1

2    MR. KOSTANTINOS A. STAMOULIS (Orcid ID : 0000-0003-2688-4695)

3

4

5    Article type    : Articles

6

7


**Title:** Seascape Models Reveal Places to Focus Coastal Fisheries Management


**Running head:** Focusing coastal fisheries management

**Authors and affiliation:** Kostantinos A Stamoulis[1,2] *, Jade MS Delevaux[2], Ivor D Williams[3], Matthew Poti[4,5], Joey Lecky[2,3,6], Bryan Costa[4], Matthew S Kendall[4], Simon J Pittman[4,7], Mary K Donovan[2], Lisa M Wedding[8], Alan M Friedlander[2,9]


[1]Curtin University, Kent St, Bentley WA 6102, Australia.

[2]University of Hawaiʻi at Mānoa, 2500 Campus Rd, Honolulu, HI 96822, USA.

[3]NOAA Pacific Islands Fisheries Science Center, 1845 Wasp Blvd. Building 176, Honolulu, HI 96818, USA.

[4]NOAA National Centers for Coastal Ocean Science, 1305 East West HighwayN-SCI-1, SSMC 4, 9th Floor #9232, Silver Spring, MD 20910, USA.

[5]CSS Inc., 10301 Democracy Lane, Suite 300, Fairfax, Virginia 22030, USA.

[6]Joint Institute for Marine and Atmospheric Research, University of Hawaiʼi at Mānoa, 1000 Pope Road, Marine Sciences Building 312, Honolulu, HI 96822, USA.

[7]Marine Conservation and Policy Research Group, Marine Institute, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK.

[8]Center for Ocean Solutions, Stanford University, 473 Via Ortega, Room 193, Stanford, CA 94305, USA.

[9]National Geographic Society, 1145 17th Street NW Washington, D.C. 20090, USA.

**\*Corresponding author:** Kostantinos A. Stamoulis, E-mail: <u>kostanti@hawaii.edu</u>, PO BOX 61064, Honolulu, HI 96839.

## 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 which 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.

## 1. 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

14  management of fisheries worldwide, including the implementation of additional marine reserves

15  to recover fish biomass and restore key ecosystem functions (Edgar et al. 2014). Numerous

16  studies have documented the benefits of spatial protection on exploited fish assemblages, such as

17  increased biodiversity and resilience (Mellin et al. 2016), resistance to invasive species

18  (Giakoumi and Pey 2017), and fisheries enhancement (Weigel et al. 2014). Increases in biomass

19  and size of targeted fish species in marine reserves have been particularly well documented

20  (Lester et al. 2009). Current research includes a focus on maximizing reserve benefits by

21  incorporating connectivity, the demographic linking of local populations through dispersal of

22  individuals as larvae, juveniles or adults, and habitat quality as explicit considerations in marine

23  reserve design (Almany et al. 2009, Green et al. 2015). As larval export from marine reserves has

24  been shown to replenish stocks in fished areas (Harrison et al. 2012), reserves that support

25  healthy spawning populations which act as larval sources may be key for fisheries recovery.

26  Thus, identifying areas with habitats that have the potential to support reproductive populations

27  of targeted fishes is critical to the design of effective place-based fisheries restoration strategies.

28       Rarely, however, do studies of coastal marine ecosystems integrate local context and

29  stressors in estimates of recovery potential. Specifically, fishing patterns must be considered to

30  inform effective placement of marine reserves intended to enhance fisheries. Fishing effects vary

31  geographically and are difficult to disentangle from other factors that influence targeted fish

32  distributions, creating a spatially complex challenge for understanding patterns of fishing

33  impacts on these assemblages (Taylor et al. 2015, Nash and Graham 2016). Spatial ecological

34  modeling techniques, where predicted variable distributions are mapped across geographical

35  space, have proven useful to examine spatial trends and fill gaps in coverage of empirical

36  datasets (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009).

37  Models can be calibrated using ecological field survey data to establish relationships between

38  fish species and/or assemblage characteristics and remotely sensed habitat and environmental

39  variables. These calibrated models, referred to here as seascape models, can then be used to

40  make spatial predictions of fish, or fishery indicators, across the area of interest (Pittman and

41  Knudby 2014).  However, these approaches have yet to incorporate spatially explicit estimates of

42  fishing pressure and are rarely applied to prioritize areas to inform fisheries replenishment

43  strategies in coastal marine ecosystems.

44        Seascape variables such as seafloor topography, benthic cover, and wave exposure, at

45    varying spatial scales, have been shown to be important predictors of fish assemblages

46    (Friedlander et al. 2003, Bouchet et al. 2015, Galaiduk et al. 2017). Impacts from fishing have

47    been inferred by comparing fish populations in populated versus remote areas (eg. Friedlander et

48    al. 2017) and by using proxies such as local human population density and distance to markets

49    (Williams et al. 2008, Cinner et al. 2013). Fishing effects have also been investigated through

50    studies of fish populations along gradients of protection ranging from gear restrictions (Campbell

51    et al. 2017), to rotational closures (Cohen and Foale 2013), to marine protected areas (MPAs)

52    including full no-take marine reserves (Sciberras et al. 2013). Due to increased availability and

53    coverage of empirical and remotely sensed datasets, there is opportunity to build on these studies

54    by using seascape models to better understand fish habitat relationships in the context of fishing

55    impacts and make realistic and spatially explicit estimates of recovery potential.

56        We address these knowledge and capacity gaps by developing a set of fishing effort map

57    layers at high resolution and employing machine-learning techniques to create regional-scale

58    seascape models and predictive maps of targeted reef fish biomass and body length for the Main

59    Hawaiian Islands (MHI). We use a large and geographically comprehensive database of reef fish

60    surveys and of predictor variables that includes measures of two-dimensional and three-

61    dimensional spatial patterning of the seafloor and the distribution of wave energy. Study

62    objectives were to 1) quantify and map fishing effort and habitat patterns around the MHI, 2)

63    identify and characterize key habitat variables which promote high targeted fish biomass and

64    body length, 3) model and quantify the recovery potential of targeted fish assemblages in the

65    absence of fishing pressure (in terms of mean biomass and body length), and 4) identify areas

66    with the highest recovery potential to prioritize for management actions.

67

## 2. Methods

68    **2. Methods**

69    **2.1 Study area**

70        The Hawaiian Islands are located near the center of the Pacific Ocean and are the most

71    isolated archipelago in the world. The MHI consist of high volcanic mountain peaks, with steep

72    topographic relief to the coastline and fringing reefs accreting on the submerged slopes. There

73    are eight islands that comprise the MHI, six of which were evaluated in this study (from north to

74    south): Kauaʻi, Niʻihau, Oʻahu, Molokaʻi, Maui, and Hawaiʻi islands (Fig. 1). The islands of

75    Lānaʻi and Kahoʻolawe were not included due to the lack of high-resolution bathymetry data.

76

**2.2 Reef fish survey data**

78            A spatially comprehensive dataset of reef fish surveys of the MHI conducted between

79    2010 and 2016 was contributed by the Pacific Islands Fisheries Science Center's Coral Reef

80    Ecosystem Program (Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center

81    2016). Fish surveys utilized a paired stationary point count (SPC) protocol and were conducted

82    on hard bottom habitat, stratified by reef zone and depth (McCoy et al. 2017). A total of 1,184

83    independent survey locations across the MHI were used for modeling (Fig. 1). Spatial

84    predictions were generated on a 60x60 m resolution grid to account for the dimensions of the

85    survey method and the positional uncertainty of the global positioning systems used to navigate

86    to survey locations.

87            Targeted species of the MHI nearshore fishery were defined as coral reef fishes having ≥

88    450 kg of annual recreational or commercial harvest for the past 10 years (2000-2010), or

89    otherwise recognized as important for recreational, subsistence, or cultural fishing

90    (http://dlnr.hawaii.gov/dar/fishing/hmrfs/). Biomass was estimated using the allometric length-

91    weight conversion: $W = aTL^{b}$, where parameters $a$ and $b$ are species-specific fitting parameters,

92    TL is total length (cm), and W is weight (g). Parameters were obtained from a comprehensive

93    assessment of Hawaiʻi length-weight fitting parameters (M. Donovan, unpublished data) and

94    FishBase (Froese and Pauly 2017). Cryptic and soft-bottom species were excluded due to low

95    sampling effectiveness. Planktivores were excluded due to patchy distributions and weak

96    benthic-habitat relationships, as were pelagic species (Table S1). Targeted species biomass was

97    calculated as the sum biomass of modeled species at each survey location. Targeted species body

98    length was calculated as the average recorded body length of modeled species at each survey

99    location.

100

**2.3 Predictor data**

102    *2.3.1 Fishing Effort*

103    We modeled and mapped spatial patterns of fishing effort based on non-commercial island-scale

104    effort estimates (McCoy 2015), following the methods of Lecky (2016). This previous work

105    mapped spatial patterns of catch, though did not incorporate measures of human population in

106    the distribution of shore-based fishing estimates. We did not consider nearshore commercial

107    fishing because it only represents a small fraction of total estimated effort and data quality is

108    questionable (McCoy 2015). Furthermore, commercial fishing data are recorded for large

109    reporting blocks that would obscure fine-scale spatial patterns of fishing effort.  Shore and boat

110    fishing were modeled separately by major gear type (line, net, and spear), which were assumed

111    to have different spatial footprints. Despite different magnitudes, patterns of total shore effort

112    hours between gear types were very similar among islands (Appendix S1: Fig. S1) and both

113    shore and boat fishing effort layers were highly correlated among gear types (> 0.8 Pearson r).

114    Because spear fishing had the largest spatial footprint, highest catch per unit effort, and targets

115    the greatest variety of species, it was used as a proxy of total effort for both shore and boat

116    fishing, respectively.

117        We used average annual fishing effort (hrs/yr) for reef fish by island from ten years of

118    recreational fishery data (2004-2013) compiled by McCoy (2015) and distributed these values

119    into the nearshore marine area based on weighting factors related to accessibility to fishers.

120    Fishing effort showed a declining trend over time for all islands with the exception of Lānaʻi

121    (McCoy 2015), so estimated values were conservative. Marine managed areas where fishing is

122    prohibited were set to zero. For shore fishing, proximity and type of roads along with shoreline

123    steepness were used as proxies for accessibility, and values were weighted by human population

124    within 30 km. To model spear fishing, a logistic decay function was used so effort decreased

125    with depth to a maximum distance of 2 km from shore. The parameters of the function were set

126    based on discussions with fishing experts in Hawaiʻi and assume the vast majority of

127    spearfishing effort is shallower than 20 m and there is no effort beyond 40 m (Lecky 2016). For

128    boat fishing, accessibility measures were based on distance to boat launch/harbor weighted by

129    human population within 30 km. There was no recreational fishery data available for Niʻihau

130    (pop. 170) and while subsistence fishing does occur, shore fishing effort was assumed to be zero.

131    To ground-truth the fishing effort maps, estimated shore-based spear fishing effort values were

132    compared to total shore fishing effort values from 12 independent fishing (creel) survey locations

133    across the MHI. Total shore fishing effort values were obtained from Delaney et al. (2017) and

134    compared to derived spear fishing effort maps based on the sum of pixel values within polygons

135    matching the description of each survey area. Empirical boat based fishing effort estimates were

136    not available for comparison.

137

138    *2.3.2 Habitat variables*

139           A set of 62 gridded environmental datasets at 60x60 m resolution was generated for each

140    island as potential predictor variables used to model reef fish assemblage metrics (Stamoulis et

141    al. 2016). Selection of predictors was based on an extensive literature review and input from

142    experts in Hawaiian reef ecology (Delevaux 2017). There were four types of predictor variables:

143    seafloor topography, benthic habitat composition, geographic, and wave energy.

144           Seafloor topography variables were included to account for variation in reef fish

145    distributions due to direct and indirect effects of depth and seafloor structure. A gridded

146    synthesis of multibeam sonar and Light Detection and Ranging (LiDAR) bathymetry at 5 m

147    resolution was used as the depth variable and to derive the suite of seafloor topography metrics.

148    For example, the morphometric, slope-of-the-slope (a second derivative of bathymetry),

149    measures the maximum rate of change in slope between cells within the specified analytical

150    neighborhood. Slope-of-the-slope is a measure of surface topographic complexity, sometimes

151    called terrain roughness, and has been shown to be positively correlated with finer scale *in situ*

152    measures of rugosity such as chain-tape measurements (Pittman et al. 2009, Pittman and Brown

153    2011). The modeled area was limited by gaps in the LiDAR bathymetry data. For this reason, the

154    islands of Lānaʻi and Kahoʻolawe were not modeled, as well as much of the nearshore area

155    around Niʻihau, and large portions of the north-east and south-east coasts of Hawaiʻi island.

156           Benthic habitat composition variables from existing habitat maps (Battista et al. 2007)

157    were included to account for variation in reef fish assemblages arising from the direct and

158    indirect effects of the spatial configuration of benthic habitats. Geographic variables were used to

159    account for variation in reef fish assemblages arising from spatial location. Wave energy

160    variables were included to account for variation in reef fish assemblages arising from the direct

161    and indirect effects of ocean wave dynamics.

162           A pairwise correlation analysis was performed on the full set of predictors for the whole

163    study area (MHI). Highly correlated predictors (Spearman $|\rho| > 0.7$) were identified, and those

164    highly correlated with two or more other predictors were removed. In cases where only two

165    predictors were highly correlated, those with greater ecological importance (based on expert

166    opinion and scientific literature) were retained. After the correlation analysis, 25 out of 62

167    seascape predictors were retained for model development (Table 1, Table S2).

168

169    **2.4 Seascape models**

170    Boosted regression trees (BRT) were used to estimate relationships between targeted fish

171    assemblage metrics (biomass and length) and the predictor datasets (De'ath 2007, Elith et al.

172    2008). These modeled relationships were then used to create spatial predictions of targeted fish

173    biomass and body length. Each metric was modeled independently at the archipelago scale. To

174    make predictions with fishing pressure removed, fishing predictors were set to zero. Statistical

175    models and spatial predictions were generated in R (R Core Team 2014) using the dismo

176    (Hijmans et al. 2014) and raster (Hijmans 2014) packages. BRT is effective at modeling

177    nonlinearities, discontinuities (threshold effects), and interactions between variables (Breiman

178    1996, 2001, De'ath and Fabricius 2000).

179    BRT can accommodate many types of response variables. Since the targeted fish

180    assemblage metrics were continuous variables, they were modeled using a Gaussian (normal)

181    distribution, and appropriate data transformations were applied to improve normality. Targeted

182    fish biomass was fourth root transformed and targeted fish body length was square root

183    transformed. Prior to model fitting, reef fish survey data were randomly divided into model

184    training (70%) and test (30%) subsets. The test data set was withheld from model fitting and

185    used only to evaluate predictive performance (map accuracy). Although boosting makes BRT

186    models less prone to overfitting (Friedman 2002, Elith et al. 2008), predictive performance was

187    evaluated using the test data to measure how well the model generalized to new data.

188    Model fitting and selection was accomplished following the procedures detailed in Elith

189    et. al. (2008). To increase parsimony, selected models were then simplified to remove less

190    informative predictor variables. This was accomplished by dropping the least contributing

191    predictor, re-fitting the model, and computing the change in predictive deviance relative to the

192    initial model (Elith et al. 2008). The predictive deviance indicates the amount of variation in the

193    response variable not explained by the model. This process was repeated and the predictive

194    deviance was plotted over the full range of predictors. The final number of predictors was

195    selected at the inflection point in the predictive deviance curve, where change in predictive

196   deviance increased relative to previous values. In general, this resulted in removal of predictors

197   which explained < 5% of the variation in the response variable.

198         Bootstrapping was used to create spatially explicit predictions and calculate prediction

199   precision. The model training dataset was repeatedly sampled with replacement to create 20

200   bootstrap samples. Using the optimal parameter value combination and simplified set of

201   predictor variables, a BRT model was fit to each bootstrap sample and used to make predictions

202   to a spatially explicit gridded map using the values of the predictor variables at each grid cell.

203   This resulted in a total of 20 spatial prediction grids that were used to calculate the mean and

204   coefficient of variation (CV) in each grid cell (Leathwick et al. 2006), where low CV values

205   indicate high precision. Prediction means and CVs were plotted against each other to visualize

206   the relationship between the magnitude and precision of predictions. The mean of the

207   bootstrapped predictions was used for interpretation and further analysis.

208         Model performance was evaluated using the cross-validation percent deviance explained

209   (PDE) and test PDE. The cross-validation PDE is the 10-fold cross-validation estimate of the

210   percent deviance explained for the best model (as described above). Similarly, the test PDE was

211   determined by calculating the percent deviance explained by the model when evaluated using the

212   model test dataset. Both metrics indicate overall model fit, but the test PDE also provides a

213   measure of model performance when predicting data that were independent of model fitting. To

214   better understand the relationship between measured and predicted values, average measured

215   values by island were compared with predicted values under current fishing levels and with

216   fishing pressure removed. Finally, the relative importance of predictor variables for each model

217   was evaluated and partial dependence plots were generated for each predictor variable to

218   interpret their individual effects on the response variables (De'ath 2007, Elith et al. 2008).

219

220   **2.5 Recovery potential in the absence of fishing**

221         Final BRT models were used to generate gridded predictions of targeted fish biomass and

222   body length across the MHI study area (60x60 m resolution) under current fishing levels and

223   with fishing pressure removed. Values from these layers were used to create distribution curves

224   of predicted biomass and body length under each fishing scenario for each island. Differences

225   were assessed visually and tested using a two-sample Kolmogorov-Smirnov test. Overall change

226   in spatial patterns of high predicted targeted fish biomass and body length were assessed using

227   maps of predicted values. Finally, means and percent change between predicted values across all

228   modeled habitats for present conditions and with fishing effort set to zero were calculated by

229   island to estimate recovery potential at the island scale.

230

231   **2.6 Spatial prioritization for management**

232       To identify places that could be prioritized for management actions which would support

233   fisheries restoration, we evaluated spatial differences between predictions of targeted fish

234   biomass and body length under current fishing levels and predictions with fishing effort set to

235   zero. We assumed that areas with the greatest differences have the highest potential for fisheries

236   replenishment if fishing pressure were limited or removed through management actions. To

237   identify areas where predictions differed significantly between models, we applied the

238   methodology of Januchowski et al. (2010) using the SigDiff function in the R package

239   SDMTools (VanDerWal et al. 2014). We computed the significance of the pairwise differences

240   (for each grid cell) for the response variables (biomass and length) relative to the mean and

241   variance of all differences for each island. The resulting probability values represent the area

242   under the curve of a Gaussian distribution defined by the mean and variance across all cells for

243   that island. The spatial grids representing the individual significance values were reclassified to

244   indicate cells where predictions with fishing pressure removed were significantly higher than

245   present predictions ($p < 0.10$). Mean absolute difference and mean percent change relative to

246   modeled values under current fishing pressure were calculated for cells showing significant

247   increase by island. Finally, the spatial grids representing regions of significant increase for

248   biomass and body length were combined into a single map for interpretation.

249

250   **3. Results**

251   **3.1 Fishing and habitat patterns**

252       Modeled shore spearing effort values under-estimated total shore effort from creel

253   surveys by a factor of two. However, there was a strong positive relationship ($r^2$=0.7) across all

254   sites indicating that this measure of shore spearing effort provides a reliable proxy for overall

255   shore fishing effort (Fig. 2). The highest intensity of shore fishing effort was estimated to be near

256   the highly populated areas of Hawaiʻi Island near Hilo and Kona, followed by the south and

257   southeast shores of Oʻahu and near the populated areas around Kahalui and Kihei on Maui (Fig.

258    3A). Boat fishing effort for reef fish was generally much lower than shore fishing effort (Fig.

259    3B). The highest values for boat fishing effort were found offshore of south Oʻahu. Moderate

260    boat fishing effort was found along the southwest shore of Kauaʻi, south Molokaʻi, northwest

261    Maui, and near Kona and Hilo on Hawaiʻi Island (Fig. 3B).

262          While a more complete description of marine habitat patterns in the MHI is outside the

263    scope of this study, here we focus on several key variables shown to be important determinants

264    of targeted fish biomass and body length. Seafloor topographic complexity (slope of slope) was

265    highly variable within islands. Generally, areas with low values (indicating flat bottom)

266    encompassed the greatest area, while high values (indicating complex structure) were few and

267    widely dispersed. Islands with more shallow water habitat such as Oʻahu tended to have more

268    flat bottom. Sine aspect represents the E/W exposure of benthic habitats. The highest values were

269    located on east-facing shores and the lowest values on west-facing shores. Eastern exposures are

270    most exposed to the predominate trade winds and associated short-period swells. Wave power

271    was highest on the north shores of all islands, with the exception of Hawaiʻi Island, and generally

272    decreased among islands from north to south. Depth increased with distance from shore on all

273    islands, and the largest shallow water areas were found on Oʻahu and the south shore of

274    Molokaʻi.

275

276    **3.2 Seascape models**

277          The final BRT model for targeted fish biomass had nine predictors. Cross-validation PDE

278    was 37.5%, and test PDE was 35.3%. The final BRT model for targeted fish body length had

279    nine predictors, a cross-validation PDE of 21.2%, and a test PDE of 21.4%. Based on these

280    metrics, the biomass model fit better than the length model, and had higher predictive accuracy.

281    Plots of prediction means vs CVs showed that higher predicted values generally had higher

282    precision (CV < 0.5 – Appendix S1: Fig. S2).  When predictions for biomass and length under

283    present fishing levels were compared to fish survey data at the island level, BRT predictions

284    tended to underestimate means of field measured values within one standard deviation

285    (Appendix S1: Fig. S3). This effect increased with the magnitude of the measured values.

286    However, the BRT predicted values well represented the relative differences between islands

287    (Appendix S1: Fig. S3).

288    Biomass was largely driven by shore fishing, while length responded primarily to boat

289    fishing (Fig. 4). In terms of habitat, biomass was primarily driven by topographic complexity

290    (slope of slope) and length was most associated with exposure (sine aspect). Depth and wave

291    power were other key habitat variables that influenced both targeted fish biomass and body

292    length (Fig. 4). These habitat variables all had positive relationships with the assemblage

293    indicators, whereas the fishing variables had negative relationships (Fig. 4).

294

295    **3.3 Effects of fishing and habitat on fish biomass and body length**

296    Targeted fish biomass and body length had similar negative relationships with fishing

297    predictors. Both declined rapidly from 0-2 hrs/ha/yr of shore (spear) fishing effort and 0-0.2

298    hrs/ha/yr of boat (spear) fishing effort, then were relatively flat across a wide range of increasing

299    effort values (Fig. 5, Appendix S1: Fig. S5). Areas of shore fishing effort < 2 hrs/ha/yr include

300    the less populated islands, Niʻihau, Molokaʻi, and Lānaʻi, as well as remote and difficult to

301    access areas of the more populated islands such as west Kauaʻi, east Maui, and south Hawaiʻi

302    Island (Fig. 3A). Areas of low boat fishing effort (< 0.2 hrs/ha/yr) included Niʻihau, northwest

303    Kauaʻi, north Oʻahu, north Molokaʻi, west Lānaʻi, and north and south Hawaiʻi (Fig. 3B).

304    Slope of slope, a measure of topographic complexity, was the most important habitat

305    predictor for targeted reef fish biomass, which increased rapidly at the low end of the scale (0-8°)

306    (Appendix S1: Fig. S4). Seafloor depth had a strong positive relationship with targeted fish

307    biomass, which increased with depth before leveling off at around 17 m. Maximum slope in a

308    240 m radius was also positively related to biomass with a steep increase from 0-10°. Sine aspect

309    (exposure) was positively related to biomass, which increased linearly from -1 (west facing) to 1

310    (east facing), and wave power, responding more at higher levels (> 10,000 kW/hr, Appendix S1:

311    Fig. S4). Predictor relationships for fish body length were similar to those for biomass (Appendix

312    S1: Fig. S5). However, there was a stronger relationship with wave power and a weaker

313    relationship with slope of slope. In addition, the relationship of average body length and sine

314    aspect was not linear and length increased with depth up to 25 m before leveling off. Targeted

315    fish body length was also positively related to maximum slope of slope within a 240 m radius,

316    peaking between 25-40°; and slope, increasing from 0-5° (Appendix S1: Fig. S5). Thus, in the

317    absence of fishing pressure, targeted fish biomass and body length were generally predicted to

318    reach their highest values in habitats with slope of slope > 8°, eastern exposures (sine aspect >

319    0), wave power > 10,000 kW/hr, and at depths > 17 m.

320

321    **3.3 Recovery potential in the absence of fishing**

322           All islands except for Niʻihau (which was assumed to have negligible fishing pressure)

323    showed a significant increase in predicted biomass when the influence of fishing was removed

324    (Fig. 6). Biomass predictions for these islands under present fishing levels had distributions that

325    were right skewed, indicating primarily low biomass levels. When fishing effort was set to zero,

326    these distributions flattened out, shifted right, and became more symmetrical, indicating overall

327    increases in mean biomass (Fig. 6). Targeted fish biomass was highest in areas less accessible to

328    humans such as the north shores of most islands and the east shore of Maui. However, when

329    fishing pressure was removed biomass increased across all suitable habitats with the highest

330    increases in deeper areas with high topographic complexity (Appendix S1: Figs S6-S7). Oʻahu

331    (the most populated island, with highest overall fishing effort) showed the largest predicted

332    increase in biomass, followed by Kauaʻi, Molokaʻi, Maui, Hawaiʻi, and then Niʻihau (Table 2).

333           All islands except for Niʻihau showed a significant increase in predicted fish body length

334    when the influence of fishing was removed (Fig. 7). Under current fishing levels, the shapes of

335    predicted fish length distributions varied by island. When fishing effort was set to zero, predicted

336    length distributions maintained their general shape and shifted to the right indicating an increase

337    in average body length (Fig. 7). Similar to biomass, larger fishes were located in areas that are

338    less accessible to humans such as north shores of most islands and the east shore of Maui

339    (Appendix S1: Figs S8-S9). When fishing effort was set to zero, fish length increased in all areas

340    with the highest increases along eastern exposures and areas with high wave power. As with

341    biomass, Oʻahu showed the largest relative increase in fish body length when fishing pressure

342    was removed; the other islands showed smaller increases (Table 3).

343

344    **3.4 Spatial prioritization for management**

345    These analyses identified areas with the highest recovery potential (i.e., areas with high quality

346    habitat and currently under high fishing pressure), which would be expected to respond

347    positively to management of fishing effort. Because current fishing effort was assumed to be

348    zero in existing marine reserves, these areas were not selected. Areas with highest recovery

349 potential for targeted reef fish biomass tended to be patchy, while areas with highest projected

350 recovery for body length were more continuous. Locations with high recovery potential for

351 targeted fish biomass and body length were usually found in the same areas, though often with

352 little direct spatial overlap (Fig. 8). In general, these areas were located on the east-facing shores

353 of Kauaʻi and Oʻahu, the southeast shore of Molokaʻi, and the west shore of west Maui (Fig. 8).

354 In addition, the prioritization analysis identified areas on the north shore of Kauaʻi, around

355 Mōkapu point and the southeast shore of Oʻahu, Māʻili point on west Oʻahu,

356 northwest Molokaʻi , Maʻalaea bay on Maui, west Hawaiʻi Island just north of Makoleʻa point,

357 and east Hawaiʻi Island around Cape Kumukahi and north of Kaloli point (Fig. 8). The largest

358 relative change in biomass for regions of significant increase were on Oʻahu and Kauaʻi, while

359 largest relative increases in body length for these areas were on Oʻahu, with smaller levels of

360 increase on Kauaʻi, Molokaʻi, and Maui (Table 4). Niʻihau showed minimal change in biomass

361 and body length.

362

363 **4. Discussion**

364 Inferred fishing effort patterns were highly variable around the MHI and seascape models

365 indicated a low threshold beyond which targeted fish assemblages were severely impacted.

366 Sparsely populated islands Niʻihau and Molokaʻi had fishing effort below this threshold, as did

367 large, and often remote, areas on the other islands. Seascape models also identified seafloor

368 topographic complexity, exposure, wave power, and depth as the key variables that influenced

369 the distribution of high targeted fish biomass and body length and characterized productive

370 habitats. Fish biomass was most sensitive to shore and boat-based fishing, as well as topographic

371 complexity, whereas average body length responded primarily to boat fishing and was strongly

372 influenced by exposure. While the highest targeted reef fish biomass and body lengths were

373 mostly restricted to areas not easily accessed by humans; when fishing effort was set to zero,

374 high values of biomass and body length were widely distributed among suitable habitats. By

375 comparing modelled current targeted fish distributions with those predicted when fishing

376 pressure was removed, areas with high recovery potential were revealed, with significant

377 increases in average biomass and length across the MHI (Table 4).

378

379 **4.1 Fishing effort**

380         An integral component of this research was the application of spatially continuous fishing

381 effort layers developed for the MHI. We chose to use fishing effort rather than catch because

382 derived catch estimates incorporate catch per unit effort (CPUE) which varies in relation to a

383 number of factors including fish abundance (Maunder et al. 2006). Because fish biomass is also

384 related to fish abundance, fish catch - unlike fishing effort – would not be independent of our

385 response variable. Our derived fishing effort layers represent the most spatially comprehensive,

386 high resolution, and broad-scale products yet created to quantify spatial patterns of coral reef

387 fishery effort. However, a number of simplifying assumptions were made in order to develop

388 these layers, primarily that fishers are more likely to frequent accessible areas, more likely to fish

389 close to home, and that numbers of fishers are proportional to total population (Stewart et al.

390 2010). For these reasons, our fishing effort maps may possibly capture additional impacts related

391 to accessibility and proximity to humans, such as land based source pollution. Though our

392 fishing layers were strong predictors of fishery indicators and have been corroborated with fine

393 scale effort data from creel surveys, there is considerable scope to improve them further. Future

394 studies should focus on testing large-scale drivers of fishing effort based on local-scale empirical

395 data.

396         Our results show the greatest impacts on targeted reef fishes within the first 10% of

397 modeled ranges for shore and boat fishing effort. This is supported by previous research

398 indicating that the greatest impacts from fishing occur at low fishing levels (Jennings and

399 Polunin 1996, Jennings and Kaiser 1998). There are few examples in the literature showing this

400 relationship for coral reef fisheries; it has important implications for management as it highlights

401 the importance of no-take MPAs and suggests that fishing effort in rotational closures should be

402 carefully managed.

403

404 **4.2 Fish response variables**

405         Biomass and size of targeted fish species have often been used to evaluate the effects of

406 fishing pressure (Nicholson and Jennings 2004, Dulvy et al. 2004). The theoretical basis is that

407 larger fishes are generally more targeted; the accumulated effects of fishing mortality reduce the

408 number of older, and therefore larger, fishes in a population; and that large-bodied species are

409 more vulnerable to fishing due to slow population turnover (Jennings et al. 1998, 1999). Both

410 biomass and fish length are thought to represent the relative abundance of large and small

411    individuals (Shin et al. 2005). However, our results suggest they are not interchangeable and

412    instead capture different aspects of the fished assemblage. Biomass was more sensitive to fishing

413    compared to mean length. While higher average length always reflects greater relative

414    abundance of large individuals, high biomass can also result from high abundance of small

415    individuals. This was supported by the fact that slope of slope (60 m) was the top habitat

416    predictor for biomass, while maximum slope of slope in a 240 m radius explained more

417    variability in average length. Larger individuals and species generally have a broader

418    geographical range of movements and thus respond to broader-scale measures of seascape

419    structure (Pittman et al. 2007, Wedding et al. 2008, Kendall et al. 2011). It is important to

420    consider both fished assemblage biomass and size distribution because large individuals

421    represent high-value species and high reproductive capacity (Birkeland and Dayton 2005).

422         Our response variables were derived from pooling all targeted coral reef fish species (49)

423    for which we had adequate data. These species represent a range of trophic guilds, life history

424    traits, and vulnerability to fishing (Table S1). The majority were herbivores (23), followed by

425    mobile invertivores (15), piscivores (9), and detritivores (2). Maximum species sizes ranged

426    from 19 cm to over two meters and known life-spans from 4 to 50 years. This level of variability

427    is common in coral reef fisheries and managers are in need of simple, yet meaningful metrics to

428    guide management actions (Nash and Graham 2016). While species differences in terms of life-

429    span and age at maturity will influence timelines of recovery, habitats characteristics which

430    support targeted fish assemblages can be identified and used to select priority areas for

431    management (Pittman and Knudby 2014). In addition to their practicality, a significant advantage

432    of using assemblage level metrics for spatial modeling is the low prevalence of null values which

433    improves model performance (Wisz et al. 2008). Furthermore, using a large number of species

434    provides more stable spatial solutions when conducting multi-species prioritization (Kujala et al.

435    2017).

436

437    **4.3 Habitat and waves**

438         Of the 27 seascape predictors selected for model development, slope of slope, sine aspect,

439    wave power, and depth were selected as final predictors and showed positive relationships for

440    both targeted fish biomass and body length. Topographically complex habitats offer more

441    potential niches and provide refuges from predation (Hixon and Beets 1989, Almany 2004).

442  Slope of slope is a measure of topographic complexity, which along with related LiDAR derived

443  metrics, has been shown to be highly correlated with in-situ rugosity (Wedding et al. 2008,

444  Stamoulis and Friedlander 2013) and a strong positive spatial predictor for the distribution of fish

445  biomass (Wedding and Friedlander 2008, Pittman et al. 2009). Depth has also been shown to be

446  a key predictor of fish distributions with higher fish biomass generally associated with greater

447  depths (Friedlander and Parrish 1998a, Pittman and Brown 2011), suggesting that deeper waters

448  may represent a refuge from fishing (Lindfield et al. 2014).

449       Both targeted fish biomass and body length showed strong positive relationships with

450  sine aspect. Sine aspect measures east/west exposure with the highest values facing east towards

451  the prevailing trade-winds. Windward reefs may be more productive due to nutrient inputs from

452  increased terrestrial runoff (Ringuet and Mackenzie 2005, Giambelluca et al. 2012), and

453  predominantly rough seas along eastern shores likely limit boat and shore fishing activity. In

454  contrast, wave power is highest along north and northwest facing shores due winter storms in the

455  north Pacific (Fletcher et al. 2008). The positive relationships between wave energy and targeted

456  fish biomass and body length have several possible explanations. High waves may provide a

457  refuge from fishing pressure (Branch and Odendaal 2003, McLean et al. 2016) and flush reefs

458  and mitigate land based source pollution, thus improving habitat quality (Fabricius 2005, 2011).

459  Highly wave exposed areas also have less small-scale structure such as from branching corals

460  and support fewer small species, while larger fishes are stronger swimmers and thus able to

461  subsist in areas with high wave energy (Friedlander and Parrish 1998b, Friedlander et al. 2003).

462  Further research is needed to confirm these patterns and identify causal mechanisms.

463       Productive habitats for targeted fishes were characterized by eastern exposures and a

464  combination of high topographic complexity, wave power, and depth. Topographic complexity

465  provides ecological benefits, though it may also provide some refuge from fishing. High wave

466  power, wind exposure, and depth likely provide refuges from fishing pressure due to reduced

467  accessibility, which may in part explain why targeted fish biomass and body length showed

468  strong positive relationships with these factors.

469

470  **4.4 Recovery patterns in the absence of fishing**

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

472  with fishing pressure removed clearly shows the strong limiting influence of fishing. Because our

473    fishing effort layers were partly based on accessibility to humans and human population, some of

474    the variability they account for in models of targeted fish assemblage indicators may be due to

475    human impacts other than fishing. While current productive and healthy targeted fish

476    assemblages were largely restricted to areas less accessible to fishers, when fishing pressure was

477    removed they expanded throughout all suitable habitats. This is supported by previous research

478    which showed that structurally complex habitats harbored greater fish biomass (Graham and

479    Nash 2013, Darling et al. 2017). When converted to percent depletion, our island-scale estimates

480    of biomass recovery potential are generally lower than estimates of depletion reported by

481    Williams et al. (2015), though relative differences among islands were fairly consistent. This is

482    unsurprising given that models used in Williams et al. (2015) estimated total fish biomass and

483    were calibrated on a suite of Pacific Islands ranging from pristine to highly degraded. Our

484    models were calibrated only on the main Hawaiian Islands, which are far from pristine. Also

485    Ni'ihau was assumed to have negligible fishing impact, which is not strictly accurate as

486    subsistence fishing occurs on the island (pop. 170), and there are reports of fishing from boats

487    based on Kaua'i. Furthermore, due to gaps in the bathymetry datasets the shallow nearshore

488    areas around Ni'ihau were not included in our analysis.

489         Areas with significant projected biomass and length recovery had little direct spatial

490    overlap. This is because they represent different aspects of the fished assemblage and are

491    primarily influenced by different seascape predictors, especially in terms of fishing effort. Shore

492    fishing explained the most variability in targeted fish biomass, while boat fishing was most

493    important for fish body length. As a result, when fishing pressure was removed, predicted

494    biomass increase was highest in accessible, nearshore areas with currently high shore fishing

495    effort, and body length showed greatest projected increases in well populated areas close to

496    boating facilities with currently high boat fishing effort. After fishing effort, high biomass was

497    primarily driven by high topographic complexity (slope of slope) which is patchily distributed.

498    This resulted in fragmented patterns for areas of high biomass recovery potential. In contrast, top

499    habitat predictors for body length were high exposure (sine aspect) and wave power which have

500    more continuous patterns, resulting in similarly unbroken spatial patterns for areas with high

501    length recovery potential.

502

503    **4.5 Management applications**

504    In September, 2016 the governor of Hawai'i made a commitment at the International

505    Union for Conservation of Nature (IUCN) World Conservation Conference to effectively

506    manage 30% of Hawai'i's nearshore waters by 2030 (Ige 2016). "Effective management" will be

507    achieved through a broad suite of approaches including area closures for fisheries replenishment,

508    as well as identifying areas that are already healthy (Hawaii Division of Aquatic Resources

509    2016). Therefore, identifying presently productive areas and those with high recovery potential is

510    a priority, and an effective approach to accomplish this at the scale of the MHI is timely and

511    could serve as a template for similar efforts elsewhere.

512    The prioritization approach presented in this study incorporates current fishing levels into

513    estimates of recovery potential, thus identifying areas where management actions will be most

514    effective in restoring coral reef fisheries. This was a result of comparing spatial predictions of

515    fishery indicators under current fishing levels with predictions after fishing is removed. Each of

516    these predicted maps also has utility for management. Spatial patterns of targeted fish biomass

517    and body length under current fishing levels allows for identification of areas that presently

518    harbor healthy fish assemblages. Effectively managing fishing in these areas would ensure that

519    they continue to supplement adjacent fisheries, through larval export and spillover of adults and

520    juveniles (Harrison et al. 2012, Stamoulis and Friedlander 2013). Because these areas generally

521    have low fishing pressure, management actions would incur minimal cost in terms of fisher

522    displacement. Predicted maps of targeted fish distributions with fishing removed identify habitats

523    capable of supporting high biomass and larger fishes. This information can be used to

524    characterize these essential habitats for coral reef fisheries. Comparing predictions with and

525    without fishing pressure reveals areas to focus fisheries management and provides estimates of

526    recovery potential. Targeted fish biomass recovery in these areas represented a 517% increase on

527    average relative to current values for O'ahu with smaller increases for the other islands where

528    fishing pressure is not as high. These areas show potential mean targeted fish size increases of up

529    59% on O'ahu with smaller increases for the other islands. Long-term monitoring data shows

530    over a ten-fold increase in total fish biomass during the first 16 years of protection at Hanauma

531    Bay, the oldest no-take reserve on O'ahu (Friedlander and Brown, 2004), suggesting that these

532    estimates are likely conservative.

533    The intrinsic rate of population growth ($r$) is the major driver of population recovery after

534    fishing pressure is removed (Jennings 2000). However, the rate of population recovery also

535  depends on the size of the remaining population and degree of compensation or depensation, as
536  well as other factors (Jennings 2000). In the absence of this information, rough estimates of
537  recovery rates inside no-take marine reserves can be inferred from life history traits such as
538  trophic level, maximum body size and longevity (Abesamis et al. 2014). The targeted reef fish
539  species included in this analysis exhibit a broad range of life history characteristics (Table S1)
540  and thus timelines of recovery will vary. The first species likely to recover are the goatfish
541  (Mullidae) and several of the parrotfish (Scaridae - $A_{max} < 7$ yrs) based on their short lifespans,
542  and full recovery for these species may be possible within 10 years (Abesamis et al. 2014). In
543  overfished regions such as the MHI, full recovery of moderate to highly vulnerable targeted reef
544  fish such as jacks (Carangids), wrasses (Labrids), surgeonfish (Acanthurids), and large parrotfish
545  is likely to take 20-40 years (Abesamis et al. 2014).

546      Areas with significant ($\alpha$=0.1) projected biomass and length recovery were selected for
547  prioritization, though the threshold could be adjusted based on management needs. Spatial
548  predictions of high biomass and fish body length generally had high precision (CV < 0.5),
549  providing confidence in the results. This prioritization approach identified areas where
550  management actions will have the most scope to restore fisheries and could be used as a starting
551  point for marine reserve selection. These areas are capable of supporting high numbers of large
552  fishes which constitute high reproductive capacity (Berkeley et al. 2004, Birkeland and Dayton
553  2005). The next most important criteria to consider is larval connectivity to ensure that adequate
554  portions of larvae are exported into fished areas (Green et al. 2015). While larval transport
555  modeling is still in its infancy, recent work has modeled potential connectivity based on
556  oceanographic circulation in the Hawaiian islands and identified potential larval sources and
557  sinks at 4 $km^2$ resolution (Wren et al. 2016). Places that are capable of supporting high spawner
558  biomass, which are also important larval source areas for connected reefs, would be good
559  candidates for enhanced fishery management or protection. Such areas, identified by these
560  ecological criteria, should be additionally evaluated based on social, economic, and other
561  considerations important for management (Smith and Wilen 2003, Charles and Wilson 2009,
562  Jones et al. 2013).

563

564  **5. Conclusions**

565    The development of spatially continuous and comprehensive fishing effort layers,

566    combined with seascape models of targeted fish assemblage indicators for the entire MHI,

567    allowed us to make spatially explicit estimates of recovery potential and thus identify areas that

568    would benefit most from focused coral reef fisheries management. These areas are generally

569    located on the east-facing shores of Kaua'i and O'ahu, the southeast shore of Moloka'i, the west

570    shore of west Maui, and isolated locations in west and east Hawai'i Island.  However, the high

571    resolution maps show considerable spatial heterogeneity in the geographical distribution of

572    recovery potential as defined by habitat and fishing patterns. While targeted fish biomass and

573    body length were chosen here to characterize key attributes of reef fisheries, this approach could

574    also be applied using other fish response variables that are important to managers. The

575    information provided is well suited for both local scale management and regional marine spatial

576    planning efforts that aim to sustain and enhance coastal fisheries.

577    This study is the first of its kind to develop regional-scale seascape models that integrate

578    spatially explicit estimates of fishing pressure. The high resolution of our model inputs and

579    predictions (60x60 m) is consistent with movement patterns of most targeted fish species and

580    fishers (Weeks et al. 2017). Tree-based modeling approaches are well suited to handling non-

581    linear relationships and high-order interactions of complex ecological data (De'ath and Fabricius

582    2000). The ability to make spatial predictions, or predictive mapping, expands upon field-based

583    measurements that are expensive and spatially limited, and produces spatial information at the

584    scope and scale necessary for large-scale assessments and marine spatial planning (Stamoulis

585    and Delevaux 2015). Spatially comprehensive, continuous input and output datasets eliminate

586    the need for the simplifying assumptions common in traditional approaches that can increase

587    uncertainty when results are extrapolated across the area of interest. Predictive mapping fills

588    gaps in survey coverage, allows for testing of management scenarios, and provides spatially

589    comprehensive information for managers including estimates of prediction precision (Pittman

590    and Knudby 2014). Finally, the approach is flexible so that it can be applied anywhere where

591    demersal fish populations are targeted, and any response variable derived from fish survey data

592    can be modeled depending on the research or management question.

593

594    **Acknowledgements**

610

611   **Literature Citations**

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

615   Almany, G., S. Connolly, D. Heath, J. Hogan, G. Jones, L. McCook, M. Mills, R. Pressey, and
616         D. Williamson. 2009. Connectivity, biodiversity conservation and the design of marine
617         reserve networks for coral reefs. Coral Reefs 28:339–351.

618   Almany, G. R. 2004. Does increased habitat complexity reduce predation and competition in
619         coral reef fish assemblages? Oikos 106:275–284.

620   Battista, T. A., B. M. Costa, and S. M. Anderson. 2007. Shallow-water benthic habitats of the
621         main eight Hawaiian Islands. Technical Memorandum, Biogeography Branch, Silver
622         Spring, MD.

623   Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries Sustainability via
624         Protection of Age Structure and Spatial Distribution of Fish Populations. Fisheries 29:23–
625         32.

626     Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big
627         ones. Trends in Ecology & Evolution 20:356–358.

628     Bouchet, P. J., J. J. Meeuwig, C. P. Salgado Kent, T. B. Letessier, and C. K. Jenner. 2015.
629         Topographic determinants of mobile vertebrate predator hotspots: current knowledge and
630         future directions. Biological Reviews 90:699–728.

631     Branch, G. M., and F. Odendaal. 2003. The effects of marine protected areas on the population
632         dynamics of a South African limpet, Cymbula oculus, relative to the influence of wave
633         action. Biological Conservation 114:255–269.

634     Breiman, L. 1996. Bagging predictors. Machine Learning 24:123–140.

635     Breiman, L. 2001. Statistical Modeling: The Two Cultures (with comments and a rejoinder by
636         the author). Statistical Science 16:199–231.

637     Campbell, S. J., G. J. Edgar, R. D. Stuart-Smith, G. Soler, and A. E. Bates. 2017. Fishing-gear
638         restrictions and biomass gains for coral reef fishes in marine protected areas.
639         Conservation Biology:n/a-n/a.

640     Charles, A., and L. Wilson. 2009. Human dimensions of Marine Protected Areas. ICES Journal
641         of Marine Science 66:6–15.

642     Cinner, J. E., N. a. J. Graham, C. Huchery, and M. A. Macneil. 2013. Global Effects of Local
643         Human Population Density and Distance to Markets on the Condition of Coral Reef
644         Fisheries. Conservation Biology 27:453–458.

645     Cohen, P. J., and S. J. Foale. 2013. Sustaining small-scale fisheries with periodically harvested
646         marine reserves. Marine Policy 37:278–287.

647     Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center. 2016. National Coral
648         Reef Monitoring Program: Stratified Random Surveys (StRS) of Reef Fish, including
649         Benthic Estimate Data of U.S. Pacific Reefs since 2007. NOAA National Centers for
650         Environmental Information. Unpublished Dataset.

651     Darling, E. S., N. A. J. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S.
652         K. Wilson. 2017. Relationships between structural complexity, coral traits, and reef fish
653         assemblages. Coral Reefs:1–15.

654     De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

655     De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple
656         technique for ecological data analysis. Ecology 81:3178–3192.

657    Delaney, D. G., L. T. Teneva, K. A. Stamoulis, J. L. Giddens, H. Koike, T. Ogawa, A. M.
658        Friedlander, and J. N. Kittinger. 2017. Patterns in artisanal coral reef fisheries reveal best
659        practices for monitoring and management.

660    Delevaux, J. 2017, July. Data and tools to operationalize ridge-to-reef management and build
661        island resilience in oceanic island environments. PhD Dissertation, University of Hawaii
662        at Manoa, Honolulu, HI.

663    Dulvy, N. K., N. V. C. Polunin, A. C. Mill, and N. A. J. Graham. 2004. Size structural change in
664        lightly exploited coral reef fish communities: evidence for weak indirect effects.
665        Canadian Journal of Fisheries and Aquatic Sciences 61:466–475.

666    Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S.
667        Barrett, M. A. Becerro, A. T. F. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A.
668        T. Cooper, M. Davey, S. C. Edgar, G. Försterra, D. E. Galván, A. J. Irigoyen, D. J.
669        Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. A. Strain, and R. J.
670        Thomson. 2014. Global conservation outcomes depend on marine protected areas with
671        five key features. Nature 506:216–220.

672    Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and
673        Prediction Across Space and Time. Annual Review of Ecology, Evolution, and
674        Systematics 40:677–697.

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

677    Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs:
678        review and synthesis. Marine Pollution Bulletin 50:125–146.

679    Fabricius, K. E. 2011. Factors Determining the Resilience of Coral Reefs to Eutrophication: A
680        Review and Conceptual Model. Pages 493–505 in Z. Dubinsky and N. Stambler, editors.
681        Coral Reefs: An Ecosystem in Transition. Springer Netherlands.

682    Fletcher, C. H., C. Bochicchio, C. L. Conger, M. S. Engels, E. J. Feirstein, N. Frazer, C. R.
683        Glenn, R. W. Grigg, E. E. Grossman, J. N. Harney, E. Isoun, C. V. Murray-Wallace, J. J.
684        Rooney, K. H. Rubin, C. E. Sherman, and S. Vitousek. 2008. Geology of Hawaii Reefs.
685        Pages 435–487 in B. M. Riegl and R. E. Dodge, editors. Coral Reefs of the USA.
686        Springer Netherlands.

687    Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of
688        habitat, wave exposure, and marine protected area status on coral reef fish assemblages in
689        the Hawaiian archipelago. Coral Reefs 22:291–305.

690    Friedlander, A. M., M. K. Donovan, K. A. Stamoulis, I. D. Williams, E. K. Brown, E. J. Conklin,
691        E. E. DeMartini, K. S. Rodgers, R. T. Sparks, and W. J. Walsh. 2017. Human-induced
692        gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of
693        traditional management boundaries. Aquatic Conservation: Marine and Freshwater
694        Ecosystems:n/a-n/a.

695    Friedlander, A. M., and J. D. Parrish. 1998a. Habitat characteristics affecting fish assemblages
696        on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1–
697        30.

698    Friedlander, A. M., and J. D. Parrish. 1998b. Temporal dynamics of fish communities on an
699        exposed shoreline in Hawaii. Environmental Biology of Fishes 53:1–18.

700    Friedman, J. H. 2002. Stochastic gradient boosting. Computational Statistics & Data Analysis
701        38:367–378.

702    Froese, R., and D. Pauly. 2017. FishBase. Online database. www.fishbase.org.

703    Galaiduk, R., A. R. Halford, B. T. Radford, C. H. Moore, and E. S. Harvey. 2017. Regional-scale
704        environmental drivers of highly endemic temperate fish communities located within a
705        climate change hotspot. Diversity and Distributions:n/a-n/a.

706    Giakoumi, S., and A. Pey. 2017. Assessing the Effects of Marine Protected Areas on Biological
707        Invasions: A Global Review. Frontiers in Marine Science 4.

708    Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid,
709        and D. M. Delparte. 2012. Online Rainfall Atlas of Hawai'i. Bulletin of the American
710        Meteorological Society 94:313–316.

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

713    Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G.
714        Gleason, P. J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of
715        coral reef fishes, and implications for marine reserve network design. Biological Reviews
716        90:1215–1247.

717     Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple

718           habitat models. Ecology Letters 8:993–1009.

719     Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology.

720           Ecological Modelling 135:147–186.

721     Harrison, H. B., D. H. Williamson, R. D. Evans, G. R. Almany, S. R. Thorrold, G. R. Russ, K. A.

722           Feldheim, L. van Herwerden, S. Planes, M. Srinivasan, M. L. Berumen, and G. P. Jones.

723           2012. Larval Export from Marine Reserves and the Recruitment Benefit for Fish and

724           Fisheries. Current Biology 22:1023–1028.

725     Hawaii Division of Aquatic Resources. 2016, September 1. Hawaiʻi 30 by 30 Oceans Target.

726           http://dlnr.hawaii.gov/dar/announcements/hawaii-30-by-30-oceans-target/.

727     Hijmans, R. J. 2014. Raster: Geographic data analysis and modeling. http://CRAN.R-

728           project.org/package=raster.

729     Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2014. dismo: Species distribution

730           modeling. http://CRAN.R-project.org/package=dismo.

731     Hixon, M. A., and J. P. Beets. 1989. Shelter Characteristics and Caribbean Fish Assemblages:

732           Experiments with Artificial Reefs. Bulletin of Marine Science 44:666–680.

733     Ige, D. Y. 2016, September 10. DLNR NEWS RELEASE: IUCN World Conservation Congress

734           is pau & now the work begins. http://governor.hawaii.gov/newsroom/latest-news/dlnr-

735           news-release-iucn-world-conservation-congress-is-pau-now-the-work-begins/.

736     Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R.

737           H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange,

738           H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R.

739           Warner. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems.

740           Science 293:629–637.

741     Januchowski, S. R., R. L. Pressey, J. VanDerWal, and A. Edwards. 2010. Characterizing errors

742           in digital elevation models and estimating the financial costs of accuracy. International

743           Journal of Geographical Information Science 24:1327–1347.

744     Jennings, S. 2000. Patterns and prediction of population recovery in marine reserves. Reviews in

745           Fish Biology and Fisheries 10:209–231.

746 Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural change in an exploited
747     fish community: a consequence of differential fishing effects on species with contrasting
748     life histories. Journal of Animal Ecology 68:617–627.

749 Jennings, S., and M. J. Kaiser. 1998. The Effects of Fishing on Marine Ecosystems. Advances in
750     Marine Biology 34:201–352.

751 Jennings, S., and N. V. C. Polunin. 1996. Effects of Fishing Effort and Catch Rate Upon the
752     Structure and Biomass of Fijian Reef Fish Communities. Journal of Applied Ecology
753     33:400–412.

754 Jennings, S., J. D. Reynolds, and S. C. Mills. 1998. Life history correlates of responses to
755     fisheries exploitation. Proceedings of the Royal Society of London B: Biological
756     Sciences 265:333–339.

757 Jones, P. J. S., W. Qiu, and E. M. De Santo. 2013. Governing marine protected areas: Social–
758     ecological resilience through institutional diversity. Marine Policy 41:5–13.

759 Kendall, M., T. Miller, and S. Pittman. 2011. Patterns of scale-dependency and the influence of
760     map resolution on the seascape ecology of reef fish. Marine Ecology Progress Series
761     427:259–274.

762 Kujala, H., A. Moilanen, and A. Gordon. 2017. Spatial characteristics of species distributions as
763     drivers in conservation prioritization. Methods in Ecology and Evolution:n/a-n/a.

764 Leathwick, J. R., J. Elith, M. P. Francis, T. Hastie, and P. Taylor. 2006. Variation in demersal
765     fish species richness in the oceans surrounding New Zealand: an analysis using boosted
766     regression trees. Marine Ecology Progress Series 321:267–281.

767 Lecky, J. 2016. Ecosystem Vulnerability and Mapping Cumulative Impacts on Hawaiian Reefs.
768     University of Hawaii at Manoa, Honolulu, HI.

769 Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S.
770     Airamé, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a
771     global synthesis. Marine Ecology Progress Series 384:33–46.

772 Lindfield, S. J., J. L. McIlwain, and E. S. Harvey. 2014. Depth Refuge and the Impacts of
773     SCUBA Spearfishing on Coral Reef Fishes. PLoS ONE 9:e92628.

774 Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M.
775     Kidwell, M. X. Kirby, C. H. Peterson, and J. B. Jackson. 2006. Depletion, degradation,
776     and recovery potential of estuaries and coastal seas. Science 312:1806–1809.

777 Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley. 2006.
778         Interpreting catch per unit effort data to assess the status of individual stocks and
779         communities. ICES J. Mar. Sci. 63:1373–1385.

780 McCoy, K. 2015, December. Estimating Nearshore Fisheries Catch for the main Hawaiian
781         Islands. University of Hawaii at Manoa, Honolul, HI.

782 McCoy, K., A. Heenan, J. Asher, P. Ayotte, K. Gorospe, A. Gray, K. Lino, J. Zamzow, and I.
783         Williams. 2017. Pacific Reef Assessment and Monitoring Program Data Report
784         Ecological monitoring 2016 - reef fishes and benthic habitats of the main Hawaiian
785         Islands, Northwestern Hawaiian Islands, Pacific Remote Island Areas, and American
786         Samoa. PIFSC Data Report, NOAA Pacific Islands Fisheries Science Center.

787 McLean, M., J. Cuetos-Bueno, O. Nedlic, M. Luckymiss, and P. Houk. 2016. Local Stressors,
788         Resilience, and Shifting Baselines on Coral Reefs. PLOS ONE 11:e0166319.

789 Mellin, C., M. Aaron MacNeil, A. J. Cheal, M. J. Emslie, and M. Julian Caley. 2016. Marine
790         protected areas increase resilience among coral reef communities. Ecology Letters
791         19:629–637.

792 Nash, K. L., and N. A. J. Graham. 2016. Ecological indicators for coral reef fisheries
793         management. Fish and Fisheries 17:1029–1054.

794 Nicholson, M. D., and S. Jennings. 2004. Testing candidate indicators to support ecosystem-
795         based management: the power of monitoring surveys to detect temporal trends in fish
796         community metrics. ICES Journal of Marine Science 61:35–42.

797 Norström, A. V., M. Nyström, J.-B. Jouffray, C. Folke, N. A. Graham, F. Moberg, P. Olsson, and
798         G. J. Williams. 2016. Guiding coral reef futures in the Anthropocene. Frontiers in
799         Ecology and the Environment 14:490–498.

800 Pittman, S. J., and K. A. Brown. 2011. Multi-Scale Approach for Predicting Fish Species
801         Distributions across Coral Reef Seascapes. PLoS ONE 6:e20583.

802 Pittman, S. J., C. Caldow, S. D. Hile, and M. E. Monaco. 2007. Using seascape types to explain
803         the spatial patterns of fish in the mangroves of SW Puerto Rico. Marine Ecology Progress
804         Series 348:273–284.

805 Pittman, S. J., B. M. Costa, and T. A. Battista. 2009. Using Lidar Bathymetry and Boosted
806         Regression Trees to Predict the Diversity and Abundance of Fish and Corals. Journal of
807         Coastal Research:27–38.

808    Pittman, S., and A. Knudby. 2014. Predictive mapping of coral reef fish species and

809        communities. Pages 219–236 *in* P. Bortone, editor. Interrelationships Between Corals and

810        Fisheries. CRC Press.

811    R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for

812        Statistical Computing, Vienna, Austria.

813    Ringuet, S., and F. T. Mackenzie. 2005. Controls on nutrient and phytoplankton dynamics during

814        normal flow and storm runoff conditions, southern Kaneohe Bay, Hawaii. Estuaries

815        28:327–337.

816    Sciberras, M., S. R. Jenkins, R. Mant, M. J. Kaiser, S. J. Hawkins, and A. S. Pullin. 2013.

817        Evaluating the relative conservation value of fully and partially protected marine areas.

818        Fish and Fisheries:n/a–n/a.

819    Shin, Y.-J., M.-J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. Using size-based

820        indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science:

821        Journal du Conseil 62:384–396.

822    Smith, M. D., and J. E. Wilen. 2003. Economic impacts of marine reserves: the importance of

823        spatial behavior. Journal of Environmental Economics and Management 46:183–206.

824    Stamoulis, K. A., and J. M. S. Delevaux. 2015. Data requirements and tools to operationalize

825        marine spatial planning in the United States. Ocean & Coastal Management 116:214–

826        223.

827    Stamoulis, K. A., and A. M. Friedlander. 2013. A seascape approach to investigating fish

828        spillover across a marine protected area boundary in Hawai'i. Fisheries Research 144:2–

829        14.

830    Stamoulis, K. A., M. Poti, J. M. S. Delevaux, M. K. Donovan, A. Friedlander, and M. S.

831        Kendall. 2016. Chapter 4: Fishes - Reef Fish. Pages 156–196 Marine Biogeographic

832        Assessment of the Main Hawaiian Islands. Bureau of Ocean Energy Management and

833        National Oceanic and Atmospheric Administration.

834    Stewart, K. R., R. L. Lewison, D. C. Dunn, R. H. Bjorkland, S. Kelez, P. N. Halpin, and L. B.

835        Crowder. 2010. Characterizing Fishing Effort and Spatial Extent of Coastal Fisheries.

836        PLOS ONE 5:e14451.

837    Taylor, B. M., S. J. Lindfield, and J. H. Choat. 2015. Hierarchical and scale-dependent effects of
838        fishing pressure and environment on the structure and size distribution of parrotfish
839        communities. Ecography 38:520–530.

840    VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2014. SDMTools: Species
841        Distribution Modelling Tools.

842    Wedding, L. M., and A. M. Friedlander. 2008. Determining the influence of seascape structure
843        on coral reef fishes in Hawaii using a geospatial approach. Marine Geodesy 31:246–266.

844    Wedding, L. M., A. M. Friedlander, M. McGranaghan, R. S. Yost, and M. E. Monaco. 2008.
845        Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for
846        management of reef fish assemblages in Hawaii. Remote Sensing of Environment
847        112:4159–4165.

848    Weeks, R., A. L. Green, E. Joseph, N. Peterson, and E. Terk. 2017. Using reef fish movement to
849        inform marine reserve design. Journal of Applied Ecology 54:145–152.

850    Weigel, J.-Y., K. O. Mannle, N. J. Bennett, E. Carter, L. Westlund, V. Burgener, Z. Hoffman, A.
851        Simão Da Silva, E. A. Kane, J. Sanders, C. Piante, S. Wagiman, and A. Hellman. 2014.
852        Marine protected areas and fisheries: bridging the divide. Aquatic Conservation: Marine
853        and Freshwater Ecosystems 24:199–215.

854    Williams, I. D., J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, and R. E. Brainard. 2015.
855        Human, Oceanographic and Habitat Drivers of Central and Western Pacific Coral Reef
856        Fish Assemblages. PLoS ONE 10:e0120516.

857    Williams, I. D., W. J. Walsh, R. E. Schroeder, A. M. Friedlander, B. L. Richards, and K. A.
858        Stamoulis. 2008. Assessing the importance of fishing impacts on Hawaiian coral reef fish
859        assemblages along regional-scale human population gradients. Environmental
860        Conservation 35:261–272.

861    Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and NCEAS
862        Predicting Species Distributions Working Group. 2008. Effects of sample size on the
863        performance of species distribution models. Diversity and Distributions 14:763–773.

864    Wren, J. L. K., D. R. Kobayashi, Y. Jia, and R. J. Toonen. 2016. Modeled Population
865        Connectivity across the Hawaiian Archipelago. PLOS ONE 11:e0167626.

866

867    Supporting Information

868    Additional supporting information may be found in the online version of this article at

869    http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

870

871    Data Availability

872    Habitat and wave predictor layers at NOAA National Centers for Environmental Information:

873    https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0155189

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

875    Fishing effort layers and predicted maps at Research Data Australia:

876    http://dx.doi.org/10.4225/06/5a572a1f1406a

**Tables:**

Table 1: Final predictor datasets used in model development. Number of individual datasets of each type indicated in parenthesis. 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. See table S2 for more details.

| Predictor dataset types | Datasets | 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, BPI | Seafloor topography metrics derived from bathymetry including depth, slope, structural complexity, exposure, curvature and bathymetric position index (BPI). Slope, slope of slope, and BPI were calculated at two scales. |
| Benthic habitat composition (7) | Percent cover of CCA, 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 * wave period. |

890 Table 2: Predicted mean biomass and percent increase for targeted reef fishes under present
891 conditions and with fishing pressure removed. N is the sample size representing total number of
892 spatially predicted grid cells per island. SD is standard deviation. Islands are ordered from north
893 to south.

894

| Biomass (g m$^{-2}$) | 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% |

895
896
897
898
899
900
901
902
903
904
905
906
907
908 Table 3: Predicted mean body length and percent increase for targeted reef fishes under present
909 conditions and with fishing pressure removed. N is the sample size representing total number of
910 spatially predicted grid cells per island. SE is standard error of the mean.

911

Present                        No fishing

| Length (cm) | N | mean | SD | mean | SD | % Increase |
|---|---|---|---|---|---|---|
| Kauaʻi | 67,967 | 17.9 | 2.4 | 21.8 | 1.6 | 22% |
| Niʻihau | 10,677 | 23.0 | 1.2 | 23.0 | 1.2 | 0% |
| Oʻahu | 84,870 | 15.1 | 2.0 | 20.0 | 1.6 | 33% |
| Molokaʻi | 38,220 | 17.7 | 3.2 | 21.3 | 2.0 | 21% |
| Maui | 43,830 | 18.0 | 2.9 | 21.1 | 1.6 | 17% |
| Hawaiʻi | 30,702 | 18.6 | 2.1 | 21.0 | 1.3 | 13% |

912

913

914

915

916

917

918

919

920

921

922

923

924

925

926 Table 4: Biomass (g m$^{-2}$) and fish length (cm) mean, standard deviation (SD), mean percent

927 increase, and standard deviation of percent increase between MHI model predictions for regions

928 of significant difference shown in figure 7.

929

| | Biomass Increase | | | | Length Increase | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | **Mean %** | SD % | Mean | SD | **Mean %** | SD % |
| Kauaʻi | 29.4 | 2.6 | **383%** | 184% | 6.5 | 0.6 | **45%** | 7% |
| Niʻihau | 3.6 | 0.9 | **11%** | 2% | 0.0 | 0.0 | **0%** | 0% |
| Oʻahu | 25.9 | 2.8 | **517%** | 268% | 7.3 | 0.5 | **59%** | 10% |
| Molokaʻi | 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% |

**Figure Legends:**

**Figure 1:** Main Hawaiian Islands study domain with reef fish survey locations used for modeling.

**Figure 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 spear fishing effort maps based on the sum of pixel values within polygons matching the description of the survey area in each report. The equation of the fitted line is y = 0.48x - 1660.

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

**Figure 4:** Final predictors for MHI models based on 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).
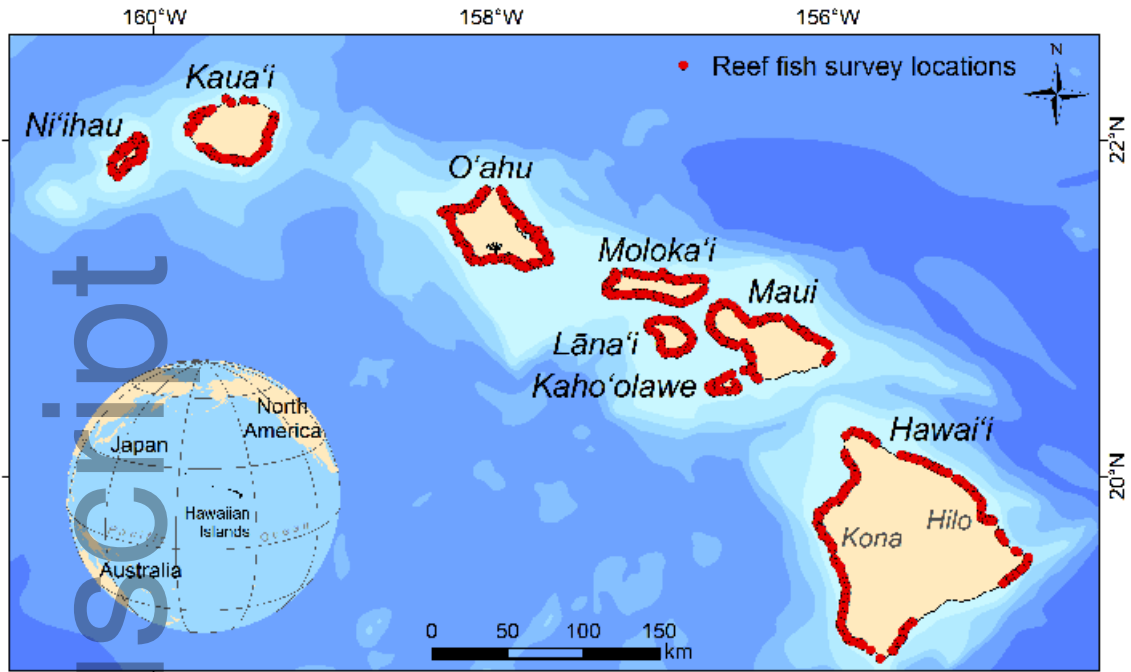
959    **Figure 5:** Partial dependence plots of fishing predictors for the targeted reef fish biomass model.

960    Y-axis is transformed biomass (4th root) and x-axis is predictor variable (units in table S1). Plots

961    represent the relationship of biomass with each predictor individually when all other predictors

962    are held at their mean. Lines are the mean of bootstrapped models plus and minus the standard

963    deviation.

964    **Figure 6:** Distributions of predicted biomass values under present fishing levels and with fishing

965    removed for each island. X-axis is biomass values per 60x60 m grid cell and y-axis is frequency

966    of biomass values as a proportion of the total number of grid cells per island (density).

967    **Figure 7:** Distributions of predicted length values under present fishing levels and with fishing

968    removed for each island. X-axis is length values per 60x60 m grid cell and y-axis is frequency of

969    length values as a proportion of the total number of grid cells per island (density).

970    **Figure 8:** Regions of significant increase ($\alpha = 0.1$) in MHI model predictions of biomass and

971    length after removal of fishing. Existing no-take reserves and restricted access areas are outlined
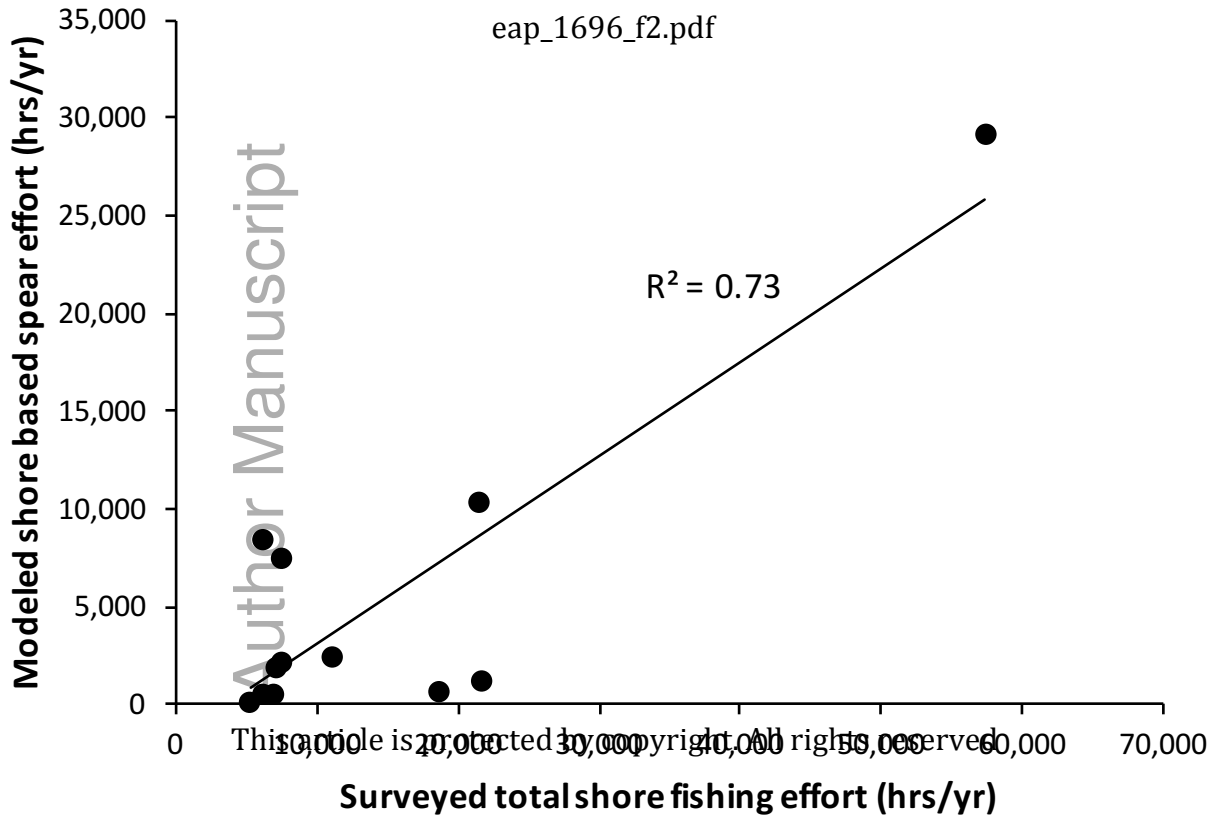
972    in black.

eap_1696_f1.tif
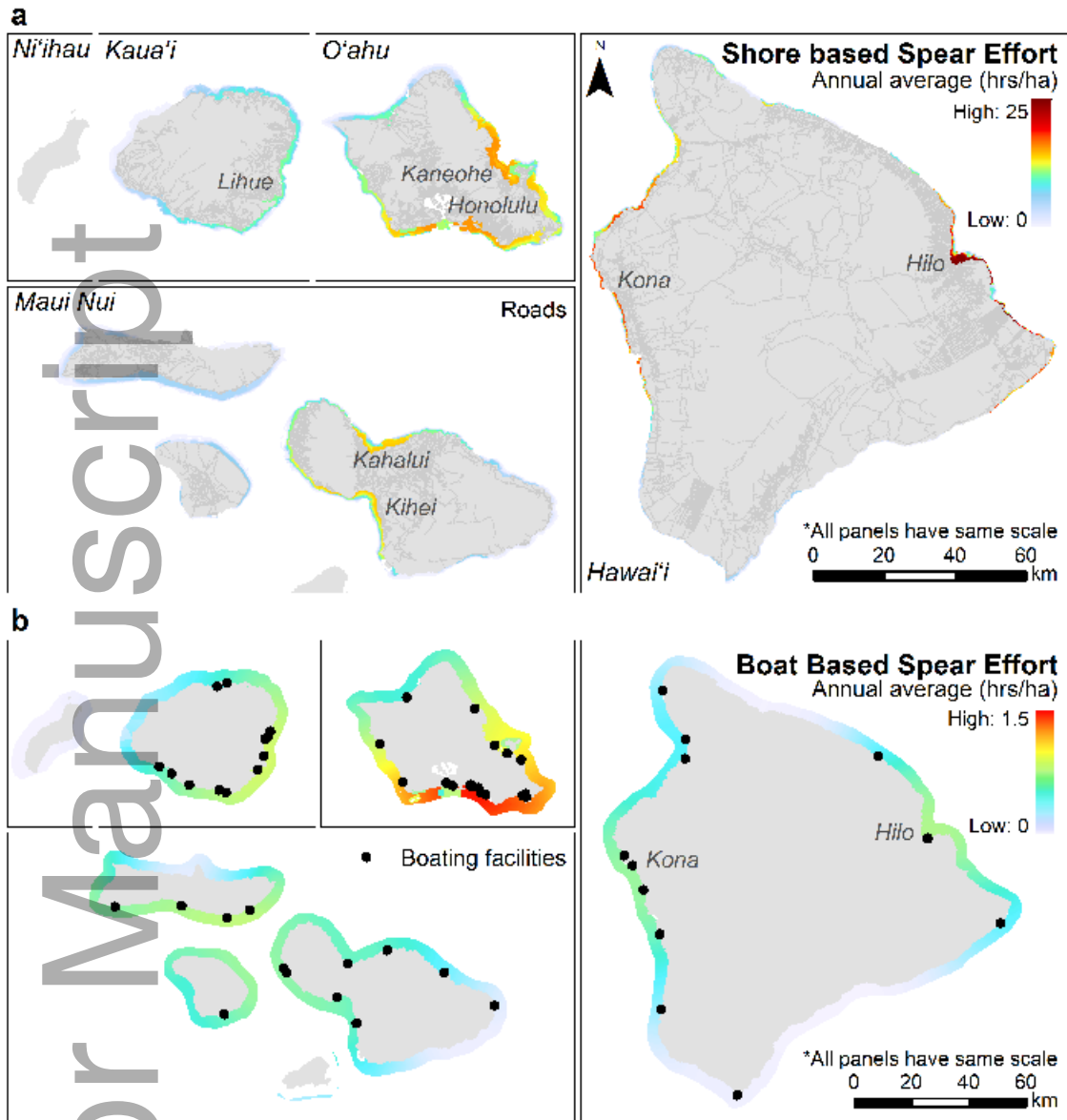
a

*Ni'ihau* *Kaua'i* *O'ahu*

*Lihue* *Kaneohe* *Honolulu*

*Maui Nui* Roads

*Kahalui* *Kihei*

**Shore based Spear Effort**
Annual average (hrs/ha)

High: 25

Low: 0

*Kona* *Hilo*

*All panels have same scale
0   20   40   60
km

*Hawai'i*

b

Boating facilities

**Boat Based Spear Effort**
Annual average (hrs/ha)

High: 1.5

Low: 0

*Kona* *Hilo*

*All panels have same scale
0   20   40   60
km

eap_1696_f3.tif

**a**

Biomass

| Category | |
|---|---|
| Shore fishing | |
| Boat fishing | |
| Slope of slope | |
| Depth | |
| Longitude | |
| Slope 240m | |
| Sine Aspect | |
| Latitude | |
| Wave power | |

% variation explained

**b**

Body length

| Category | |
|---|---|
| Boat fishing | |
| Longitude | |
| Sine aspect | |
| Shore fishing | |
| Wave power | |
| Slope of slope 240m | |
| Depth | |
| Slope | |
| Slope of slope | |
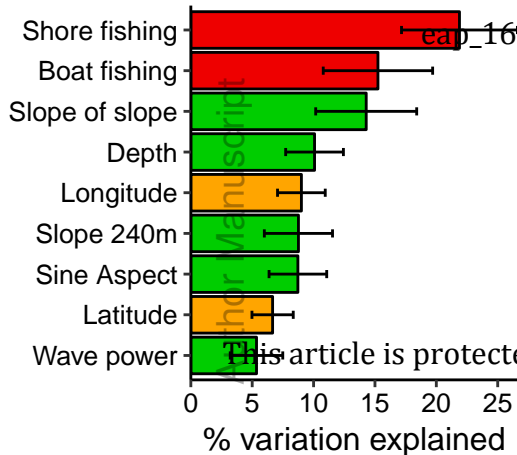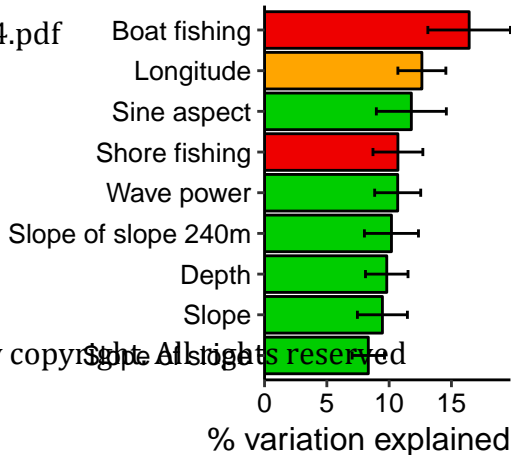
% variation explained
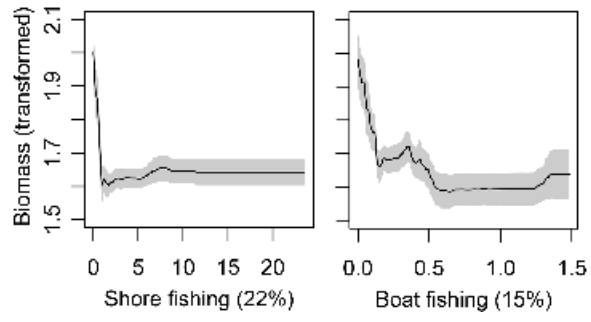
eap_1696_f5.tif
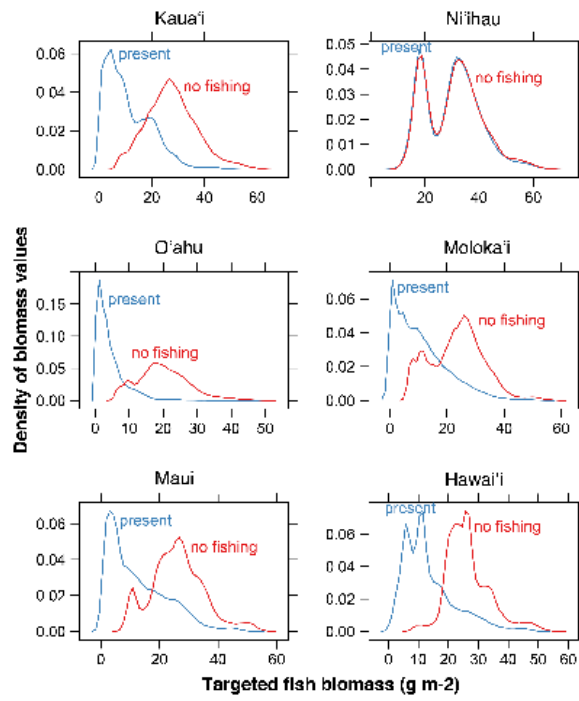
eap_1696_f6.tif

eap_1696_f7.tif

None
Biomass
Length
Both

*Ni'ihau*

*Kaua'i*

*O'ahu*

Mōkapu Pt.

Mā'ili Pt.

*Moloka'i*

*Maui*

Ma'alaea
Bay

Makole'a
Pt.

Kaloli
Pt.

Cape Kumukahi

*East
Hawai'i*

*West Hawai'i*

Coastline

Existing MPAs

15 km

eap_1696_f8.tif