Contents lists available at ScienceDirect

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management



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ARTICLE INFO

Article history: Received 25 February 2016 Received in revised form 22 March 2016 Accepted 22 March 2016

Keywords: Fisheries m

Fisheries management Essential fish habitat Ecosystem-based fisheries management Species distribution modelling Generalised Additive Models Boosted Regression Trees Maximum Entropy Hawaiian bottom fishery

ABSTRACT

A major limitation to fully integrated ecosystem based fishery management approaches is a lack of information on the spatial distribution of marine species and the environmental conditions shaping these distributions. This is particularly problematic for deep-water species that are hard to sample and are data poor. The past decade has seen the rapid development of a suite of advanced species distribution, or ecological niche, modelling approaches developed specifically to support efficient and targeted management. However, model performance can vary significantly and the appropriateness of which methods are best for a given application remains questionable. Species distribution models were developed for three commercially valuable Hawaiian deep-water eteline snappers: Etelis coruscans (Onaga), Etelis carbunculus (Ehu) and Pristipomoides filamentosus (Opakapaka). Distributional data for these species was relatively sparse. To identify the best method, model performance and distributional accuracy was assessed and compared using three approaches: Generalised Additive Models (GAM), Boosted Regression Trees (BRT) and Maximum Entropy (MaxEnt). Independent spatial validation data found MaxEnt consistently provided better model performance with 'good' model predictions (AUC = > 0.8). Each species was influenced by a unique combination of environmental conditions, with depth, terrain (slope) and substrate (low lying unconsolidated sediments), being the three most important in shaping their distributions. Sustainable fisheries management, marine spatial planning and environmental decision support systems rely on an understanding species distribution patterns and habitat linkages. This study demonstrates that predictive species distribution modelling approaches can be used to accurately model and map sparse species distribution data across marine landscapes. The approach used herein was found to be an accurate tool to delineate species distributions and associated habitat linkages, account for species-specific differences and support sustainable ecosystem-based management.

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1. Introduction

Management of marine resources has evolved from single species approaches to more holistic ecosystem based management approaches in order to integrate ecosystem, bioregional and societal facets based on ecosystem boundaries rather than sectoral or jurisdictional boundaries [1–3]. The National Oceanic and

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Atmospheric Administration (NOAA) defines an ecosystem approach as "management that is adaptive, specified geographically, takes account of ecosystem knowledge and uncertainties, considers multiple external influences, and strives to balance diverse social objectives". The approach recognises the full suite of interactions within an ecosystem as well as human influences [2,4]. This shift in focus involves the implementation of a range of marine management strategies, including improved marine spatial planning, to balance conservation objectives with sustainable resource use [3,5]. As ecosystem-based management encompasses a vast array of interactions, it can be seen as a complex process that



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is difficult to implement [4,6]. Therefore, defining clear objectives has been one of the most important steps. This often involves identifying focal species or groups of species, such as threatened, indicator, commercially valuable, predator or prey species, to provide a thorough understanding of critical ecosystem components [7–11]. These species are useful for monitoring an ecosystem's status, to provide feedback on management progress and to feed into integrated ecosystem modelling approaches and marine spatial planning [6, 10, 12, 13].

Commercial scale deep-water fishing in the tropical and subtropical region of the Pacific Ocean began in the 1970 s [14–17]. This so called "bottomfish" fishery targets a group of deep-water species including snappers (Lutianidae), groupers (Epinephelidae), and jacks (Carangidae). Most of these species have a relatively high age at maturity, long life span and slow growth rate, making them particularly susceptible to overfishing and therefore in need of careful management [16, 18-21]. Historically, these species have been targeted using deep handlines from canoes. While the modern fishery employs similar handline gear, the use of powered vessels and advances in technology, such as powered reels to haul gear and global positioning systems (GPS) to find fishing grounds, have meaningfully increased fishing efficiency (e.g. [22-24]). As a result, it has only been in a few places, with extensive and productive fishing grounds (e.g. Hawaii, Fiji and Tonga), that larger commercial ventures have persisted [16, 25].

Recently, with limited potential to further develop commercial shallow water reef and lagoon fisheries, many Pacific Island countries have expressed renewed interest in developing their deep-water fisheries [14, 16, 26]. However, many deep-water fisheries in the Pacific have proved unviable as catch rates have quickly dropped from virgin to sustainable levels, and in some areas, localised depletions have been reported [14, 27]. For example, the two most commercially valuable deep-water species in the Main Hawaiian Islands (MHI), Etelis coruscans and Etelis carbunculus, were identified as being in a state of overfishing from as early as 1989 [27, 28]. In response to steady declines and unfavourable biological indicators the State of Hawaii implemented several measures in an effort to restore the fishery [23, 29]. This included bottomfish restricted fishing areas (BRFAs), a bottomfish boat registry and the introduction of a non-commercial bag limit. Further management actions, including temporal closures, have subsequently been implemented [29]. The BRFAs were designed to protect 20% of the deeper portion (100-400 m) of the 0-400 m bottomfish essential fish habitat (EFH) across all islands and banks. EFH is defined as 'the water and substrate necessary for fish spawning, feeding or growth to maturity' [30, 31], and closing 20% of the portion occupied by E. coruscans and E. carbunculus was expected to help replenish their stocks across the Main Hawaiian Islands. Since their implementation, responses in the size and abundance of bottomfish within the BRFAs has been variable but in most cases the most commercially important species increased in size [32, 33].

When the Hawaiian BRFAs were originally created, the identification of suitable geographic areas was difficult as there was a lack of adequate species distribution and essential fish habitat data. This problem is not uncommon for many marine species, particularly deep-water species, as preferred habitat and species distribution data is often sparse. A subsequent review and revision of the BRFAs in 2005 successfully incorporated more extensive distribution and habitat data (i.e. fishing records, submersible and ROV transects, multibeam mapping and commercial catch records) enabling a more rigorous assessment of how well the BRFAs were sited. However, more recent developments in the field of species distribution modelling has seen advances in the accuracy and power of modelling individual species-environment relationships providing detailed information on the geographical extent of species and the environmental drivers shaping their distributions. These spatially explicit and quantitative assessments of individual and combined species distributions can contribute to the advice provided to fishery managers.

Species distribution modelling has developed as a powerful tool for understanding species-environment relationships and predicting species distributions across unsampled locations [34. 35]. While initially more commonly used for the terrestrial environment, research has demonstrated that species distributions can also be reliably predicted across marine landscapes using bathymetry and derived terrain variables [8, 36, 37]. Species distribution modelling approaches have been demonstrated to provide important and cost-effective tools to reliably model and map EFH [8, 36]. As sustainable fisheries management shifted towards ecosystem-based approaches, a restructuring of the management framework in many areas has moved from species-based Fishery Management Plans to a place-based Fishery Ecosystem Plans [38]. Developing an accurate understanding of the type and distribution of EFH supporting these commercially valuable deep-water species is a critical need. This requires accurate species distribution data, as well as accurate environmental and habitat data. Novel flexible modelling approaches being developed in the speciesenvironment modelling domain can be explored to fill this data gap. These approaches not only can be used to inform spatial management of bottomfish species in Hawaii, but also to potentially provide key inputs for ecosystem-based management of deep-water stocks across the Indo-Pacific. Indeed, a recent study has used an ensemble predictive modelling framework to predict deep-water genera (Etelis, Pristipomoides, and Aphareus) across the Western Central Pacific Ocean [39]. While the study provides much needed broadscale information on the spatial distribution (a resolution of 0.016° or \sim 1 nmi) of these genera across the region it acknowledges a need for this information at both a higher taxonomic and spatial resolution.

The aim of this study was to identify a robust modelling method to further improve the accuracy of EFH designations. Three species distribution modelling approaches were tested to see which provided the most accurate and ecologically interpretable predictive model; the modelling approaches were: Generalised Additive Models (GAM), Boosted Regression Trees (BRT) and Maximum Entropy (MaxEnt). These methods were chosen as they are widely used and have been demonstrated to provide strong predictive performance but differ substantially in their statistical approach [40–42]. The model providing the best predictive performance was chosen to define the species-environment relationships and to predict and describe accurate spatial maps of preferred bottomfish habitat across the area under consideration. Developing an effective modelling approach provides additional decision support tools for the sustainable management of the Hawaiian bottomfish fishery and, even more importantly, for the data sparse deep-water fisheries across the Indo Pacific.

2. Materials and methods

2.1. Study area

The location of this study was in BRFA "F" on the south side of Penguin Bank off the coast of Molokai, Hawaii (Fig. 1). Historically, Penguin Bank is one of the most important bottomfish fishing grounds in the MHI, as it is an extensive relatively shallow shelf area within easy reach of major population centres and is a site known to support significant populations of bottomfish [18].



Fig. 1. Details the location of the bottomfish restricted fishing areas (BRFA) across the main Hawaiian Islands (insert) and the location of the research area within BRFA F on Penguin Banks. Figure details fish survey sites and the spatial extent of the analysis (Penguin Banks), overlayed on the bathymetry.

2.2. Fish sampling

Bottomfish were surveyed using a baited stereo-video camera system designed specifically as a fishery-independent tool for monitoring Hawaiian deep-water fish. The system has been established as a flexible and economic tool for assessing bottomfish [43]. Details of the system are described in Merritt et al. [44] and an overview of its implementation across the MHI to assess bottomfish populations is reported in Moore et al. [32]. The fish records used here were collected as part of a monitoring program that assessed the effectiveness of the BRFAs [32, 33]. Demersal fish were sampled from April 2008 to December 2011, with a total of 128 samples (independent baited stereo-video camera samples) collected within BRFA F (Fig. 1).

2.3. Environmental variables

Environmental variables available for the analysis included; fine scale bathymetry (resolution of 5×5 m) and secondary topographic derivatives calculated in ArcGIS 10.2 including; slope,

[45]). Because aspect is a circular variable, it was transformed into two variables; northness (calculated as cos(aspect)) and eastness (calculated as sin(aspect)). These variables described sites of north–south aspect and sites of east–west aspect [46]. Substrate variables were based on slope and a binary classification of backscatter data into either hard or soft substrate. These categories had previously been defined by Kelley et al. [47] based on the type of habitat categories known to be important to Hawaiian bottomfish [30, 48]. This categorical data was transformed into a continuous percentage of habitats present using a 50×50 m moving window analysis in ArcGIS.

aspect and curvature (detailed in Table 1: see also Holmes at al

2.4. Model formulation and evaluation

Three Hawaiian bottomfish species; *E. coruscans, E. carbunculus* and *Pristipomoides filamentosus* were chosen for this study because they are the most abundant of the deep-water bottomfishes and have the greatest commercial importance to the fishery [18, 32, 33, 49]. Three different species distribution modelling procedures

Table 1

Description of the geophysical data used in the modelling.

Predictor variable	Definition
Terrain variables	
Bathymetry (depth)	Elevation (5 m resolution)
Slope ^a	First derivative of elevation: average change in elevation/distance
Aspect ^a	Azimuthal direction of steepest slope
Northness ^a	Calculated as cos(aspect) representing north-south aspect
Eastness ^a	Calculated as sin(aspect) representing east-west aspect
Curvature ^a	Combined index of profile curvature and plan curvature
Plan curvature ^a	Second derivative of elevation: concavity/convexity perpendicular to the slope
Profile curvature ^a	Second derivative of elevation: concavity/convexity parallel to the slope
Substrate variables	
Hard substrate, high slope ^b	Based on backscatter data analysis and a slope of $\geq 20^{\circ}$
Hard substrate, low slope ^b	Based on backscatter data analysis and a slope of $\leq 20^{\circ}$
Soft substrate, high slope ^b	Based on backscatter data analysis and a slope of $\geq 20^{\circ}$
Soft substrate, low slope ^b	Based on backscatter data analysis and a slope of $\leq 20^{\circ}$

 $^{\rm a}$ Continuous variable calculated using a 15 \times 15 m moving window analysis.

^b Continuous variable calculated as % substrate based on a 50 × 50 m moving window analysis.

were employed and assessed; Generalised Additive Models (GAM), Boosted Regression Trees (BRT) and Maximum Entropy (MaxEnt). The three modelling approaches differ substantially in their statistical formulation. GAMs use non-parametric smoothing functions to allow flexible description of complex species responses [50, 51]. Boosted regression trees (BRT) combine both statistical and machine learning techniques and use boosting to combine large numbers of simple hierarchical tree models to optimize predictive performance (e.g. Elith et al. [40]; Leathwick et al. [51, 52]). MaxEnt [42] is a machine-learning method using the maximum entropy method for modelling species geographic distributions and unlike the other two methods it uses presence-only data. The modelling algorithms for each approach are described in Hastie & Tibshirani [50] for GAM; Leathwick et al. [52] for BRT; and Elith et al. [53]. These species distribution modelling approaches are reviewed in Guisan and Zimmermann [54], Elith and Graham [34] and Robinson et al. [55].

GAMs were developed on presence-absence data in R (version 2.15.1, 2012 the R Foundation for Statistical Computing) using the GAM function. Models were created with a backward stepwise selection eliminating variables from a full model with all predictors until a minimum AIC was reached. BRTs were also developed in R using the GBM (generalised boosted models) function with the custom scripts of Elith et al. [56], and a selected bag fraction of 0.5, tree complexity of 3 and a learning rate of 0.001. Regression based models can be sensitive to correlated predictor variables therefore variables with a correlation greater than 0.7 were removed from the analysis [41, 57]. Maximum Entropy (MaxEnt) modelling was conducted using version 3.3.3 of the MaxEnt software package. Presence only samples were modelled using the default settings with a random 10,000 background samples selected. Phillips and Dudik [58] argue for default settings when applying MaxEnt to small or biased datasets as fine tuning can be unreliable. For all models, 25% of the data was withheld for independent evaluation of predictive performance. Values were extracted from the predicted ASCII files in ArcGIS using the point intercept method and independently evaluated using the threshold-independent AUC (area under the curve) of the ROC (receiver operating characteristic) curve. Other metrics evaluated included threshold dependent percentage correctly classified and this information was corrected for probability of occurrence using the Kappa statistic. The best performing model was chosen to predict each species' distributions and the continuous predicted probability surface was then converted to presence-absence using the threshold-dependent P-krit statistic [45] This statistic was calculated using P-fair which balances model sensitivity and specificity (Type I and Type II errors).

3. Results

3.1. Model performance

Independent evaluation demonstrated that MaxEnt consistently produced more reliable spatial predictions for all three species (Table 2). AUC values were between 0.8 and 0.9 indicating the models provided good predictive performance and further, map accuracy was consistently high (> 78% correct). Predictions produced from the GAMs and BRTs were less accurate and more variable (Table 2). The GAM provided notably lower predictive performance for *E. carbunculus* (an AUC of 0.797% and 78% correctly classified as opposed to an AUC of 0.869% and 87.5% correctly classified by MaxEnt) and lower predictive performance for *E. coruscans* and *P. filamentosus*. The BRT failed to provide an informative model for *P. filamentosus* (AUC = 0.607% and 50% correct) while also providing lower predictive performance

Table 2

Model performance assessed using 25% of the data withheld from the analysis.

Species	Model	AUC	P-krit ^a	% Correct ^a	Kappa ^a
E. coruscans	GAM	0.859	0.21	0.875	0.71
	BRT	0.84	0.142	0.75	0.455
	MaxEnt	0.874	0.342	0.812	0.565
E. carbunculus	GAM	0.797	0.205	0.781	0.508
	BRT	0.835	0.115	0.781	0.508
	MaxEnt	0.869	0.375	0.875	0.71
P. filamentosus	GAM	0.825	0.56	0.718	0.433
	BRT	0.607	0.37	0.5	0.5
	MaxEnt	0.841	0.442	0.781	0.559

^a Values calculated using the threshold-dependent P-fair statistic balancing model sensitivity and specificity.

for E. coruscans and E. carbunculus.

3.2. Species-environment relationships

The variable percent contributions produced by the three modelling approaches are shown in Table 3. Species-environment relationships identified by MaxEnt show each species responded to a unique combination of environmental conditions with depth, terrain (slope) and substrate (low lying unconsolidated sediments) being the three most important in shaping their distributions. *E. coruscans* preferred deep (approx. 200–300 m), steeply sloping habitats with little flat, unconsolidated substrate while *E. carbunculus* preferred slightly deeper (approx. 250–300 m), but similar habitats. In contrast, *P. filamentosus* preferred relatively shallow (approx. 125–225 m), less steeply sloping habitats with little flat, unconsolidated substrate.

There was some consistency in environmental variables chosen across modelling approaches (Table 3). For example, depth was an important explanatory variable across all modelling approaches. However, the relative importance of other environmental variables varied substantially. MaxEnt consistently selected depth, slope and soft low slope as the three most important explanatory variables. However, depth provided the greatest percent contribution for *E. carbunculus* only, while soft low slope provided the most for *E. coruscans* and slope for *P. filamentosus*. In contrast, the GAMs indicated a higher relative importance of the substrate variables (e.g. soft low slope and soft high slope) while the BRTs indicated a higher relative importance of the terrain variables (e.g. slope, curvature and aspect).

3.3. Predicting species distributions

Predicted species distributions using MaxEnt are shown for the three species in Fig. 2. Response curves for the three most important predictor variables (depth, slope and % soft low slope substrate) in each model are also displayed. The response curves provide a relatively smooth fit indicating the models are not overfitting the data. Differences in the spatial extent of habitat predicted, by each of the three models, for each of the three species, are displayed in Fig. 3. Most notable differences can be seen in for the BRT for E. coruscans and E. carbunculus and the GAM for P. filamentosus. In the first case the BRTs are including more of the deeper flat areas for E. coruscans and E. carbunculus while in the second, the GAM is including more of the shallow flat areas for P. filamentosus. In both cases the alternative models provide lower predictive performance and are likely to be overestimating the spatial extent of habitat. Sampling did extend across the deeper basin where the BRTs predicted E. coruscans and E. carbunculus to be present and neither were detected. Therefore, the models are overestimating the spatial extent of habitat. In contrast, limited

Table 3 Variable percent contribution produced by MaxEnt, GAM and BRT. The three most important predictor variables for each species is highlighted in bold.

Predictor variable	Percent contribution								
	E. coruscans			E. carbunculus			P. filamentosus		
	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt	GAM	BRT	MaxEnt
Depth	8.6	38.5	36.7	76.8	62.3	48	54	61	9.9
Slope	0.5	4.2	7.8	-	5.9	4.6	-	39	36.6
Curvature	0.01	6.8	0.2	-	6.6	0.2	-	-	-
Plan Curvature	-	8.4	-	0.3	2.3	-	-	-	-
Profile Curvature	-	7.5	0.5	-	6.7	0.7	1.7	-	-
Sin(aspect)	0.05	9.7	1.6	-	4.8	1.2	-	-	3.2
Cos(aspect)	-	4.3	0.9	-	2.5	0.1	1.2	-	7.7
Hard High Slope	5.9	3	6.3	7.2	1.4	0.3	0.1	-	7.8
Hard Low Slope	-	15.2	1.6	15.3	3.3	-	-	-	0.5
Soft High Slope	19.4	1.6	1.5	-	0.2	0.1	42.9	-	1.4
Soft Low Slope	65.5	-	43	0.3	4	44.8	0.1	-	32.8

sampling of the shallowest sections of this basin area means the predicted spatial extent for *P. filamentosus* by the GAM remains inconclusive. Additional sampling of these areas would provide greater discriminatory power.

With MaxEnt consistently providing the most reliable predictive performance, these models were used to provide an example of how they can inform management. Fig. 4 presents the three species 'core' habitat (where all three species are predicted to co-occur), 'combined' habitat (where one or more species are predicted to occur) and 'unique' habitat (where each species exists on its own). The current EFH definition of 0–400 m equates to around 74.5% of the research area and 100% of the 100–300 m depth zone. In contrast, the 'combined' bottomfish habitat covers 18.9% of the 100–300 m depth zone, while the predicted 'core' bottomfish habitat covers just 2.1%. Unique habitat includes an additional 0.7% for *E. coruscans*, 6.7% for *E. carbunculus* and 7.3% for *P. filamentosus*.

4. Discussion

The management of marine resources has evolved to be more holistic and now involves consideration of multiple facets to address cumulative impacts by using an ecosystem-based management approach [1, 2, 59]. However, the transition from single species approaches to ecosystem-based management and placebased management has been hampered by a paucity of data on species distributions and the environmental variables shaping these distributional patterns [2, 8]. Under these circumstances, modelling approaches can make a significant contribution by potentially identifying important environmental drivers and thus improving habitat predictions for multiple species across unknown, and spatially contiguous, locations.

In this study, predictive species distribution modelling was used to provide both ecological information and spatial information to increase the resolution of the EFH designations for each species. Having an accurate understanding of the extent of EFH supporting a fishery enables fisheries managers to better target spatial management arrangements and provide key inputs into ecosystem models (e.g. Ecosim and Ecospace) in support of ecosystem-based fisheries management [11–13, 60]. In the past a major deficiency of ecosystem modelling approaches used to evaluate the impacts of fisheries on ecosystems was the implicit assumption of homogeneous spatial behaviour [11]. By combining accurate EFH models with spatially explicit ecosystem models, such as Ecospace [60], model outputs can be modified by defining whether a location is a preferred habitat or not. Characterisation of EFH data provides a platform to evaluate the impacts of fisheries on ecosystems both in time and space [11].

Outcomes from this study show that the choice of modelling approach is important when identifying species distributions from sparse data. Due to the uncertainly associated with model performance, using a number of different modelling approaches enables the best and most informative to be chosen. In our case MaxEnt consistently provided the best predictive performance. Had the alternative modelling approaches provided similar predictive performance, but varying predicted distributions, combining them in an ensemble can improve overall prediction [39, 61]. Modelling found the three species responded to a unique combination of environmental conditions, with the majority of the predicted habitat unique to each species, highlighting the importance of considering individual requirements when managing deep-water Hawaiian bottomfish as a single management unit. In light of this, what was define as 'core' bottomfish habitat (habitat where all species are predicted to co-occur) was also calculated to enable managers to identify the most important spatial areas of multi-species resource use for management consideration. While it was established that individual distributions are important, this approach also enables the highest priority habitat to be identified and can be used to significantly improve the spatial management of Hawaiian bottomfish.

The application of species distribution modelling (SDM) in the marine environment has, until more recently, been rare [55, 62]. Model performance between studies has been highly variable and dependent on the type of data being modelled, the intended application and ultimately the shape of the species responses [34, 54, 63]. The selection of which method is best for a certain application is still in debate [34, 55]. Elith et al. [40] in their review found MaxEnt's predictive performance to be consistently competitive with the highest performing methods. This study also demonstrates that it is a powerful method for modelling sparse data, outperforming both the GAM and BRT. The models developed are consistent with the known ecology of the species, accurately describing the preferred habitat of the three species. However, the subject is complex and will vary with the species ecology, quality of the data, shape of the response curve and scale of analysis [53, 54, 64].

Reasons why MaxEnt outperformed the two presence-absence models is likely to be a combination of sample size, model calibration and the shape of the species response. Some studies suggest that presence-only data addresses the problem of poor detectability or 'false' absences (i.e. locations where a species occurs but was not detected [65]). However, Elith et al. [53] argues that if detectability of a species varies from site to site, it will affect both



Fig. 2. Essential bottomfish habitat predictions using MaxEnt (between 100 and 300 m). First panel (a) depicts distribution of habitat (displayed in green) across Penguin Banks for the three species; (1) *Etelis coruscans*, (2) *Etelis carbunculus* and (3) *Pristipomoides filamentosus*. The second panel (b) provides more detail at a higher spatial resolution. The third panel (c) provides the response curves for the three most important predictor variables. Fish illustrations by Les Hata©, Hawaii Department of Land and Natural Resources.

the presence and the absence data. Therefore, removing the absence data will not address limitations of poor detectability. In general, it is recommended that presence-absence data are used, when available, as they are less susceptible to sample selection bias and provide more information for model calibration enabling better predictive performance [34]. However, in this case the presence only model outperformed the presence-absence models. A number of factors contributed to this outcome. First, the default



Fig. 3. Difference in spatial extent of habitat predicted, by each of the three models, for each of the three species (between 100 and 300 m). First panel (a) depicts differences in predicted habitat for the three species; 1) *Etelis coruscans*, 2) *Etelis carbunculus* and 3) *Pristipomoides filamentosus*. The second panel (b) provides more detail at a higher spatial resolution. Continuous probabilities of occurrence were converted to presence-absence using the P-fair threshold statistic balancing model sensitivity and specificity. Fish illustrations by Les Hata©, Hawaii Department of Land and Natural Resources.

settings within MaxEnt were appropriate for the small sample size, the species prevalence and the shape of the species response. In addition, data quality was good and sampling used a stratified systematic sampling design to minimize bias. Finally, the modelled response curves did not overfit the data. Therefore, MaxEnt provided good predictive performance. In contrast, the GAMs and BRTs were sensitive to the sparse data. For GAMs, small sample sizes can result in incorrect 'peaks' or 'troughs' in the modelled



Fig. 4. Combined predicted habitat using MaxEnt for the three bottomfish species (between 100 and 300 m) to illustrate differences in spatial extent: (1) core bottomfish habitat (where all three species are predicted to co-occur); (2) combined bottomfish habitat (where one or more species are predicted to occur); and 3) unique bottomfish habitat (where each species exists on its own). The second panel (b) provides more detail at a higher spatial resolution. Continuous probabilities of occurrence were converted to presence-absence using the P-fair threshold statistic balancing model sensitivity and specificity. Fish illustrations by Les Hata©, Hawaii Department of Land and Natural Resources.

response as a consequence of the complexity of the fit allowed [34]. Few replicates in the shallowest sections of the study area lead to the GAM overestimating the occurrence of *P. filamentosus* and thus reducing predictive performance. BRTs can also be strongly influenced by sample size with small samples found to provide models with higher predictive error and small changes in training data can result in a very different series of splits [56, 66]. In addition, BRTs can have difficulties modelling smooth functions

[34, 56]. Therefore, this study suggests MaxEnt will outperform more traditional presence-absence modelling when data is sparse, the sampling unbiased and the environmental response a smooth function.

The most important outcome from the modelling was that it demonstrated that each species responded to a unique combination of environmental conditions, with little overlap. To effectively manage deep-water snappers as a single management unit, differences in these species distributions must be taken into account. For many years, the overall EFH for the MHI bottomfish fishery has been the depth range between 0 and 400 m around each island and bank. This equates to 74.5% of the research area. This designation was purposely broad to encompass all 12 species in the fishery as well as all life history stages for each species. However, in the last couple of decades, research using submersible observations and fishing surveys has provided more data on life stage preferences as well as individual species preferences, showing clear differences in how that depth range is being utilised and the importance of substrate and terrain, namely hard, high slope substrates [30,47,48,67]. All studies have found a strong relationship with depth, however studies with access to fine scale substrate and terrain data (e.g. bathymetric slope) have also been able to demonstrate its importance [37,39,49,67]. For example, Misa et al. [49] assessed habitat preferences for 4 targeted bottomfish species and found species-specific differences to both depth and substrate. In contrast, the study by Gomez et al. [39] found bathymetric slope to be the poorest predictor of bottomfish distributions, while depth provided good predictive performance at very broad spatial scales ($> 1000 \text{ m}^2$). They suggest that finer scale data is needed for more precise predictions of deep-water groups. Using fine scale bathymetry and backscatter data this research was able to provide more precise, and species-specific, EFH designations and identified that the area utilised by bottomfish to be much reduced with individual predicted EFH covering between 9.3% and 10.6% of the research area (P. filamentosus and E. car*bunculus* respectively). This highlights an urgent need for fine scale data and an accurate method for predicting habitat preferences for all bottomfish species to understand factors shaping their distributions and for assessing whether management actions, such as spatial closures, are achieving their intended purpose in assisting the long term sustainable management of the fishery. This study identified unique species-specific distributions and responses to environmental conditions; therefore each deep-water species should be modelled separately. The present results suggest that when treating bottomfish species as an assemblage, a logistical necessity for management, individual differences must be accounted for to ensure effective management of this fishery.

5. Conclusion

Sustainable fisheries management, marine spatial planning and environmental decision support systems require a solid understanding of species distributions and habitat linkages. This study demonstrates that predictive species distribution modelling approaches can be used to accurately model and map sparse species distribution data across marine seascapes. The approach was found to be both a cost-effective and accurate tool to support spatial, or place-based, fisheries management and feed into ecosystem models to support sustainable ecosystem-based fisheries management. Currently managers and policy makers are looking for effective tools to support this new management approach. This study illustrates an approach that fully accounts for individual differences when treating groups of species as management units. These models provide the basis from which spatially explicit ecosystem models can be compiled. As more fine scale environmental data is collected and processed, the application of this approach across Hawaii and regions of the Indo-Pacific would give valuable additional insight into the extent of EFH supporting deepwater species and assess the potential for regions to support commercially viable deep-water fisheries.

Acknowledgements

This study was based on data collected by the University of Hawaii as part of a program independently assessing the deepwater bottom fishery for the State of Hawaii DLNR-Division of Aquatic Resources. The authors acknowledge D. Merritt, K. Wong, and the Coral Reef Ecosystem Division of the NOAA Pacific Islands Fisheries Science Center for their technical support and thank captains R. Cates (Wailoa) and G. Jones (Red Raven; Huki Pono) for supporting the field operations. The authors are grateful to C. Demarke, B. Alexander, J. Yeh, J. Friedman, V. Moriwake and B. Schumacher for undertaking the field surveys and processing the video imagery.

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