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Habitat-based species distribution modelling of the Hawaiian deepwater snapper-grouper complex

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ABSTRACT

Deepwater snappers and groupers are valuable components of many subtropical and tropical fisheries globally and understanding the habitat associations of these species is important for spatial fisheries management. Habitat-based species distribution models were developed for the deepwater snapper-grouper complex in the main Hawaiian Islands (MHI). Six eteline snappers (*Pristipomoides* spp., *Aphareus rutilans*, and *Etelis* spp.) and one endemic grouper (*Hyporthodus quernus*) comprise the species complex known as the Hawaiian Deep Seven Bottomfishes. Species occurrence was recorded using baited remote underwater video stations deployed between 30 and 365 m (n = 2381) and was modeled with 12 geomorphological covariates using GLMs, GAMs, and BRTs. Depth was the most important predictor across species, along with ridge-like features, rugosity, and slope. In particular, ridge-like features were important habitat predictors for *E. coruscans* and *P. filamentosus*. Bottom hardness was an important predictor especially for the two *Etelis* species. Along with depth, rugosity and slope were the most important habitat predictors for *A. rutilans* and *P. zonatus*, respectively. Models built using GAMs and BRTs generally had the highest predictive performance. Finally, using the BRT model output, we created species-specific distribution maps and demonstrated that areas with high predicted probabilities of occurrence were positively related to fishery catch rates.

1. Introduction

Snappers (Family Lutjanidae) and groupers (Family Serranidae) are commercially important marine species in many tropical-subtropical fisheries. These fishes are often characterized as large, long-living species with high site fidelity and thus are vulnerable to fishing pressure (Jennings et al., 1999; Coleman et al., 2000; Morris et al., 2000; Newman et al., 2016). For many countries in the Indo-Pacific region, there has been limited fisheries management of deepwater snappers and groupers and assessments of stock status (Newman et al., 2016). Improvements to increase and standardize fisheries, habitat, and life history data for this species complex are ongoing and top priorities for the Indo-Pacific region (Newman et al., 2015).

In the main Hawaiian Islands (MHI), the deepwater snapper-grouper or "bottomfish" complex is a commercially and culturally valuable fishery (Pooley, 1993; Hospital and Pan, 2009; Hospital and Beavers, 2012). The Hawaiian Deep Seven Bottomfishes is a state and US federally managed species complex consisting of six eteline snappers and one endemic grouper: *Etelis coruscans, E. carbunculus, Pristipomoides*

filamentosus, P. sieboldii, P. zonatus, Aphareus rutilans, and *Hyporthodus quernus*. Two species, *E. coruscans* and *P. filamentosus*, comprise the majority of the Deep Seven bottomfish catch (Brodziak et al., 2014). The major component of fisheries data is a 60+ year time series of catch and effort data, with ongoing efforts to establish a fisheries-independent surveying program using invasive and non-invasive techniques (Richards et al., 2016). Regulations for this fishery include: annual catch limits, size and gear restrictions, bag limits, fisher and boat registrations, and permanent restricted fishing areas.

Habitat information is an important piece of knowledge that informs the spatial management of fisheries. Depth is a consistent habitat feature found to delineate bottomfish species distributions (Sundberg and Richards, 1984; Ralston and Williams, 1998; Martinez-Andrade, 2003; Gomez et al., 2015). Misa et al. (2013) and Moore et al. (2016) established preliminary habitat associations for the top four commercially important species in the MHI (*E. carbunculus, E. coruscans, P. filamentosus*, and *P. sieboldii*). They noted depth segregations among the species complex, and high-relief, hard-bottom areas as important habitat features. Raised physical features like promontories and pinnacles

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allow for an upward advection and retention of deeper-dwelling zoo-plankton to shallower waters that may attract fish predators, and is concurrent with submersible observations of bottomfishes (e.g., *P. fi-lamentosus*) near underwater headlands, especially in upcurrent lo-calities (Ralston et al., 1986; Kelley et al., 2006). Macrohabitat features like substrate rugosity and natural cavities also serve as important predator rufugia (Kelley and Ikehara, 2006).

Our main research objective was to develop habitat-based species distribution models for each of the Hawaiian Deep Seven Bottomfishes throughout the MHI. Species occurrence was collected using Baited Remote Underwater Videos (BRUVs) deployed between 30 and 365 m across the MHI. Probability of occurrence was modelled with various benthic habitat landscape variables using Generalized Linear Models (GLMs), Generalized Additive Models (GAMs), and Boosted Regression Trees (BRTs). To account for possible spatial autocorrelation (SAC) in the model residuals, a residual autocovariate (RAC) model (Crase et al., 2012, 2014) was included as an additional model to the GLMs, GAMs, and BRTs. The model output was then interpolated to the entire MHI between 50 and 400 m depth, resulting in a predictive map of prob-ability of occurrence for each of the seven species. Finally, as an ap-plication of the species distribution models, we related model output with fishery catch rates within statistical fishery reporting areas to examine whether model predictions of species hotspots were positively related to fishery yields.

2. Material and methods

2.1. Data sources

Presence-absence data for each of the seven species were collected at 2381 sites from 2007 to 2015 across the MHI (Fig. 1) ranging 30–365 m via Bottom Baited Camera Stations (BotCam; Merritt et al., 2011). The main goal of the BotCam surveys was to monitor bottomfish populations inside and adjacent to bottomfish restricted fishing areas (BRFAs). BotCam locations were selected using a stratified-random design with protection (inside or outside of BRFAs) and coarse habitat features (soft-bottom/low slope, hard-bottom/low slope, soft-bottom/high slope, hard-bottom/high slope (Misa et al., 2013)) as the sampling strata. The BotCam system used two ultralow-light video cameras that recorded under ambient light conditions and was propped 3 m above the sea floor to optimize the field of view for observations. At each site, species presence was recorded over a 30–40 min soak period, a soak period found to be adequate for stereo-video surveys for these species (Misa et al., 2016). Full details on the BotCam protocol are provided in Misa et al. (2013), Moore et al. (2013) and Sackett et al. (2014). Species occurrence as a percentage of the total dataset ranged from 5.45% for *H. quernus* to 28.3% for *P. filamentosus*. Bathymetry layers at 5-m re-solution were provided by the Hawaii Mapping Research Group (HMRG). A backscatter synthesis at 60-m resolution was accessed from the HMRG website (http://www.soest.hawaii.edu/HMRG/multibeam/index.php). Fisheries logbook data from 2003 to 2014 were provided by the State of Hawaii Division of Aquatic Resources. For each commercial bottomfish trip, fishers reported the date caught and fishery reporting area (Fig. 1) and the total number of pieces, weight, and number of hours and lines used for each species caught.

2.2. Habitat variables

Bathymetry-derived variables—slope, aspect, and curvature—were calculated in ArcGIS (V.10.3) with an eight-cell neighborhood (Burrough and McDonnell, 1998). Terrain ruggedness, referred to as rugosity hereafter, was calculated with an eight-cell neighborhood using ArcGIS Benthic Terrain Modeler (Wright et al., 2005) and ranged from 0 (no variation) to 1 (complete variation). Rugosity was log-transformed to normalize the positively skewed distribution. Bathy-metry-derived variables were calculated at two resolutions of bathy-metry (5-m and 60-m) to provide different scales of habitat features.

Bathymetric position index (BPI; Lundblad et al., 2006) describes a particular point in relation to the overall landscape similar to the to-pographic position index (Weiss, 2001; Iampietro and Kvitek, 2002). BPI was calculated using ArcGIS Benthic Terrain Modeler using scale factors of 125 (fine-scale BPI) and 1250 (broad-scale BPI), and then standardized similar to the protocol of Lundblad et al. (2006). Under standardized bpi units, values > 100 indicate scale-specific ridge-like structures, values < -100 indicate scale-specific depressions, and va-lues between -100 and 100 indicate either slopes or flat plains. Maps of each of the 12 habitat covariates can be viewed in the supplementary material (Figs. S8–S19).

2.3. Model parameterization

Due to the differences in observed depth ranges for the seven spe-cies, creating a model that included sites outside of the depth range would have produced overly confident model predictions. Thus, for
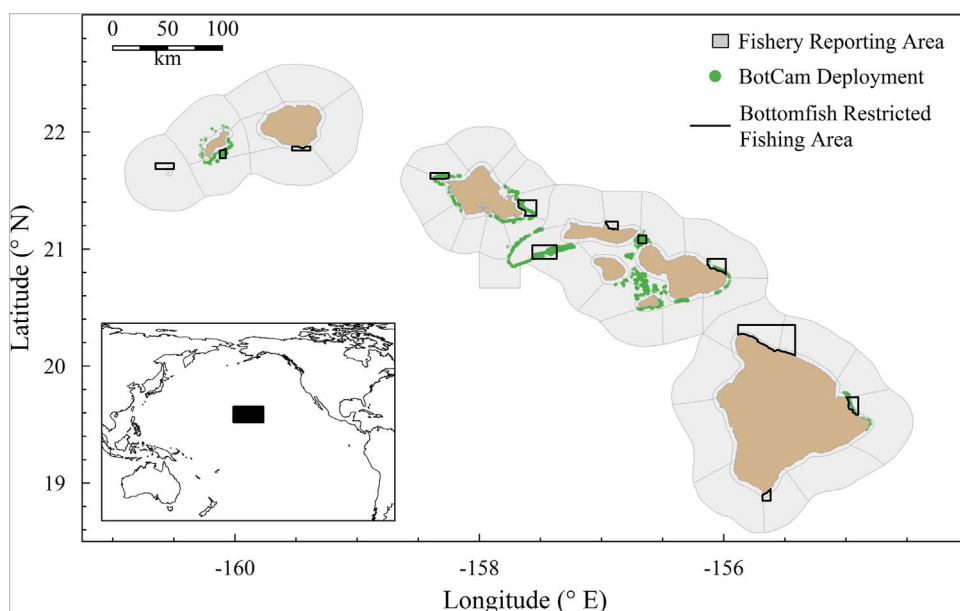

Fig. 1. Location of Bottom Camera Bait Station (BotCam) sites (green dots) within the main Hawaiian Islands (located within the solid black box in insert) deployed during 2007–2015. The State of Hawaii statistical fishery reporting areas (gray areas) and current bottomfish restricted fishing areas (bold outlines) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

each species, only records within the observed depth range were used, then randomly partitioned into a training and test dataset with 70% and 30% of the data, respectively. GLMs, GAMs, and BRTs were built on the training set, and evaluation metrics were calculated on the test dataset. These three models were chosen to represent models in increasing complexity, respectively. All models were fitted within the R statistical environment (R Core Team, 2016).

GLMs and GAMs were fitted with a binomial (Bernoulli) error distribution with a logit-link. GAMs were fitted using the mgcv R-package. The pdredge function in the MuMIn R-package was used to compare combinations of first-order variable models. Corrected Akaike Information Criterion (AICc) was used as the metric to rank the different candidate models. Delta-AICc values were calculated by subtracting each model's AICc by the lowest AICc. The "best" model was chosen as the most parsimonious combination of habitat variables with "substantial support" (i.e., delta-AICc < 2.0; Burnham and Anderson (2004)). Of the habitat variables that were chosen in the final GLMs and GAMs, the only pair of habitat variables that was strongly correlated (r > 0.8) were slopes calculated at 5 m and 60 m resolutions. Boosted Regression Trees were fitted using the dismo R-package and customized code similar to Elith et al. (2008). Optimal model settings were chosen using 10-fold cross-validation by evaluating factorial combinations of learning rate (0.001, 0.005, or 0.010), bagging rate (0.50 or 0.75) and tree complexity (1–5) similar to the protocol of Franklin et al. (2013). The combination of model settings that produced the lowest cross-validated residual deviance with > 1000 trees (Elith et al., 2008) was chosen for each of the seven species models.

A residual-autocovariate model following Crase et al. (2012, 2014) was also implemented to account for possible SAC in the model residuals. First, models were fitted as described in this section, then the residual on the logit-link scale was calculated for each datum. The RAC was calculated for each datum as the mean residual using a 1 km moving window. Models fitted without the RAC are hereafter referred to as environment-only models (i.e., ENV-GLM, ENV-GAM, and ENV-BRT) and models fitted with the RAC are hereafter referred to as RAC models (i.e., RAC-GLM, RAC-GAM, and RAC-BRT).

2.4. Model evaluation

A set of common evaluation metrics of predictive performance was calculated on the models fitted to the test datasets. Spatial autocorrelation of the model residuals was evaluated on the test datasets using Moran's I (Cliff and Ord, 1981), calculated using the ape R-package. Moran's I values range from −1 to +1 with a value of zero indicating a random spatial pattern. Area Under the Receiving Operating Curve (AUC) calculates the ability of a model to discriminate between a presence or absence observation. Values of AUC are coarsely interpreted as: bad: 0.50–0.59; poor: 0.60–0.69; fair: 0.70–0.79; good: 0.80–0.89; excellent: 0.90–1.0 (Hosmer et al., 2013). Specificity, Sensitivity, and the True Skill Statistic (TSS) were calculated using a probability threshold that balances sensitivity and specificity similar to Schröder and Richter (2000). True Skill Statistic values range from −1 to +1 where values < 0 indicating a predictive model worse than random, zero indicating an indiscriminate predictive model, and +1 indicating a perfect predictive model. Lastly, percent deviance explained was calculated as: *%Deviance Explained = 100%(1 − Residual Deviance/Null Deviance)*.

2.5. Linking model output with fishery catch rates

The model output from the ENV-BRT was chosen to map the species distribution across the MHI, and then used to link habitat quality (i.e., areas with high species probability of occurrence) with fishery catch rates. Species-specific mean annual catch-per-unit effort (CPUE) over the 2003–2014 time period was calculated for each statistical fishery reporting area (Fig. 1) as total catch divided by total line-hours

(Supplementary material, Figs. S1–S7). Because predicted probabilities were highly clustered and geographically sparse, conventional mean or median probabilities of occurrence would not have been a representative index of the upper distribution habitat quality of the fishing area. Thus, within each fishery reporting area, the probability of occurrence associated with the 99th percentile was chosen as a coarse but representative index of habitat quality. A generalized linear mixed model (GLMM) was used to model the natural logarithm of CPUE of the jth species in the ith reporting area:

$$\ln(CPUE_{ij}) = \beta_0 + \beta_j SPECIES_{ij} + \beta_1 99PROB.OC_{ij} + AREA_i + \varepsilon_{ij}$$

$$AREA_i \sim N(0, \sigma^2_{AREA})$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

where β_j are the species-specific intercepts, $99\_PROB\_OC_{ij}$ is the 99th percentile cell value of probability of occurrence for the jth species in the ith fishery reporting area, and the slope of the linear relationship between log-CPUE and 99_PROB_OC is denoted as β_1. The analysis was not sensitive to the choice of the percentile threshold, and thus we concluded that the 99th percentile was representative of the upper distribution of the probability of occurrence values within a fishery reporting area. Species-specific landings within a fishery reporting area were expected to be highly correlated and thus, fishery reporting area was included as a random effect with variance σ^2_{AREA} representing the inter-area variation. ε_{ij} are normally distributed zero-centered residuals with variance σ^2. Psuedo-R^2 values were calculated using the r.squaredGLMM function in the MuMIn R-package. This method calculates the marginal (fixed effects only) and conditional (fixed and random effects) coefficient of determination based on Nakagawa and Schielzeth (2013).

3. Results

3.1. Overall model performance

3.1.1. Environment-only species distribution models

Area Under the Receiving Operating Curve (AUC) and TSS values trended similarly across species models (Tables 1 and 2, respectively). *Pristipomoides zonatus* and the two *Etelis* species had the best-performing models and *H. quernus* models consistently had the lowest predictive performance across model types. For the *P. filamentosus*, *P. sieboldii*, and *E. carbunculus* models, the AUC values noticeably increased from GLMs to GAMs and BRTs. The BRT models had the highest threshold-dependent metrics compared to GLMs and GAMs except for the *A. rutilans* and *P. zonatus* models (Table 2). Consistent across species, percent deviance explained increased from GLMs to GAMs to BRTs.

3.1.2. Residual autocovariate species distribution models

Model residuals for the environment-only models showed weak positive spatial autocorrelation with Moran's I values between 0.02 - 0.18 (Table 1). The RAC models either had Moran's I values shifted closer to zero or Moran's I values of the same magnitude but in the opposite (negative) direction. Area Under the ROC values all increased with the inclusion of the RAC (AUC > 0.90) and did not vary much across model types. Deviance explained was also higher for the RAC models, with the largest increase in deviance explained between environment-only GLMs and RAC-GLMs. True Skill Statistic values were also higher for the RAC models compared to the environment-only models, however there was no clear pattern in TSS values across model types (Table 2).

3.2. Habitat associations from ENV-BRT models

3.2.1 Aphareus rutilans

Bathymetry and log-rugosity at 60 m resolution had > 60% relative importance in the BRT models (Fig. 2). *A. rutilans* was observed at

Table 1

Moran's I of model residuals, Area Under the Receiver Operating Curve (AUC), and percentage of deviance explained for the environment-only (ENV) and residual autocovariate (RAC) models across model types–Generalized Linear Models (GLM), Generalized Additive Models (GAM), and Boosted Regression Trees (BRT)–and species. Species codes: ARU (*Aphareus rutilans*), ECA (*Etelis carbunculus*), ECO (*E. coruscans*), HQU (*Hyporthodus quernus*), PFI (*Pristipomoides filamentosus*), PSI (*P. sieboldii*), and PZO (*P. zonatus*).

Species-Model Code	Moran's I			AUC			% Deviance Explained		
	GLM	GAM	BRT	GLM	GAM	BRT	GLM	GAM	BRT
ARU-ENV	0.03	0.04	0.06	0.79	0.80	0.78	17	19	28
ARU-RAC	− 0.04	− 0.07	− 0.08	0.94	0.96	0.96	56	66	51
ECA-ENV	0.18	0.10	0.13	0.78	0.85	0.84	19	36	45
ECA-RAC	− 0.01	− 0.02	0.01	0.95	0.95	0.92	56	61	67
ECO-ENV	0.09	0.08	0.13	0.80	0.83	0.83	25	34	46
ECO-RAC	− 0.07	− 0.08	− 0.05	0.93	0.92	0.93	57	65	68
HQU-ENV	0.08	0.04	0.08	0.71	0.72	0.73	10	33	30
HQU-RAC	− 0.07	− 0.05	− 0.14	0.97	0.93	0.95	59	69	55
PFI-ENV	0.09	0.09	0.07	0.73	0.77	0.79	12	23	33
PFI-RAC	0.01	0.01	− 0.05	0.92	0.93	0.91	48	56	44
PSI-ENV	0.09	0.07	0.06	0.73	0.77	0.81	14	23	38
PSI-RAC	− 0.05	− 0.07	− 0.04	0.93	0.93	0.92	46	53	55
PZO-ENV	0.03	0.02	0.03	0.88	0.88	0.90	30	45	58
PZO-RAC	0.01	− 0.07	− 0.08	0.96	0.97	0.95	61	60	57

depths between 108 and 273 m, with a near linear decrease in probability of occurrence with increasing depths and increasing probability of occurrence with log-rugosity at 60 m resolution (Fig. 3). Probability of occurrence was positively associated with lower slope values at both scales (Fig. 3; Supplementary material, Fig. S20), a pattern unlike the other species in the complex.

3.2.2. Etelis spp.

Both *Etelis* spp. were observed at the deepest depths among the seven species, with an observed depth range of 175–365 m. Bathymetry and backscatter were consistently important variables in the BRT models, as well as log-rugosity at 60 m (Fig. 2). Ridge-like features at fine scales were associated with *E. carbunculus* occurrence whereas ridge-like features at broad scales were associated with *E. coruscans* occurrence (Fig. 3; Supplementary material, Fig. S21). Probability of occurrence for both species increased near linearly with depth and backscatter (Fig. 3). Slope at both resolutions were more important for *E. carbunculus* than *E. coruscans*, with higher probabilities of occurrence associated with higher slope values (i.e., slope > 30°; Fig. 3; Supplementary material, Fig. S20).

3.2.3. Hyporthodus quernus

There were no habitat variables that were especially important for the *H. quernus* BRT model (Fig. 2). The observed depth range was between 81 and 264 m, with peak probability of occurrence at approximately 175 m (Fig. 3). Probability of occurrence increased linearly with backscatter and was greater in areas with slopes > 25° and lower values of log-rugosity, both at 5-m and 60-m scales (Fig. 3; Supplementary material, Fig. S20). Ridge-like features at broad scales were also associated with *H. quernus* occurrence (Supplementary material, Fig. S21).

3.2.4. Pristipomoides spp.

Bathymetry, broad-scale BPI, backscatter, and slope and log-rugosity at 60 m resolution were the most important variables for *P. filamentosus* and *P. sieboldii* (Fig. 2). *Pristipomoides filamentosus* had the shallowest observed presence at 41 m, whereas *P. sieboldii* and *P. zonatus* had deeper depth ranges with peaks at approximately 250 and 175 m, respectively (Fig. 3). Slope at 60 m resolution had the highest relative importance for the *P. zonatus* BRT model across species models (Fig. 2), with slopes > 30° associated with higher probabilities of

Table 2

Threshold-dependent True Skill Statistic (TSS), sensitivity, and specificity for environment-only (ENV) and residual autocovariate (RAC) models across model types–Generalized Linear Models (GLM), Generalized Additive Models (GAM), and Boosted Regression Trees (BRT)–and species. Threshold chosen to balance model specificity and sensitivity based on (Schröder and Richter, 1999). Species codes: ARU (*Aphareus rutilans*), ECA (*Etelis carbunculus*), ECO (*E. coruscans*), HQU (*Hyporthodus quernus*), PFI (*Pristipomoides filamentosus*), PSI (*P. sieboldii*), and PZO (*P. zonatus*).

Species-Model Code	Threshold			TSS			Sensitivity/Specificity		
	GLM	GAM	BRT	GLM	GAM	BRT	GLM	GAM	BRT
ARU-ENV	0.10	0.10	0.06	0.46	0.48	0.40	0.73/0.74	0.73/0.74	0.71/0.70
ARU-RAC	0.07	0.06	0.07	0.70	0.77	0.80	0.86/0.84	0.89/0.88	0.90/0.90
ECA-ENV	0.32	0.32	0.30	0.46	0.46	0.50	0.72/0.73	0.72/0.73	0.75/0.75
ECA-RAC	0.29	0.29	0.30	0.73	0.75	0.67	0.86/0.87	0.87/0.88	0.84/0.83
ECO-ENV	0.22	0.24	0.43	0.44	0.52	0.54	0.74/0.72	0.77/0.76	0.78/0.77
ECO-RAC	0.22	0.22	0.24	0.77	0.74	0.66	0.89/0.88	0.87/0.87	0.83/0.83
HQU-ENV	0.08	0.08	0.04	0.22	0.24	0.30	0.63/0.61	0.63/0.62	0.66/0.65
HQU-RAC	0.06	0.06	0.07	0.79	0.75	0.77	0.90/0.89	0.87/0.88	0.88/0.89
PFI-ENV	0.32	0.36	0.33	0.34	0.40	0.42	0.68/0.67	0.69/0.70	0.72/0.76
PFI-RAC	0.32	0.32	0.29	0.66	0.68	0.67	0.83/0.83	0.84/0.84	0.84/0.83
PSI-ENV	0.17	0.17	0.16	0.38	0.48	0.52	0.69/0.69	0.73/0.74	0.76/0.76
PSI-RAC	0.15	0.15	0.14	0.74	0.69	0.63	0.87/0.87	0.85/0.84	0.81/0.82
PZO-ENV	0.10	0.10	0.08	0.64	0.64	0.56	0.82/0.82	0.85/0.82	0.79/0.78
PZO-RAC	0.07	0.07	0.07	0.83	0.84	0.76	0.92/0.91	0.92/0.92	0.88/0.88

% Importance	ARU	ECA	ECO	HQU	PFI	PSI	PZO
Bathymetry	31	20	22	12	28	22	10
Backscatter	3	15	18	10	8	10	5
BPI broad	3	6	16	10	19	10	3
BPI fine	4	10	3	4	2	6	10
Aspect 60 m-scale	2	4	4	10	4	2	1
Curvature 60 m-scale	6	4	7	8	3	7	8
Log-Rugosity 60 m-scale	31	8	10	8	6	11	5
Slope 60 m-scale	2	9	4	8	10	12	40
Aspect 5 m-scale	4	2	2	5	4	2	1
Curvature 5 m-scale	4	5	3	9	4	6	4
Log-Rugosity 5 m-scale	4	8	5	9	4	7	5
Slope 5 m-scale	7	9	5	7	7	4	9

Legend (% Importance): 0–5%, 5–10%, 10–15%, 15–20%, 20–25%, 25–30%, 30–35%, 35–40%

Fig. 2. Percent relative contributions of each habitat covariate based on environment-only Boosted Regression Trees models fitted for each species. BPI refers to bathymetric positioning index. Species codes: ARU (*Aphareus rutilans*), ECA (*Etelis carbunculus*), ECO (*E. coruscans*), HQU (*Hyporthodus quernus*), PFI (*Pristipomoides filamentosus*), PSI (*P. sieboldii*), and PZO (*P. zonatus*).

occurrence. The association with slope for the other two *Pristipomoides* species were similar, but were less important (Fig. 2). Broad-scale BPI was an important variable especially for *P. filamentosus*, with higher occurrences associated with broad-scale ridges.

3.3. Species distribution maps

The 12 habitat layers were inputted into the BRT models for each species to produce spatial distribution maps of probability of occurrence across the MHI between 50 and 400 m (Supplementary material, Figs. S22–S28). As an example, Fig. 4 highlights a popular fishing area, Penguin Banks, off the southwestern coast of Molokai island. The bottomfish restricted fishing area in Penguin Banks (solid black rectangle, Fig. 4) encapsulates hotspots of probability of occurrence for most of the species complex. Species distribution map layers for each species across the MHI at 60 m resolution can be accessed in the Dryad Digital Repository (http://www.datadryad.org).

3.4. Linking model output with fishery management zones

The GLMM including both species and habitat suitability (i.e., 99th percentile predicted probability of occurrence) fitted the data with reasonable model fit, with a marginal (fixed effects only) pseudo-R^2 of 0.48 and a conditional (random and fixed effects) pseudo-R^2 of 0.76. The 99th percentile probability of occurrence was significantly positively related to log-CPUE with a slope estimate of 1.66 (SE: 0.242, $p < 0.001$), meaning an average 1.66 increase in log-CPUE across the range of probability of occurrence. The positive log-linear slope means that CPUE increases exponentially across the range of habitat suitability, and the magnitude of this increase is scaled by the species intercepts. For example, *E. coruscans* and *P. filamentosus* had higher intercepts in the model relative to the other species, and thus the largest scaling of the species complex (Fig. 5), whereas *H. quernus* and *A. rutilans* had the smallest scaling.

4. Discussion

Across species and model types for the environment-only models, depth, slope, BPI, rugosity, and backscatter described the majority of the habitat associations. Depth was an important habitat predictor

among the 12 covariates, with species occupying different depth ranges (). Bathymetry is a common descriptor of habitat among snapper species globally (Martinez-Andrade, 2003) and was a good predictor of occurrence for deepwater snappers in the western central Pacific (Gomez et al., 2015). Previous work on habitat associations for the *Etelis* and *Pristipomoides* species in Hawaii also showed depth as the most important habitat predictor (Misa et al., 2013; Moore et al., 2016). From our analysis, the species complex can be segregated by depth, with *P. filamentosus* having the shallowest distributions, the two *Etelis* spp. occupying deeper areas > 200 m, and the other species having intermediate depth distributions. The differences in depth ranges between the *Etelis* spp. and *P. filamentosus* is reflective of bottomfish catch composition in the Pacific (Ralston and Polovina, 1982; Ralston and Williams, 1998).

Rugosity and backscatter were important habitat features for each of the seven species highlighting the importance of quantifying structural complexity when characterizing habitat. The rugosity metric calculated in our study was the best approximation for habitat complexity, and the incorporation of the two spatial scales allowed for different levels of habitat complexity to be analyzed. Observations from submersible dives have noted the importance of natural cavities and the complexity of the substrate as predator refugia (Kelley et al., 2006). The inclusion of local habitat features generally increases model fit and performance (Mitchell et al., 2001; Thompson et al., 2012), however is subject to differences in the ecology and life history of the species (Mitchell et al., 2001). Including local habitat variables like substrate type and porosity, possibly garnered from the video at each location, may have further increased the predictive power of the models, however would have complicated the use of these models to produce species distribution maps.

Raised physical structures like ridges, banks, and seamounts were also important habitat features for many of these species, specifically for *E. coruscans* and *P. filamentosus*. High relief underwater structures are of particular interest to fisheries because, though not always evident, some may concentrate or retain biological productivity due to various oceanographic processes (Pitcher et al., 2007). Across all species, regardless of the importance of broad-scale BPI, higher probabilities of occurrence were associated with broad-scale ridge-like structures rather than broad-scale depressions. The restricted fishing area southwest of the island of Niihau encapsulates such a raised physical feature (Supplementary material, Figs. S22–S28) as well as the "fingers" in the restricted fishing area at Penguin Banks (Moore et al., 2016). Both *Etelis* spp. and *P. filamentosus* had high predicted probabilities of occurrences around these features, but at different depths, with the *Etelis* spp. having deeper distributions than *P. filamentosus*. Ralston et al. (1986) observed *E. coruscans* and *P. filamentosus* aggregated near underwater headlands but at different depths. These raised physical features, as well as the steep drop-offs associated with the island slope were consistent hotspots of predicted bottomfish occurrence.

High-relief is generally an important habitat feature for adult snappers and groupers (Ralston et al., 1986; Sluka et al., 2001). Unexpectedly, slope was not a consistently important habitat variable across species models. This result is also concurrent with habitat-based species distribution models of western central Pacific snappers from Gomez et al. (2015) and earlier work from Penguin Banks off the southwest coast of the island of Molokai (Moore et al., 2016). Slope had intermediate importance across models with the exception of *P. zonatus* where slope was the most important habitat variable in the ENV-BRT (Fig. 2). Although outside of the scope of this study, the distribution of bottomfishes is likely influenced by their prey distributions. Ralston et al. (1986) reported higher catch rates of *P. filamentosus* on the up-current sides of high-relief features. Current flow in high-relief areas has been hypothesized to aggregate prey (Haight et al., 1993). The biophysical relationship between oceanographic currents and bottomfish aggregations was partly addressed with the slope and BPI variables,
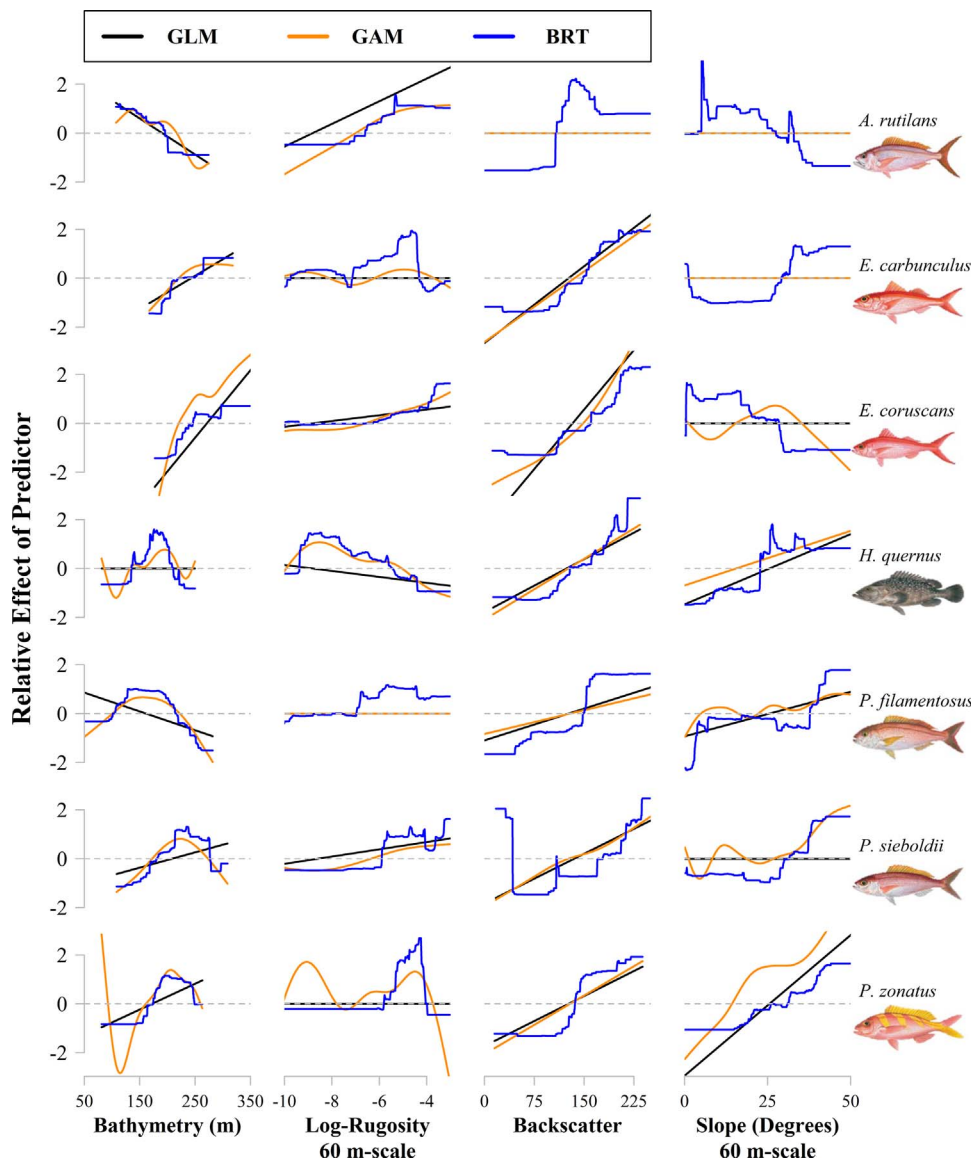
Fig. 3. Partial fitted plots of bathymetry, log-rugosity (60 m-scale), backscatter, and slope (60 m-scale) across environment-only model types—Generalized Linear Models (GLM; black), Generalized Additive Models (GAM; orange), and Boosted Regression Trees (BRT; blue)—and species. Fish illustrations by Les Hata©, Hawaii Department of Land and Natural Resources. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

however information on surface and bottom currents unavailable in this study could have been particularly insightful.

The connection between benthic habitat associations and feeding behavior is important for this species complex, as the observations of bottomfishes in this study were collected just off the bottom, whereas bottomfishes are usually fished at depths higher in the water column where they are presumably feeding. Thus, the positive relationship between log-CPUE and probability of occurrence suggests concurrence between the spatial distributions of fishing and BotCam observations, bolstering the applicability of our results to fishery management. For example, habitat variables can be related to catch rates when standardizing CPUE (Bigelow et al., 2002; Maunder et al., 2006; Bigelow and Maunder, 2007).

The use of a wide range of modelling frameworks in this study showed the advantages of relatively novel machine-learning approaches in niche-based modelling. This work contributes to the examples of BRTs in niche-based modeling (e.g., Leathwick et al., 2006; Froeschke and Froeschke, 2011; Compton et al., 2012; Franklin et al., 2013; Moore et al., 2016) popularized by Elith et al. (2008). The increase in model complexity characteristic of GAMs and BRTs (e.g., non-linear relationships, variable interactions) did increase the deviance explained, but its effect on predictive performance was varied. Predictive performance metrics did increase from GLMs to GAMs to BRTs

in general, but for some species like *A. rutilans* and *P. zonatus*, predictive performance was similar across model types. In these cases, near-linear relationships for key habitat variables (e.g. depth, slope, backscatter) could have been approximated by GLMs just as well as GAMs or BRTs (Fig. 3).

A plethora of methods to account for spatial autocorrelation in niche modelling include autoregressive models, GLMMs, GAMMs, spatial eigenvector mapping, and autocovariate regressions as used in our study (see review by Dormann et al., 2007). The advantages of the RAC models were better performing predictive models with higher deviance explained compared to their environment-only model counterparts. Because residual spatial autocorrelation was relatively low under environment-only models, accounting for the spatial autocorrelation using the RAC approach served to more to increase the predictive performance of the model and less to ensure that the spatial independence of residuals assumption was met. Extrapolation in space or interpolation of non-sampled areas using the current methods used to correct for SAC is problematic due to the assumption of transferability of non-linear and interactive effects, as well as the variance-covariance structure (Dormann et al., 2007). Augustin et al. (1996) used a Gibbs sampler to predict the distribution of species in non-surveyed grids, however convergence is not guaranteed and such an approach may be sensitive to initial conditions (Dormann, 2007). Crase et al. (2012, 2014) used
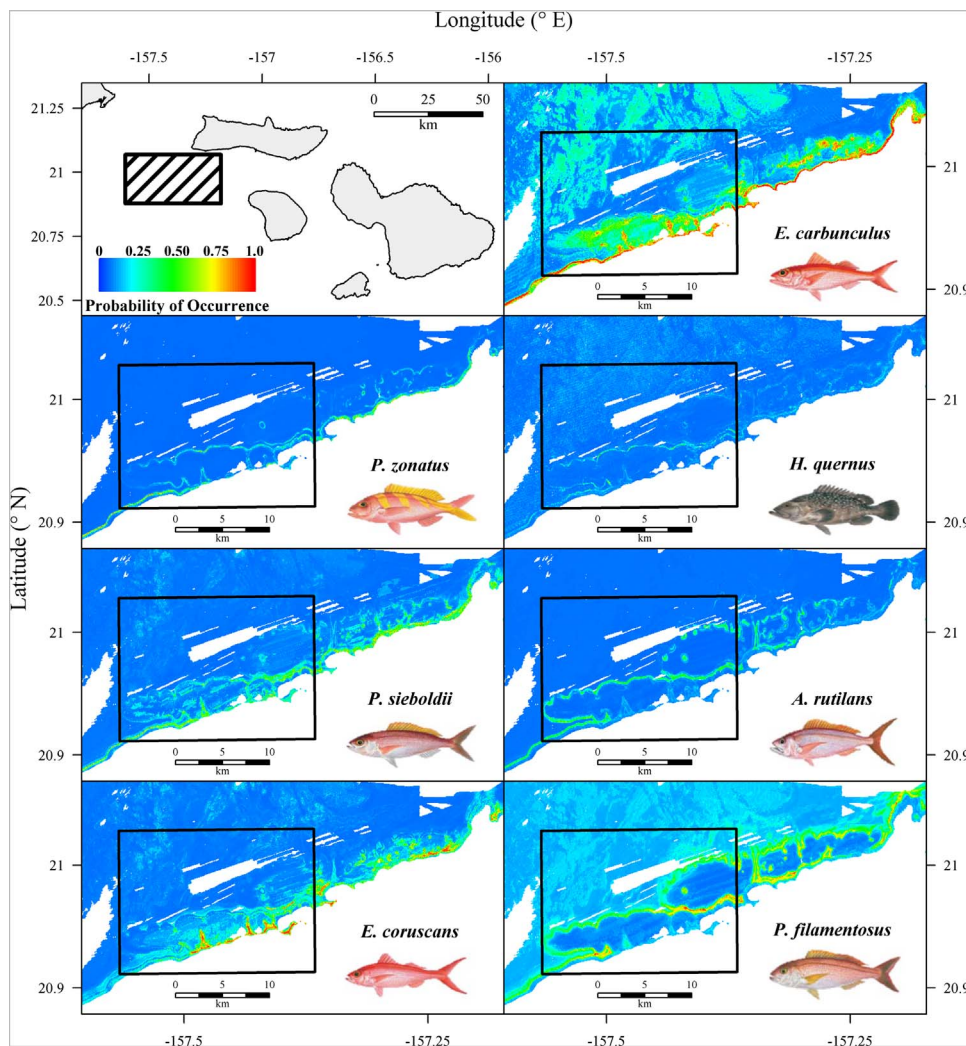
Fig. 4. Predicted probability of occurrence within Penguin Banks (textured box in inset) for each species using environment-only Boosted Regression Trees. The rectangle represents a bottomfish restricted fishing area. Fish illustrations by Les Hata©, Hawaii Department of Land and Natural Resources.

the RAC approach using an example in which the data were structured in a grid and every cell in the grid had an observation (presence or absence). Raphael et al. (2015) used the RAC-BRTs to model marbled murrelet (*Brachyramphus marmoratus*) along a nearly contiguous coastal domain on the US Northwest Coast including Puget Sound. In these examples, the domains of the samples were relatively continuous in space, and thus predicted species distribution maps could be created directly. We provided the results from the RAC models to highlight the value of the method, however the most pragmatic predictions for interpolating cells in our spatial domain came from the environment-only models.

Not addressed in our work was the habitat associations of juvenile bottomfish populations. The BotCam video surveys were initially purposed to monitor adult populations, however the size ranges observed in these deployments also included pre-adult stages of bottomfishes (Misa et al., 2013). Future research priorities should focus on delineating juvenile habitat associations, especially in relation to their adult counterparts. The most extensive work on juvenile habitat associations of Hawaiian bottomfishes was conducted for *P. filamentosus* observed in relatively shallow waters on the islands of Oahu, Maui, and Hawaii Island over low relief sandy or rocky substrates and *Halimeda* spp. beds (Parrish, 1989; Moffitt and Parrish, 1996; Parrish et al., 1997; Misa et al., 2013). Juvenile *E. coruscans* have been observed in low-relief rocky bottoms between the islands of Maui and Molokai (Misa et al., 2013). There is some evidence that the overlap in juvenile and adult habitat associations range from similar (e.g., *Etelis* spp.; Ikehara, 2006) to divergent (e.g., *P. filamentosus*; Parrish, 1989). The merging of

juvenile and adult habitat ranges would help better define Essential Fish Habitat and Habitat Areas of Particular Concern for the Hawaiian Deep Seven Bottomfishes.

5. Conclusions

Despite their current/potential economic importance in many Indo-Pacific nations, deepwater snappers and groupers are relatively understudied species (Newman et al., 2016). Our study refined the habitat associations for adult Hawaiian Deep Seven Bottomfishes, the product being a high-resolution habitat-based mapped distribution for each of the species across the entire main Hawaiian archipelago. For most of these species, information on habitat associations contributes to the current dearth of life history information and research attention in general. As useful as these models are in highlighting ecological habitat associations, they can also provide the foundation for other fisheries management-driven questions. The model-based maps clearly showed hotspots of bottomfish occurrence and can be used to more clearly delineate Essential Fish Habitat and Habitat Areas of Particular Concern for these species in the main Hawaiian Islands (Parke, 2007; Moore et al., 2016). These habitat models can be applied to the design of fisheries-independent surveys and can also provide useful insight to fishery managers relating to the effectiveness of the placement of marine protected areas.
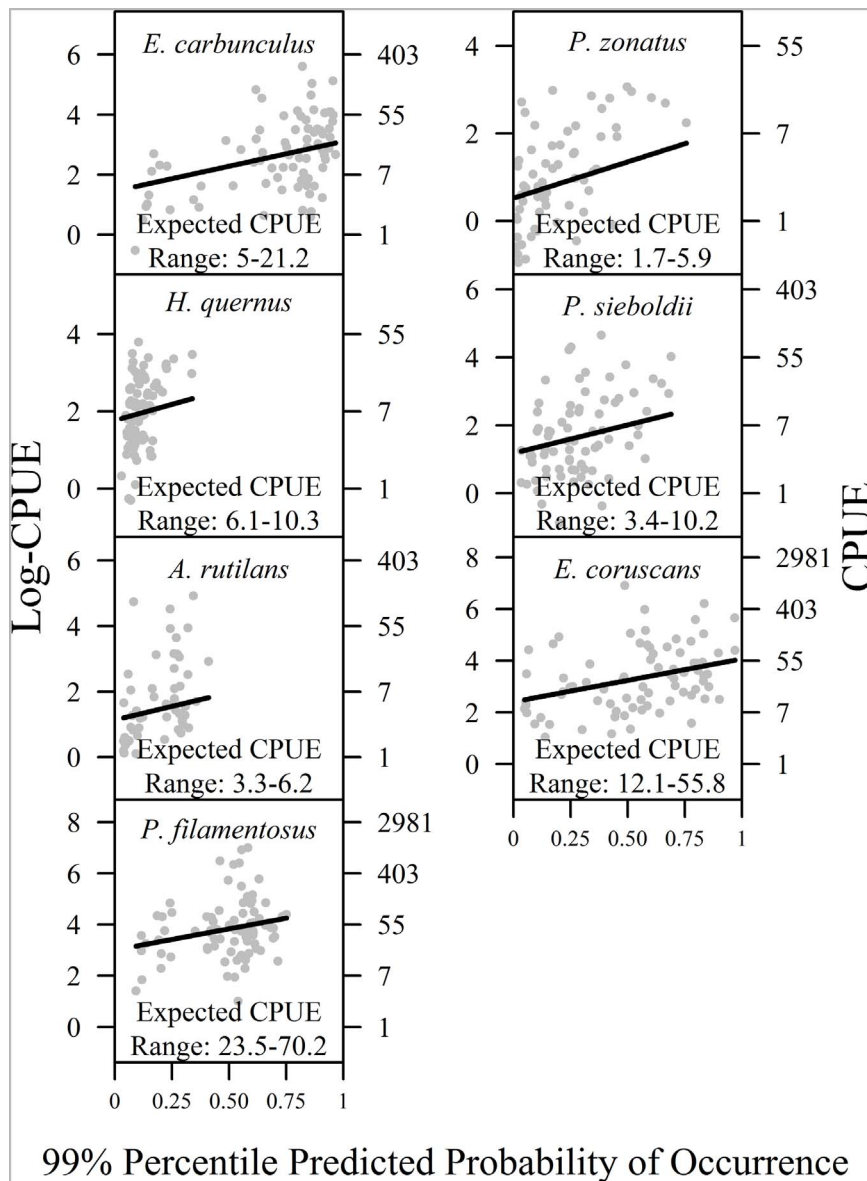
Fig. 5. Log-CPUE against model-predicted (environment-only Boosted Regression Trees) 99% percentile probability of occurrence across State of Hawaii fishery statistical reporting areas with log-linear model prediction (solid black line) for each species. The range of the expected CPUE over the domain of probabilities of occurrences are given at the bottom of each plot.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.06.011.

References

Augustin, N.H., Mugglestone, M.A., Buckland, S.T., 1996. An autologistic model for the spatial distribution of wildlife. J. Appl. Ecol. 33, 339–347. http://dx.doi.org/10.2307/2404755.

Bigelow, K.A., Maunder, M.N., 2007. Does habitat or depth influence catch rates of pelagic species? Can. J. Fish. Aquat. Sci. 64, 1581–1594. http://dx.doi.org/10.1139/F07-115.

Bigelow, K.A., Hampton, J., Miyabe, N., 2002. Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). Fish. Oceanogr. 11, 143–155. http://dx.doi.org/10.1046/j.1365-2419.2002.00196.x.

Brodziak, J., Yau, A., O'Malley, J., Andrews, A., Humphreys, R., DeMartini, E., Pan, M., Parke, M., Fletcher, E., 2014. Stock Assessment Update for the Main Hawaiian Islands Deep7 Bottomfish Complex Through 2013 with Projected Annual Catch Limits Through 2016. NOAA Technical Memorandum NMFS-PIFSC-43. National Oceanic and Atmospheric Administration, Silver Spring, MD p.61.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Method. Res. 33, 261–304. http://dx.doi.org/10.1177/0049124104268644.

Burrough, P.A., McDonnell, R.A., 1998. Principals of Geographic Information Systems

(revised Edition). Clarendon Press, Oxford, pp. p.333.

Cliff, A.D., Ord, J.K., 1981. Spatial Processes: Models and Applications. Pion, London, England p.266.

Coleman, F., Koenig, C., Huntsman, G., Musick, J., Eklund, A., McGovern, J., Sedberry, G., Chapman, R., Grimes, C., 2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25, 14–21. http://dx.doi.org/10.1577/1548-8446(2000) 025<0014:LRF>2.0. CO;2.

Compton, T.J., Morrison, M.A., Leathwick, J.R., Carbines, G.D., 2012. Ontogenetic habitat associations of a demersal fish species, Pagrus auratus, identified using boosted regression trees. Mar. Ecol. Prog. Ser. 462, 219–230. http://dx.doi.org/10.3354/meps09790.

Crase, B., Liedloff, A.C., Wintle, B.A., 2012. A new method for dealing with residual spatial autocorrelation in species distribution models. Ecography 35, 879–888. http://dx.doi.org/10.1111/j. 1600-0587.2011.07138.x.

Crase, B., Liedloff, A., Vesk, P.A., Fukuda, Y., Wintle, B.A., 2014. Incorporating spatial autocorrelation into species distribution models alters forecasts of climate-mediated range shifts. Glob. Chang. Biol. 20, 2566–2579. http://dx.doi.org/10.1111/gcb. 12598.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., et al., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609–628. http://dx.doi.org/10.1111/j. 2007.0906-7590.05171.x.

Dormann, C.F., 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Glob. Ecol. Biogeogr. 16, 129–138. http://dx.doi.org/10. 1111/j.1466-8238.2006.00279.x.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. http://dx.doi.org/10.1111/j.1365-2656.2008.01390.x.

Franklin, E.C., Jokiel, P.L., Donahue, M.J., 2013. Predictive modeling of coral distribution and abundance in the Hawaiian Islands. Mar. Ecol. Prog. Ser. 481, 121–132. http://dx.doi.org/10.3354/meps10252.

Froeschke, J.T., Froeschke, B.F., 2011. Spatio-temporal predictive model based on environmental factors for juvenile spotted seatrout in Texas estuaries using boosted regression trees. Fish. Res. 111, 131–138. http://dx.doi.org/10.1016/j.fishres.2011. 07.008.

Gomez, C., Williams, A.J., Nicol, S.J., Mellin, C., Loeun, K.L., Bradshaw, C.J., 2015. Species distribution models of tropical deep-sea snappers. PLoS One 10, e0127395. http://dx.doi.org/10.1371/journal.pone.0127395.

Haight, W.R., Kobayashi, D.R., Kawamoto, K.E., 1993. Biology and management of deepwater snappers of the Hawaiian Archipelago. Mar. Fish. Rev. 55, 20–27.

Hosmer, J.D.W., Lemeshow, S., Sturdivant, R.X., 2013. Applied Logistic Regression. John Wiley & Sons, Inc., Hoboken, NJ p.528.

Hospital, J., Beavers, C., 2012. Economic and Social Characteristics of Bottomfish Fishing in the Main Hawaiian Islands. NOAA Technical Memorandum NMFS-PIFSC- H-12-01. National Oceanic and Atmospheric Administration, Silver Spring, MD p.44.

Hospital, J., Pan, M., 2009. Demand for Hawaii Bottomfish Revisited: Incorporating Economics into Total Allowable Catch Management. NOAA Technical Memorandum NMFS-PIFSC-20. National Oceanic and Atmospheric Administration, Silver Spring, MD p.19.

Iampietro, P., Kvitek, R., 2002. Quantitative seafloor habitat classification using GIS terrain analysis: effects of data density, resolution and scale (Poster). In: Symposium on Effects of Fishing Activities on Benthic Habitats: Linking Geology, Biology, Socioeconomics, and Management. Tampa, FL.

Ikehara, W., 2006. Bottomfish management and monitoring in the main Hawaiian Islands. In: Shotton, R. (Ed.), In Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries. Part 2: Conference Poster Papers and Workshop Papers. Queenstown, New Zealand, 1–5 December 2003, Dunedin, New Zealand, 27–29 November 2003. pp. 289–300 FAO Fisheries Proceedings 3/2. FAO, Rome.

Jennings, S., Reynolds, J.D., Polunin, N.V.C., 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conserv. Biol. 13, 1466–1475. http://dx.doi.org/10.1046/j. 1523-1739.1999.98324.x.

Kelley, C., Ikehara, W., 2006. The impacts of bottomfishing on raita and west St. rogatien banks in the northwestern hawaiian islands. Atoll Res. Bull. 543, 319–332.

Kelley, C., Moffitt, R., Smith, J.R., 2006. Mega-to micro-scale classification and description of bottomfish essential fish habitat on four banks in the Northwestern Hawaiian Islands. Atoll Res. Bull. 543, 319–332.

Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T., Taylor, P., 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Mar. Ecol. Prog. Ser. 321, 267–281. http://dx.doi.org/10. 3354/meps321267.

Lundblad, E.R., Wright, D.J., Miller, J., Larkin, E.M., Rinehart, R., Naar, D.F., Donahue, B.T., Anderson, S.M., Battista, T., 2006. A benthic terrain classification scheme for American Samoa. Mar. Geod. 29, 89–111. http://dx.doi.org/10.1080/01490410600738021.

Martinez-Andrade, F., 2003. A Comparison of Life Histories and Ecological Aspects Among Snappers (Pisces: Lutjanidae). Ph.D. Dissertation. Louisiana State University and Agricultural and Mechanical College p.194.

Maunder, M.N., Hinton, M.G., Bigelow, K.A., Langley, A.D., 2006. Developing indices of abundance using habitat data in a statistical framework. B. Mar. Sci. 79, 545–559.

Merritt, D., Donovan, M.K., Kelley, C., Waterhouse, L., Parke, M., Wong, K., Drazen, J.C., 2011. BotCam: a baited camera system for nonextractive monitoring of bottomfish species. Fish. Bull. 109, 56–67.

Misa, W.F., Drazen, J.C., Kelley, C.D., Moriwake, V.N., 2013. Establishing species?habitat associations for four eteline snappers with the use of a baited stereo-video camera system. Fish. B-NOAA 111, 293–308. http://dx.doi.org/10.7755/FB.111.4.1.

Misa, W.F.X.E., Richards, B.L., DiNardo, G.T., Kelley, C.D., Moriwake, V.N., Drazen, J.C., 2016. Evaluating the effect of soak time on bottomfish abundance and length data

from stereo-video surveys. J. Exp. Mar. Biol. Ecol. 479, 20–34. http://dx.doi.org/10. 1016/j.jembe.2016.03.001.

Mitchell, M.S., Lancia, R.A., Gerwin, J.A., 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. Ecol. Appl. 11, 1692–1708. http://dx.doi.org/10.1890/1051-0761(2001)011[1692:ULLDTP]2.0.CO;2.

Moffitt, R.B., Parrish, F.A., 1996. Habitat and life history of juvenile Hawaiian pink snapper, Pristipomoides filamentosus. Pac. Sci. 50, 371–381. http://hdl.handle.net/10125/2912.

Moore, C.H., Drazen, J.C., Kelley, C.D., Misa, W.F., 2013. Deepwater marine protected areas of the main Hawaiian Islands: establishing baselines for commercially valuable bottomfish populations. Mar. Ecol-Prog. Ser. 476, 167–183. http://dx.doi.org/10. 3354/meps10132.

Moore, C., Drazen, J., Radford, B., Kelley, C., Newman, S., 2016. Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. Mar. Policy 69, 32–41. http://dx.doi.org/10.1016/j.marpol.2016.03.021.

Morris, A.V., Roberts, C.M., Hawkins, J.P., 2000. The threatened status of groupers (Epinephelinae). Biodivers. Conserv. 9, 919–942. http://dx.doi.org/10.1023/A:1008996002822.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. http://dx. doi.org/10.1111/j.2041-210x.2012.00261.x.

Newman, S.J., Wakefield, C.B., Williams, A.J., O'Malley, J.M., Nicol, S.J., DeMartini, E.E., Halafihi, T., Kaltavara, J., Humphreys, R.L., Taylor, B.M., Andrews, A.H., Nichols, R.S., 2015. International workshop on methodological evolution to improve estimates of life history parameters and fisheries management of data-poor deep-water snappers and groupers. Mar. Policy 60, 182–185. http://dx.doi.org/10.1016/j. marpol.2015.06.020.

Newman, S.J., Williams, A.J., Wakefield, C.B., Nicol, S.J., Taylor, B.M., O'Malley, J.M., 2016. Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. Rev. Fish. Biol. Fisher. 26, 537–562. http://dx.doi.org/10.1007/s11160-016-9442-1.

Parke, M., 2007. Linking Hawaii Fisherman Reported Commercial Bottomfish Catch Data to Potential Bottomfish Habitat and Proposed Restricted Fishing Areas Using GIS and Spatial Analysis. NOAA Technical Memorandum NMFS-PIFSC-11. National Oceanic and Atmospheric Administration, Silver Spring, MD p.37.

Parrish, F., DeMartini, E., Ellis, D., 1997. Nursery habitat in relation to production of juvenile pink snapper, Pristipomoides filamentosus, in the Hawaiian Archipelago. Fish. B-NOAA 95, 137–148.

Parrish, F., 1989. Identification of habitat of juvenile snappers in Hawaii. Fish. B-NOAA 87, 1001–1005.

Pitcher, T.J., Morato, T., Hart, P.J., Clark, M.R., Haggan, N., Santos, R.S., 2007. Seamounts: Ecology, Fisheries & Conservation. John Wiley & Sons, Inc., Hoboken, NJ p.552.

Pooley, S.G., 1993. Hawaii's marine fisheries: some history, long-term trends, and recent developments. Mar. Fish. Rev. 55, 7–19.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria, URL: http://www.Rproject. org/.

Ralston, S., Polovina, J.J., 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. B-NOAA 80, 435–448.

Ralston, S., Williams, H.A., 1998. Depth Distributions, Growth, and Mortality of Deep Slope Fishes from the Mariana Archipelago. NOAA Technical Memorandum NMFS-SWFC-113. National Oceanic and Atmospheric Administration, Silver Spring, MD p.47.

Ralston, S., Gooding, R.M., Ludwig, G.M., 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. B-NOAA. 84, 141–156.

Raphael, M.G., Shirk, A.J., Falxa, G.A., Pearson, S.F., 2015. Habitat associations of marbled murrelets during the nesting season in nearshore waters along the Washington to California coast. J. Mar. Syst. 146, 17–25. http://dx.doi.org/10.1016/j.jmarsys.2014.06.010.

Richards, B.L., Smith, S.G., Ault, J.S., DiNardo, G.T., Kobayashi, D., Domokos, R., Anderson, J., Taylor, J., Misa, W., Giuseffi, L., 2016. Design and Implementation of a Bottomfish Fishery-independent Survey in the Main Hawaiian Islands. NOAA Technical Memorandum NMFS-PIFSC-53. National Oceanic and Atmospheric Administration, Silver Spring, MD p.54.

Sackett, D.K., Drazen, J.C., Moriwake, V.N., Kelley, C.D., Schumacher, B.D., Misa, W.F., 2014. Marine protected areas for deepwater fish populations: an evaluation of their effects in Hawaii. Mar. Biol. 161, 411–425. http://dx.doi.org/10.1007/s00227-013-2347-9.

Schröder, B., Richter, O., 2000. Are habitat models transferable in space and time? J. Nat. Conserv. 8, 195–205.

Sluka, R.D., Chiappone, M., Sealey, K.M.S., 2001. Influence of habitat on grouper abundance in the Florida Keys, U.S.A. J. Fish. Biol. 58, 682–700 1095-8649.2001.tb00522.x.

Sundberg, P., Richards, A., 1984. Deep-sea bottom handline fishing in Papua New Guinea: a pilot study. Papua New G. J. Agr. Forest. Fish. 33, 55–67.

Thompson, F.R., Robbins, M.B., Fitzgerald, J.A., 2012. Landscape-Level forest cover is a predictor of cerulean warbler abundance. Wilson. J. Orinthol. 124, 721–727. http://dx.doi.org/10.1676/1559-4491-124.4.721.

Weiss, A., 2001. Topographic position and landforms analysis (Poster). In: ESRI User Conference. San Diego CA.

Wright, D., Lundblad, E., Larkin, E., Rinehart, R., Murphy, J., Cary-Kothera, L., Draganov, K., 2005. ArcGIS Benthic Terrain Modeler (BTM), v. 3.0. Environmental Systems Research Institute, NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management.