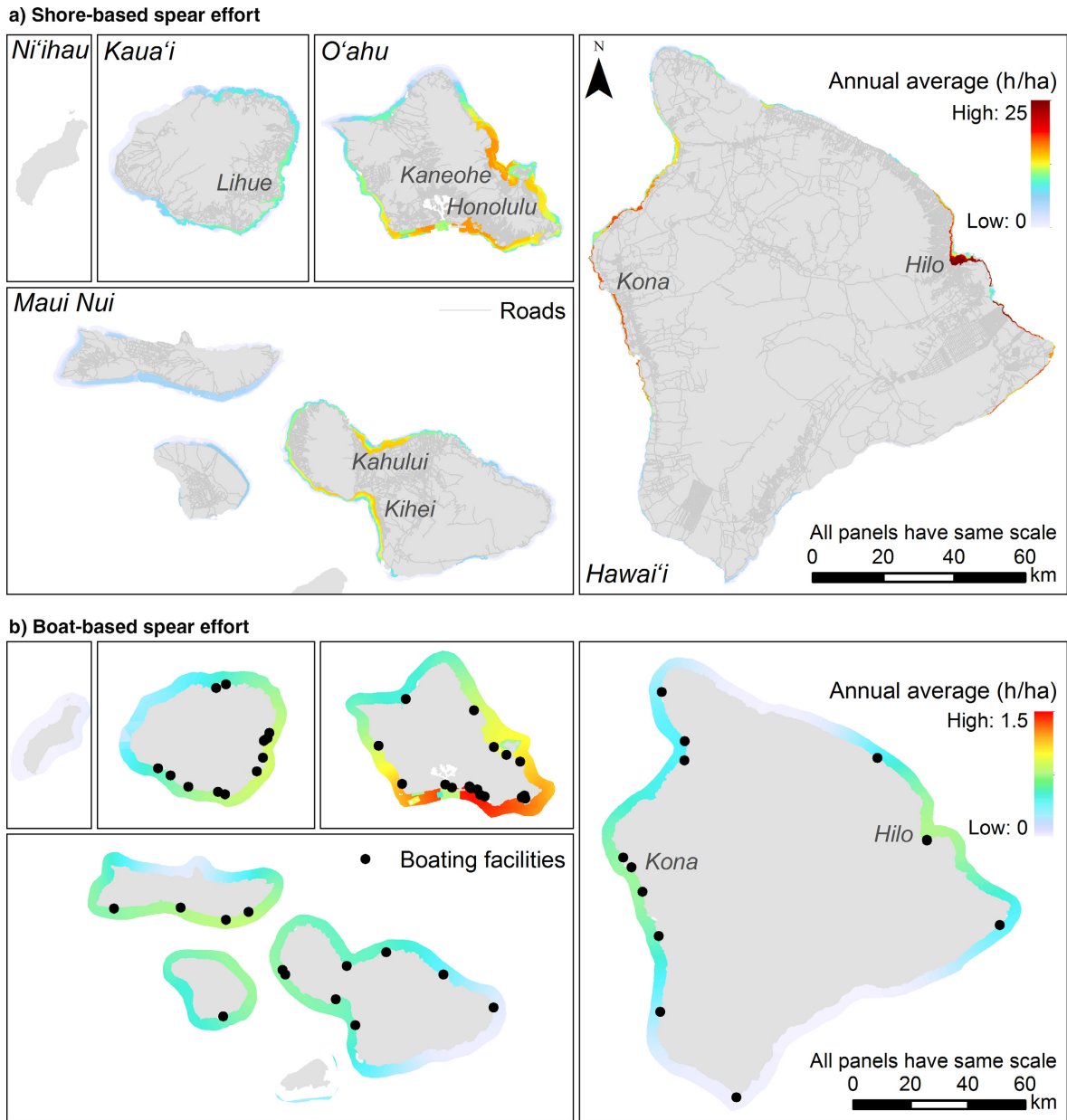


FIG. 3. Shore fishing effort around the MHI as represented by (a) shore-based spear effort (h/ha). Boat fishing effort around the MHI as represented by (b) boat-based spear effort (h/ha). Maui Nui encompasses the islands of Maui, Moloka'i, and Lāna'i.

and a test PDE of 21.4%. Based on these metrics, the biomass model fit better than the length model, and had higher predictive accuracy. Plots of prediction means vs. CVs showed that higher predicted values generally had higher precision ( $CV < 0.5$ ; Appendix S1: Fig. S2). When predictions for biomass and length under present fishing levels were compared to fish survey data at the island level, BRT predictions tended to underestimate means of field measured values within one standard deviation (Appendix S1: Fig. S3). This effect increased with the magnitude of the measured values. However, the BRT predicted values well represented the relative differences between islands (Appendix S1: Fig. S3).

Biomass was largely driven by shore fishing, while length responded primarily to boat fishing (Fig. 4). In terms of

habitat, biomass was primarily driven by topographic complexity (slope of slope) and length was most associated with exposure (sine aspect). Depth and wave power were other key habitat variables that influenced both targeted fish biomass and body length (Fig. 4). These habitat variables all had positive relationships with the assemblage indicators, whereas the fishing variables had negative relationships (Fig. 4).

*Effects of fishing and habitat on fish biomass and body length*

Targeted fish biomass and body length had similar negative relationships with fishing predictors. Both declined rapidly from 0 to 2 h/ha/yr of shore (spear) fishing effort and

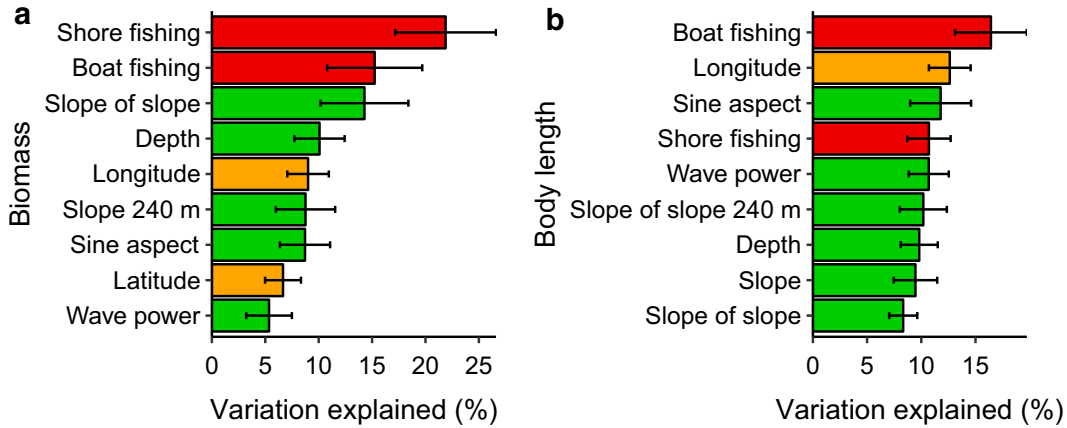


FIG. 4. Final predictors for MHI models based on boosted regression tree (BRT) model results for (a) biomass and (b) body length. Relative percent variation explained is shown on the x-axis and the color represents the directionality of the relationship (red, negative; green, positive; orange, non-directional). Values are mean  $\pm$  standard deviation.

0–0.2 h/ha/yr of boat (spear) fishing effort, then were relatively flat across a wide range of increasing effort values (Fig. 5; Appendix S1: Fig. S4, Fig. S5). Areas of shore fishing effort <2 h/ha/yr include the less populated islands, Ni‘i-hau, Moloka‘i, and Lāna‘i, as well as remote and difficult to access areas of the more populated islands such as west Kaua‘i, east Maui, and south Hawai‘i Island (Fig. 3a). Areas of low boat fishing effort (<0.2 h/ha/yr) included Ni‘ihau, northwest Kaua‘i, north O‘ahu, north Moloka‘i, west Lāna‘i, and north and south Hawai‘i (Fig. 3b).

Slope of slope, a measure of topographic complexity, was the most important habitat predictor for targeted reef fish biomass, which increased rapidly at the low end of the scale (0–8°; Appendix S1: Fig. S4). Seafloor depth had a strong positive relationship with targeted fish biomass, which increased with depth before leveling off at around 17 m. Maximum slope in a 240 m radius was also positively related to biomass with a steep increase from 0 to 10°. Sine aspect (exposure) was positively related to biomass, which increased linearly from –1 (west facing) to 1 (east facing), and wave power, responding more at higher levels (>10,000 kW/m, Appendix S1: Fig. S4). Predictor relationships for fish body length were

similar to those for biomass (Appendix S1: Fig. S5). However, there was a stronger relationship with wave power and a weaker relationship with slope of slope. In addition, the relationship of average body length and sine aspect was not linear and length increased with depth up to 25 m before leveling off. Targeted fish body length was also positively related to maximum slope of slope within a 240 m radius, peaking between 25° and 40°; and slope, increasing from 0° to 5° (Appendix S1: Fig. S5). Thus, in the absence of fishing pressure, targeted fish biomass and body length were generally predicted to reach their highest values in habitats with slope of slope >8°, eastern exposures (sine aspect > 0), wave power >10,000 kW/m, and at depths >17 m.

*Recovery potential in the absence of fishing*

All islands except for Ni‘ihau (which was assumed to have negligible fishing pressure) showed a significant increase in predicted biomass when the influence of fishing was removed (Fig. 6). Biomass predictions for these islands under present fishing levels had distributions that were right skewed, indicating primarily low biomass levels. When fishing effort was set to zero, these distributions flattened out, shifted right, and became more symmetrical, indicating overall increases in mean biomass (Fig. 6). Targeted fish biomass was highest in areas less accessible to humans such as the north shores of most islands and the east shore of Maui. However, when fishing pressure was removed biomass increased across all suitable habitats with the highest increases in deeper areas with high topographic complexity (Appendix S1: Figs. S6 and S7). O‘ahu (the most populated island, with highest overall fishing effort) showed the largest predicted increase in biomass, followed by Kaua‘i, Moloka‘i, Maui, Hawai‘i, and then Ni‘ihau (Table 2).

All islands except for Ni‘ihau showed a significant increase in predicted fish body length when the influence of fishing was removed (Fig. 7). Under current fishing levels, the shapes of predicted fish length distributions varied by island. When fishing effort was set to zero, predicted length distributions maintained their general shape and shifted to the right indicating an increase in average body length

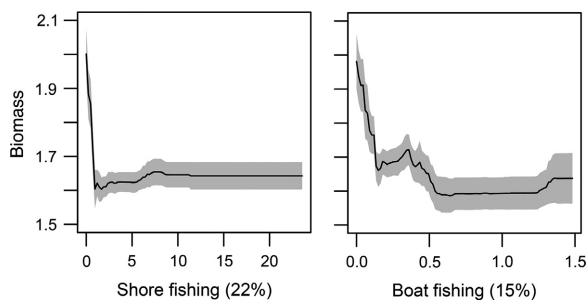


FIG. 5. Partial dependence plots of fishing predictors for the targeted reef fish biomass model. The y-axis is transformed biomass (fourth-root) and the x-axis is the fishing predictor variable (h/ha/yr). Plots represent the relationship of biomass with each predictor individually when all other predictors are held at their mean. Lines are the mean of bootstrapped models plus and minus the standard deviation.

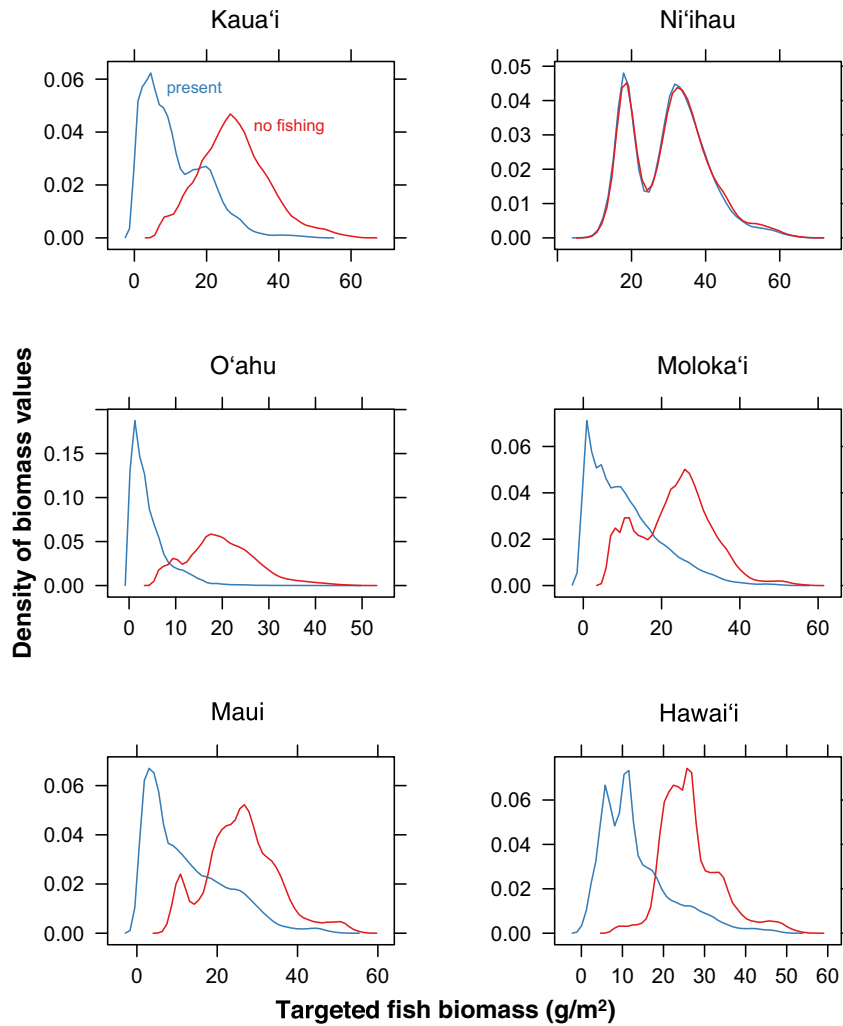


FIG. 6. Distributions of predicted biomass values under present fishing levels (blue) and with fishing removed (red) for each island. The x-axis is biomass values per 60 × 60 m grid cell and the y-axis is frequency of biomass values as a proportion of the total number of grid cells per island (density).

(Fig. 7). Similar to biomass, larger fishes were located in areas that are less accessible to humans such as north shores of most islands and the east shore of Maui (Appendix S1: Figs. S8 and S9). When fishing effort was set to zero, fish length increased in all areas with the highest increases along eastern exposures and areas with high wave power. As with biomass, O'ahu showed the largest relative increase in fish body length when fishing pressure was removed; the other islands showed smaller increases (Table 3).

*Spatial prioritization for management*

These analyses identified areas with the highest recovery potential (i.e., areas with high quality habitat and currently under high fishing pressure), which would be expected to respond positively to management of fishing effort. Because current fishing effort was assumed to be zero in existing marine reserves, these areas were not selected. Areas with highest recovery potential for targeted reef fish biomass tended to be patchy, while areas with highest projected recovery for body length were more continuous. Locations with high recovery

potential for targeted fish biomass and body length were usually found in the same areas, though often with little direct spatial overlap (Fig. 8). In general, these areas were located on the east-facing shores of Kaua'i and O'ahu, the southeast shore of Moloka'i, and the west shore of west Maui (Fig. 8). In

TABLE 2. Predicted mean biomass (g/m<sup>2</sup>) and percent increase for targeted reef fishes under present conditions and with fishing pressure removed.

Island	N	Present		No fishing		Increase (%)
		Mean	SD	Mean	SD	
Kaua'i	67,967	11.2	8.7	27.6	9.7	147
Ni'ihau	10,677	30.0	10.2	30.5	10.4	2
O'ahu	84,870	4.2	4.1	19.9	7.6	370
Moloka'i	38,220	10.9	9.2	23.5	9.4	116
Maui	43,830	12.5	10.0	26.1	9.1	110
Hawai'i	30,702	13.4	8.7	26.6	7.3	98

Notes: N is the sample size representing total number of spatially predicted grid cells per island. SD is standard deviation. Islands are ordered from north to south.



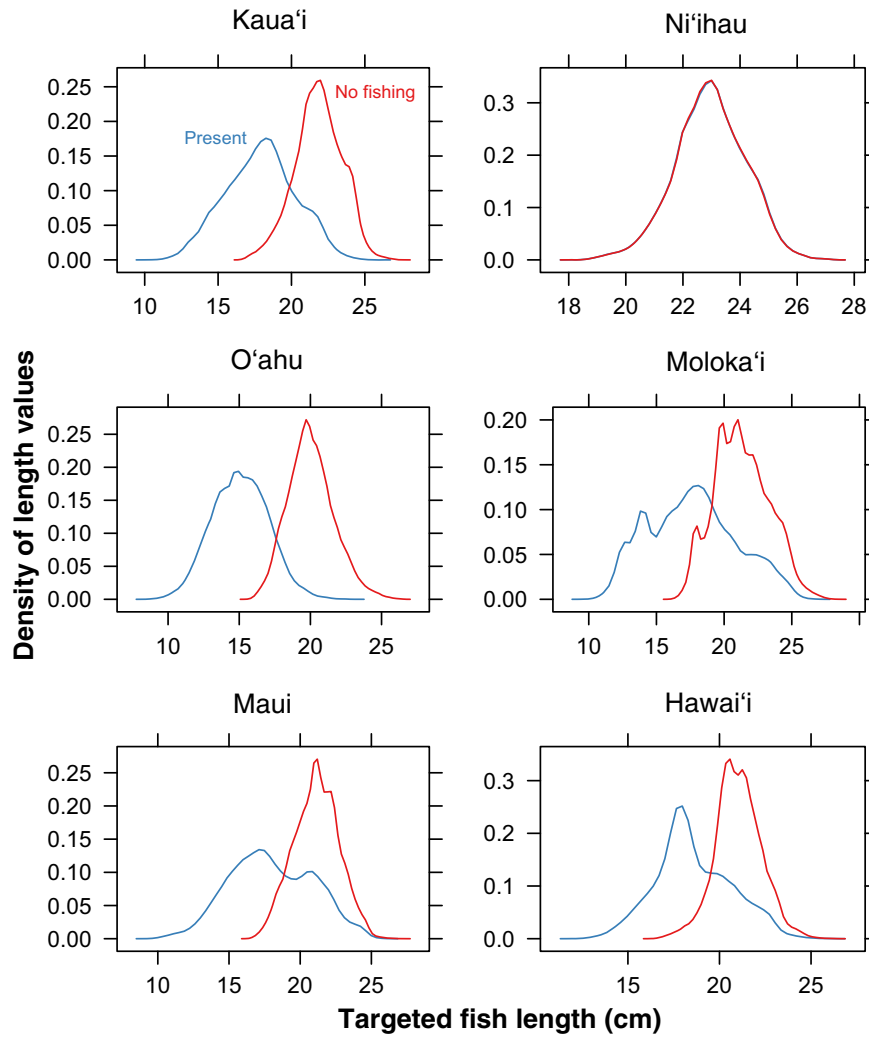


FIG. 7. Distributions of predicted length values under present fishing levels (blue) and with fishing removed (red) for each island. The *x*-axis is length values per 60 × 60 m grid cell and *y*-axis is frequency of length values as a proportion of the total number of grid cells per island (density).

TABLE 3. Predicted mean body length (cm) and percent increase for targeted reef fishes under present conditions and with fishing pressure removed.

Island	<i>N</i>	Present		No fishing		Increase (%)
		Mean	SD	Mean	SD	
Kaua'i	67,967	17.9	2.4	21.8	1.6	22
Ni'ihau	10,677	23.0	1.2	23.0	1.2	0
O'ahu	84,870	15.1	2.0	20.0	1.6	33
Moloka'i	38,220	17.7	3.2	21.3	2.0	21
Maui	43,830	18.0	2.9	21.1	1.6	17
Hawai'i	30,702	18.6	2.1	21.0	1.3	13

Notes: *N* is the sample size representing total number of spatially predicted grid cells per island. SE is standard error of the mean.

addition, the prioritization analysis identified areas on the north shore of Kaua'i, around Mōkapu point and the southeast shore of O'ahu, Mā'ili point on west O'ahu, northwest Moloka'i, Ma'alaea bay on Maui, west Hawai'i Island just north of Makole'a point, and east Hawai'i Island around Cape Kumukahi and north of Kaloli point (Fig. 8). The largest

relative change in biomass for regions of significant increase were on O'ahu and Kaua'i, while largest relative increases in body length for these areas were on O'ahu, with smaller levels of increase on Kaua'i, Moloka'i, and Maui (Table 4). Ni'ihau showed minimal change in biomass and body length.

#### DISCUSSION

Inferred fishing effort patterns were highly variable around the MHI and seascape models indicated a low threshold beyond which targeted fish assemblages were severely impacted. Sparsely populated islands Ni'ihau and Moloka'i had fishing effort below this threshold, as did large, and often remote, areas on the other islands. Seascape models also identified seafloor topographic complexity, exposure, wave power, and depth as the key variables that influenced the distribution of high targeted fish biomass and body length and characterized productive habitats. Fish biomass was most sensitive to shore- and boat-based fishing, as well as topographic complexity, whereas average body length

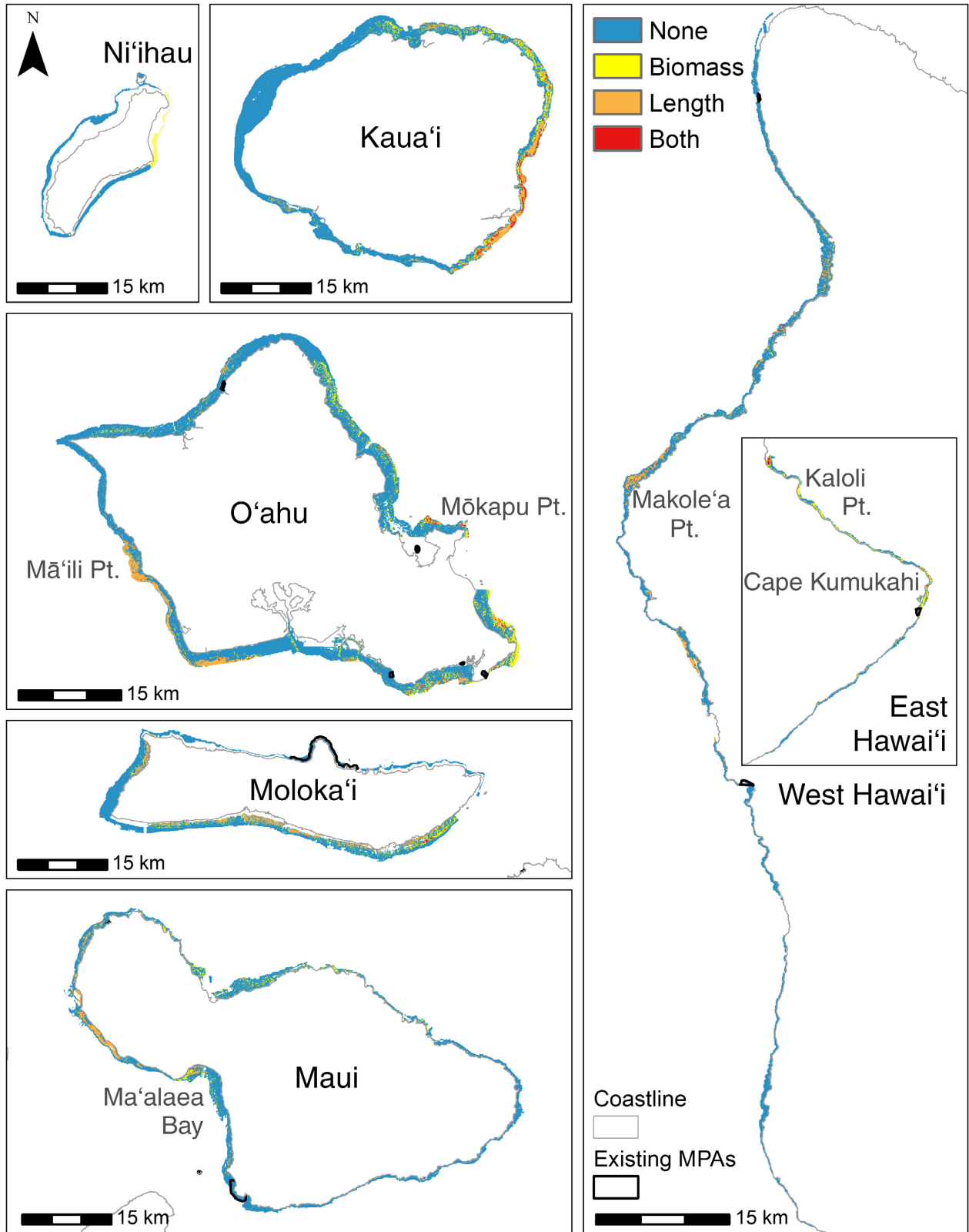


FIG. 8. Regions of significant increase ( $\alpha = 0.1$ ) in MHI model predictions of biomass and length after removal of fishing. Existing no-take reserves and restricted access areas are outlined in black.

TABLE 4. Biomass (g/m<sup>2</sup>) and fish length (cm) mean, standard deviation (SD), mean percent increase, and standard deviation of percent increase between MHI model predictions for regions of significant increase shown in Fig. 8.

Island	Biomass increase				Length increase			
	Mean	SD	Mean %	SD %	Mean	SD	Mean %	SD %
Kaua'i	29.4	2.6	383	184	6.5	0.6	45	7
Ni'i'hau	3.6	0.9	11	2	0.0	0.0	0	0
O'ahu	25.9	2.8	517	268	7.3	0.5	59	10
Moloka'i	21.6	2.2	349	200	5.8	0.2	43	4
Maui	23.4	2.2	256	125	6.2	0.6	46	9
Hawai'i	21.9	2.1	203	114	4.5	0.4	29	4

responded primarily to boat fishing and was strongly influenced by exposure. While the highest targeted reef fish biomass and body lengths were mostly restricted to areas not easily accessed by humans; when fishing effort was set to zero, high values of biomass and body length were widely distributed among suitable habitats. By comparing modelled current targeted fish distributions with those predicted when fishing pressure was removed, areas with high recovery potential were revealed, with significant increases in average biomass and length across the MHI (Table 4).

#### *Fishing effort*

An integral component of this research was the application of spatially continuous fishing effort layers developed for the MHI. We chose to use fishing effort rather than catch because derived catch estimates incorporate catch per unit effort (CPUE), which varies in relation to a number of factors including fish abundance (Maunder et al. 2006). Because fish biomass is also related to fish abundance, fish catch, unlike fishing effort, would not be independent of our response variable. Our derived fishing effort layers represent the most spatially comprehensive, high resolution, and broad-scale products yet created to quantify spatial patterns of coral reef fishery effort. However, a number of simplifying assumptions were made in order to develop these layers, primarily that fishers are more likely to frequent accessible areas, more likely to fish close to home, and that numbers of fishers are proportional to total population (Stewart et al. 2010). For these reasons, our fishing effort maps may possibly capture additional impacts related to accessibility and proximity to humans, such as land based source pollution. Though our fishing layers were strong predictors of fishery indicators and have been corroborated with fine scale effort data from creel surveys, there is considerable scope to improve them further. Future studies should focus on testing large-scale drivers of fishing effort based on local-scale empirical data.

Our results show the greatest impacts on targeted reef fishes within the first 10% of modeled ranges for shore and boat fishing effort. This is supported by previous research indicating that the greatest impacts from fishing occur at low fishing levels (Jennings and Polunin 1996, Jennings and Kaiser 1998). There are few examples in the literature showing this relationship for coral reef fisheries; it has important implications for management as it highlights the importance of no-take MPAs and suggests that fishing effort in rotational closures should be carefully managed.

#### *Fish response variables*

Biomass and size of targeted fish species have often been used to evaluate the effects of fishing pressure (Dulvy et al. 2004, Nicholson and Jennings 2004). The theoretical basis is that larger fishes are generally more targeted; the accumulated effects of fishing mortality reduce the number of older, and therefore larger, fishes in a population; and that large-bodied species are more vulnerable to fishing due to slow population turnover (Jennings et al. 1998, 1999). Both biomass and fish length are thought to represent the relative abundance of large and small individuals (Shin et al. 2005). However, our results suggest they are not interchangeable and instead capture different aspects of the fished assemblage. Biomass was more sensitive to fishing compared to mean length. While higher average length always reflects greater relative abundance of large individuals, high biomass can also result from high abundance of small individuals. This was supported by the fact that slope of slope (60 m) was the top habitat predictor for biomass, while maximum slope of slope in a 240 m radius explained more variability in average length. Larger individuals and species generally have a larger geographical range of movements and thus respond to broader-scale measures of seascape structure (Pittman et al. 2007, Wedding et al. 2008, Kendall et al. 2011). It is important to consider both fished assemblage biomass and size distribution because large individuals represent high-value species and high reproductive capacity (Birkeland and Dayton 2005).

Our response variables were derived from pooling all targeted coral reef fish species (49) for which we had adequate data. These species represent a range of trophic guilds, life history traits, and vulnerability to fishing (Appendix S1: Table S1). The majority were herbivores (23), followed by mobile invertivores (15), piscivores (9), and detritivores (2). Maximum species sizes ranged from 19 cm to >2 m and known life spans from 4 to 50 yr. This level of variability is common in coral reef fisheries and managers are in need of simple, yet meaningful metrics to guide management actions (Nash and Graham 2016). While species differences in terms of life span and age at maturity will influence timelines of recovery, habitat characteristics that support targeted fish assemblages can be identified and used to select priority areas for management (Pittman and Knudby 2014). In addition to their practicality, a significant advantage of using assemblage-level metrics for spatial modeling is the low prevalence of null values, which improves model

performance (Wisz et al. 2008). Furthermore, using a large number of species provides more stable spatial solutions when conducting multi-species prioritization (Kujala et al. 2017).

#### *Habitat and waves*

Of the 25 habitat predictors retained for model development, slope of slope, sine aspect, wave power, and depth were selected as final predictors and showed positive relationships for both targeted fish biomass and body length. Topographically complex habitats offer more potential niches and provide refuges from predation (Hixon and Beets 1989, Almany 2004). Slope of slope is a measure of topographic complexity, which, along with related LiDAR derived metrics, has been shown to be highly correlated with in-situ rugosity (Wedding et al. 2008, Stamoulis and Friedlander 2013) and a strong positive spatial predictor for the distribution of fish biomass (Wedding and Friedlander 2008, Pittman et al. 2009). Depth has also been shown to be a key predictor of fish distributions with higher fish biomass generally associated with greater depths (Friedlander and Parrish 1998a, Pittman and Brown 2011), suggesting that deeper waters may represent a refuge from fishing (Lindfield et al. 2014).

Both targeted fish biomass and body length showed strong positive relationships with sine aspect. Sine aspect measures east-west exposure with the highest values facing east towards the prevailing tradewinds. Windward reefs may be more productive due to nutrient inputs from increased terrestrial runoff (Ringuet and Mackenzie 2005, Giambelluca et al. 2012), and predominantly rough seas along eastern shores likely limit boat and shore fishing activity. In contrast, wave power is highest along north- and northwest-facing shores due to winter storms in the north Pacific (Fletcher et al. 2008). The positive relationships between wave energy and targeted fish biomass and body length have several possible explanations. High waves may provide a refuge from fishing pressure (Branch and Odendaal 2003, McLean et al. 2016) and flush reefs and mitigate land based source pollution, thus improving habitat quality (Fabricius 2005, 2011). Highly wave exposed areas also have less small-scale structure such as from branching corals and support fewer small species, while large fishes are stronger swimmers and thus able to subsist in areas with high wave energy (Friedlander and Parrish 1998b, Friedlander et al. 2003). Further research is needed to confirm these patterns and identify causal mechanisms.

Productive habitats for targeted fishes were characterized by eastern exposures and a combination of high topographic complexity, wave power, and depth. Topographic complexity provides ecological benefits, though it may also provide some refuge from fishing. High wave power, wind exposure, and depth likely provide refuges from fishing pressure due to reduced accessibility, which may in part explain why targeted fish biomass and body length showed strong positive relationships with these factors.

#### *Recovery patterns in the absence of fishing*

Our comparison of predicted targeted fish distributions under current fishing levels and with fishing pressure

removed clearly shows the strong limiting influence of fishing. Because our fishing effort layers were partly based on accessibility to humans and human population, some of the variability they account for in models of targeted fish assemblage indicators may be due to human impacts other than fishing. While current productive and healthy targeted fish assemblages were largely restricted to areas less accessible to fishers, when fishing pressure was removed, they expanded throughout all suitable habitats. This is supported by previous research that showed that structurally complex habitats harbored greater fish biomass (Graham and Nash 2013, Darling et al. 2017). When converted to percent depletion, our island-scale estimates of biomass recovery potential are generally lower than estimates of depletion reported by Williams et al. (2015), though relative differences among islands were fairly consistent. This is unsurprising given that models used in Williams et al. (2015) estimated total fish biomass and were calibrated on a suite of Pacific Islands ranging from pristine to highly degraded. Our models were calibrated only on the main Hawaiian Islands, which are far from pristine. Also Ni'ihau was assumed to have negligible fishing impact, which is not strictly accurate as subsistence fishing occurs on the island (population 170), and there are reports of fishing from boats based on Kaua'i. Furthermore, due to gaps in the bathymetry data, the shallow nearshore areas around Ni'ihau were not included in our analysis.

Areas with significant projected biomass and length recovery had little direct spatial overlap. This is because they represent different aspects of the fished assemblage and are primarily influenced by different seascape predictors, especially in terms of fishing effort. Shore fishing explained the most variability in targeted fish biomass, while boat fishing was most important for fish body length. As a result, when fishing pressure was removed, predicted biomass increase was highest in accessible, nearshore areas with currently high shore-fishing effort, and body length showed greatest projected increases in well populated areas close to boating facilities with currently high boat fishing effort. After fishing effort, high biomass was primarily driven by high topographic complexity (slope of slope), which is patchily distributed. This resulted in fragmented patterns for areas of high biomass recovery potential. In contrast, top habitat predictors for body length were high exposure (sine aspect) and wave power, which have more continuous patterns, resulting in similarly unbroken spatial patterns for areas with high length recovery potential.

#### *Management applications*

In September 2016, the governor of Hawai'i made a commitment at the International Union for Conservation of Nature (IUCN) World Conservation Conference to effectively manage 30% of Hawai'i's nearshore waters by 2030 (Ige 2016). "Effective management" will be achieved through a broad suite of approaches including area closures for fisheries replenishment, as well as identifying areas that are already healthy (Hawaii Division of Aquatic Resources 2016). Therefore, identifying presently productive areas and those with high recovery potential is a priority, and an effective approach to accomplish this at the scale of the MHI is timely and could serve as a template for similar efforts elsewhere.

The prioritization approach presented in this study incorporates current fishing levels into estimates of recovery potential, thus identifying areas where management actions will be most effective in restoring coral reef fisheries. This was a result of comparing spatial predictions of fishery indicators under current fishing levels with predictions after fishing is removed. Each of these predicted maps also has utility for management. Spatial patterns of targeted fish biomass and body length under current fishing levels allows for identification of areas that presently harbor healthy fish assemblages. Effectively managing fishing in these areas would ensure that they continue to supplement adjacent fisheries, through larval export and spillover of adults and juveniles (Harrison et al. 2012, Stamoulis and Friedlander 2013). Because these areas generally have low fishing pressure, management actions would incur minimal cost in terms of fisher displacement. Predicted maps of targeted fish distributions with fishing removed identify habitats capable of supporting high biomass and larger fishes. This information can be used to characterize these essential habitats for coral reef fisheries. Comparing predictions with and without fishing pressure reveals areas to focus fisheries management and provides estimates of recovery potential. Targeted fish biomass recovery in these areas represented a 517% increase on average relative to current values for O'ahu with smaller increases for the other islands where fishing pressure is not as high. These areas show potential mean targeted fish size increases of up 59% on O'ahu with smaller increases for the other islands. Long-term monitoring data shows over a ten-fold increase in total fish biomass during the first 16 yr of protection at Hanauma Bay, the oldest no-take reserve on O'ahu (Friedlander and Brown 2004), suggesting that these estimates are likely conservative.

The intrinsic rate of population growth ( $r$ ) is the major driver of population recovery after fishing pressure is removed (Jennings 2000). However, the rate of population recovery also depends on the size of the remaining population and degree of compensation or depensation, as well as other factors (Jennings 2000). In the absence of this information, rough estimates of recovery rates inside no-take marine reserves can be inferred from life history traits such as trophic level, maximum body size, and longevity (Abesamis et al. 2014). The targeted reef fish species included in this analysis exhibit a broad range of life history characteristics (Appendix S1: Table S1) and thus timelines of recovery will vary. The first species likely to recover are the goatfish (Mullidae) and several of the parrotfish (Scaridae;  $A_{\max} < 7$  yr) based on their short life spans, and full recovery for these species may be possible within 10 yr (Abesamis et al. 2014). In overfished regions such as the MHI, full recovery of moderate to highly vulnerable targeted reef fish such as jacks (Carangids), wrasses (Labrids), surgeonfish (Acanthurids), and large parrotfish is likely to take 20–40 yr (Abesamis et al. 2014).

Areas with significant ( $\alpha = 0.1$ ) projected biomass and length recovery were selected for prioritization, though the threshold could be adjusted based on management needs. Spatial predictions of high biomass and fish body length generally had high precision ( $CV < 0.5$ ), providing confidence in the results. This prioritization approach identified areas where management actions will have the most scope to restore fisheries and could be used as a starting point for

marine reserve selection. These areas are capable of supporting high numbers of large fishes, which constitute high reproductive capacity (Berkeley et al. 2004, Birkeland and Dayton 2005). The next most important criteria to consider is larval connectivity to ensure that adequate portions of larvae are exported into fished areas (Green et al. 2015). While larval transport modeling is still in its infancy, recent work has modeled potential connectivity based on oceanographic circulation in the Hawaiian islands and identified potential larval sources and sinks at 4 km<sup>2</sup> resolution (Wren et al. 2016). Places that are capable of supporting high spawner biomass, which are also important larval source areas for connected reefs, would be good candidates for enhanced fishery management or protection. Such areas, identified by these ecological criteria, should be additionally evaluated based on social, economic, and other considerations important for management (Smith and Wilen 2003, Charles and Wilson 2009, Jones et al. 2013).

## CONCLUSIONS

The development of spatially continuous and comprehensive fishing effort layers, combined with seascape models of targeted fish assemblage indicators for the entire MHI, allowed us to make spatially explicit estimates of recovery potential and thus identify areas that would benefit most from focused coral reef fisheries management. These areas are generally located on the east-facing shores of Kaua'i and O'ahu, the southeast shore of Moloka'i, the west shore of west Maui, and isolated locations in west and east Hawai'i Island. However, the high resolution maps show considerable spatial heterogeneity in the geographical distribution of recovery potential as defined by habitat and fishing patterns. While targeted fish biomass and body length were chosen here to characterize key attributes of reef fisheries, this approach could also be applied using other fish response variables that are important to managers. The information provided is well suited for both local scale management and regional marine spatial planning efforts that aim to sustain and enhance coastal fisheries.

This study is the first of its kind to develop regional-scale seascape models that integrate spatially explicit estimates of fishing pressure. The high resolution of our model inputs and predictions (60 × 60 m) is consistent with movement patterns of most targeted fish species and fishers (Weeks et al. 2017). Tree-based modeling approaches are well suited to handling non-linear relationships and high-order interactions of complex ecological data (De'ath and Fabricius 2000). The ability to make spatial predictions, or predictive mapping, expands upon field-based measurements that are expensive and spatially limited, and produces spatial information at the scope and scale necessary for large-scale assessments and marine spatial planning (Stamoulis and Delevaux 2015). Spatially comprehensive, continuous input and output data sets eliminate the need for the simplifying assumptions common in traditional approaches that can increase uncertainty when results are extrapolated across the area of interest. Predictive mapping fills gaps in survey coverage, allows for testing of management scenarios, and provides spatially comprehensive information for managers including estimates of prediction precision (Pittman and Knudby 2014). Finally,

the approach is flexible so that it can be applied anywhere where demersal fish populations are targeted, and any response variable derived from fish survey data can be modeled depending on the research or management question.

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#### LITERATURE CITED

- Abesamis, R. A., A. L. Green, G. R. Russ, and C. R. L. Jadloc. 2014. The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. *Reviews in Fish Biology and Fisheries* 24:1033–1063.
- Almany, G. R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284.
- Almany, G., S. Connolly, D. Heath, J. Hogan, G. Jones, L. McCook, M. Mills, R. Pressey, and D. Williamson. 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351.
- Battista, T. A., B. M. Costa, and S. M. Anderson. 2007. Shallow-water benthic habitats of the main eight Hawaiian Islands. Technical Memorandum. Biogeography Branch, NOAA National Centers for Coastal Ocean Science (NCCOS), Silver Spring, Maryland, USA.
- Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29:23–32.
- Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution* 20:356–358.
- Bouchet, P. J., J. J. Meeuwig, C. P. Salgado Kent, T. B. Letessier, and C. K. Jenner. 2015. Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. *Biological Reviews* 90:699–728.
- Branch, G. M., and F. Odendaal. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biological Conservation* 114:255–269.
- Breiman, L. 1996. Bagging predictors. *Machine Learning* 24:123–140.
- Breiman, L. 2001. Statistical modeling: the two cultures (with comments and a rejoinder by the author). *Statistical Science* 16:199–231.
- Campbell, S. J., G. J. Edgar, R. D. Stuart-Smith, G. Soler, and A. E. Bates. 2017. Fishing-gear restrictions and biomass gains for coral reef fishes in marine protected areas. *Conservation Biology*. Accepted Author Manuscript. <https://doi.org/10.1111/cobi.12996>
- Charles, A., and L. Wilson. 2009. Human dimensions of marine protected areas. *ICES Journal of Marine Science* 66:6–15.
- Cinner, J. E., N. A. J. Graham, C. Huchery, and M. A. Macneil. 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conservation Biology* 27:453–458.
- Cohen, P. J., and S. J. Foale. 2013. Sustaining small-scale fisheries with periodically harvested marine reserves. *Marine Policy* 37:278–287.
- Darling, E. S., N. A. J. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S. K. Wilson. 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36:561–575.
- De'ath, G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88:243–251.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- Delaney, D. G., L. T. Teneva, K. A. Stamoulis, J. L. Giddens, H. Koike, T. Ogawa, A. M. Friedlander, and J. N. Kittinger. 2017. Patterns in artisanal coral reef fisheries reveal best practices for monitoring and management. *PeerJ* 5:e4089
- Delevaux, J. 2017. Data and tools to operationalize ridge-to-reef management and build island resilience in oceanic island environments. Dissertation. University of Hawaii at Manoa, Honolulu, Hawaii, USA.
- Dulvy, N. K., N. V. C. Polunin, A. C. Mill, and N. A. J. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences* 61:466–475.
- Edgar, G. J., et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–220.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802–813.
- Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125–146.
- Fabricius, K. E. 2011. Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model. Pages 493–505 in Z. Dubinsky and N. Stambler, editors. *Coral reefs: an ecosystem in transition*. Springer Netherlands, Dordrecht, The Netherlands.
- Fletcher, C. H., et al. 2008. Geology of Hawaii reefs. Pages 435–487 in B. M. Riegl and R. E. Dodge, editors. *Coral reefs of the USA*. Springer Netherlands, Dordrecht, The Netherlands.
- Friedlander, A. M., and J. D. Parrish. 1998a. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224:1–30.
- Friedlander, A. M., and J. D. Parrish. 1998b. Temporal dynamics of fish communities on an exposed shoreline in Hawaii. *Environmental Biology of Fishes* 53:1–18.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305.
- Friedlander, A. M., E. K. Brown. 2004. *Marine Protected Areas and Community-based Fisheries Management in Hawai'i*. Pages 208–230 Status of Hawaii's coastal fisheries in the new millennium. 2004 revised edition. American Fisheries Society, Hawaii Chapter, Honolulu, HI.
- Friedlander, A. M., M. K. Donovan, K. A. Stamoulis, I. D. Williams, E. K. Brown, E. J. Conklin, E. E. DeMartini, K. S. Rodgers, R. T. Sparks, and W. J. Walsh. 2018. Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28:146–157.

- Friedman, J. H. 2002. Stochastic gradient boosting. *Computational Statistics and Data Analysis* 38:367–378.
- Froese, R., and D. Pauly. 2017. FishBase. [www.fishbase.org](http://www.fishbase.org)
- Galaiduk, R., A. R. Halford, B. T. Radford, C. H. Moore, and E. S. Harvey. 2017. Regional-scale environmental drivers of highly endemic temperate fish communities located within a climate change hotspot. *Diversity and Distributions* 23:1256–1267.
- Giakoumi, S., and A. Pey. 2017. Assessing the effects of marine protected areas on biological invasions: a global review. *Frontiers in Marine Science* 4:49.
- Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid, and D. M. Delporte. 2012. Online rainfall atlas of Hawai'i. *Bulletin of the American Meteorological Society* 94:313–316.
- Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326.
- Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G. Gleason, P. J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* 90:1215–1247.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Harrison, H. B., et al. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* 22:1023–1028.
- Hawaii Division of Aquatic Resources. 2016. September 1. Hawai'i 30 by 30 oceans target. <http://dlnr.hawaii.gov/dar/announcements/hawaii-30-by-30-oceans-target/> Hawaii Division of Aquatic Resources. 2018. Hawaii marine recreational fishing survey. <http://dlnr.hawaii.gov/dar/fishing/hmrf/>
- Heenan, A., I. D. Williams, T. Acoba, A. DesRochers, R. K. Kosaki, T. Kanemura, M. O. Nadon, and R. E. Brainard. 2017. Long-term monitoring of coral reef fish assemblages in the Western central pacific. *Scientific Data* 4:170176.
- Hijmans, R. J. 2014. Raster: Geographic data analysis and modeling. <http://CRAN.R-project.org/package=raster>
- Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2014. dismo: Species distribution modeling. <http://CRAN.R-project.org/package=dismo>
- Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* 44:666–680.
- Ige, D. Y. 2016. September 10. DLNR NEWS RELEASE: IUCN World Conservation Congress is pau & now the work begins. <http://governor.hawaii.gov/newsroom/latest-news/dlnr-news-release-iucn-world-conservation-congress-is-pau-now-the-work-begins/>
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Januchowski, S. R., R. L. Pressey, J. VanDerWal, and A. Edwards. 2010. Characterizing errors in digital elevation models and estimating the financial costs of accuracy. *International Journal of Geographical Information Science* 24:1327–1347.
- Jennings, S. 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* 10:209–231.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34:201–352.
- Jennings, S., and N. V. C. Polunin. 1996. Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *Journal of Applied Ecology* 33:400–412.
- Jennings, S., J. D. Reynolds, and S. C. Mills. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B* 265:333–339.
- Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* 68:617–627.
- Jones, P. J. S., W. Qiu, and E. M. De Santo. 2013. Governing marine protected areas: Social-ecological resilience through institutional diversity. *Marine Policy* 41:5–13.
- Kendall, M., T. Miller, and S. Pittman. 2011. Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish. *Marine Ecology Progress Series* 427:259–274.
- Kujala, H., A. Moilanen, and A. Gordon. 2017. Spatial characteristics of species distributions as drivers in conservation prioritization. *Methods in Ecology and Evolution* 00:1–12.
- Leathwick, J. R., J. Elith, M. P. Francis, T. Hastie, and P. Taylor. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series* 321:267–281.
- Lecky, J. 2016. Ecosystem vulnerability and mapping cumulative impacts on Hawaiian reefs. University of Hawaii at Manoa, Honolulu, Hawaii, USA.
- Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airamé, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384:33–46.
- Lindfield, S. J., J. L. McIlwain, and E. S. Harvey. 2014. Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. *PLoS ONE* 9:e92628.
- Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.
- Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science* 63:1373–1385.
- McCoy, K. 2015. Estimating nearshore fisheries catch for the main Hawaiian Islands. University of Hawaii at Manoa, Honolulu, Hawaii, USA.
- McLean, M., J. Cuetos-Bueno, O. Nedlic, M. Luckymiss, and P. Houk. 2016. Local stressors, resilience, and shifting baselines on coral reefs. *PLoS ONE* 11:e0166319.
- Mellin, C., M. Aaron MacNeil, A. J. Cheal, M. J. Emslie, and M. Julian Caley. 2016. Marine protected areas increase resilience among coral reef communities. *Ecology Letters* 19:629–637.
- Nash, K. L., and N. A. J. Graham. 2016. Ecological indicators for coral reef fisheries management. *Fish and Fisheries* 17:1029–1054.
- Nicholson, M. D., and S. Jennings. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. *ICES Journal of Marine Science* 61:35–42.
- Norström, A. V., M. Nyström, J.-B. Jouffray, C. Folke, N. A. Graham, F. Moberg, P. Olsson, and G. J. Williams. 2016. Guiding coral reef futures in the Anthropocene. *Frontiers in Ecology and the Environment* 14:490–498.
- Pittman, S. J., and K. A. Brown. 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS ONE* 6:e20583.
- Pittman, S., and A. Knudby. 2014. Predictive mapping of coral reef fish species and communities. Pages 219–236 *in* P. Bortone, editor. *Interrelationships between corals and fisheries*. CRC Press, Boca Raton, Florida, USA.
- Pittman, S. J., C. Caldwell, S. D. Hile, and M. E. Monaco. 2007. Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. *Marine Ecology Progress Series* 348:273–284.
- Pittman, S. J., B. M. Costa, and T. A. Battista. 2009. Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *Journal of Coastal Research* 10053:27–38.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Ringuet, S., and F. T. Mackenzie. 2005. Controls on nutrient and phytoplankton dynamics during normal flow and storm runoff conditions, southern Kaneohe Bay, Hawaii. *Estuaries* 28:327–337.
- Sciberras, M., S. R. Jenkins, R. Mant, M. J. Kaiser, S. J. Hawkins, and A. S. Pullin. 2013. Evaluating the relative conservation value of fully and partially protected marine areas. *Fish and Fisheries* 16:58–77.
- Shin, Y.-J., M.-J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science: Journal du Conseil* 62:384–396.
- Smith, M. D., and J. E. Wilen. 2003. Economic impacts of marine reserves: the importance of spatial behavior. *Journal of Environmental Economics and Management* 46:183–206.
- Stamoulis, K. A., and J. M. S. Delevaux. 2015. Data requirements and tools to operationalize marine spatial planning in the United States. *Ocean and Coastal Management* 116:214–223.
- Stamoulis, K. A., and A. M. Friedlander. 2013. A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai'i. *Fisheries Research* 144:2–14.
- Stamoulis, K. A., M. Poti, J. M. S. Delevaux, M. K. Donovan, A. M. Friedlander, and M. S. Kendall. 2016. Chapter 4: Fishes – Reef Fish. Pages 156–196 in B. M. Costa and M. S. Kendall, editors. *Marine Biogeographic Assessment of the Main Hawaiian Islands*. Bureau of Ocean Energy Management and National Oceanic and Atmospheric Administration, Silver Spring, M.D.
- Stewart, K. R., R. L. Lewison, D. C. Dunn, R. H. Bjorkland, S. Kelez, P. N. Halpin, and L. B. Crowder. 2010. Characterizing fishing effort and spatial extent of coastal fisheries. *PLoS ONE* 5:e14451.
- Taylor, B. M., S. J. Lindfield, and J. H. Choat. 2015. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* 38:520–530.
- VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2014. SDMTtools: species distribution modelling tools. <https://CRAN.R-project.org/package=SDMTtools>
- Wedding, L. M., and A. M. Friedlander. 2008. Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy* 31:246–266.
- Wedding, L. M., A. M. Friedlander, M. McGranaghan, R. S. Yost, and M. E. Monaco. 2008. Using bathymetric lidar to define near-shore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment* 112:4159–4165.
- Wedding, L. M., J. Lecky, J. M. Gove, H. R. Walecka, M. K. Donovan, G. J. Williams, J.-B. Jouffray, L. B. Crowder, A. Erickson, K. Falinski, A. M. Friedlander, C. V. Kappel, J. N. Kittinger, K. McCoy, A. Norström, M. Nyström, K. L. L. Oleson, K. A. Stamoulis, C. White, and K. A. Selkoe. 2018. Advancing the integration of spatial data to map human and natural drivers on coral reefs. *PLoS ONE* 13:e0189792.
- Weeks, R., A. L. Green, E. Joseph, N. Peterson, and E. Terk. 2017. Using reef fish movement to inform marine reserve design. *Journal of Applied Ecology* 54:145–152.
- Weigel, J.-Y., et al. 2014. Marine protected areas and fisheries: bridging the divide. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:199–215.
- Williams, I. D., W. J. Walsh, R. E. Schroeder, A. M. Friedlander, B. L. Richards, and K. A. Stamoulis. 2008. Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation* 35:261–272.
- Williams, I. D., J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, and R. E. Brainard. 2015. Human, oceanographic and habitat drivers of central and western pacific coral reef fish assemblages. *PLoS ONE* 10:e0120516.
- Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14: 763–773.
- Wren, J. L. K., D. R. Kobayashi, Y. Jia, and R. J. Toonen. 2016. Modeled population connectivity across the Hawaiian Archipelago. *PLoS ONE* 11:e0167626.

#### SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1696/full>

#### DATA AVAILABILITY

Habitat and wave predictor layers at NOAA National Centers for Environmental Information: <https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0155189>.

Fish survey data at Figshare: <https://doi.org/10.6084/m9.figshare.c.3808039>.

Fishing effort layers and predicted maps at Research Data Australia: <https://doi.org/10.4225/06/5a572a1f1406a>.