



Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management

Owen F. Anderson^{a,*}, John M. Guinotte^b, Ashley A. Rowden^a, Malcolm R. Clark^a, Sophie Mormede^a, Andrew J. Davies^c, David A. Bowden^a

^a NIWA, Wellington, New Zealand

^b Marine Conservation Institute, Seattle, USA

^c School of Ocean Sciences, Bangor University, Menai Bridge, Wales, LL59 5AB, UK

ARTICLE INFO

Article history:

Received 29 July 2015

Received in revised form

26 November 2015

Accepted 26 November 2015

Available online 17 December 2015

Keywords:

Vulnerable marine ecosystems

Habitat suitability models

Boosted Regression Trees

MaxEnt

Deep-sea corals

Scleractinia

Louisville Seamount Chain

ABSTRACT

Management of human activities which impact the seafloor in the deep ocean is becoming increasingly important as bottom trawling and exploration for minerals, oil, and gas continue to extend into regions where fragile ecosystems containing habitat-forming deep-sea corals and sponges may be found. Spatial management of these vulnerable marine ecosystems requires accurate knowledge of their distribution. Predictive habitat suitability modelling, using species presence data and a suite of environmental predictor variables, has emerged as a useful tool for inferring distributions outside of known areas. However, validation of model predictions is typically performed with non-independent data. In this study, we describe the results of habitat suitability models constructed for four deep-sea reef-forming coral species across a large region of the South Pacific Ocean using MaxEnt and Boosted Regression Tree modelling approaches. In order to validate model predictions we conducted a photographic survey on a set of seamounts in an un-sampled area east of New Zealand. The likelihood of habitat suitable for reef-forming corals on these seamounts was predicted to be variable, but very high in some regions, particularly where levels of aragonite saturation, dissolved oxygen, and particulate organic carbon were optimal. However, the observed frequency of coral occurrence in analyses of survey photographic data was much lower than expected, and patterns of observed versus predicted coral distribution were not highly correlated. The poor performance of these broad-scale models is attributed to lack of recorded species absences to inform the models, low precision of global bathymetry models, and lack of data on the geomorphology and substrate of the seamounts at scales appropriate to the modelled taxa. This demonstrates the need to use caution when interpreting and applying broad-scale, presence-only model results for fisheries management and conservation planning in data poor areas of the deep sea. Future improvements in the predictive performance of broad-scale models will rely on the continued advancement in modelling of environmental predictor variables, refinements in modelling approaches to deal with missing or biased inputs, and incorporation of true absence data.

© 2015 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

The concept of vulnerable marine ecosystems (VMEs) is one that has become important in recent years for the management of impacts of bottom trawling on benthic habitats in the deep sea (e.g., Ardron et al., 2014). VMEs are found in areas that may be subjected

to negative impacts from human activities such as bottom trawling, offshore oil/gas development, and deep sea mining. Potential VMEs are identified by biological characteristics that express the vulnerability of their species, communities, and/or habitats to damage or disturbance (FAO, 2009; CCAMLR, 2009). The United Nations General Assembly (UNGA) Resolutions 61/105 and 64/72 state the urgent need to identify and map VMEs in order to effectively implement cohesive networks of Marine Protected Areas (MPAs) and the need for Regional Fisheries Management Organisations to

* Corresponding author.

E-mail address: owen.anderson@niwa.co.nz (O.F. Anderson).

implement a precautionary approach to fishing on the high seas.

The South Pacific Regional Fisheries Management Organisation (SPRFMO) was formed to manage high-sea fisheries across a large area of the South Pacific Ocean, to ensure the sustainable use of fishery resources, and to safeguard the marine ecosystems in which they occur. This non-governmental organisation aims to implement management strategies to protect VMEs and thereby conserve biodiversity and ecosystem function in the deep sea. The SPRFMO convention area comprises the region of the South Pacific beyond areas of national jurisdiction, an area of about 59 million km². Currently, SPRFMO has some interim measures in place to protect VMEs (Penney et al., 2009) but the efficacy of these measures has been questioned (Penney and Guinotte, 2013). A general need for improved protection of VMEs in areas of the High Seas based on more robust spatial management planning has been recognised (Ardron et al., 2014).

Very little information exists on the spatial distribution of VMEs within the SPRFMO area, which is an impediment to the design of management strategies. The SPRFMO area is too large for cost-effective and comprehensive survey programmes to directly determine the location of all VMEs so predictive methods have been explored to help fill this management need (Rowden et al., 2013). Many studies have used habitat suitability models to predict the potential distribution of benthic fauna that may be indicators of VMEs in other areas (e.g., Davies and Guinotte, 2011; Yesson et al., 2012; Rengstorff et al., 2013, 2014). The use of such models has been recommended as part of a process for designing effective management plans for protecting VMEs from the adverse effects of fishing on the high seas (Ardron et al., 2014; Vierod et al., 2014), and for benthic ecosystem management in general (Reiss et al., 2014), even though the practical application of model outputs into conservation management can be difficult to achieve (Marshall et al., 2014).

While there are many recognised VME indicator taxa (Parker et al., 2009; Parker and Bowden, 2010), it is the reef-forming deep-sea scleractinian corals which have attracted the most attention because of their role in providing habitat which is associated with diverse fish and invertebrate communities (McCloskey, 1970; Jensen and Frederiksen, 1992; Husebø et al., 2002; Jonsson et al., 2004; Buhl-Mortensen and Mortensen, 2005; Costello et al., 2005; Stone, 2006; Henry and Roberts, 2007; Moore et al., 2008; Mortensen et al., 2008; D'Onghia et al., 2010; Mastrototaro et al., 2010). Coral reefs throughout the deep sea, including in the South Pacific, have suffered damage over the last 30 years from bottom trawling (Koslow et al., 2001; Fossa et al., 2002; Hall-Spencer et al., 2002; Rogers, 2005; Reed et al., 2007; Waller et al., 2007; Clark and Rowden, 2009; Althaus et al., 2009; Williams et al., 2010) and continue to be threatened by this activity. In addition, deep-sea coral reef VMEs are also threatened by changes in the physical environment including the shoaling of the aragonite saturation horizon and increasing ocean temperatures (Guinotte et al., 2006; Maier et al., 2009; Tittensor et al., 2010; Thresher et al., 2015).

In the northern hemisphere, *Lophelia pertusa* is the species primarily responsible for deep-sea coral reef formation. These reefs can grow to be tens of kilometres in length and tens of metres in height (e.g. Huehnerbach et al., 2007). This species is uncommon in the southern hemisphere where other reef-forming scleractinian species dominate including *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enalllopsammia rostrata*, and *Madrepora oculata* (Tracey et al., 2011). The distributions of these coral species are well described for the New Zealand EEZ and environs from compilations of data records and from regional habitat suitability models (Tracey et al., 2011). These four species are widely distributed throughout the region, have well defined depth zonation ranges, and are strongly associated with seamounts around New Zealand (Tracey

et al., 2011). Prior habitat suitability modelling studies conducted in the New Zealand region indicated depth, slope, surface water primary productivity, and tidal currents were all strong predictors of their distribution (Tracey et al., 2011).

Few studies have attempted to verify modelled predictions of deep-sea corals by direct comparison with independent field data, despite many stressing the need for such surveys (e.g. Tittensor et al., 2009; Davies and Guinotte, 2011; Guinotte and Davies, 2014). One example, highlighted by Dullo et al. (2008), characterized known *Lophelia pertusa* reef locations by the ambient water density (sigma-theta), temperature, salinity, oxygen levels, bottom relief, and current regimes. A manned submersible was used to “ground-truth” coral locations on the Norwegian continental shelf predicted from CTD casts and bathymetric analysis, but correspondence between predictions and observations was not quantified. Field validation of model results is often not carried out due to the expense of such surveys, which leads to uncertainty surrounding the accuracy of the modelled results and by extension, reluctance of managers and stakeholders to use the model results for management decisions. There is a clear and urgent need to test the ability of habitat suitability models to correctly predict suitable habitat for VME indicator taxa by conducting field surveys that sample the seafloor directly in areas with gradients of predicted habitat suitability. Such validation is particularly important in data-poor areas that are of high commercial interest. A prime example of this within the SPRFMO area is the Louisville Seamount Chain. The Louisville Seamount Chain lies in international waters and is an important area for New Zealand's commercial fishing interests, primarily for orange roughy (*Hoplostethus atlanticus*) (Clark, 1999). The seafloor habitats of the Louisville Seamount Chain have only rarely been sampled by independent research studies and only a limited number of records of reef-forming scleractinian corals and other VME indicator taxa exist from these seamounts.

In this study we produced broad-scale habitat suitability models for four species of reef-forming corals in the SPRFMO area using two statistical modelling approaches that are commonly used in deep-sea applications. We then tested these models using data from a systematic independent visual survey of a sub-region of the area to enable assessment of the correspondence between habitat suitability as predicted by the models, and actual presence or absence of corals. In order to assess which factors may drive differences between observed and predicted values, we compared the measured characteristics of the study region against the broad-scale environmental data used in the models. We discuss shortcomings of the modelling approaches and the implications of these results for fisheries management and conservation planning.

2. Methods

2.1. Study area

The Louisville Seamount Chain lies near the southern centre of the SPRFMO area, the region of the South Pacific beyond areas of national jurisdiction from 10° N to 60° S, and 120° E to about 67° W (Fig. 1). It is made up of over 80 seamounts and extends over 4000 km from the junction of the Pacific and Indo-Australian Plates (latitude ~27° S) south eastwards into the central southwest Pacific (latitude ~47° S) (Fig. 1). Many of the seamounts in the chain are large guyots (flat-topped seamounts, formed by erosion and subsequent submersion of islands). The region is known from New Zealand fisheries observer records to host VME indicator taxa including Porifera (sponges), Actiniaria (anemones), Alcyonacea (soft corals and gorgonians), Pennatulacea (sea pens), Scleractinia (stony corals), Antipatharia (black corals), Stylasterida (hydrocorals); and VME-associated taxa such as Crinoidea (sea lilies and

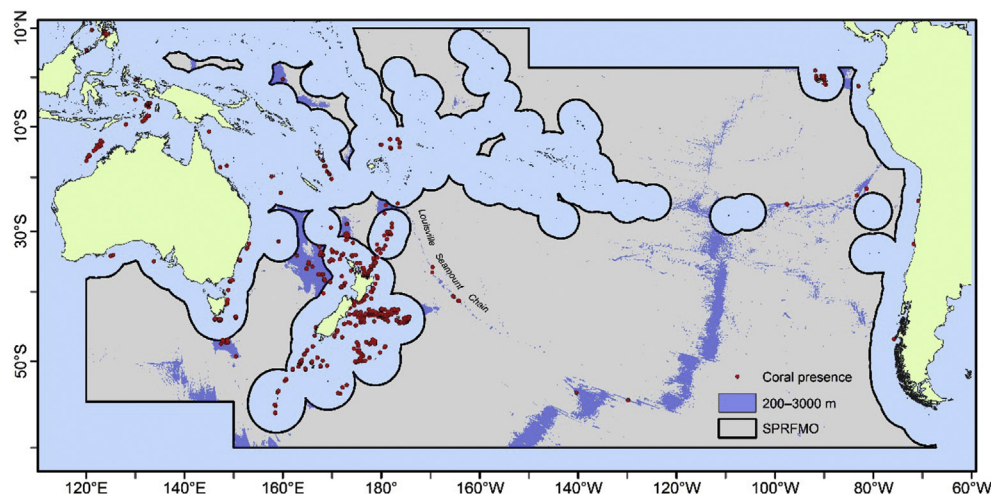


Fig. 1. The SPRFMO convention area (grey), comprising the waters of the Pacific Ocean beyond areas of national jurisdiction from 10° N to 60° S, and 120° E to about 67° W as shown (see <https://www.sprfmo.int/> for precise definition), and location of the Louisville Seamount Chain study area. Dark blue shading indicates regions within the SPRFMO convention area in water depths of 200–3000 m; red dots indicate the location of the 1643 presence records of reef-forming scleractinian corals used in the habitat suitability models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

feather stars) and Brisingida (“Armless” starfish) (Parker et al., 2009).

2.2. Species presence data

A comprehensive set of presence records for the wider Pacific region were compiled from a range of sources from several countries: *Chile*, Instituto de Fomento Pesquero (IFOP); *New Zealand*, Ministry for Primary Industries (MPI) fisheries observer and research trawl databases (*cod* and *trawl*), NIWA Invertebrate Collection (NIC) database (*Specify*), and databases of the Museum of New Zealand Te Papa Tongarewa; *Australia*, Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) databases; *other*, taxonomic lists from a 2003 biodiversity survey of the Norfolk Ridge and Lord Howe Ridge (NORFANZ) (Clark and Roberts, 2008), and the Ocean Biogeographic Information System (OBIS) databases (<http://www.iobis.org/>). The final dataset comprised a total of 202,579 records of VME indicator taxa, including 120,792 of Scleractinia. Records from outside the outer boundaries of the SPRFMO area (i.e. north of 10° N, south of 60° S, west of 120° E, and east of 67° W) were excluded from the models, as were those shallower than 200 m or deeper than 3000 m (outside the likely depth range of bottom trawling in the region and the accepted depth distribution of the four coral species), and any duplicate records (ESM 1 Table 1). The 1643 records of the four focal reef-forming species (*Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia rostrata*, *Madrepore oculata*) were not widely distributed across the SPRFMO area, with nearly 75% coming from the New Zealand EEZ and environs, and most of the remainder from the northwestern corner of the SPRFMO area (Australia, Indonesia, Philippines, and Melanesia) (Fig. 1). Records from eastern regions of the SPRFMO area were limited to the Galapagos Islands and Chile. The large central region of the SPRFMO area contained very few records, highlighting the uneven distribution of sampling effort.

2.3. Habitat suitability models

Two commonly used machine-learning model approaches were used to model potential habitat for scleractinian reef-forming corals based on species presence data and a set of environmental variables for the study area. These models were maximum entropy

(MaxEnt, Phillips et al., 2006) and Boosted Regression Trees (BRT, De'ath, 2007; Elith et al., 2008). The primary models were based on data for all four reef-forming coral species combined, in order to predict the overall distribution of likely VME habitat across the study area. Separate models were also constructed for each of the four species to examine factors affecting distribution patterns of individual species. The model extent was the SPRFMO area and adjoining EEZs between 200 m and 3000 m, although ultimately the model results were used to map only predicted suitable habitat in the SPRFMO area and the New Zealand EEZ. The spatial resolution of the models was 30 arc-seconds (approximately 1 km²), which is the same as the SRTM30 global bathymetry dataset and, by extension, the environmental variables re-scaled using SRTM30 and used as model inputs for this study (see Section 2.5). Many coral presence records were from physical samples of the seafloor, obtained using either dredges or research and commercial trawls, which are typically towed along the seafloor for several minutes to an hour. The median tow distance for the subset of 750 tows that recorded scleractinian reef-forming species and had complete start and end location data was 0.8 km, indicating that the ~1 km² spatial resolution of the environmental data was an appropriate match to coral presence and fishing effort data.

2.3.1. MaxEnt model

MaxEnt is a presence-only modeling approach that has been widely used to model deep-sea species distributions (e.g. Davies and Guinotte, 2011; Yesson et al., 2012; Guinotte and Davies, 2014). MaxEnt's underlying assumption is that the best way to determine an unknown probability distribution is to maximize entropy (Jaynes, 1957) based on constraints derived from environmental variables (Phillips et al., 2006). MaxEnt version 3.3.3a (Phillips et al., 2006) was used with default model parameters as they have performed well in other studies (a convergent threshold of 1025, maximum iteration value of 500 and a regularization multiplier of 1). A set of 10,000 background absence records were randomly selected from the depth range 200–3000 m across the entire study area. If more than one coral record from the same taxon occurred in the same 1 km² grid cell, they were removed and treated as spatial duplicates (following Davies and Guinotte, 2011; Guinotte and Davies, 2014). If spatial duplicates are retained, they can skew model results towards environmental conditions where

Table 1

Physico-chemical, terrain, and biological variables used in the BRT and MaxEnt habitat suitability models. Due to strong correlations with other variables, depth was not used directly in the models (see text).

Variable name	Native resolution	Model	Source
<i>Physico-chemical variables</i>			
Phosphate	1°	BRT only	Garcia et al. (2006)
Nitrate	1°	BRT only	Garcia et al. (2006)
Dissolved oxygen	1°	Both	Garcia et al. (2006)
Aragonite saturation state	1°	Both	Steinacher et al. (2009)
Salinity	0.25°	Maxent only	Boyer et al. (2005)
Salinity residuals	—	BRT only	(see text)
Temperature	0.25°	Maxent only	Boyer et al. (2005)
Temperature residuals	—	BRT only	(see text)
<i>Terrain variables</i>			
Slope	0.25° × 0.2°	Both	Becker and Sandwell (2008)
Depth (not used)	0.0083°	Neither	Becker et al. (2009)
<i>Biological variables</i>			
Particulate organic carbon flux	0.08°	Both	Lutz et al. (2007)

most sampling has taken place resulting in distorted model predictions. No weighting was applied to either the presence or background absences.

2.3.2. BRT model

BRT models use presence-background or presence-absence data to calculate habitat suitability probabilities by incorporating recursive binary splits within a regression tree structure to explain the relationship between the response and predictor variables (Elith et al., 2008). This approach, whilst less popular than MaxEnt is growing in utilization (De'ath, 2007) and has also been used to model distributions of deep-sea species (e.g. Tracey et al., 2011). Model fitting in BRT is controlled by three main parameters, which were set to typical levels: (1) Tree-complexity (*tc*) specifies the size (number of nodes) in each tree, and relates to the level of variable interaction; in these models *tc* was set to 3 (allowing three-way interactions between terms), (2) the learning rate (*lr*) shrinks the contribution of each tree added sequentially to the model and allows the model to be built up slowly with the contribution of a large number of trees, (3) the optimal number of trees (*nt*) is then determined based on *tc* and *lr*, using the cross-validation method described by Elith et al. (2008). In this case, a value for *lr* of 0.05 was found to be a suitable value to produce models with a relatively large number of trees (>1500). Estimation of the relative influence of predictor variables was based on the number of times a variable was selected for splitting (Friedman, 2001), scaled so that the sum across all variables was 100. Background absence records, equal in number to the presence records, were randomly selected from the portion of the study area within the depth range 200–3000 m as recommended by Barbet-Massin et al. (2012). These background data points do not suffer from the spatial bias inherent in presence data due to the highly clumped nature of sampling effort, and this will affect model accuracy if unaccounted for (Vierod et al., 2014). Unlike the approach taken for MaxEnt, duplicate records within a cell were not removed. BRT instead provides an option for weighting records to deal with spatial bias and this was used to weight presence records by 1/*n*, where *n* = the number of records in each cell; absence records were weighted so as to be constant and equal to the sum of the presence weights (after Tracey et al., 2011).

2.4. Model performance and interpretation

Model accuracy was assessed initially by partitioning the presence-only data into training and test datasets (75% of records used to train the model, 25% of records used to test). A threshold-

independent procedure was employed that used a receiver operating characteristic curve with areas under curve (AUC) for the test localities and a threshold-dependent procedure that assessed misclassification rate. With presence-background models, Phillips et al. (2006) define the AUC statistic as the probability that a presence site is ranked above a random background site, in terms of the likelihood of suitable habitat being present. In this situation, AUC scores of 0.5 indicate that the discrimination of the model is no better than random, with the maximum achievable AUC value being 1, which implies perfect discrimination of validation data. AUC values of >0.7 are considered to produce 'useful' model outputs (Swets, 1988; Guisan et al., 2006). Final map outputs were based on a model trained on all presence data.

Neither MaxEnt nor BRT are able to provide genuine species occurrence probabilities as this is not possible without the use of true absence data points. Therefore, model outputs are better described as estimates of relative habitat suitability. Final habitat suitability grids were produced by applying the calculated models to all cells in the study area, using a logistic link function to yield a habitat suitability index (HSI) between zero and one (Phillips and Dudik, 2008).

2.5. Environmental variables

Eleven environmental variables were included in the models (Table 1), based on global seafloor estimates for these parameters. These variables were derived from Davies and Guinotte (2011), who developed an approach to extrapolate and re-scale 3-dimensional gridded datasets of existing climatologies (e.g. dissolved oxygen, temperature, salinity, carbonate chemistry) using the highest resolution (~1 km²) dataset of global bathymetry available (SRTM30, Becker et al., 2009). This provides seafloor estimates for these variables in areas where high-resolution multibeam bathymetry and local environmental data have not yet been collected.

Variables used in the models were selected based on factors known to influence deep-sea coral settlement, growth, and survival. Temperature, salinity, slope (a proxy for current acceleration and mixing), carbonate chemistry, and nutrient availability have all been found to be important variables in previous modelling studies of deep-sea corals (Davies et al., 2008; Tracey et al., 2011; Davies and Guinotte, 2011; Rengstorf et al., 2013; Guinotte and Davies, 2014; Rengstorf et al., 2014). Deep-sea scleractinian reef-forming corals, including the four species modeled in this study, use aragonite to build their calcium carbonate skeletons and several global studies indicate calcium carbonate saturation state has a strong influence on their distributions (e.g. Guinotte et al., 2006;

Davies and Guinotte, 2011; Thresher et al., 2011; Yesson et al., 2012; Bostock et al., 2015; Thresher et al., 2015). Because depth was found to be highly correlated with several key variables (especially temperature (~80%) and aragonite saturation (Ω_{arag}) (~70%)) it was not used as a predictor variable in either the MaxEnt or BRT models. To be consistent with BRT modelling methods used in other New Zealand studies to avoid the influence of strong correlations between depth and temperature (e.g., Leathwick et al., 2006; Tracey et al., 2011), the temperature predictor was adjusted for depth by fitting a non-linear regression describing the relationship between depth and temperature—the predictor comprising the residuals from this regression (*temperature residuals*). A similar regression method was used to adjust salinity in relation to both temperature and depth (*salinity residuals*). These adjustments were not made to temperature and salinity used in the MaxEnt models but the influence of such correlations on model results is likely to be minimal, as machine-learning methods in general tend to be highly robust to correlations between variables (Archer and Kimes, 2008).

2.6. Independent model validation

For the independent model validation exercise, six large seamounts in the Louisville Seamount Chain were selected for survey (Fig. 2) with the aim to represent as wide a geographic range as possible given the available survey time. Within the chosen seamounts there is a general gradient of increasing historical bottom trawling effort from north to south, mainly targeting orange roughy. Bottom trawling has taken place on all of these seamounts and much of the area (excluding Forde and Censeam seamounts) remains open to fishing by New Zealand bottom trawlers under SPRFMO regulations. These regulations permit continued fishing in designated 20-min latitude/longitude blocks by vessels flagged to SPRFMO Member States, based on a 'bottom fishing footprint' established during the 2002–06 SPRFMO reference period (SPRFMO CMM2.03, <https://www.sprfmo.int/>, Penney et al., 2009). All six surveyed seamounts have a vertical elevation of more than

1 km from the surrounding seafloor. Details of the six seamounts are given in ESM 1 Table 2, and the survey methodology is described in Clark et al. (2015).

A random-stratified survey was designed to test both the ability of the models to predict presence of reef-forming corals and the relative performances of the two models against each other. In order to maximize the likelihood of being able to resolve performance with limited sampling effort, strata were constructed to enable sampling across the full range of model indices. These strata comprised cells of either low or high habitat suitability as predicted by the BRT model; and cells with either statistically similar or different habitat suitability for the two model types. The BRT model indices were much higher overall than the MaxEnt indices, therefore high habitat suitability was set at 0.8 for the BRT model and statistically similar cells were those in which the difference in habitat suitability between models was 0.44 or less. This was based on a power analysis for a minimum detectable difference with a sample size of 20. High suitability strata were further partitioned according to whether they had been subjected to any bottom trawling activity (Table 2) based on fine-scale effort data collected from New Zealand vessels – responsible for most historical bottom trawling activity on the Louisville Seamounts (Clark, 2008). The survey cells were the 1 km² habitat suitability model grid. Cells were selected for photographic survey transects randomly within each stratum: 6 from within Stratum 1 (high probability in both models), and up to 4 each from within the other strata. Some seamounts had no, or few, available cells of some strata (usually Stratum 2, which were typically deeper than 1500 m, or Stratum 5 where northern seamounts had less fishing). In these cases, additional random transects were completed in the other strata where possible.

Prior to running photographic transects on each seamount, a bathymetric survey was conducted using a 30 KHz Kongsberg EM302 Multibeam Echosounder (MBES), producing a bathymetry resolution of 25 m². The length of each photographic transect was approximately 1 nautical mile (1.85 km), and covered at least two

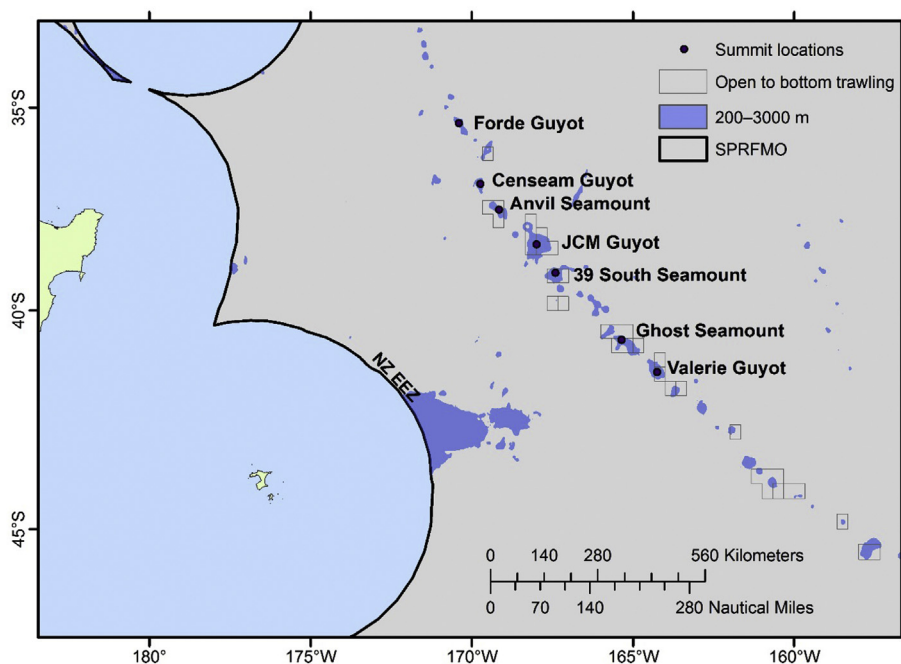


Fig. 2. The general survey area on the Louisville Seamount Chain, showing the six survey seamounts (plus JCM Guyot) and the 20-min latitude/longitude blocks open to bottom trawling (with or without a move-on rule) by New Zealand vessels (source www.nablis.govt.nz). Dark blue shading indicates regions within the SPRFMO convention area (grey) in depths of 200–3000 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Characteristics of validation survey strata. Strata were designed to enable sampling across the full range of model indices, and comprised areas of either low (≤ 0.44) or high (≥ 0.80) probability of suitable habitat as predicted by the BRT model for four reef-forming scleractinian corals, and areas with either statistically similar or different probability for the two model types, based on a sample size 20 samples per stratum. High probability strata were further partitioned according to whether they had been subjected to any bottom trawling activity.

Stratum	Suitable habitat probability	Conditions
1	High	High probability of suitable habitat for stony corals (BRT ≥ 0.80) and models agree (difference between BRT and MaxEnt model in that cell < 0.44), unfished
2	Low	Low probability (BRT model in that cell ≤ 0.20) and models agree (difference between BRT and MaxEnt model in that cell < 0.44) of suitable habitat for stony corals, unfished
3	Models differ	Different probability between models (difference between BRT and MaxEnt model in that cell ≥ 0.44), unfished
4	Intermediate	Intermediate probability (BRT model in that cell = 0.20–0.80) of suitable habitat for stony corals, unfished
5	High (fished)	High probability of suitable habitat for stony corals (BRT model in that cell ≥ 0.80), and models agree (difference between BRT and MaxEnt model in that cell < 0.44), fished.

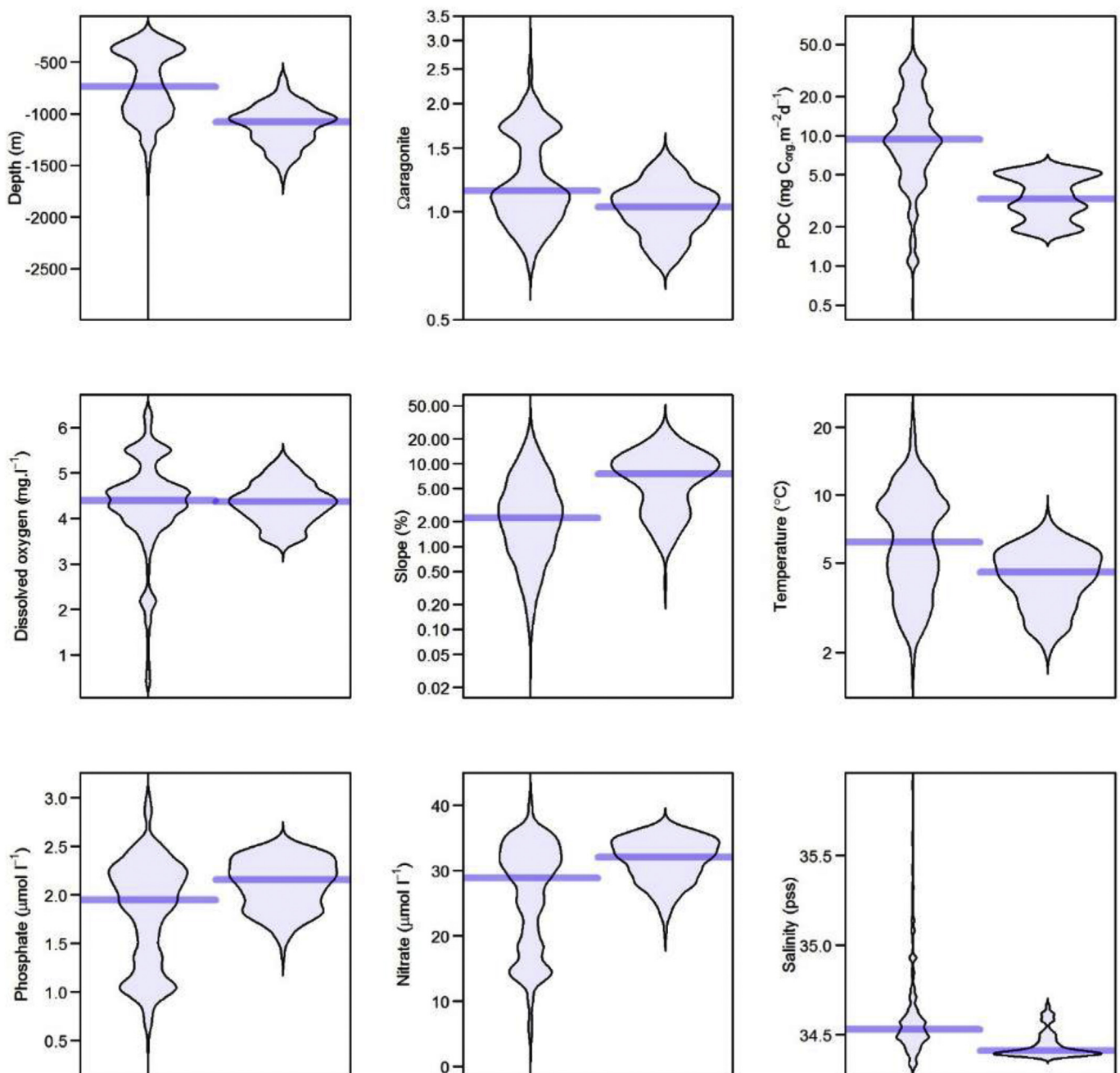


Fig. 3. Bean plots of environmental variables associated with reef-forming scleractinian coral presence locations. The beans are mirrored density traces, with the median value shown as a horizontal line. In each panel the bean on the left is based on point values associated with all presence data used in the broad-scale models and the bean on the right is based on the values assigned to each cell of the photographic survey. Environmental variables are the model values (as described in Table 1) for all beans except for depth, which is based on the recorded depth for the model presence locations, and the mean transect depth for the camera observations.

Table 3

Correlations between model indices and observed frequencies (for all reef-forming scleractinian corals, and for *Solenosmilia variabilis* alone) in the validation survey area, overall and by survey stratum; the mean of BRT and MaxEnt model habitat suitability indices (HSI) in the sampled cells in each stratum; and coral prevalence (the mean of the fractions of observed corals in the sampled time segments of all cells in each stratum). Random transects only.

Stratum (n.cells sampled)	Correlation				Mean HSI (four-species model)		Coral prevalence
	Four-species model		<i>Solenosmilia</i> model				
	BRT	MaxEnt	BRT	MaxEnt	BRT	MaxEnt	
All cells (233)	−0.07	0.10	0.00	0.09	0.75	0.43	0.13
1-High (82)	0.00	0.22	−0.03	−0.04	0.91	0.54	0.13
2-Low (20)	−0.22	0.23	−0.22	0.24	0.10	0.18	0.20
3-Models differ (55)	0.21	0.22	0.28	0.27	0.90	0.39	0.09
4-Intermediate (57)	0.01	0.14	−0.03	0.09	0.57	0.35	0.12
5-High (fished) (19)	0.29	0.22	0.16	0.51	0.94	0.56	0.17

adjacent cells of the same stratum. After completion of all the photographic transects, a CTD cast was conducted at each seamount. Data from these casts were used to help derive and assign values for Q_{arag} to each survey cell. Epibenthic sled deployments were also made to collect physical samples for verification of visual identifications and other research. A total of 24 sled deployments was made, with between 1 and 8 tows per seamount.

Photographic transects were carried out using NIWA's deep towed imaging system (DTIS, Hill, 2009), which incorporates high definition video and still camera systems and an ultra-short baseline positioning system (USBL, Kongsberg HiPAP) for tracking and recording the precise seabed position of the equipment (accurate

under ideal conditions to within 1 m). DTIS provides a live video link to the vessel, and coral individuals and colonies, other invertebrates, fish, and substrate information were recorded in real time into georeferenced files by teams of observers using Ocean Floor Observation Protocol (OFOP) software (www.ofop-by-sams.eu). The OFOP transect data were compiled into a single master file comprising all 115 transects (89 random and 26 target) completed on the survey.

All occurrence records for reef-forming coral were assigned to one of the 326 cells sampled during the survey. For each cell a frequency of occurrence was calculated for records of live reef-forming corals for comparison with model habitat suitability

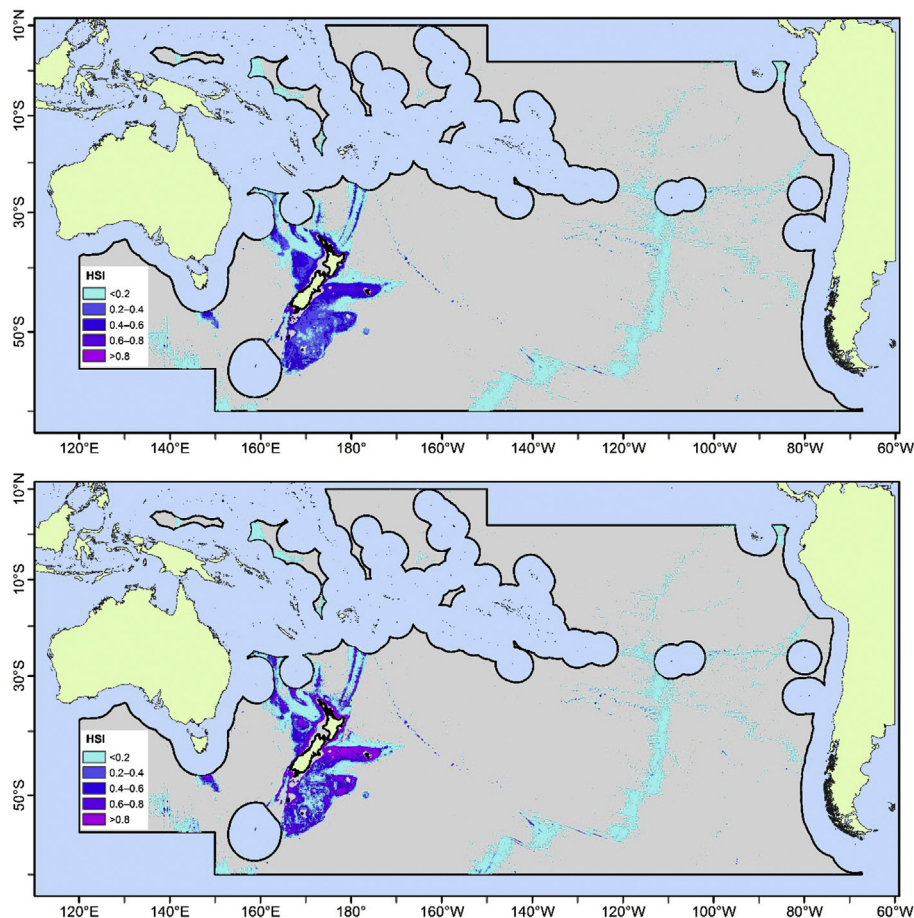


Fig. 4. Model results: top MaxEnt, bottom BRT. Predictive relative habitat suitability index (HSI, 0–1) for the SPRFMO convention area and the New Zealand EEZ from the habitat suitability models for the four reef-forming scleractinian coral species.

indices, using the following protocol: the elapsed time from the beginning of the transect was calculated for each record, and the transects split into 60 s segments. Any segment that crossed two or more cells was arbitrarily assigned to one or the other rather than being split, to avoid having to include short segments in the analysis. The frequency of coral occurrence was then derived for each cell by dividing the number of segments with corals by the total number of segments sampled in that cell. Confidence intervals (95th percentiles) were calculated for these frequencies by:

$$CI = p \pm 2\sqrt{\frac{0.25}{n}}$$

where p = the frequency of occurrence and n = the number of segments sampled. These CIs are approximate only because the calculation assumes a normal distribution of the data and the n segments in each transect are not independent.

Correspondence between measured frequency of occurrence and model habitat suitability indices was assessed using correlations (Pearson correlation coefficients), with Fisher's z' transformation used for testing the significance of differences in correlations between models and strata. Coral prevalence was calculated as the mean fraction of observed reef-forming corals in the time segments of the randomly sampled cells. Prevalence values were calculated for the survey area as a whole and for each stratum separately, for comparison with mean habitat suitability indices.

2.7. Comparison of actual depth versus depth estimated by SRTM30 bathymetry

Accuracy of the re-scaled environmental predictor variables used in the habitat suitability models is highly dependent on the accuracy of the SRTM30 bathymetry used. Any depth errors in SRTM30 will be propagated through the predictor variables created using reported depths from SRTM30 and by extension, the habitat suitability model outputs. This issue may be especially relevant in remote areas of the ocean such as the Louisville Seamount Chain, where there is a paucity of ship sounding data available to refine global bathymetry models.

A mean depth value was calculated for each cell based on every available spatially referenced depth record in the OFOP transect data. These values provide an accurate measure of the mean depth of the transect, and an approximate measure of the mean depth of the whole cell. Depth values from the SRTM30 bathymetry model were also assigned to each survey cell so that comparisons could be made between measured and modelled depths.

3. Results

3.1. Species niches based on presence records and data from CTD casts

The coral presence records used in the models were collected over a depth range from 200 to 2850 m with a median depth of approximately 740 m. Individual depth distributions of the four species analysed resulted in a bimodal depth distribution when data from all four species were combined (Fig. 3). This was largely due to the influence of *Madrepora oculata*, for which many records were in depths of 200–500 m.

About 29% of the observed corals were located in potentially undersaturated conditions, with estimated Ω_{arag} as low as 0.65. However, aragonite saturation based on CTD casts showed higher overall levels in the survey area than estimated, suggesting that only 25% of cells containing live *Solenosmilia variabilis* were

in water undersaturated with aragonite compared to 41% of cells based on estimated values. The lowest CTD-based Ω_{arag} value was 0.87, at a depth of 1752 m on 39 South Seamount, but corals were not observed deeper than 1500 m on this feature. Lower Ω_{arag} values (to a minimum of 0.71 on Forde Seamount) were otherwise only attributed to a few records based on extrapolation of the CTD data to depths beyond where bottle samples were taken, and are therefore unreliable. In comparison, the minimum Ω_{arag} value for a cell with live *Solenosmilia variabilis* from the predictor variable used in the habitat suitability models was 0.69.

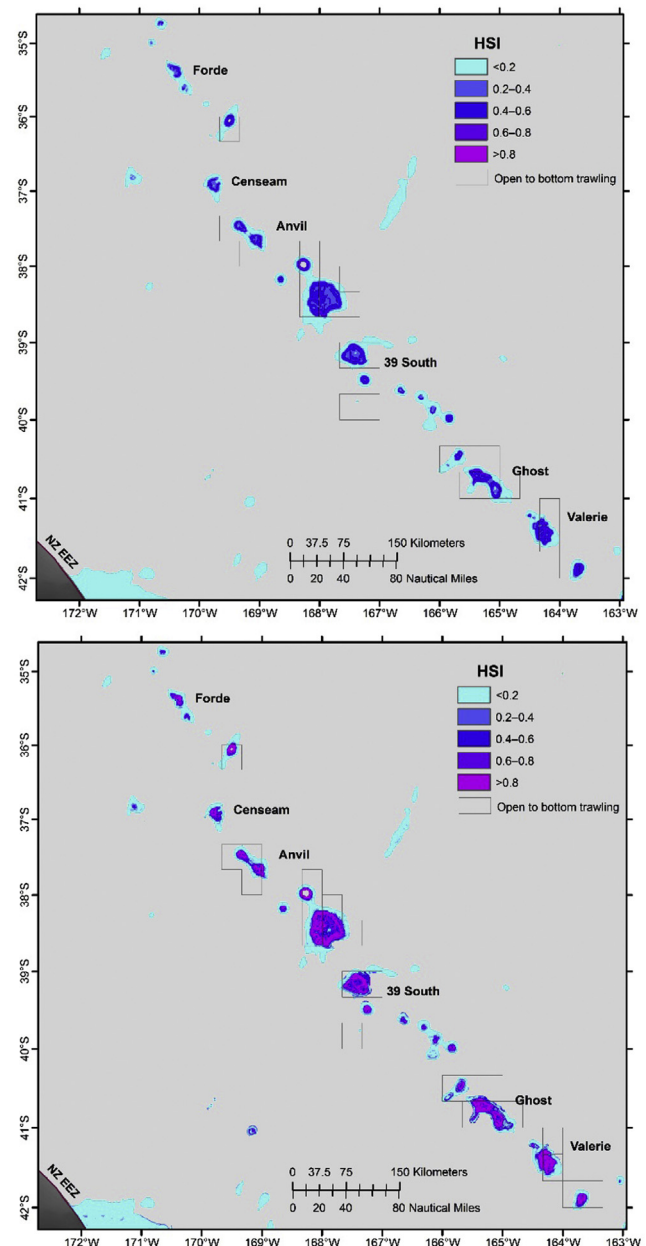


Fig. 5. Model results: top MaxEnt, bottom BRT. Predictive relative habitat suitability index (HSI, 0–1) for reef-forming scleractinian corals in the sampled region of the Louisville Seamount Chain. The peaks of all seamounts are far deeper than the minimum depth modelled (200 m) but predictions are limited to the maximum modelled depth (3000 m). Also shown are the 20-min latitude/longitude blocks open to bottom trawling (with or without a move-on rule) by New Zealand vessels.

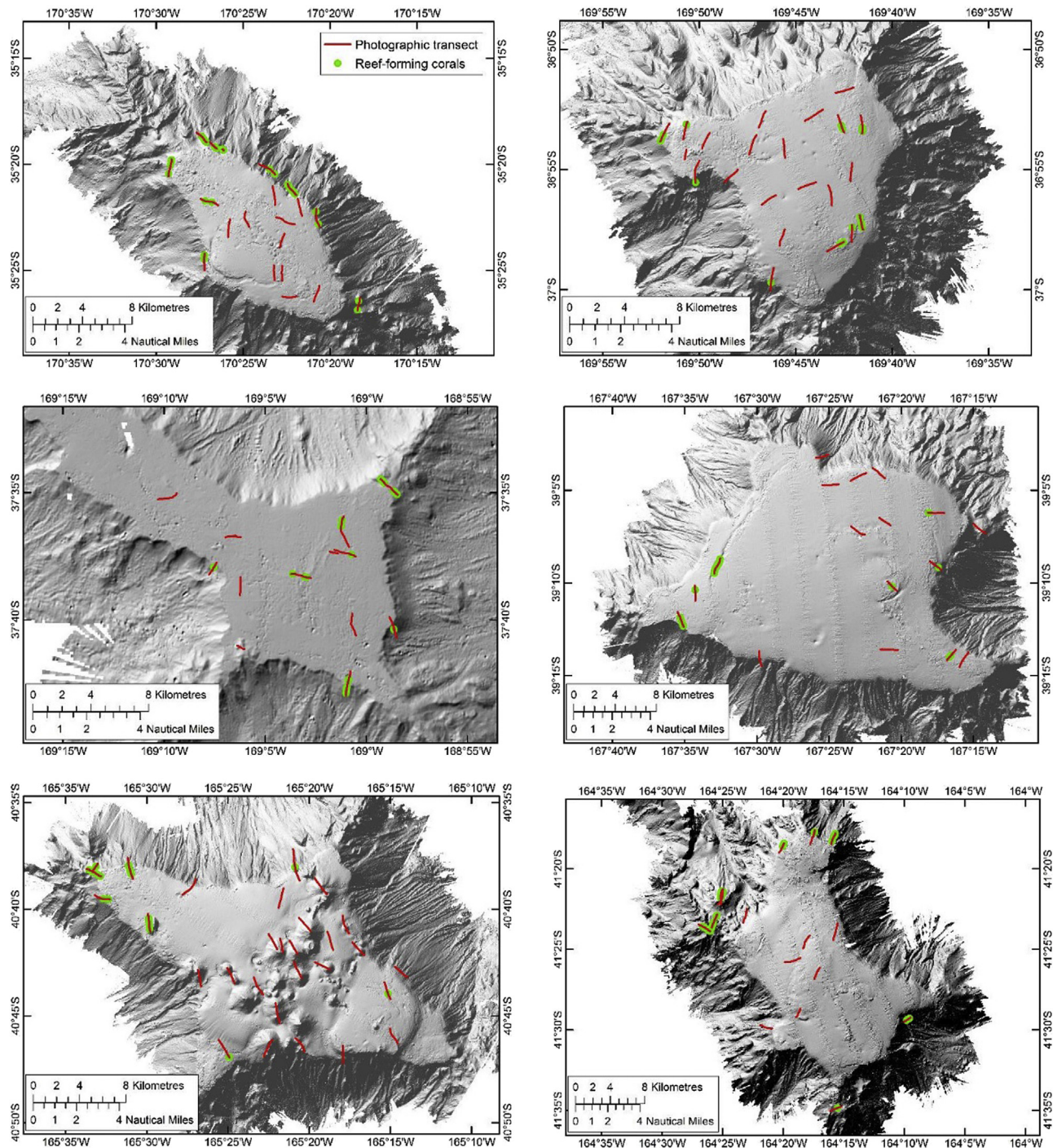


Fig. 6. Photographic transect tracks and observations of reef-forming scleractinian corals on the six seamounts surveyed. From left to right, top to bottom: Forde, Censeam, Anvil, 39 South, Ghost, Valerie.

3.2. Model predictions

For the combined four-species BRT model, the AUC value calculated from the 25% test data subset was 0.95; the equivalent AUC statistic from MaxEnt was 0.88. Similarly high values were calculated for the four models based on individual species (BRT, 0.93–0.97; MaxEnt, 0.92–0.97; see ESM 1 Table 3 for full details).

Only a small fraction of the SPRFMO area lies within the modelled depth range (200–3000 m), mainly confined to areas of the northern Tasman Sea between Australia and New Zealand, parts

of Micronesia east of Papua New Guinea, the Kermadec and Colville Ridge systems north of New Zealand, and large sections of the Pacific-Antarctic Rise in the east (Fig. 4). Over much of this region both models produce a habitat suitability index of less than 0.20, with higher suitability levels largely restricted to shallower sections of the Kermadec and Colville Ridges, the West Norfolk Ridge and Lord Howe Rise west of New Zealand, the Tasman Rise south of Tasmania, and the Louisville Seamount Chain. Large areas of relatively high habitat suitability (>0.40 for MaxEnt, 0.80 for BRT) exist within the EEZ of New Zealand and are included in Fig. 4 for

comparison. The models show a high level of agreement in the extent of the region of these higher levels of habitat suitability, however the BRT model produces much higher predictions of habitat suitability overall.

Within the Louisville Seamount Chain study area, the highest suitability values for both models were around the shallower parts of the seamounts, with extensive areas across the flat tops of the seamounts predicted to be suitable habitat (Fig. 5). The higher suitability values from the BRT model are especially apparent. Although both models predicted habitat suitability of less than 0.20 in about 50% of all cells within the entire Louisville Seamount Chain, BRT predicted habitat suitability of less than 0.50 in 68% of all cells compared with 78% for MaxEnt. The greatest difference between models was at the highest levels of habitat suitability, with BRT predicting habitat suitability of greater than 0.80 in 22% of cells compared with <1% of cells for MaxEnt.

Aragonite saturation was the primary predictor of suitable habitat for the combined four species of reef-forming corals in both the BRT and MaxEnt models, with a relative contribution of around 60% in each, and indicating a strongly positive response to increasing $\mathcal{Q}_{\text{arag}}$. In the BRT model particulate organic carbon was the next selected predictor, followed by dissolved oxygen and slope; in the MaxEnt model dissolved oxygen was the second strongest predictor, followed by particulate organic carbon and temperature.

The main explanatory variable in the BRT models for separate coral species were generally similar to the overall model, with aragonite saturation the primary predictor in each case and particulate organic carbon and dissolved oxygen also important. An exception to this was the model for *Enallopsammia rostrata*, in which the relative influence of phosphate was very high (29%). The MaxEnt models differed, in that although aragonite saturation was the primary predictor for *Madrepora oculata*, dissolved oxygen was most important for the other three species, and in each case temperature had a stronger influence than in the combined model. (see ESM 1 Tables 3 and 4 for full details of model fits).

3.3. Independent model validation

Photographic transects were concentrated on the flat tops and upper flanks of the seamounts where the models had predicted the highest levels of habitat suitability. Depth in these areas ranged from about 770–1000 m on Valerie Seamount to about 1100–1250 m on Anvil Seamount, and the full depth range of the transect data points was from 614 m (on Ghost seamount) to over 1600 m (on 39 South, Ghost, and Valerie Seamounts). Live reef-forming corals were found on each of the six seamounts surveyed (Fig. 6), but their distribution was uneven, with more observations associated with transects which ran across the generally hard substrate around the edges of the seamount summit than those which ran across the generally sandy substrate of the flat top of the seamount. Areas of intact but dead coral matrix were more extensive than live colonies (Fig. 7), but for the purposes of this study were not counted as records of coral presence. These dead corals were found on all seamounts surveyed, especially around the flanks, but also occasionally on sandy areas of the summits. Samples of these dead corals recovered by sled sampling were coated with a thin ferromanganese layer, particularly noticeable on those from the northern seamounts.

In none of the photographic transects was it possible to identify damage to or removal of coral colonies due to the impact of passing trawl gear. However, trawl marks were clearly visible on the substrate in five of the photographic transects; one each on Censeam and Anvil seamounts, and two on Ghost Seamount.

Observed frequencies of occurrence in sampled cells showed

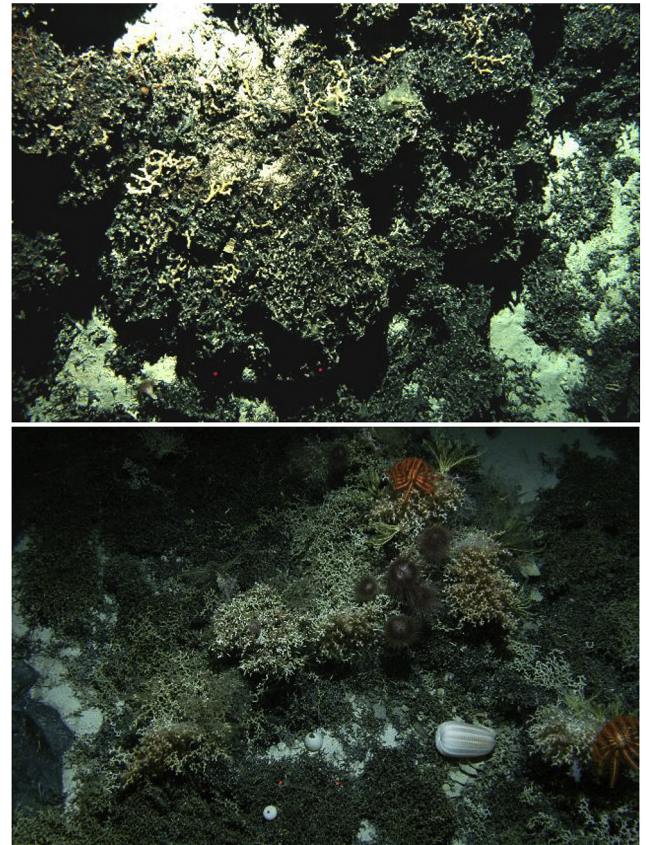


Fig. 7. Top, dead coral reef with ferromanganese coating at 1205 m on Anvil Seamount; Bottom, live coral reef (*Solenosmilia variabilis*) with associated echinoids, brisingid asteroids, and comatulid crinoids. The laser points near the bottom centre of the images are 20 cm apart.

low correlation with habitat suitability values from the four-species model, with overall correlations of −7% (BRT) and 10% (MaxEnt) (Table 3). Models for *Solenosmilia variabilis* alone might have been expected to perform better as this was the sole reef-forming species observed during the validation survey, but correlations for these models were both less than 10%. Although MaxEnt model values were generally more correlated with frequency of occurrence than BRT model values, the difference was not significant in any strata, either for the four-species model or for the *Solenosmilia variabilis* model (Fisher's z transformation, $p = 0.05$).

Correlations also indicated some variability in model performance among survey strata, although they were relatively constant

Table 4

Summary statistics for comparison of model habitat suitability indices (HSI) with observed frequencies and their confidence intervals (CIs) in the validation survey area overall, and by survey stratum. Random transects only.

Stratum	Total no. of cells surveyed	% Cells with model HSI within CI of observed frequency		% Cells with model HSI greater than observed frequency	
		BRT	MXE	BRT	MXE
All combined	233	17	34	92	90
1-High	82	6	26	99	95
2-Low	20	65	65	40	55
3-Models differ	55	9	24	96	93
4-Intermediate	57	28	47	93	88
5-High (fished)	19	0	26	99	95

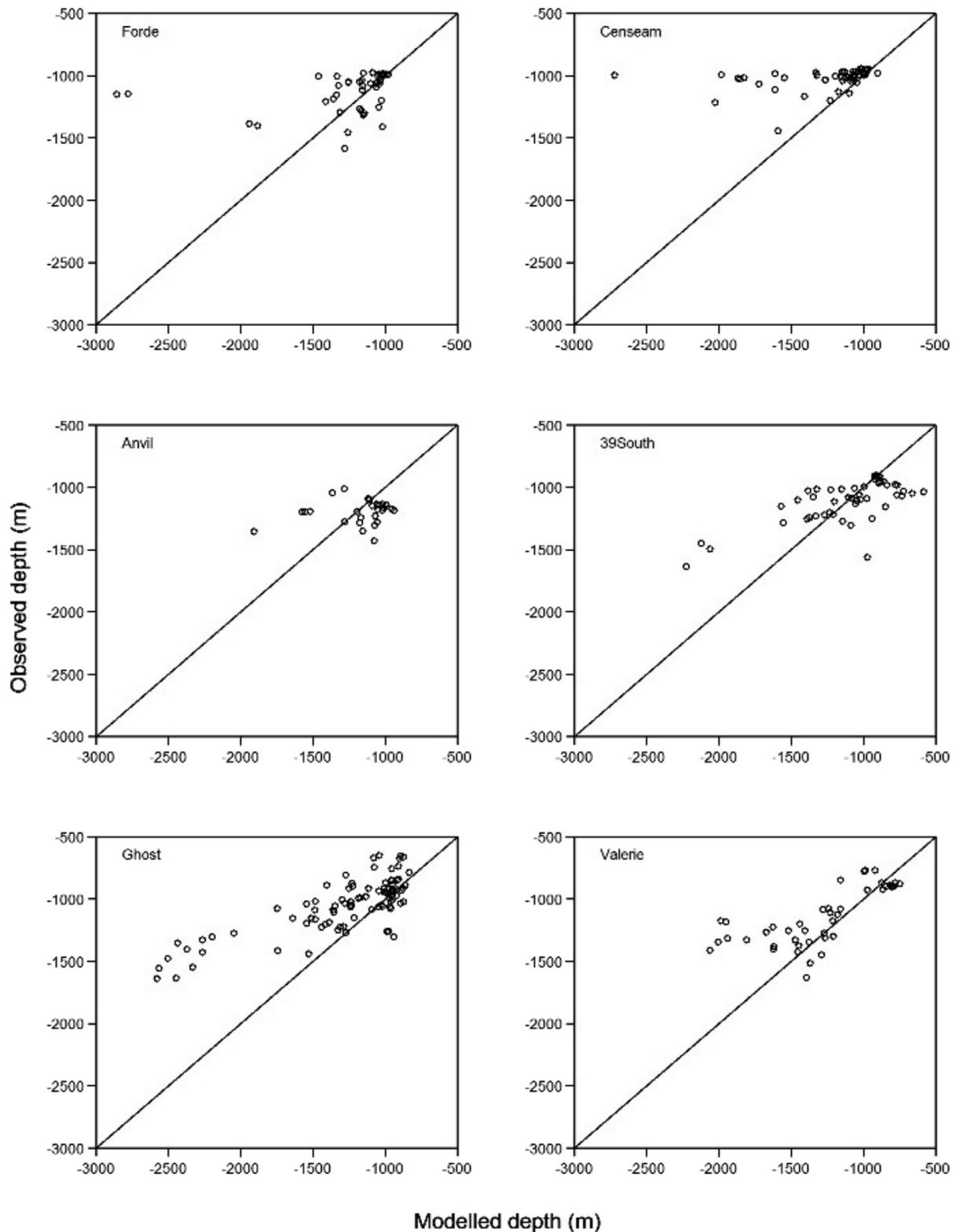


Fig. 8. Observed vs modelled depth on each of the six seamounts sampled on the Louisville Seamount Chain. Points above the line in each panel indicate model overestimation of depth; points below the line indicate model underestimation.

for the MaxEnt four-species model, but again no significant differences were identified between any strata for any of the four model/species combinations.

Overall coral prevalence in the survey area was 0.13 (Table 3). In

comparison, the mean habitat suitability values for the sampled cells were far higher at 0.75 (BRT) and 0.43 (MXE). There was little correspondence between prevalence values and strata, with the greatest value (0.20) occurring in stratum 2, where both models

Table 5

Pearson correlation coefficients of modelled depth (SRTM30) with the mean observed depth across each of the sampled cells (random and target) on the validation survey seamounts.

Seamount	Correlation coefficient	Number of cells
Forde	0.26	46
CenSeam	0.35	57
Anvil	0.17	28
39 South	0.70	49
Ghost	0.78	95
Valerie	0.73	47
All seamounts ^a	0.58	326

^a Including JCM.

predicted low habitat suitability and the lowest value (0.09) occurring in stratum 3, where model predictions differed. Notably, coral prevalence in fished areas (stratum 5) was not lower than in equivalent un-fished areas (stratum 1).

Confidence intervals around the observed frequencies in individual sampled cells were broad (between 0.15 and 1.0 depending on the number of time segments in the cell) and often encompassed the model habitat suitability value for the cell. Overall, however, model habitat suitability values were mostly higher than the observed frequencies and fell within these confidence intervals in fewer than half of the cells sampled for both models in all strata except stratum 2 (low habitat suitability) (Table 4). By this measure the poorest agreement between observed frequency of coral occurrence and predicted habitat suitability indices was in stratum 3 (models differ) and strata 1 and 5 (high habitat suitability and high habitat suitability-fished respectively), and the highest agreement was in stratum 2.

3.4. Reliability of environmental variables used in the models

Comparison of mean observed depth with SRTM30 depth revealed consistent patterns of depth overestimation by the SRTM30 data set in the survey area. Mean depths for the observed cells ranged from 650 m to 1641 m whereas the SRTM30 depth range for the same cells was much wider (581–2855 m). Differences between SRTM30 depth and observed depth exceeded 1000 m in some cells, especially on Forde, CenSeam, and Ghost seamounts (Fig. 8). Overall there was a low level of correlation between the depth values, particularly on Forde (26%), CenSeam (35%), and Anvil (17%) Seamounts (Table 5).

4. Discussion

This study is the first formal attempt that we are aware of to validate habitat suitability models for deep-sea VME indicator taxa using a purpose-designed field survey. Broad-scale habitat suitability models were generated using the best available scientific data for the SPRFMO area and New Zealand EEZ, using the two types of model that feature prominently in deep-sea species distribution modelling literature (e.g. Leathwick et al., 2006; Tracey et al., 2011; Davies and Guinotte, 2011; Rengstorf et al., 2013; García-Alegre et al., 2014). High AUC values indicated a good fit of the models to internally retained test data, even though this statistic may be overinflated as it is not based on fully independent data and the coral presence data has inherent spatial autocorrelation (Vierod et al., 2014). Despite this, neither model was successful in accurately predicting suitable habitat for reef-forming deep-sea corals at the scale of individual grid cells surveyed in the field validation region of the Louisville Seamount Chain. This failure is likely caused by a combination of several issues: 1) limitations of the SRTM30 bathymetry dataset, which affect the precision of each

of the environmental predictor variables; 2) missing critical predictor variables, particularly substrate type; 3) lack of true absence data; 4) spatial bias as a result of the majority of presence records coming from within the New Zealand EEZ; and 5) aspects of the topography of the seamounts in the Louisville Seamount Chain study area. These issues and a number of other observations are expanded on below, followed by a discussion on the implications of the results produced by this study for fisheries management. Suggestions for future habitat suitability modelling of VMEs are also made.

4.1. Influence of SRTM30 depth error on predictor variable precision

The error and bias detected in the SRTM30 data has significant implications for the habitat suitability models, as it directly affects the reliability of predictor variables. Because SRTM30 depths were used to re-scale seafloor values for all of the predictor variables used in both in the BRT and MaxEnt models, any inherent discrepancies between the SRTM30 depth and actual sampled depth will have been transferred to the predictor variables. Although validations of environmental variables re-scaled in this way using measurements from water samples have shown generally high agreement globally (Davies and Guinotte, 2011), few measurements exist for large areas of the SPRFMO area. So, although accuracy of SRTM30 data may be high in some well-sampled areas, significant inaccuracies are probable throughout the SPRFMO area where depth estimation is more heavily reliant on satellite altimetry data alone. Such errors are likely to be particularly large with steeply-rising topography including banks and seamounts (Davies et al., 2008).

Our comparison of depths recorded along camera transects to SRTM30 data for the same locations indicated that the upper flanks of the surveyed seamounts were particularly susceptible to large discrepancies in SRTM30 bathymetry. In these areas SRTM30 frequently overestimated true depth by hundreds of meters. Depth discrepancies in the survey area and their flow-on effects to environmental predictors are likely to have led to overestimation of the variability in habitat across the relatively homogeneous flat tops of the seamounts, and to have strongly contributed to the poor predictive power of the models. An example of this error being perpetuated through to the environmental predictor variables was evident in the estimated Q_{arag} (derived using SRTM30 depths) for observed corals being as low as 0.65, well below the minimum value derived from survey CTD casts (0.87) (see also Section 4.6).

4.2. Missing critical predictor variables

An important reason for the poor prediction of suitable habitat by both models is likely to be the lack of a predictor describing the distribution of hard substrate; a factor which can be highly variable over small spatial scales and is known to limit the distribution of reef-forming coral species (Mackay et al., 2014; Davies and Guinotte, 2011; Tracey et al., 2011; Guinotte and Davies, 2014). The photographic transects showed that the flat tops of the surveyed seamounts were dominated by sand, an unsuitable substrate for the settlement of most stony coral species. Where high-resolution bathymetry data are available, backscatter, fine-scale slope parameters, and terrain variables such as roughness, rugosity, and benthic position index (BPI, Wright et al., 2005) can be derived, which are useful proxies for substrate type and can enable development of high-performing habitat suitability models (e.g., Howell et al., 2011; Rengstorf et al., 2013; García-Alegre et al., 2014; Rengstorf et al., 2014). For such variables to be useful for predicting suitable coral habitat, they must be paired with presence data at a similar resolution. The lack of substrate data and high-resolution

bathymetry across the SPRFMO area will continue to be a challenge for increasing the predictive accuracy of broad-scale models.

4.3. Lack of true absence data

Because both models used background data, rather than true absence data, to define the physical environment of the study area, they do not provide a precise estimate of the probability of presence and may not even be proportional to it (Phillips et al., 2009). MaxEnt applies an arbitrary default parameter to map its relative output into a 0–1 scale, while for BRT the relative level of the probabilities in the model were driven to a large extent by the number of background points used and the weighting applied to them. Nevertheless, if the models were accurately referencing suitable habitat, good correlations between model outputs and observed coral frequencies would be found, especially at low and high levels of habitat suitability. In practice, however, correlations were not significantly better in the low and high habitat suitability survey strata than in other strata.

BRT is primarily designed for use with true absence data, and if true absence data are available they can be used to transform MaxEnt output into absolute probabilities (Guillera-Arroita et al., 2014). The lack of true absence data is a shortcoming of many attempts to model suitable habitat for VME indicator taxa (Vierod et al., 2014). The use of random background points rather than true absence data in our study has likely contributed to a bias in habitat suitability towards values nearer to 1 in both the BRT and MaxEnt models, as the spatial bias in the presence data is not matched by the background data, and the removal of duplicates (MaxEnt) and weighting procedures (BRT) do not appear to have fully accounted for this bias. If suitable absence data cannot be obtained, then the assembly of non-random background data methods could be attempted. Target-group methods, which utilize records collected or observed for a broad set of species using the same methods or equipment as the target species (Phillips et al., 2009; Tracey et al., 2011; Wood et al., 2013; Vierod et al., 2014) and methods which weight data according to environmental envelopes around the presence data (Barbet-Massin et al., 2012) should, if possible, be more widely adopted in future presence-background modelling attempts.

4.4. Spatial bias of presence records

An important assumption in presence-background habitat suitability models is that sampling is either random or representative throughout the environmental extent (Yackulic et al., 2013). Sensitivity to this assumption can be lessened by correcting for variation in sampling intensity. Duplicate removal or data weighting were used here, but given the strong bias in the spatial distribution of presence records towards heavily sampled areas around New Zealand and away from regions of the SPRFMO area far from land, this is unlikely to have been sufficient. The habitat suitability models produced here were mainly based on corals in environmental conditions associated with the highly complex topography and oceanography of the New Zealand continental shelf and slope, and may not be as applicable to an oceanic setting such as the Louisville Seamount Chain.

4.5. Topography of seamounts in the Louisville Seamount Chain

Additional factors specific to the topography of seamounts in the Louisville Seamount Chain are also likely to have contributed to poor model performance. The majority of the seamount-based coral presence records used to train and test both models came from conical or semi-conical seamounts of the Chatham Rise and

other major oceanic features around New Zealand, which typically have exposed rocky substrate over much of their extent which is suitable for coral colonization. In contrast, the surveyed seamounts in the Louisville Seamount Chain were much larger, flat-topped guyots where it was observed that suitable hard substrate for coral colonization and growth was mostly limited to the upper edges of the flanks or small volcanic peaks on the summit. The full extent of these differences in seamount geomorphology and substrate type was unforeseen, and could have influenced the success of the model results. However, where environmental conditions described by the model predictor variables were similar between New Zealand and Louisville Seamount Chain seamounts of similar depth, models may predict high suitability for the Louisville Seamount Chain despite the differences in topography and substrate around the seamount summits. Nonetheless, to improve future modelling attempts the inclusion of categorical environmental data such as feature type (e.g., seamount, guyot, ridge) or substrate type (see Section 4.2) may better explain the influence of physical differences in potential habitats not captured by continuous topographic variables such as slope.

4.6. Additional observations

Reef-forming corals observed on the surveyed seamounts occurred deeper than recorded in the New Zealand region. Over 73% of *Solenosmilia variabilis* observations were deeper than 1000 m and 16% were deeper than 1400 m. The median depth of the observations on the survey (1082 m) is 60–80 m deeper than otherwise reported for the region (Tracey et al., 2011; Bostock et al., 2015). Depth is strongly linked to carbonate saturation state and previous research has shown that *Solenosmilia variabilis* and other species of reef-forming scleractinians are sensitive to low levels of aragonite saturation (Guinotte et al., 2006; Thresher et al., 2011; 2015), and are less common below the depth of the aragonite saturation horizon (ASH) where it becomes increasingly difficult for them to extract calcium carbonate to form skeletons. The model-based Ω_{arag} values for the survey area indicated nearly a third of the observed corals were in undersaturated water, but the over-estimation of depths in the SRTM30 data would have caused predicted Ω_{arag} to be much lower than reality. This suspicion was confirmed by water samples collected on CTD casts, which showed the ASH to be variable across the survey area (from about 1130 m on Valerie to about 1443 m on Ghost Seamount) and although the distribution of reef-forming corals extended to slightly below the ASH on all seamounts, the minimum Ω_{arag} value measured (0.87) is within previously recorded tolerances for these corals (e.g., Thresher et al., 2011, 2015). Depth errors of the SRTM30 bathymetry data, and by extension the environmental and chemical variables derived using SRTM30 depths, skewed predicted Ω_{arag} (the strongest predictor in both BRT and MaxEnt models) to lower levels than exist in the survey area. This issue could further explain overly-high habitat suitability being predicted by the models for the shallower tops of the seamounts.

The observation that large areas of dead, intact coral matrix (coated with ferro-manganese crust) exist on some seamounts of the Louisville Seamount Chain appears to indicate that either conditions were previously more suitable for coral growth and have changed over time, or that some catastrophic event in the past caused a large-scale die off of coral reefs, which are now still in a process of recovery. Ferro-manganese crusts are known to form very slowly, about 1–7 mm per million years (Hein et al., 2000), suggesting that these corals have been dead for thousands of years. Preliminary radiocarbon dating of similar samples of ferro-manganese coated *Solenosmilia variabilis* collected from south of Tasmania suggested an age of 11–15 kyr (Thresher et al., 2014). A

catastrophic die-off scenario has implications for the accurate modeling of suitable habitat for reef-forming deep-sea corals, for if current conditions are similar to those that prevailed when these reefs were at their greatest extent, and they are now in a rebuilding phase, then the potential for coral presence on these seamounts may be far higher than predicted or observed. Aging of samples of dead coral matrix collected during the survey will be attempted, with the hope of establishing a link between coral die off and past significant geological or climatic events.

Coral mortality due to the impact of bottom trawling had the potential to confound model validation if photographic transects passed over affected areas, causing artificially low observed frequency of presence. However, coral prevalence and correlations between model predictions and observed frequencies were relatively high in the fished survey stratum compared with other strata. This result, and the lack of accuracy in the habitat suitability model outputs, precluded the ability to usefully compare differences in coral presence between fished and unfished areas.

4.7. Implications for fisheries management and conservation planning

Prior to this survey, reef-forming corals were known only from Censeam, Ghost, and Valerie Seamounts. Following the model validation survey we now know corals exist on several other seamounts in this chain. Although large areas of living coral reef were not frequently seen on the photographic transects, areas that could be defined as VME habitat (based on structure-forming species densities of 15% or more in a visual imaging survey of 100 m² or more, the definition of a coral reef/thicket under the New Zealand EEZ and Continental Shelf (Environmental Effects) Act regulations, 2013) were noted in transects on 4 of the 6 seamounts surveyed. Five such VMEs were located within the 20-min blocks currently open to New Zealand bottom trawlers (on 39 South, Ghost, and Valerie Seamounts). According to the interim measures implemented by New Zealand for VME protection in the SPRFMO area, the known presence of VMEs requires the review and potential modification of the open status of blocks (Penney et al., 2009). Whether such a review would apply in this situation depends upon the SPRFMO interpretation of the density of a VME indicator species, which is typically based on catch weights, rather than the visual definition of “sensitive environments” under the EEZ Act regulations.

The results of this modeling work and the validation survey were intended to inform proposals for effective management measures for the orange roughy fishery by SPRFMO, with an intention that the model outputs would allow SPRFMO to evaluate new spatial-based management planning options for protecting VMEs in the SPRFMO area (Rowden et al., 2015). However, both models failed to accurately differentiate high suitability from low suitability at the individual seamount scale in the Louisville Seamount Chain region of the SPRFMO area, and thus the usefulness of these broad-scale models for their intended purpose is questionable. Nonetheless, the models are useful in identifying seamounts at a regional scale that are likely to contain habitat suitable for coral-reef VME habitat as evidenced by survey confirmation of living scleractinian corals on all 6 seamounts surveyed, 4 of which contained potential VME level coral habitats. This result is an important aspect for managers to consider, given the need to adopt a precautionary approach to management of deep-sea fisheries (FAO, 2009), and the strong overlap between the deep-sea reef-building corals and the depth range at which orange roughy fisheries operate (Clark & O'Driscoll, 2003). The total area of predicted habitat suitability for reef-forming corals in the SPRFMO area is low due to the seafloor of the South Pacific Ocean being very deep

on average. However, in addition to the Louisville Seamount Chain, there are some other isolated seamount chains within the SPRFMO area that the broad-scale models predicted to contain highly suitable habitat for reef-forming corals, including: Sala y Gomez Ridge, Nazca Ridge, Foundation Seamounts, Eltanin Fracture Zone, Geracyl Ridge, and other un-named features of the East Pacific Rise and Pacific-Antarctic Rise. These seamounts, like the Louisville Seamount Chain, are remote and largely data poor and represent potential candidate areas where predictive habitat suitability models would be applied. Any future modelling efforts should ideally consider the issues raised by our study.

4.8. Future VME modelling

Lack of suitable data on the distribution of sediment types is a significant shortcoming common to many attempts to model species habitat in the world's oceans (e.g. Guinotte and Davies, 2014; García-Alegre et al., 2014). Proxies for sediment type, such as terrain variables derived from high-resolution bathymetry, and multibeam backscatter data, can be useful but these variables too are lacking the necessary spatial resolution over the broad areas of the world's oceans where reliable habitat suitability models are most needed for management purposes. Efforts to assemble high resolution sediment maps should be given a high priority in future modelling attempts. Until this and other issues affecting our ability to accurately model VME habitat on the SPRFMO-wide scale can be resolved (in particular obtaining more accurate bathymetry data, and ideally real absence data) models should focus on regional to local scales where higher quality input data is available.

Improved bathymetry models at a finer resolution (250 m) of the New Zealand region (including the Louisville Seamount Chain and other important regions of the SPRFMO area such as the Lord Howe Rise and Northwest Challenger Plateau) have recently been produced and sediment maps for this region are also under development, although data for remote areas such as the Louisville Seamount Chain are sparse. The new bathymetry data can be used to derive benthic terrain variables such as slope and bottom roughness measures at a resolution that begins to approach the scale of variability in faunal distribution in localized areas, and can also be used to re-scale global climatologies of oceanographic variables using the methods developed by Davies et al. (2008) and Davies and Guinotte (2011). Finer model resolution will help models to better discriminate small-scale habitats, and can reduce model over-estimation of suitable habitat (Ross and Howell, 2013). Regional-scale models for VME indicator taxa are now being prepared for the New Zealand region, although models may still be limited by a lack of presence and absence records at a similar scale.

If true absence data are not available, improvements in model performance may be achieved if structured background datasets can be created that help to minimize spatial bias—a significant source of error in model prediction. Data from sample collections from the same sources and sample methods used to construct the presence datasets could be used to build target-group background datasets with similar spatial bias, as an alternative to the weighting and duplicate removal approach used here. Such an approach has been used with some success in a range of modeling methods, including BRT and MaxEnt (Phillips et al., 2009).

The best performing models are likely to be those which use true absence data along with presence data and predictor variables at high spatial resolutions. Such a dataset is being prepared for the Louisville Seamount Chain, based on high-resolution video and bathymetry data collected during the survey for this study. This dataset will be used to produce local-scale models of VME indicator taxa and habitat for the Louisville Seamount Chain survey region, enabling an examination of spatial variability in suitable habitat at

the level of the individual seamount.

Our study was designed in part to help determine which of the two modelling methods was better for prediction of suitable habitat for VME indicator taxa but this question must remain unanswered as neither model was able to make useful predictions at the scale of individual seamounts given the available data. Nevertheless, as no single model type has been shown to be consistently superior for habitat suitability modelling in general, more than one method should continue to be applied. With multiple methods an ensemble approach using weighted model outputs (e.g., Oppel et al., 2012) may help to provide increased confidence in the results.

5. Conclusions

This study is the first full-scale field evaluation of habitat suitability modelling approaches as a tool for identifying the likelihood of VME occurrence in previously unsampled oceanic regions beyond areas of national jurisdiction. As such, it represents a significant step in understanding the limitations of such approaches for use in data-poor regions and suggests several caveats on data sets and their modelling that should be considered before habitat suitability model outputs are adopted in management of environmental effects of fisheries and other activities in deep-sea ecosystems. The spatial scale at which habitat suitability model predictions are interpreted has a strong influence on their credibility: both models here predicted high probability of coral occurrence on all of the seamounts surveyed and the presence of such corals was confirmed by sampling, but predictions at intra-seamount scales (the grid scale of the predictor variables) were not useful. This suggests that *a priori* definition of appropriate scales at which model outputs should be interpreted is a critical step. Refinements in modelling methods will, no doubt, improve the ways in which missing or biased inputs are handled. However, for broad-scale habitat suitability models to be reliable in remote and data poor areas of the ocean, it is clear from this study that significant improvements in the input data will be required as the main priority, in terms of both the types and spatial resolutions of environmental layers, and the completeness and reliability of datasets describing the distribution and abundance of modelled taxa in the deep sea.

Acknowledgements

This research under the NIWA project “Predicting the occurrence of vulnerable marine ecosystems for planning spatial management in the South Pacific region” was funded by the New Zealand Ministry of Business, Innovation and Employment (C01X1229). We thank the crew and survey staff on R.V. *Tangaroa* during the Louisville Seamount Chain voyage (TAN1402). The following people are also thanked for their important input to the project: Alan Williams and Franzis Althaus (CSIRO) provided valuable data from the Australian region; Edwin Niklitschek (Universidad de los Lagos) and Rodolfo Serra (Instituto de Fomento Pesquero) supplied data from Chile; Kevin Mackay and Di Tracey (NIWA) were responsible for compiling all the biological data used for the habitat suitability models; Helen Bostock, Kim Currie (NIWA), and Judith Murdoch (University of Otago) processed the carbonate chemistry samples and data. Miles Dunkin (NIWA) produced the maps in Fig. 6. The Marine Conservation Institute would like to thank Esri's Nonprofit Organization Program for providing Esri software. We gratefully acknowledge the pre-survey guidance provided by the project's Stakeholder Advisory Group. Finally, we also thank one anonymous reviewer for their very helpful comments on the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ocecoaman.2015.11.025>.

References

- Althaus, F., Williams, A., Schlacher, T.A., Kloser, R.J., Green, M.A., Barker, B.A., 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. *Mar. Ecol. Prog. Ser.* 397, 279–294.
- Archer, K.J., Kimes, R.V., 2008. Empirical characterization of random forest variable importance measures. *Comput. Statistics Data Anal.* 52, 2249–2260.
- Ardron, J.A., Clark, M.R., Penney, A.J., Hourigan, T.F., Rowden, A.A., Dunstan, P.K., Watling, L.E., Shank, T., Tracey, D.M., Dunn, M., Parker, S.J., 2014. A systematic approach towards the identification and protection of vulnerable marine ecosystems. *Mar. Policy* 49, 146–154.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many. *Methods Ecol. Evol.* 3, 327–338.
- Becker, J.J., Sandwell, D.T., 2008. Global estimates of seafloor slope from singlebeam ship soundings. *J. Geophys. Res.* 113, C05028.
- Becker, J.J., Sandwell, D.T., Smith, W.H.F., Braud, J., Binder, B., et al., 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Mar. Geod.* 32, 355–371.
- Bostock, H.C., Tracey, D.M., Currie, K.I., Dunbar, G.B., Handler, M.R., Mikaloff-Fletcher, S.E., Smith, A.M., Williams, M.J.M., 2015. The carbonate mineralogy and distribution of habitat-forming deep-sea corals in the southwest pacific region. *Deep Sea Res. I* 100, 88–104.
- Boyer, T.P., Levitus, S., Garcia, H.E., Locamini, R.A., Stephens, C., et al., 2005. Objective analyses of annual, seasonal, and monthly temperature and salinity for the world ocean on a 0.25° grid. *Int. J. Climatol.* 25, 931–945.
- Buhl-Mortensen, L., Mortensen, P.B., 2005. Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer Publishing House, Heidelberg, Germany, pp. 849–879.
- CCAMLR, 2009. Schedule of Conservation Measures in Force, 2009/10. CCAMLR, Hobart, Australia, 232 pp.
- Clark, M.R., 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. *Oceanol. Acta* 22 (6), 593–602.
- Clark, M.R., 2008. Descriptive Analysis of Orange Roughy Fisheries in the New Zealand Region outside the EEZ: Lord Howe Rise, Northwest Challenger Plateau, West Norfolk Ridge, and Louisville Ridge to the End of the 2006–07 Fishing Year. New Zealand Fisheries Assessment Report 2008/66. 24 pp.
- Clark, M., O'Driscoll, R., 2003. Deepwater fisheries and aspects of their impact on seamount habitat in New Zealand. *J. Northwest Atl. Fish. Sci.* 31, 441–458.
- Clark, M.R., Roberts, C.D., 2008. Fish and Invertebrate Biodiversity on the Norfolk Ridge and Lord Howe Rise, Tasman Sea (NORFANZ Voyage, 2003). New Zealand Aquatic Environment and Biodiversity Report No. 28. 131 pp.
- Clark, M.R., Rowden, A.A., 2009. Effects of deepwater trawling on the macro-invertebrate assemblages of seamounts on the Chatham Rise, New Zealand. *Deep Sea Res. I* 56, 1540–1544.
- Clark, M.R., Anderson, O.F., Bowden, D.A., Chin, C., George, S.G., Glasgow, D.A., Guinotte, J.M., Hererra, S., Osterhage, D.M., Pallentin, A., Parker, S.J., Rowden, A.A., Rowley, S.J., Stewart, R., Tracey, D.M., Wood, S.A., Zeng, C., 2015. Vulnerable Marine Ecosystems of the Louisville Seamount Chain: Voyage Report of a Survey to Evaluate the Efficacy of Preliminary Habitat Suitability Models. New Zealand Aquatic Environment and Biodiversity Report No. 149, p. 86.
- Costello, M.J., McCrea, M., Freiwald, A., Lundalv, T., Jonsson, L., Bett, B.J., van Weering, T.C.E., de Haas, H., Roberts, J.M., Allen, D., 2005. Role of cold-water *Lophelia pertusa* coral reefs as habitat in the NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, pp. 771–805.
- Davies, A.J., Wisshak, M., Orr, J.C., Roberts, J.M., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep Sea Res. I* 55, 1048–1062.
- Davies, A.J., Guinotte, J., 2011. Global habitat suitability for framework-forming coldwater corals. *PLoS One* 6, 1–15 e18483.
- De'ath, G., 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88, 243–251.
- D'Onghia, G., Maiorano, P., Sion Giove, L.A., Capezzuto, F.R., Carlucci, R., Tursi, A., 2010. Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. *Deep Sea Res. II* 57, 397–411.
- Dullo, W.-C., Flögel, S., Rüggeberg, A., 2008. Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. *Mar. Ecol. Prog. Ser.* 371, 165–176. <http://dx.doi.org/10.3354/meps07623>.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- FAO, 2009. International Guidelines for the Management of Deep-Sea Fisheries in the High-seas. Food and Agriculture Organisation of the United Nations, Rome, Italy, 73 pp.
- Fossa, J.H., Mortensen, P.B., Furevik, D.M., 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*

- 471, 1–12.
- Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. *Ann. Stat.* 29, 1189–1232.
- García, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., 2006. World ocean atlas 2005, volume 3: dissolved oxygen, apparent oxygen utilization, and oxygen saturation. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 63. U.S. Government Printing Office, Washington, D.C., 342 pp.
- García-Alegre, A., Sánchez, F., Gómez-Ballesteros, M., Hinz, H., Serrano, A., Parra, S., 2014. Modelling and mapping the local distribution of representative species on the Le Danois bank, El Cachucho marine protected area (Cantabrian sea). *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 106, 151–164. <http://dx.doi.org/10.1016/j.dsr2.2013.12.012>.
- Guillera-Aroita, G., Lahoz-Monfort, J.J., Elith, J., 2014. MaxEnt is not a presence-absence method: a comment on Thibaud et al. *Methods Ecol. Evol.* 2014 (5), 1192–1197.
- Guinotte, J.M., Orr, J., Cairns, S., Freiwald, A., Morgan, L., George, R., 2006. Will human induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front. Ecol. Environ.* 4, 141–146.
- Guinotte, J.M., Davies, A.J., 2014. Predicted deep-sea coral habitat suitability for the U.S. West coast. *PLoS One* 9 (4), e93918. <http://dx.doi.org/10.1371/journal.pone.0093918>.
- Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.M.C.C., Aspinall, R., Hastie, T., 2006. Making better biogeographical predictions of species distributions. *J. Appl. Ecol.* 43, 386–392.
- Hall-Spencer, J.V., Allain, V., Fossa, J.H., 2002. Trawling damage to Northeast Atlantic ancient coral reefs. *Proc. R. Soc. Lond. Ser. B* 269, 507–511.
- Hein, J.R., Koschinsky, A., Bau, M., Manheim, F.T., 2000. Cobalt-rich ferromanganese crusts in the Pacific. In: Cronan, D.S. (Ed.), *Handbook of Marine Mineral Deposits*. CRC Press, Boca Raton, FL, pp. 239–279.
- Henry, L.A., Roberts, J.M., 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Res. I* 54, 654–672.
- Hill, P., 2009. Designing a deep-towed camera vehicle using single conductor cable. *Sea Technol.* 50 (12), 49–51.
- Howell, K.L., Holt, R., Endrino, I.P., Stewart, H., 2011. When the species is also a habitat: comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. *Biol. Conserv.* 144 (11), 2656–2665.
- Husebø, A., Nøttestad, L., Fosså, J.H., Furevik, D.M., Jørgensen, S.B., 2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471, 91–99.
- Huehnerbach, V., Blondel, P., Huvenne, V., Freiwald, A., 2007. Habitat mapping on a deep-water coral reef off Norway, with a comparison of visual and computer-assisted sonar imagery interpretation. In: Todd, B., Greene, G. (Eds.), *Mapping the Seafloor for Habitat Characterization*, vol. 47. Geol. Assoc. Can. Spec. Pap., pp. 297–308.
- Jaynes, E.T., 1957. Information theory and statistical mechanics. *Phys. Rev.* 106, 620–630.
- Jensen, A., Frederiksen, R., 1992. The fauna associated with the bankforming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. *Sarsia* 77, 53–69.
- Jonsson, L.G., Nilsson, P.G., Floruta, F., Lundälv, T., 2004. Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Mar. Ecol. Prog. Ser.* 284, 163–171.
- Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B., Williams, A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar. Ecol. Prog. Ser.* 213, 111–125.
- 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.
- Lutz, M.J., Caldeira, K., Dunbar, R.B., Behrenfeld, M.J., 2007. Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *J. Geophys. Res.* 112, C10011.
- Mackay, K.A., Rowden, A.A., Bostock, H.C., Tracey, D.M., 2014. Revisiting Squires' coral Coppice, Campbell plateau, New Zealand. *N. Z. J. Mar. Freshw. Res.* 48 (4) <http://dx.doi.org/10.1080/00288330.2014.897635>.
- Maier, C., Hegeman, J., Weinbauer, M.G., Gattuso, P., 2009. Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6, 1671–1680. <http://dx.doi.org/10.5194/bg-6-1671-2009>.
- Marshall, C.E., Clegg, G.A., Howell, K.L., 2014. Species distribution modelling to support marine conservation planning: the next steps. *Mar. Policy* 45, 330–332. <http://dx.doi.org/10.1016/j.marpol.2013.09.003>.
- Mastrototaro, F., D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P., Gherardi, M., Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C., Boero, F., Taviani, M., Tursi, A., 2010. Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. *Deep Sea Res. II* 57, 412–430.
- McCloskey, L.R., 1970. The dynamics of the community associated with a marine scleractinian coral. *Int. Rev. Gesamten Hydrobiol.* 55, 13–81.
- Moore, J., Auster, P., Calini, D., Heinonen, K., Barber, K., Hecker, B., 2008. The false boarfish *Neocyttus helgae* in the western North Atlantic. *Bull. Peabody Mus. Nat. Hist.* 49, 31–41.
- Mortensen, P.B., Buhl-Mortensen, L., Gebruk, A.V., Krylov, E.M., 2008. Occurrence of deep-water corals on the mid-Atlantic ridge based on MAR-ECO data. *Deep Sea Res. II* 55, 142–152.
- Oppel, S., Meirinho, A., Ramirez, I., Gardner, B., O'Connell, A.F., Miller, P.I., Louzao, M., 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol. Conserv.* 156, 94–104.
- Parker, S.J., Penney, A.J., Clark, M.R., 2009. Detection criteria for managing trawl impacts on vulnerable marine ecosystems in high seas fisheries of the South Pacific Ocean. *Mar. Ecol. Prog. Ser.* 397, 309–317.
- Parker, S.J., Bowden, D.A., 2010. Identifying taxonomic groups vulnerable to bottom longline fishing gear in the Ross Sea region. *CCAMLR Sci.* 17, 105–127.
- Penney, A.J., Parker, S.J., Brown, J.H., 2009. Protection measures implemented by New Zealand for vulnerable marine ecosystems in the South Pacific Ocean. *Mar. Ecol. Prog. Ser.* 397, 341–354.
- Penney, A.J., Guinotte, J.M., 2013. Evaluation of New Zealand's high-seas bottom Trawl closures using predictive habitat models and quantitative risk assessment. *PLoS One* 8 (12), e82273. <http://dx.doi.org/10.1371/journal.pone.0082273>.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Dudik, M., 2008. Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Dudik, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19 (1), 181–197.
- Reed, J.K., Koenig, C.C., Shepard, A.N., 2007. Impacts of bottom Trawling on a deep-water *Oculina* coral ecosystem off Florida. *Bull. Mar. Sci.* 81 (3), 481–496.
- Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., van Hoey, G., Zettler, M.L., Degraer, S., 2014. Benthos distribution modelling and its relevance for marine ecosystem management. *ICES J. Mar. Sci.* 72 (2), 297–315. <http://dx.doi.org/10.1093/icesjms/fsu107>.
- Rengstorf, A.M., Yesson, C., Brown, C., Grehan, A.J., 2013. High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. *J. Biogeogr.* 40, 1702–1714.
- Rengstorf, A., Mohn, M., Brown, C., Wisz, M.S., Grehan, A.J., 2014. Predicting the distribution of deep-sea vulnerable marine ecosystems using high-resolution data: considerations and novel approaches. *Deep Sea Res. I* 93, 72–82.
- Rogers, A.D., 2005. Concern over deep-sea reefs is widespread. *Nature* 434 (7030), 137–137.
- Ross, R.E., Howell, K.L., 2013. Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. *Divers. Distrib.* 19, 433–445. <http://dx.doi.org/10.1111/ddi.12010>.
- Rowden, A.A., Guinotte, J.M., Baird, S.J., Tracey, D.M., Mackay, K.A., Wadhwa, S., 2013. Developing Predictive Models for the Distribution of Vulnerable Marine Ecosystems in the South Pacific Ocean Region. New Zealand Aquatic Environment and Biodiversity Report No. 120, 70 pp.
- Rowden, A.A., Clark, M.R., Lundquist, C.J., Guinotte, J.M., Anderson, O.F., Julian, K.A., Mackay, K.A., Tracey, D.M., Gerring, P.K., 2015. Developing spatial management options for the protection of vulnerable marine ecosystems in the South Pacific Ocean region. *N. Z. Aquat. Environ. Biodivers. Rep.* No. 155, 76.
- Steinacher, M., Joos, F., Frölicher, T.L., Plattner, G.-K., Doney, S.C., 2009. Imminent ocean acidification projected with the NCAR global coupled carbon cycleclimate model. *Biogeosciences* 6, 515–533.
- Stone, R.P., 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25, 229–238.
- Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.
- Thresher, R.E., Tilbrook, B., Fallon, S., Wilson, N.C., Adkins, J., 2011. Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. *Mar. Ecol. Prog. Ser.* 442, 87–99. <http://dx.doi.org/10.1035/meps09400>.
- Thresher, R., Althaus, F., Adkins, J., Gowlett-Holmes, K., Alderslade, P., et al., 2014. Strong depth-related zonation of megabenthos on a rocky continental margin (–700–4000 m) off southern Tasmania, Australia. *PLoS One* 9 (1), e85872. <http://dx.doi.org/10.1371/journal.pone.0085872>.
- Thresher, R.E., Guinotte, J.M., Matear, R.J., Hobday, A.J., 2015. Options for managing impacts of climate change on a deep-sea community. *Nat. Clim. Change* 5, 635–639. <http://dx.doi.org/10.1038/NCLIMATE2611>.
- Tittensor, D.P., Baco-Taylor, A.R., Brewin, P., Clark, M.R., et al., 2009. Predicting global habitat suitability for stony corals on seamounts. *J. Biogeogr.* 36, 1111–1128.
- Tittensor, D.P., Baco, A.R., Hall-Spencer, J.M., Orr, J.C., Rogers, A.D., 2010. Seamounts as refugia from ocean acidification for cold-water stony corals. *Mar. Ecol. Prog. Ser.* 410, 1–22.
- Tracey, D.M., Rowden, A.A., Mackay, K.A., Compton, T., 2011. Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. *Mar. Ecol. Prog. Ser.* 430, 1–22.
- Vierod, A.D.T., Guinotte, J.M., Davies, A.J., 2014. Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models. *Deep Sea Res. II* 99, 6–18.
- Waller, R., Watling, L., Auster, P., Shank, T., 2007. Anthropogenic impacts on the corner rise seamounts, NW Atlantic ocean. *J. Mar. Biol. Assoc. U. K.* 87, 1075–1076.
- Williams, A., Schlacher, T.A., Rowden, A.A., Althaus, F., Clark, M.R., Bowden, D.A., Stewart, R., Bax, N.J., Consalvey, M., Kloser, R.J., 2010. Seamount megabenthic assemblages fail to recover from trawling impacts. *Mar. Ecol. Prog. Ser.* 401 (Suppl. 1), 183–199.
- Wood, A.C.L., Rowden, A.A., Compton, T.J., Gordon, D.P., Probert, P.K., 2013. Habitat-forming bryozoans in New Zealand: their known and predicted distribution in relation to broad-scale environmental variables and fishing effort. *PLoS One* 8

- (9), e75160. <http://dx.doi.org/10.1371/journal.pone.0075160>.
- Wright, D.J., Lundblad, E.R., Larkin, E.M., Rinehart, R.W., Murphy, J., Cary-Kothera, L., Draganov, K., 2005. ArcGIS Benthic Terrain Modeler. Oregon State University, Davey Jones Locker Seafloor Mapping/Marine GIS Laboratory and NOAA Coastal Services Center, Corvallis, Oregon. Accessible online at. <http://www.csc.noaa.gov/digitalcoast/tools/btm>.
- Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H., Veran, S., 2013. Presence-only modelling using MAXENT: when can we trust the inferences? *Methods Ecol. Evol.* 2013 (4), 236–243.
- Yesson, C., Taylor, M.L., Tittensor, D.P., Davies, A.J., Guinotte, J., et al., 2012. Global habitat suitability of cold-water octocorals. *J. Biogeogr.* 39, 1278–1292.