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Tini a Tangaroa

Developing updated predictive models for benthic taxa and communities across Chatham Rise and Campbell Plateau using photographic survey data

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EXECUTIVE SUMMARY

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Effective ecosystem-based management of the marine environment requires an understanding of the spatial distribution of species across appropriate spatial scales. However, species data generally consist of point records of taxon presences assembled from disparate sources spanning many years or decades (particularly for deepwater taxa due to the logistical difficulties and cost of data collection). Consequently, correlative modelling methods, in which statistical relationships between observed species point occurrences and continuous environmental data layers are used to predict species occurrence across unsampled space, referred to as species distribution models (SDMs). However, most SDMs are developed using presence-absence data and therefore predictions represent species' probability of occurrence. For many taxa, patterns of occurrence alone cannot indicate the range of environmental conditions under which a species is likely to thrive, rather than just survive. SDMs derived from abundance data (quantitative models), by contrast, can provide more ecologically nuanced information that is more useful for informing spatial management decisions. The lack of abundance-based models for seafloor invertebrate taxa is a consequence of the paucity of spatially consistent abundance data for non-commercial marine taxa.

The present work builds on previous projects which collected quantitative (abundance) benthic community data and predicted distribution of abundance for the Chatham Rise. Here, quantitative observation data from Campbell Plateau were incorporated to expand these predictions to encompass much of the southeastern sector of New Zealand's Exclusive Economic Zone; a region that is of importance for fisheries, encompasses areas of oil and gas exploration, and is of potential future interest for extraction of seabed minerals. The methods used were similar to those used in the Chatham Rise studies to develop a set of twenty single-taxon models and a community-level model (using gradient forests - GF) from which a spatial classification of seafloor community types was developed. The single taxon predictions were constructed from ensembles of three separate SDM methods in a hurdle model approach (a binomial model was used initially to predict the probability of occurrence, followed by a separate model with a Gaussian distribution to estimate population density for locations where presence was recorded). The modelling methods were also extended by applying a new approach, joint species distribution modelling (jSDM). jSDM is a developing field of distribution modelling in which multiple species occurrences or abundances, their functional traits and phylogenetic relationships, environmental covariates, and the spatial-temporal context in which the data were acquired are analysed explicitly and simultaneously. The study used jSDM to generate single-taxon predictions for the same set of twenty taxa that was modelled using the single-taxon models and, because the method models all taxa simultaneously, also to generate another community-level classification using the Regions of Common Profile method (RCP). As far as the authors are aware, this is the first application of jSDM to the study of marine faunal distributions in the New Zealand region.

The overall explanatory power of the single taxon and joint species distribution models for presenceabsence was high (most taxa AUC > 0.81) with relatively high predictive power (most taxa AUC > 0.70). For abundance model results, the overall explanatory power was lower (most taxa $R^2 > 0.43$) and predictive power was much lower (most taxa $R^2 > 0.12$). The model fit metrics varied by taxon, but most models had at least some explanatory and predictive power in both presence-absence and abundance models for both single-taxon models and jSDMs. Across all taxa, the majority of spatial

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patterns predicted using the single-taxon models and jSDMs were broadly similar for both presenceabsence and abundance models. However, for some taxa this was not the case, e.g., the abundance of *Goniocorella dumosa* was predicted to be highest in shallower parts of the study area when using the jSDM, compared with deeper parts of the study area (Bounty Trough) in the individual taxon model. In addition, there were marked localised differences between jSDM and single-taxon model predictions for those taxa predicted to be affected by trawling history with larger, more obvious, changes to predicted distributions in parts of the study area with high intensity of trawling for jSDMs predictions.

Community models from GF and RCP were classified at 3 levels of detail (8, 16, and 25 classes) based on an analysis assessing the optimal number of community classes. The 8-class representation can be viewed as a bioregionalisation, whereas the greater detail in the 16- and 25-class representations can be viewed as communities at increasingly finer spatial scales. Spatial predictions of classifications using both methods reflected broadscale patterns in environmental variables linked to well-defined oceanographic patterns. At the 25-class level, there were some similarities between the RCP and GF classifications but many points of difference. Similarities were most evident around western and southern flanks of Chatham Rise and extending into Bounty Trough, and in the grouping of Campbell Island Shelf, Pukaki Rise, and Bounty Islands shelf in the same class. Obvious differences were present on the Campbell Plateau. Because both classifications were based on the same input sample data, the differences between them result from the modelling methods.

Spatial variation in trawling history emerged as a key predictor of distributions for nine out of twenty taxa in the ensemble models and for twelve out of twenty taxa in the jSDM models and was the third most important variable in the Gradient Forest community model. The jSDM results also showed that the influence of trawl fishing varies across taxa, with most taxa, particularly larger-bodied ones, being negatively affected but smaller predatory or scavenging taxa positively affected. Bottom-contact trawling has been a factor in the marine environment of New Zealand for many years and these results indicate that it has influenced the distributions of benthic invertebrate taxa across broad spatial scales. Given these results, the authors suggest that trawl history should be included routinely as a candidate predictor variable in species distribution models designed to predict the distributions of benthic taxa in the region.

Here, a comprehensive and systematically collected quantitative dataset of benthic invertebrate distributions from seafloor photographic surveys was used to predict distributions for the Chatham Rise and the Campbell Plateau. These abundance predictions cover the largest geographical areas and span the broadest (ecologically relevant) environmental gradients in New Zealand to date, and likely represent the most reliable predictions of distributions for these taxa. Despite the large geographic span of the study area, the environmental conditions sampled will be very different to those in other parts of New Zealand (i.e., the warmer waters north of the Sub-Tropical Front). The Challenger Plateau has contrasting environmental conditions but similar ranges of latitude (38–45° S) and depth and is known to have shared species with the Chatham Rise and Campbell Plateau. Given the overlap in species, the Challenger Plateau represents an ideal area in which to expand current predictions and validate these with further collection of quantitative benthic invertebrate data.

1. INTRODUCTION

Effective ecosystem-based management of bottom-contacting fisheries requires understanding of how disturbances from fishing affect seafloor fauna and habitats over a wide range of spatial and temporal scales (Clark et al. 2016, Pitcher et al. 2017). A key element needed to generate such understanding is reliable knowledge about the spatial distributions of seafloor fauna. Such data are rare, however, particularly for areas where deepwater fisheries occur, with available data generally consisting of point records of taxon presences assembled from disparate sources spanning many years or decades. Consequently, correlative modelling methods, in which statistical relationships between observed point occurrences of fauna and continuous environmental data layers are used to predict faunal occurrence across unsampled space (refered to as habitat-suitability, species-environment, or species-distribution models, e.g., Elith & Leathwick 2009, Guisan & Zimmermann 2000), are used increasingly to generate full-coverage maps of either predicted habitat suitability or taxon presence for use in assessments of seafloor (benthic) impacts (Mazor et al. 2021).

In the New Zealand region, species distribution models (SDMs) have been used for more than a decade to provide predictions of benthic faunal distributions in the deep sea to inform research, environmental management, and prediction of climate change effects across a range of spatial scales (see examples and references in Stephenson et al. 2018b, Lundquist et al. 2020). Until recently, all these models other than one small-scale study (Rowden et al. 2017) have been informed by faunal occurrence data compiled from research trawl bycatch and scientific museum records, which yield information about the presence of a taxon at any given site but not its abundance (density) or absence. Such models can only yield predictions of relative habitat suitability (the likely distribution of species), rather than predictions of expected abundance. These existing models fulfil their purpose in that they still provide the best estimates of benthic distributions in an environment that remains data-limited in terms of knowledge about both faunal distributions and the physical characteristics of their habitats. However, knowledge about spatial variations in species' abundances is crucial for understanding ecosystem functioning; for instance, the presence of a single bryozoan colony at a site will not have the same ecological influence, or conservation value, as will a high density of bryozoan thickets (Wood et al. 2013). A number of studies have assessed whether presence-absence models can be used as surrogates for abundance distributions, with contrasting results. There is some evidence that correlation between probability of occurrence and density is weaker for species with broader ecological niches (e.g., as in Rullens et al. 2021 and references therein).

Acceptance of SDM outputs (whether using presence-only or abundance data) in management of impacts from fisheries and seabed mineral resource use remains limited because of a lack of confidence in their predictions, which arises because the outputs can rarely be tested against independent sample data. The lack of independent data is, of course, the main motivation for development and use of predictive modelling techniques for data-limited systems in the first instance, but the consequent lack of confidence in outputs is a serious impediment to their application in practice. Recognising the issue of low confidence in outputs from existing models, Fisheries New Zealand instigated research in 2016 with the broad objectives to assess the credibility of existing predictions and to improve on them, if possible, using enhanced modelling methods and more appropriate data. The first project under this initiative (ZBD2016-11) assessed the credibility of predictions from several existing habitat suitability models for Chatham Rise (Bowden et al. 2021) by compiling an independent dataset of benthic invertebrate faunal distributions from five photographic seafloor surveys designed specifically to quantify benthic invertebrate faunal occurrences (Bowden et al. 2019b), and then used the new dataset to generate new SDMs tuned using abundance data (termed quantitative SDMs herein) (Bowden et al. 2019a). Although the existing models proved to have generally low predictive ability when evaluated against the independent dataset, the assessment exercise highlighted a number of areas in which improvements might be made, including use of quantitative occurrence data collected using consistent sampling methods and testing against independent data, wherever possible, in preference to crossvalidation against withheld subsets of the input occurrence data (Bowden et al. 2021). The new models developed for Chatham Rise were built using quantitative data from the photographic survey dataset

and the best available modelling methods and, though they returned high scores in cross-validation tests, their credibility remained in question because of the lack of independent data.

The second project in the initiative to improve confidence in predictive model outputs (ZBD2019-01) first used the new quantitative models developed for Chatham Rise to explore the potential for predicting distributions across a neighbouring seafloor area, Campbell Plateau, beyond the spatial extent of their original training data, then ran a dedicated photographic survey to test these predictions (Anderson et al. 2020a), and finally, combined all data from Chatham Rise and Campbell Plateau to enable generation of updated models encompassing both areas. This report presents results from the final objective of ZBD2019-01: *to generate updated models with a spatial domain encompassing Chatham Rise and Campbell Plateau by merging data from the dedicated survey of Campbell Plateau with the existing Chatham Rise dataset developed under ZBD2016-11.*

For the updated models presented here, the study used similar methods to those used in the Chatham Rise studies to develop a set of twenty single-taxon models and a community-level model (using Gradient Forests, Ellis et al. 2012) from which a spatial classification of seafloor community types was developed. The main difference in these components of the study in comparison to the earlier work is that the single taxon predictions are constructed from ensembles of three separate SDM methods, rather than the two used for the Chatham Rise predictions. The modelling methods were also extended by applying a new approach; joint species distribution modelling (jSDM, Ovaskainen & Soininen 2011, Warton et al. 2015, Ovaskainen et al. 2016b) that has the potential to revolutionise how ecological community data are interpreted. Species distribution modelling methods based on single taxa can be limited by the often-weak inclusion of ecological theory, in terms of biotic interactions (e.g., predation, competition, facilitation). jSDM is a developing field of distribution modelling (Warton et al. 2015) in which multiple species occurrences or densities, their functional traits and phylogenetic relationships, environmental covariates, and the spatial-temporal context in which the data were acquired are analysed explicitly and simultaneously. This study uses jSDM to generate single-taxon predictions for the same set of twenty taxa as are modelled using the ensemble technique (above) and, because the method models all taxa simultaneously, also to generate another community-level classification using the Regions of Common Profile method (RCP, Foster et al. 2013, Ovaskainen & Abrego 2020). As far as the authors are aware, this is the first application of jSDM to the study of marine faunal distributions in the New Zealand region.

1.1 Objectives of project ZBD2019-01

Overall Objective: To expand and develop initiatives to improve confidence in predictive models of seabed fauna and habitat distributions started under ZBD201611: "Quantifying benthic biodiversity to improve predictive habitat modelling potential".

Specific Objective 1: Predict distributions of benthic taxa and communities, and gradients in faunal turnover across Campbell Plateau using relationships between faunal distributions and environmental gradients developed for Chatham Rise under project ZBD2016-11.

Specific Objective 2: Run a dedicated photographic survey of seabed habitats and fauna across Campbell Plateau, structured on the basis of predictions from Specific Objective 1.

Specific Objective 3: Use quantitative data from the Campbell Plateau survey to assess the utility of predictions from the existing Chatham Rise models when applied to a neighbouring area of the EEZ

Specific Objective 4: Generate updated models with a spatial domain encompassing both regions (Chatham Rise and Campbell Plateau) by merging data from the Campbell Plateau survey with the existing Chatham Rise dataset.

2. METHODS

2.1 Study area

The species distribution models developed in the present study span a broad segment of New Zealand's marine environment, encompassing Chatham Rise, Campbell Plateau, and the intervening areas of the Otago continental shelf and slope and Bounty Trough (Figure 1). Chatham Rise is a continental rise extending eastwards from the South Island of New Zealand for approximately 1000 km, with Mernoo Bank at its western end and the Chatham Islands at the eastern end. The Sub-Tropical Front coincides with, and is partially constrained by, the rise. Intense phytoplankton blooms propagate from west to east along the length of the rise (Chiswell 2001, Nodder et al. 2007, Nodder et al. 2012), and because of this it is the most biologically productive fisheries region in New Zealand's Exclusive Economic Zone (EEZ) (McClatchie et al. 1997, Clark et al. 2000, Marchal et al. 2009). Commercially important bottom trawl fisheries exploit populations of scampi (Metanephrops challengeri), hoki (Macruronus novaezelandiae), orange roughy (Hoplostethus atlanticus), and oreos (Pseudocyttus maculatus, Neocyttus rhomboidalis, and others). Recent summaries of bottom-contacting trawl history across Chatham Rise (Baird et al. 2011, Black et al. 2013, Black & Tilney 2015) show highest trawling intensity, primarily from the hoki fishery, at 450–700 m depth west of Mernoo Bank and on the southern and northern central flanks of Chatham Rise (Figure 2). At present, initiatives to protect benthic habitats and fauna are limited to closures, since 2000, of fisheries on some seamounts in the 'Graveyard' and 'Andes' regions on the northwest flank and southeast flanks of the rise, respectively (Clark & Dunn 2012), and establishment in 2007 of two Benthic Protection Areas (BPAs); the Mid Chatham Rise and the East Chatham Rise BPAs (Helson et al. 2010). No bottom-contacting trawling is allowed within the seamount closures and BPAs.

Campbell Plateau is a broad submarine plateau extending to the south and southeast of New Zealand's South Island. Much of the plateau lies in water depths of 500–1000 m but with shoal areas rising to the surface around Stewart Island, The Snares, Auckland Island, and Campbell Island in the west, and shoaling to less than 150 m on Pukaki Rise in the east (Figure 1). On its western and southern boundaries, the plateau descends steeply to depths greater than 3000 m. The Sub-Antarctic Front, which forms at the northern boundary of the east-going Antarctic Circumpolar Current, is constrained by the southern edge of the plateau. The Sub-Tropical Front lies generally north of the Auckland Islands, where warmer subtropical waters entrained down the west coast of the South Island recurve northwards, forming the Southland Current, which transports nutrient rich, relatively colder waters towards the southern flank of Chatham Rise to the North (Nelson & Cooke 2001, Hayward et al. 2007, Hurlburt et al. 2008, Mackay et al. 2014). Biological productivity, in terms of water column primary production, is lower than on Chatham Rise but is elevated above levels in the surrounding ocean (Gutierrez-Rodriguez et al. 2020) and supports substantial fisheries for several species including hoki (*Macruronus novaezelandiae*), hake (*Merluccius australis*), southern blue whiting (*Micromesistius australis*), jack mackerel (*Trachurus* spp.), and scampi (*Metanephrops challengeri*) (Fisheries New Zealand 2019).

Trawl fisheries operate in many areas on Campbell Plateau, the cumulative footprint of these fisheries showing a concentration of effort around the southern and eastern Stewart-Snares shelf at 500 m depth, on the Auckland Islands Shelf north and east of the Auckland Islands in depths from 200 to 400 m, and in areas of deeper water (about 700 m) between these two main shelf regions (Baird & Mules 2019) (Figure 2). Three BPAs lie at least partially on Campbell Plateau; the Campbell Heritage, Campbell East, and Sub-Antarctic Deep BPAs (Helson et al. 2010). The territorial sea (that extends 12 nm from the coast) around the Auckland Islands and Campbell Island are marine reserves and are fully protected under the *Marine Reserves Act 1971* (Figure 2). A seafloor ridge feature to the east of Auckland Island in depths of approximately 270 to 325 m and known as 'Squires' Coppice' is not currently protected but has been reported to be a potential cold water coral reef site (Mackay et al. 2014).



Figure 1: Study area, showing: approximate extents of Chatham Rise (CR) and Campbell Plateau (CP); survey sites from which benthic invertebrate density data were collated from seafloor photographic transects (five surveys on Chatham Rise, see Bowden et al. 2019b for details, and two on Campbell Plateau, TAN2004 and TAN1602); seafloor community classes from the Chatham Rise Gradient Forest model (CRGF) used as survey strata for TAN2004, and seafloor bathymetry from 50 to 2000 m depth.



Figure 2: Chatham Rise and Campbell Plateau overview showing trawl intensity (cumulative seabed swept area as km² per 5 x 5 km grid cell) for the period 1989/90 to 2006/7; Benthic Protection Areas (named red polygons without fill), and marine reserves (un-named red polygons with light red fill). Trawl data are from Baird & Mules (2019). Seabed photographic survey sites used in this study (crosses) are shown as in Figure 1.

2.2 Faunal occurrence data

The faunal occurrence dataset consisted of observations of invertebrate fauna at 467 seafloor sites compiled across seven surveys: 358 sites from five surveys of Chatham Rise (Bowden et al. 2019b) and 109 sites from Campbell Plateau compiled from voyages TAN2004 (Anderson et al. 2020a) and TAN1602 (Roberts et al. 2018). These survey data spanned a depth range from 49 to 1813 m but because there were few sites at the shallow and deep extremes of this range, model predictions here were restricted to depths from 100 to 1500 m. This range encompassed 449 sites (96% of the total available).

More than 380 individual taxa were identified from these surveys but many of these were either operational taxonomic units (OTUs) or species-level names that were often not consistently recorded within and between surveys. In an extensive audit process (see Bowden et al. 2019b), the full dataset was aggregated to a set of 139 taxa, at a range of taxonomic levels, which were reliably and consistently recorded across all studies. A subset of 66 taxa was then extracted from the aggregated taxon list by selecting only those that were observed at five or more survey sites (Table 1), with the exception of Paragorgiidae ('Bubblegum coral') because these are large and highly distinctive corals unlikely to have been missed or mis-identified during video analyses.

Table 1: Benthic invertebrate taxa for which abundance data (as individuals per 1000 m²) were used in development of species distribution models here, showing the number of individual operational taxonomic units encompassed by each taxon (OTU), the number of sites at which each taxon occurred (Site), and whether they were used for single-taxon (S) or community-level (C) models, or both. (Continued over the page)

Phylum	Class	Sub class	Taxon	Common name	OTU	Site	Use
Annelida	Polychaeta		Polychaeta	Polychaete worms	10	136	C
		Palpata	Hyalinoecia sp.	Quill worms	1	149	S, C
Arthropoda	Hexanauplia	Thecostraca	Barnacles	Barnacles	1	12	С
	Malacostraca	Eumalacostraca	Brachyura	True crabs Shrimps and	17	204	C
			Caridea	prawns	8	325	C
			Crustacean (lobster) Galatheidae /	Lobsters	2	11	C
			Chirostylidae	Squat lobsters	6	253	С
			Paguridae	Hermit crabs	1	373	S, C
			Lithodidae Metanephrops	King crabs	2	5	C
			challengeri	Scampi	2	109	S, C
			Serolidae	Serolid isopods	3	63	С
	Pycnogonida		Pycnogonida	Sea spiders	2	42	С
Brachiopoda	Rhynconellata		Brachiopoda	Lamp shells	2	90	S, C
Bryozoa	Gymnolaemata		Bryozoa	Bryozoans	9	279	S, C
Chordata	Ascidiacea		Ascidiacea	Sea squirts	7	206	С
Cnidaria	Anthozoa	Hexacorallia	Anemones	Anemones	31	409	С
			Antipatharia	Black corals Cerianthid	7	46	C
			Ceriantharia	anemones	1	220	C
			Corallimorpharia	Corallimorpharia	5	41	С
			Caryophylliidae	Solitary corals	2	97	С
			Stephanocyathus sp.	Solitary coral	1	25	C
			Enallopsammia sp.	Stony coral	1	7	S, C
			Flabellum sp.	Solitary coral	7	220	С
			Goniocorella dumosa	Stony coral	1	69	S, C
			Madrepora sp.	Stony coral	1	8	S, C
			Solenosmillia variabilis	Stony coral Commensal	1	9	S, C
			Epizoanthidae	zoanthid	1	35	С
			Zoanthidea	Zoanthid	1	53	С
		Octocorallia	Alcyonacea	Soft corals Solitary soft	5	86	C
			Taiaroa tauhou	coral	1	111	C
			Anthomastus sp.	Soft coral	1	116	C
			<i>Telesto</i> sp.	Soft coral Branching erect	1	42	C
			Gorgonacea	soft corals	4	114	C
			Isididae	Bamboo corals Bubblegum	3	53	C
			Paragorgiidae	corals	2	3	C

Table 1 contin	nued.						
Phylum	Class	Sub class	Taxon	Common name	OTU	Site	Use
			Primnoidae	Primnoid soft coals Spiral whip	6	65	C
			Radicipes sp.	corals	1	74	C
			Pennatulacea	Sea pens	12	172	S, C
			Kophobelemnon sp.	Sea pen	1	30	С
	Hydrozoa	Hydroidolina	Stylasteridae	Hydrocorals	4	109	S, C
			Hydroids	Hydroids	2	271	С
Echinodermata	Asteroidea		Asteroidea	Sea stars Suspension-	37	429	S, C
			Brisingidae	feeding sea stars	5	93	С
	Crinoidea	Articulata	Crinoidea (stalked)	Sea lilies	1	14	С
			Crinoidea (motile)	Sea lilies	2	98	С
	Echinoidea	Cidaroidea	Cidaroidea	Pencil urchins	7	206	S, C
		Euechinoidea	Euechinoidea	Regular urchins	12	203	S, C
			Dermechinus horridus	Urchin Tam O'shanter	1	27	C
			Spatangoida	urchins Burrowing urchins	4	166	۲ د د
	Ualathuraidaa		Holothuroidee	Soo ayoumbors	21	225	5, C
	Holothuloidea		Envoniastes eximia	Swimming sea	1	18	з, с
	Ophiuroidea		Ophiuroidea	Brittle stars	12	1/3	5 C
	Opiniuroidea		Correnceanhalidae	Bittle stars	12	145	3, C
Echiura			Echiuro	Dasket stars	2 1	22	C C
Eciliura			Eciliula Vananhuanhamidaa	Ciant forama	1	25	۲ د د
Malluaga	Diveluie		Riveluie		2	90 47	3, C
Monusca				Sincile (analise)	10	47	C C
	Gastropoda			Shalls (grazing)	12	305	
			Nolutidae	Whelks Large predatory	2	343 172	S, C
			Volutidae Seenhonede	Silari Tualt aballa	1	26	3, C
			Scapnopoda		1	30	C
				Sea siugs	4	49	C
Doriforo	Demospongiae	Coleoidea	Demospongies	Common	51	91 216	۲ د د
i officia	Hexactinallida		Hexactinallida	Sponges	24	1/9	5, C
	пехасипенний		Hyalasous maui	Glass sponge	54 1	140 27	3, C
			11 yalascus maul	Glass spollee	1	37	U

All 66 taxa in the final subset were included in the community-level models. For the single-taxon models, the same set of 20 taxa that was used by Bowden et al. (2021) for assessment of existing SDMs for Chatham Rise was used. This selection was developed initially to match the taxa encompassed in the existing, published models, with priority given to taxa associated with Vulnerable Marine Ecosystems (VME; Agnew et al. 2009, FAO 2009, Parker et al. 2009, Parker & Bowden 2010) or Sensitive Environments (MacDiarmid et al. 2013), and the addition of other taxa for which sufficient sample data were available (Table 1).

2.3 Explanatory variables

Explanatory variables were a subset of those explored in detail in Phase I of this project (ZBD2016-11), selected on the basis of results from the earlier models developed for Chatham Rise (Bowden et al. 2019a) and review of each layer in terms of credibility and presence of artefacts when examined visually in a Geographic Information System (GIS). The following paragraphs are modified from Bowden et al. (2019a).

A set of environmental variables that potentially influence marine organism distributions was generated from regional or global datasets upscaled to a finer resolution based on depth data from a 250 m bathymetry grid for the New Zealand region by Georgian et al. (2019) following the method of Davies & Guinotte (2011). Additional seafloor terrain metrics were derived from this bathymetry grid using Benthic Terrain Modeler in ArcGIS 10.3.1.1, with each calculated at a range of window sizes from 3 x 3 grid cells up to 15 x 15 grid cells. Some potentially important variables for explaining benthic distributions that had been used in earlier modelling studies were discarded because of artefacts observed during the review process. Thus, for instance, recently developed layers describing sediment composition were excluded because the process of extrapolating continuous gridded layers from point-source sample data (from sediment cores) resulted in obvious artefacts.

Trawl history was included as an explanatory variable because bottom-contacting fishing gear is known to affect seafloor fauna across broad spatial and temporal scales (Clark et al. 2016) and trawl intensity has emerged as an important predictor of benthic invertebrate faunal distributions on Chatham Rise (Bowden & Leduc 2017, Bowden et al. 2019a). However, this layer differs from the others in that it represents an anthropogenic disturbance that is spatially correlated with seabed type, productivity, and potentially other parameters and can be highly variable among years and across a wide range of spatial scales (Baird & Wood 2018). Trawl fishery data were provided by Fisheries New Zealand (Baird & Wood 2018), with trawl intensity calculated as the total cumulative area impacted by bottom trawling between 1 October 1989 and 30 September 2006 (i.e., all records up to the end of the last complete fishing year prior to the first of the camera surveys used in our models). The source data were calculated for a 5 x 5 km grid and these values were resampled for the 1 x 1 km grid used in the SDM models here.

In total, 58 variables were considered but many of these were strongly correlated, particularly the bathymetry-derived window-size variants. Because of the wide range of taxa to be included in the models, each of which potentially responds to different characteristics of the physical environment at different scales, the number of variables was reduced by a conservative four-stage selection process. First, variables were grouped by four categories known to influence distributions of seabed fauna: seafloor characteristics, water chemistry, water physics, and productivity. Second, each variable was examined visually (in GIS) and any with obvious processing artefacts were excluded. Third, correlations were calculated for all pairwise combinations of the remaining variables and graphical representations and cluster dendrograms were used to exclude the most highly correlated variables while also ensuring representation of each of the four high-level categories. Finally, the ecological influence of the environmental variables within each category was assessed through a set of initial exploratory Boosted Regression Tree (BRT) models for representative taxa (a combination of those most commonly recorded and those recorded to a high taxonomic resolution). This process resulted in a reduced set of 23 environmental variables.

These 23 variables were then offered as explanatory variables to an initial Chatham Rise GF model (GF is robust to large sets of correlated explanatory variables) and the ranked variable importance from this analysis was used to identify a subset of 18 variables on which to base the final GF models and as a starting point for the single-taxon models. Variables excluded in this process were either spatial scale variants (e.g., choice of the standard deviation of depth calculated using a 15 × 15 grid cell window rather than 3×3), one of a complementary pair (e.g., choice of percent gravel rather than percent mud), or strongly correlated with other more ecologically interpretable variables (e.g., choice of silicate rather than nitrate).

The eighteen predictor variables used in the final Chatham Rise GF model were used as the base set for development of models in the current project (Table 2). The full set of eighteen variables was included in GF analyses here, whereas for single-taxon ensemble models and jSDM models the number of variables was reduced using rationales and methods described under the relevant sections, below.

Table 2: Environmental explanatory variables used for species distribution models. The 18 variables are grouped into four categories: seafloor characteristics, water chemistry, water physics, and productivity.

Variable	Name	Units	Native resolution	Reference
Seafloor characteristics				
Depth ^G	bathy	metres	1 km ²	NIWA bathymetry
Depth standard deviation ^{2,G}	std	_	_	Derived from bathymetry
Profile curvature ^G	profcurv	_	_	Derived from bathymetry
Bathymetric Position Index – broad ^G	bpi_broad	_	_	Derived from bathymetry
Trawl history ⁵	trawl	m ²	5 km ²	Baird & Wood (2018)
Water chemistry				
Dissolved oxygen ^G	dissox	ml 1 ⁻¹	1°	(Garcia et al. 2014a)
Salinity ^G	salinity	_	0.25°	(Zweng et al. 2013)
Silicate	silicate	µmol l-1	1°	(Garcia et al. 2014b)
Water physics				
Temperature residuals	tempres	°C	0.25°	Derived from temperature and depth
Dynamic topography	dynoc	m	0.25°	http://www.aviso.oceanobs.com
Tidal current speed	tidalcurr	ms ⁻¹	1 km ²	NIWA
Sea surface temperature gradient	sstgrad	°C km ⁻¹	1 km ²	(Uddstrom & Oien 1999)
Productivity				
Particulate organic carbon export to seabed ^G	poc	mg C $m^{-2} d^{-1}$	0.08°	(Lutz et al. 2007)
Eppley-VGPM ^{1, 4, G}	epp_mean epp_min	mg C $m^{-2} d^{-1}$	0.167°	Oregon State University ³
Carbon-Based Productivity Model-2 ^{1,4,G}	cbpm	mg C $m^{-2} d^{-1}$	0.167°	Oregon State University ³
Dissolved organic matter	dom	<i>a</i> DOM (443) m ⁻¹	1 km ²	NIWA
Seabed POC flux	flux	$mg C m^{-2} d^{-1}$	9 km ²	Matt Pinkerton, NIWA. Long- term mean (1997–2019)

¹ Surface data derived from MODIS –Aqua (NASA) as the mean, minimum, maximum, and standard deviation from mid-2002–2016.

² Terrain metrics calculated using window sizes of 3, 5, 7, and 15 grid cells.

³ Data obtained from http://www.science.oregonstate.edu/ocean.productivity.

⁴ Calculated as mean, minimum, maximum, and standard deviation, for the period 2002 to 2016; mean values used, plus minimum for EPP.

⁵ Cumulative swept area per 5 x 5 km grid cell for the period 1989 to 2016.

^G Upscaled to 250 m bathymetry (Georgian et al. 2019).

2.4 Single taxon ensemble models

Single taxon SDMs were used to analyse and predict the spatial probability of occurrence and density of study taxa, based on inputs of taxon presence-absence data, taxon abundance data, and spatially explicit explanatory variables (e.g., see Bowden et al. 2019a). To model distribution of abundance, a two-part hurdle model was used. In this procedure, a binomial model was used initially to predict the

probability of occurrence, followed by a separate model with a Gaussian distribution to estimate population density for locations where presence was predicted. The outcomes of these two models were then multiplied to create a final density prediction. Ensemble SDMs (i.e., the combination of results from more than one SDM method) were generated using outputs from three model types: BRT, random forest (RF), and generalised additive models (GAMs). The ensemble approach limits dependence on a single model type or structural assumption and enables a more robust characterisation of the predicted spatial variation and uncertainties (Robert et al. 2016). All statistical analyses were undertaken in R (R Core Team 2020).

Selection of explanatory variables

With most species distribution modelling methods, the inclusion of many explanatory variables (e.g., more than 20 variables) should be avoided because they generally only provide minimal improvement in predictive accuracy and complicate interpretation of model outcomes (Leathwick et al. 2006). Several explanatory variables in the set selected for this study showed some co-linearity but all were considered acceptable (Pearson correlation < 0.9) for tree-based machine learning methods. To ensure parsimonious models, an automated variable selection procedure was used. First, an RF model was fitted to the taxa data with all 18 explanatory variables (Table 2) using the extendedForest package in R (Liaw & Wiener 2002). This method accounts for any co-linearity in explanatory variables when determining the relative importance of each variable in the model through the implementation of a conditional approach to calculation of variable importance (Ellis et al. 2012). Only explanatory variables with a relative influence greater than 5% were retained (Müller et al. 2013, Jouffray et al. 2019). This procedure allowed explanatory variables that may have important localised influence but low overall importance to be retained whilst removing variables with very low, or negative influence. For each taxon, the set of explanatory variables selected through this approach was used in the final RF and BRT models, but for GAM models the numbers of explanatory variables were further reduced through a stepwise backward selection process (see section 'Generalised Additive Models', below).

Random Forest models

RF models (Breiman 2001) fit an ensemble of regression (abundance data) or classification tree (presence-absence data) models describing the relationship between the distribution of an individual taxon and some set of explanatory variables (Ellis et al. 2012). Following explanatory variable selection using the initial RF model, a final RF model was tuned using the train function in the R package *caret* (Kuhn 2020). This function selects optimal values for the complexity parameters *mtry* (the number of variables used in each tree node), *maxnodes* (the maximum number of terminal nodes in each trees), and *ntree* (the number of trees to grow). RF models have previously been applied to demersal fish in the New Zealand EEZ and benthic invertebrates (Anderson et al. 2016, Stephenson et al. 2018a).

Boosted Regression Tree models

BRT modelling combines many individual regression trees (models that relate a response to their predictors by recursive binary splits) and boosting (an adaptive method for combining many simple models to give improved predictive performance) to form a single ensemble model (Elith et al. 2008). Detailed descriptions of the BRT method are given by Ridgeway (2007) and Elith et al. (2008). BRT models were fitted with a Bernoulli error distribution, a bag fraction of 0.6 and random 10-fold cross evaluation following recommendations from Leathwick et al. (2006) and Elith et al. (2008) (using the *Dismo* package (Hijmans et al. 2017)). A moderate tree complexity (2) was used. BRT models with decreasing learning rates were successively fitted (starting with a learning rate of 0.05) until a model with at least 2000 trees was fitted. The BRT method has been widely used in ecological applications and has performed well in previous studies of fish and invertebrate distributions in New Zealand (Leathwick et al. 2006, Compton et al. 2013, Anderson et al. 2016, Bowden et al. 2019a).

Generalised additive models

GAMs are generalised linear models where the linear response variable depends on smooth functions of some explanatory variables (Hastie & Tibshirani 1987). GAMs have different assumptions, strengths, and weaknesses than the flexible machine-learning tree-based approaches (RF and BRT) and provide a

complementary approach. All explanatory variables were fitted using smooth terms with 5 degrees of freedom, and each explanatory variable was tested for possible simplification of the fitted function or exclusion from the model using a stepwise backward selection method. The smoothing parameter was estimated using a Mixed model approach via restricted maximum likelihood (REML) using the *mgcv* package in R (Wood 2021).

Hurdle models and uncertainty

The two components of the hurdle models were 1) a presence-absence model based on a binary logistic regression, which predicts probability of presence, and 2) a regression model based only on the positive (i.e., non-zero) observations of species abundance, which predicts abundance at locations of species presence. For the regression model component, abundances were log transformed to provide a near-normal distribution of the response. Final estimates of abundance were made by multiplying the probabilities from the first component by the abundances from the second component.

To assess the relative confidence in predictions across the model extent, a bootstrap technique was used to produce spatially explicit uncertainty measures (Anderson et al. 2020b). Bootstrapping involved randomly drawing (with replacement) a 'training' sample with a sample size equal to the number of presence-absence or abundance records and then running the model. Presence-absence records which were not randomly selected were set aside for independent assessment of model performance (referred herein as 'evaluation' data). This process was repeated 100 times for each model type (RF, BRT, GAM) and each species with the exception of the taxa Cidaroidea and Volutidae, which were only bootstrapped 20 times because of difficulty in model convergence most likely due to the heterogeneity in abundance observations. At each BRT, RF, and GAM model iteration, geographic predictions were made using predictor variables to a 1-km² grid. Probability of occurrence and a spatially explicit measure of uncertainty (measured as the coefficient of variation, CV) were calculated for each grid cell using the 100 bootstrapped layers for models tuned with presence-absence. Abundance estimates (individuals per 1000 m²) were calculated for each grid cell by multiplying the spatial estimate of the probability of occurrence and the abundance (conditional on presence) estimate at each bootstrap. Mean abundance and a spatially explicit measure of uncertainty explicit measure of uncertainty (CV) was calculated across the 100 bootstraps.

Model performance

Model performance was assessed at each bootstrap iteration for each of the BRT, RF, and GAM models. Probability of occurrence model performances were evaluated using AUC (area under the Receiver Operating Characteristic curve) and TSS (True Skill Statistic). AUC is an effective measure of model performance and a threshold-independent measure of accuracy, whereas the TSS is a thresholddependent measure of accuracy but is not sensitive to prevalence (Allouche et al. 2006, Komac et al. 2016). AUC scores range from 0 to 1, with a score of 0.5 indicating model performance is equal to random chance, a score > 0.7 indicating adequate performance, and a score > 0.80 indicating excellent performance (Hosmer et al. 2013). TSS, which takes into account specificity and sensitivity to provide an index ranging from -1 to +1, where +1 equals perfect agreement and -1 is no better than random, and a value > 0.6 is considered useful (Allouche et al. 2006). Model fit metrics were calculated using both the 'training' dataset and the 'evaluation' dataset. The latter is considered a more robust and conservative method of evaluating goodness-of-fit of a model than using the same data with which the model was trained (Friedman et al. 2001). Abundance model performance was evaluated using R^2 (coefficient of determination which measures the proportion of the variance in the dependent variable that is predictable from the independent variables) and the Pearson correlation between the predicted and the observed density values.

Ensemble models

The ensemble model was produced by taking weighted averages of the predictions from each model type, using methods adapted from Anderson et al. (2020b). This procedure derives a two-part weighting for each component of the ensemble model, taking equal contributions from the overall model performance (TSS value derived from the 'evaluation' for presence-absence models and R^2 for abundance models) and the uncertainty measure (CV) in each cell (see Anderson et al. 2020b for further

details). The final predictions were restricted to depths between 100 and 1500 m (representing the depth range from which 99% of samples were collected).

2.5 Joint species distribution models

The full ecological community data were analysed using the joint species distribution modelling method Hierarchical Modelling of Species Communities (HMSC), which yields inference both at single-taxon and community levels from a single modelling process (Ovaskainen et al. 2017). HMSC partitions variation in species occurrences or abundances into components that can be interpreted in relation to environmental filtering, species interactions, and random processes. That is, in addition to modelling the relationship between biological data and explanatory variables, the HMSC framework can incorporate information on species biological trait data and the spatial context of the sampling design.

Trait data

Functional trait data for the modelled taxa were assembled by reference to a set of detailed trait assignments developed by Lundquist et al. (2018). A simplified suite of biological traits was selected based on the presumed sensitivity of the traits to perturbations or changes in the environment (Table 3). Trait categories were assigned using a fuzzy coding approach (Chevenet et al. 1994) in which each taxon can span more than one category for a given trait, with varying proportions or probabilities applied to each and the total summing to one. For instance, under feeding mode, whereas Bryozoa are obligate suspension feeders and thus would score 'one' against this category, the taxon Asteroidea encompasses species that can adapt their feeding between deposit, suspension, and predator-scavenger modes and thus scores 0.05, 0.20, and 0.75 against these categories. For traits with only a single category in the scheme used (*Living position* and *Longevity*), assignments were binary; i.e., all taxa are either *erect* or *not erect*, and either *long-lived*.

Table 3: Functional traits scheme used in the jSDM analyses. See Appendix 1 for trait score assignments.

Trait	Trait categories
Adult size	Small (x < 5 cm)
	Medium (5 cm $>$ x $<$ 25 cm)
	Large (> 25 cm)
Feeding mode	Filter
	Suspension
	Deposit
	Predator-scavenger
Mobility	Mobile
	Sessile
Living position	Erect
Longevity	Long-lived

Selection of explanatory variables

Six explanatory variables from the full set of eighteen (Table 2) were selected based on exploration of model fits and variable selections in the ensemble modelling process and expert knowledge: depth (*bathy*); tidal current speed (*tidcurr*); salinity (*salinity*); temperature residuals (*tempres*); profile curvature (*profcurv*); Eppley Primary Productivity (*epp*); and trawling history (*trawl*). This set included measures associated with food supply (*epp*, *tidcurr*), depth (*bathy*), water mass (*salinity* and *tempres*), and seafloor topography (*profcurv*) all of which were considered likely to influence distributions of fauna and community assembly processes.

Statistical modelling

HMSC from the *hmsc* R package (Tikhonov et al. 2020) was used to fit jSDMs to the benthic data combining simultaneously information on traits, environmental covariates, and random spatial effects

in a single model. As with single-taxon models, hurdle model predictions were generated by combining jSDMs fitted with presence-absence and abundance data.

A Bernoulli distribution was used for the presence-absence HMSC. For the (log transformed) abundance (conditional on presence) model, a Gaussian distribution was used. In addition to the explanatory variables (environmental data and trawling history) and trait data, a random spatial effect (that also models co-occurrence among species) was included at the level of sampling station using a latent factor approach (Ovaskainen et al. 2016a). The explained variation among the fixed and random effects was partitioned using methods described by Ovaskainen et al. (2017). The fitted models included parameters which measured the influences of the traits on the species-specific responses to the explanatory variables (see Ovaskainen et al. 2016b), and, therefore, it is possible to measure the portion of the among-species variation in responses to environmental covariates that is attributable to traits.

The model was fitted to the data with Bayesian inference, using the posterior sampling scheme of Tikhonov et al. (2020). Four chains, each with 250 samples and thinning parameter of 10 were used, which ensured that there was convergence of the Markov chain Monte Carlo simulations.

Model fit metrics included AUC and R^2 for each taxon for the presence-absence and abundance models, respectively. Model fit metrics were calculated using the same input data as that used to tune the models (explanatory power) and withheld data (predictive power) by performing a fourfold cross-validation. Overall model performance was assessed by calculating the mean model fits across all taxa for both presence-absence and abundance models.

Finally, the parameter estimates were explored. and spatial predictions and associated uncertainty (standard deviation of the mean) were made for the study area using the 'constructGradient' and 'predict' functions in the *hmsc* package. Taxa richness was estimated by summing the individual taxa occurrence predictions.

2.6 Community modelling

Regions of Common Profile

RCP is a multi-species, model-based approach to the delineation and mapping of species assemblages (Foster et al. 2013). RCP is a mixture model that is used to group sites based on their species profile (presence-absence or abundance) in relation to environmental conditions, thereby simultaneously grouping species and modelling the environmental variables which determine those groupings. The HMSC model (used to produce the jSDMs) is also a mixture model, although instead of grouping sites, it models continuous variation in species in their response (Ovaskainen & Abrego 2020). The two models (RCP and HMSC) share strong similarities, the clustering of community outputs from the HMSC models is referred to as RCP by its authors (Ovaskainen & Abrego 2020), and Scott Foster at CSIRO, the originator of RCP, was involved with the group that developed HMSC. Here, the implementation of RCP followed that given by Ovaskainen & Abrego (2020) using K-means clustering on the spatial predictions of the community abundances from an HSMC run using all 66 taxa available in the data, to define classifications at class levels from 2 to 75 classes.

Gradient Forest

GF is a method for modelling beta diversity (taxon turnover) based on relationships between sampled multi-species density data and environmental gradients (Pitcher et al. 2011, Ellis et al. 2012). GF builds an aggregation of RF models, each describing the environmental correlations of an individual taxon. The information from these individual models is then used to develop a set of transformations of the environmental layers, such that the correspondence between each layer and the faunal occurrence data is maximised (Compton et al. 2013, Stephenson et al. 2018a). These transformed environmental layers can then be used to generate full-coverage maps of predicted taxon turnover across the study area. These predictions can then be used with statistical clustering techniques to define hard-boundary spatial classifications of the study area at a range of class levels, with each class defining areas likely to have

similar community composition. The classifications can be generated at any level of detail, but statistical uncertainty is not propagated through to the classification stage, so there is no formal test for the optimal number of classes.

GF models were run using function gradientForest in R, with subsequent classification steps adapted from Snelder et al. (2007) and described by Stephenson et al. (2018a). Input data consisted of density measurements for 66 taxa at 467 sample sites across Chatham Rise and Campbell Plateau (see section 2.2) and fifteen environmental predictor variables from the full set of eighteen available (Table 2), excluding silicate, cbpm_min, and poc because of their low contributions to initial trial models. A $log_{10}(1+x)$ transformation was applied to the taxon density data to down-weight the influence of highly abundant taxa, enable a broader range of taxa to influence outcomes, and reduce the potential for artefacts arising from differences in density estimates derived from still image and video survey data. Models were run with 500 trees per taxon, the compact function set to false, and the correlation threshold for applying conditional permutation to allow for co-linear predictor variables set to 0.5. Model outputs include R² values for all taxa for which correlations with environmental variables were greater than zero and ranking of predictor variables in terms of their contributions to both mean accuracy of the model and mean importance weighted by the taxon R² values.

The full grid of transformed environmental predictor values (4 043 320 grid cells) was classified in two stages. First, non-hierarchical k-medoids clustering (using clara in R) was used to assign cells to 500 classes. Second, hierarchical agglomerative flexible UPGMA (unweighted pair group method with arithmetic mean) clustering with the Manhattan distance metric (using agnes in R) was used to summarise the 500 clara classes at 5-class intervals from 5 classes to 75 classes, from which maps were developed for selected class levels.

Assessing the number of community classes

Several broadscale marine environmental classifications have been developed for the New Zealand region, notably the Marine Environmental Classification (MEC, Snelder et al. 2007), the Benthic Optimised Marine Environmental Classification (BOMEC, Leathwick et al. 2012), and, more recently, GF models have been used to produce regional and national-scale environmental classifications for marine benthos (e.g., Bowden et al. 2019a, Stephenson et al. 2020). Although these latter models are based on statistical transformations applied to environmental variables (Ellis et al. 2012), the resulting classifications can be interpreted as spatial summaries of variation in seafloor community composition. Environmental classifications of this type can be generated at levels of detail from two to more than 500 classes, but a major limitation in their use for management is the lack of objective methods for defining the appropriate number of classes to use. Here, three methods for assessing the classification strength at different levels of detail were tested; two applied to the RCP outputs and the third to the GF output (any of these methods could be applied to either classification method but they are computationally demanding and the exploration here is based on what could be achieved with the resources available).

Using the jSDM outputs that defined the RCP classifications, the 'Elbow' method implemented in the *factoextra* package (Kassambara & Mundt 2017) and the 'Silhouette' method implemented in the *Nbclust* package (Charrad et al. 2014) were applied. These are both visual methods that allow assessment of the 'optimal' group number by plotting changes in the within-class sum of squares (i.e., how similar samples within a given class are to each other based on the transformed environmental space) and the mean silhouette width (a measure of how similar an object, or sample, is to other samples in the same class), respectively, with increasing number of classes in the classification.

In the elbow method, the optimal number of classes is taken to be the point in the graph at which the rate of decrease in the sum of squares metric begins to slow down. The concept is that definition of each of the first few or several classes will explain relatively large proportions of variability in the dataset but, as the number of classes begins to exceed the actual number of distinct groupings in the data, there will be no further reduction in the amount of variance explained. For a dataset in which there is a finite

number of clearly defined groupings, the plot will show a distinct change in gradient (an 'elbow') at the point at which this actual number of groups is reached. For ecological community data, as used here, however, is highly likely that there will be overlap among many classes and thus that the curve will show a gradual decline, rather than a sharp elbow, with no clearly-defined number of classes.

In the silhouette method, silhouette values for individual samples range from -1 to +1, with higher positive values for a given sample indicating stronger similarity to other samples in its class. Mean silhouette width is then calculated across all samples, yielding a metric that describes how appropriately the data have been classified. In the resulting graph, therefore, the optimal number of classes can be identified as that for which mean silhouette width reaches its highest value. As with the elbow method, real-world ecological datasets may not have a clearly defined natural number of classes and the plots are, again, subject to interpretation.

The ability of the GF classification to discriminate across classification levels with increasing group number was tested using analysis of similarities (ANOSIM, Clarke 1993), in an approach comparable with that of Snelder et al. (2007, 2010). This approach uses ANOSIM to assess how dissimilar two groups of samples are from each other. This is a similar approach to those described above, however, it differs in that the group dissimilarity is assessed using the multivariate taxon data rather than the transformed environmental space. ANOSIM calculates an R-value which ranges from -1 to +1, with higher positive values indicating greater similarity among samples within a given class than to those in other classes, and thus stronger support for the classification. Using the biological data used in the GF models, the discrimination across classification levels was assessed for each class level from 5 to 75 classes in increments of 5. The global ANOSIM-R statistic was calculated as the difference in ranked biologic similarities arising from all pairs of replicate sites between different classes, and the average of all rank similarities within classes, adjusted by the total number of sites. Global R is equal to 1 if all replicates within classes are more similar to each other than to any replicates from other classes and is approximately 0 if there is no group structure. The significance of the ANOSIM-R statistic was tested by random permutation based on the null hypothesis of no group structure, i.e., sampled communities do not differ among classes (Clarke 1993). All ANOSIM analyses were undertaken in R using the vegan package (Oksanen et al. 2013). Varying proportions of classes at any particular classification level had either few biologic sites or lacked them altogether. Therefore, only classes represented by at least five sample sites were included.

3. RESULTS

3.1 Single-taxon ensemble models

Model performance

Most ensemble models were useful to predict taxon occurrence as assessed by the withheld evaluation data (AUC > 0.7) (Table 4). Abundance models had lower explanatory power and some species had large differences between the training and evaluation estimates, indicating that the models were not able to accurately predict variation in abundance (Table 4). The highest performing taxon probability of occurrence model as assessed by the evaluation data included: *Metanephrops challengeri* (AUC: 0.85 and TSS: 0.60), Spatangidae (AUC: 0.84 and TSS: 0.58), Brachiopoda (AUC: 0.82 and TSS: 0.59), Foraminifera (AUC: 0.82 and TSS: 0.58), and *Goniocorella dumosa* (AUC: 0.81 and TSS; 0.58) (Table 4). The lowest performing taxon probability of occurrence models as assessed by the evaluation data included: Bryozoa (AUC: 0.67 and TSS: 0.35), Hexactinellida (AUC: 0.67 and TSS: 0.34), and volutidae (AUC: 0.64 and TSS: 0.26) (Table 4). The highest performing predicted abundance models as assessed by the R² evaluation data were for Spatangidae (R²: 0.33), Eucchinoidea (R²: 0.32), and *Hyalinoecia* sp. (R²: 0.28). The lowest performing predicted abundance models as assessed by the R² evaluation data were for *G. dumosa*, Foraminifera, Cidaroidea, and Volutidae, all of which had R² values of zero.

Explanatory variables

The most frequently selected environmental predictor for both the probability of occurrence and predicted abundance models was seafloor profile curvature (*profcurv*), which accounted for up to 55% of influence in individual models and was the most important predictor for the probability of occurrence and predicted abundance of Brachiopoda and branching stony coral taxa (REEF corals) (Table 5). Other important environmental variables for all taxa included sea-surface primary productivity (*epp_min*), dissolved organic material (*dom*), and dynamic oceanography (variation in sea-surface height, *dynoc*). The least important predictors included depth (*bathy*), bathymetric position index (*bpi broad*), dissolved oxygen concentration (*dissox*), and silicate concentration (*sil*). Trawl history (*trawl*) was the most important predictor for probability of occurrence of the stony coral *Goniocorella dumosa* and was also important for the predicted abundance of paguridae, the probability of occurrence and predicted abundance of *Hyalinoecia* sp., and the predicted abundance of Spatangoida.

			Abundan	ce Model		Presence	e-Absence	Model	
		\mathbb{R}^2	Pearson Co	orrelation		AUC			
Taxon	Train.	Eval.	Train.	Eval.	Train.	Eval.	Train.	Eval.	
Hyalinoecia sp.	0.60	0.28	0.78	0.57	0.85	0.73	0.65	0.42	
M. challengeri	0.53	0.09	0.76	0.41	0.92	0.85	0.80	0.60	
Paguridae	0.65	0.25	0.79	0.52	_	_	_	_	
Brachiopoda	0.67	0.15	0.83	0.50	0.92	0.82	0.79	0.59	
Bryozoa	0.62	0.12	0.77	0.43	0.84	0.67	0.69	0.35	
G. dumosa	0.70	0.00	0.84	0.26	0.93	0.81	0.82	0.58	
REEF	0.62	0.09	0.79	0.43	0.86	0.77	0.66	0.50	
Pennatulacea	0.56	0.13	0.76	0.44	0.90	0.78	0.71	0.48	
Stylasteridae	0.55	0.24	0.74	0.54	0.86	0.80	0.64	0.51	
Euechinoida	0.76	0.32	0.87	0.60	0.89	0.74	0.74	0.44	
Spatangidae	0.65	0.33	0.81	0.59	0.91	0.84	0.73	0.58	
Cidaroida	0.56	0.00	0.73	0.22	0.88	0.77	0.75	0.47	
Holothuroidea	0.59	0.00	0.75	0.26	0.92	0.75	0.81	0.44	
Asteroidea	0.60	0.11	0.75	0.38	-	-	-	-	
Xenophyophoroidea	0.66	0.00	0.82	0.22	0.91	0.82	0.77	0.58	
Hydroids	0.62	0.15	0.78	0.43	0.90	0.73	0.77	0.44	
Whelks	0.62	0.15	0.78	0.43	0.88	0.70	0.76	0.37	
Volutidae	0.24	0.00	0.52	0.22	0.83	0.64	0.59	0.26	
Demospongiae	0.62	0.10	0.77	0.42	0.91	0.75	0.80	0.47	
Hexactinellida	0.64	0.25	0.80	0.53	0.81	0.67	0.56	0.34	

 Table 4: Mean cross-validated estimates of model performance for ensemble abundance and presenceabsence models for each of the 20 single-taxon models when assessed against the data used to train the model (Train.) and against evaluation data withheld from the training (Eval.) data.

 Table 5: Environmental predictor variables and their relative importance for each taxa and model type (presence-absence, P, and abundance, A). The most important predictor for each model is highlighted in dark grey and the second most important predictor is highlighted in light grey. Presence-absence results are not shown for Paguridae or Asteroidea because these taxa were present at all survey sites. (Continued over the page)

				Seafloo	r characte	eristics		Water	chemistry		,	Water pl	hysics					Produc	ctivity
Τ	M. 1.1	1 .1	C	. 1	bpi	. 115	1	1:	.1.		1	sst	tidal	epp	epp	cbpm	1		a
Taxon	Model	bathy	projcurv	trawi	broaa	stal 5	salinity	aissox	suicate	tempres	aynoc	graa	curr	mean	mın	mean	aom	рос	fiux
<i>Hyalinoecia</i> sp.	Р			22.5							11.7			17.2		29.1	19.5		
	А			20.3							17.8			13.6		28.0	20.3		
M. challengeri	Р				7.8	10.6		13.6			11.4	7.9			11.7	10.1	8.3	18.6	
	А				10.9	18.7		14.3			10.4	6.4			8.2	12.0	11.7	7.5	
Paguridae	А	16.9		15.6	11.0		15.1							13.5	14.2	13.7			
Brachiopoda	Р		22.1					10.8						15.2		14.3	19.3		18.3
	А		24.6					16.4						12.1		16.8	12.9		17.2
Bryozoa	Р	17.0	15.4		15.4								16.9				19.1		16.1
	А	15.8	21.8		13.1								21.3				15.0		13.1
G. dumosa	Р		20.2	23.0			11.1			11.1				11.6	12.9				10.1
	А		18.6	9.3			14.3			10.8				11.5	14.9				20.5
REEF	Р		30.6				15.6					12.1		17.4	15.1				9.2
	А		23.7				14.4					13.0		17.5	19.1				12.3
Pennatulacea	Р	20.3				8.6				6.9	16.5		12.8		8.1		9.3	6.4	11.1
	А	11.9				7.7				22.6	8.0		12.3		13.2		10.7	7.4	6.3
Stylasteridae	Р		55.3			21.1						23.6							
	А		35.4			26.7						37.8							
Euechinoidea	Р	13.7	8.7			11.2		10.0	15.2		12.8		11.8		8.5	8.2			
	А	14.5	8.2			21.6		6.1	7.0		20.2		7.8		5.8	8.8			
Spatangidae	Р			4.4		9.4				10.5	7.9	28.9	14.9	6.5			17.4		
	А			15.3		9.3				15.0	18.3	11.3	12.7	8.3			9.8		
Cidaroida	Р		19.0							13.6	13.0	19.2			15.6	19.6			
	А		18.8							16.1	14.5	18.2			16.5	16.0			

				Seafloo	r charact	eristics		Water of	chemistry			Water p	hysics					Produc	ctivity
Taxon	Model	bathy	profcurv	trawl	bpi broad	std15	salinity	dissox	silicate	tempres	dynoc	sst grad	tidal curr	epp mean	epp min	cbpm mean	dom	poc	flux
Holothuroidea	Р		11.8	10.5							18.1	11.9	22.3		12.2	13.2			
	А		12.3	11.0							15.8	14.3	14.4		15.6	16.5			
Asteroidea	А	15.7			10.8	10.3		12.8	12.8			13.9		13.0			10.6		
Xenophyophoroida	Р		4.7			6.8						4.9	13.1		4.0	8.4	6.6	12.0	39.6
	А		10.4			9.0						11.0	11.4		9.9	19.0	11.4	10.3	7.4
Hydroids	Р		12.5			15.2	14.2		13.9							15.5	16.1	12.6	
	А		19.0			14.2	13.4		11.7							15.8	9.8	16.0	
Whelks	Р		13.4				18.3			16.9	20.0				15.8		15.6		
	А		12.1				15.6			13.0	16.8				17.2		25.2		
Volutidae	Р		15.5											31.2	14.6	21.9	16.8		
	А		12.8											19.5	15.7	41.5	10.4		
Demospongiae	Р		18.1		15.8		21.0			25.1	20.0								
	А		23.5		18.0		19.0			20.3	19.3								
Hexactinellida	Р		21.4			8.5					11.5	17.4						19.0	22.1

Table 5 continued.

Spatial predictions

Maps showing the probability of occurrence and the predicted abundance, with model certainty estimates for each (as coefficient of variation, CV) are shown for all twenty single-taxon ensemble models in Appendix 2 (Figures 2.1–2.28). Probability of occurrence was not estimated for Paguridae and Asteroidea because these taxa were observed at all survey sites, resulting in probability of presence of 100%. Here, mapped predictions for two mobile taxa, *Metanephrops challengeri* (scampi) and Buccinidae+Ranellidae (predatory snails, i.e., whelks), and two sessile taxa, *Goniocorella dumosa* (a branching stony coral) and Hexatinellida (glass sponges), are described as examples. Thus, for each pair there is one model at species level and the other at a coarser taxonomic level.

Metanephrops challengeri. Probability of occurrence was highest on the crest of Chatham Rise in depths from approximately 300 to 500 m, with other areas of high probability of occurrence extending down the east coast of the South Island, around Stewart Island, and to the east and southeast of Auckland Island in similar depths (Figure 3). Uncertainty for these areas was generally low, with CVs increasing with depth. Abundance was predicted to be highest in areas on the western Chatham Rise crest, to the west of Stewart Island, southeast of Auckland Island, and across a broad area in the southwest of Campbell Plateau (Figure 4). Uncertainty was, again, generally low for the areas of high predicted abundane, increasing with depth.

Buccinidae+Ranellidae. Probability of occurrence was high across much of the study area in depths greater than approximately 400 m but low in shallow areas of Chatham Rise and along western and central areas of its northern flank, and low on the Stewart-Snares and Auckland Islands shelves (Figure 5). Model uncertainty was highest on Chatham Rise, Bounty Plateau, the southern margin of Campbell Plateau and Stewart-Snares shelf. Predicted abundance (Figure 6) was highest on the northeastern, southern, and western flanks of Chatham Rise, in Mernoo Gap between Chatham Rise and the South Island, and extended southwards at similar depths along the east coast of the South Island and large areas of Campbell Plateau. Model uncertainty was highest throughout the northern half of the Chatham Rise, Stewart-Snares shelf and Puysegur, and around the Auckland Islands.

Goniocorella dumosa. Probability of occurrence was confined to the crest and upper flanks of Chatham Rise and a few locations off the east coast of the South Island, on the Otago shelf, and off the southwest coast of the South Island (Figure 7). The taxon was predicted to be absent from the Campbell and Bounty plateaux, but model uncertainty was also high across these areas. Predicted abundance of *Goniocorella dumosa* was highest on central areas of Chatham Rise, northwest Stewart-Snares shelf, and on Macquarie Ridge but also with apparently anomalous high values at depths greater than approximately 1000 m in Bounty Trough and along the outer flanks of Campbell and Bounty plateaux (Figure 8). Model uncertainty was low for much of central Chatham Rise, high at shallower depths (< 200 m) particularly off Stewart-Snares and Auckland Islands shelves but, again, apparently anomalously low for the predictions of high abundance in deeper areas.

Hexactinellida. Probability of occurrence was high throughout the study area in depths greater than approximately 1000 m, with highest values on the eastern and southern flanks of Chatham Rise, in Bounty Trough, and on the southern Campbell Plateau and Macquarie Ridge (Figure 9). Model uncertainty was highest across Chatham Rise, along the east coast of the South Island, on the Stewart-Snares and Auckland Islands shelves, and Macquarie Ridge—locations where this taxon was observed as being present, but which were predicted to have low to moderate probability of occurrence (Figure 9). Predicted abundance covered similar areas and depths to the probability of occurrence model, with highest values on Bounty Trough and Bounty Plateau, and along the southeast margin of the Campbell Plateau. The taxon was also predicted to be found in moderate densities on the outer margins of southeast Chatham Rise, southwest South Island, and along the Macquarie Ridge (Figure 10). Model uncertainty was highest in areas of low predicted abundance, with highest values along the east coast South Island shelf break and across the interior of the Campbell Plateau.



Figure 3: *Metanephrops challengeri*. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 4: *Metanephrops challengeri*. Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 5: Buccindae+Ranellidae. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 6: Buccinidae+Ranellidae. Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 7: *Goniocorella dumosa*. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 8: *Goniocorella dumosa*. Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 9: Hexactinellida. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 10: Hexactinellida. Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.

3.2 Joint species distribution models

Model performance

The overall explanatory power of the jSDMs for presence-absence results was high (AUC=0.84) with relatively high predictive power (AUC = 0.71). For abundance model results, the overall explanatory power was lower ($R^2 = 0.43$) and predictive power was much lower ($R^2 = 0.12$) (Table 6). The model fit metrics varied by taxon, but most models had at least some explanatory and predictive power in both presence-absence and abundance models (Table 6). Buccinidae+Ranellidae had the lowest explanatory power (AUC = 0.71) and hydroids and Bryozoa had almost no predictive power for the presence-absence models (AUC = 0.59 and 0.51, respectively, Table 6). In contrast, presence-absence models for *Goniocorella dumosa* and REEF had both good explanatory and predictive power (Table 6).

Volutidae abundance models had the lowest predictive and explanatory power ($R^2 = 0.09$, Table 6). *Hyalinoecia* sp. abundance models had the highest explanatory and predictive power ($R^2 = 0.5$ and 0.44, respectively, Table 6). However, for many abundance models there was a relatively large difference between explanatory and predictive power (Table 6). The biggest difference in explanatory and predictive power in abundance models were for *Goniocorella dumosa* and REEF which had very high explanatory power ($R^2 > 0.98$) but no, or negligible, predictive power ($R^2 < 0.05$, Table 6).

Table 6: Joint species distribution model performance as assessed using the same input data as were used
to tune the models (explanatory power) and withheld data from a fourfold cross-validation
(predictive power) for both presence-absence and abundance models.

_		Presence-absence	Abundance				
Taxa	AUC: Explanatory	AUC: Predictive	R ² : Explanatory	R ² : Predictive			
Asteroidea	0.78	0.65	0.25	0.06			
Brachiopoda	0.93	0.75	0.43	0.23			
Buccinidae+Ranellidae	0.71	0.64	0.26	0.19			
Cidaroida	0.86	0.72	0.38	0.06			
Stylasteridae	0.97	0.77	0.46	0.27			
Bryozoa	0.79	0.59	0.69	0.11			
Demospongiae	0.93	0.73	0.83	0.13			
Euechinoida	0.76	0.74	0.24	0.16			
Goniocorella dumosa	1.00	0.83	1.00	0.00			
Hydroids	0.85	0.51	0.46	0.06			
Hexactinellida	0.86	0.69	0.61	0.13			
Holothuroidea	0.71	0.65	0.11	0.02			
<i>Hyalinoecia</i> sp.	0.80	0.76	0.50	0.44			
Paguridae	0.78	0.74	0.25	0.17			
Pennatulacea	0.77	0.75	0.21	0.12			
REEF	1.00	0.74	0.98	0.05			
Metanephrops challengeri	0.82	0.75	0.32	0.01			
Spatangidae	0.83	0.79	0.24	0.09			
Volutidae	0.84	0.67	0.09	0.01			
Xenophyophoroidea	0.87	0.83	0.27	0.14			
Mean	0.84	0.71	0.43	0.12			

Parameter estimates

Explanatory variables

There was strong evidence (95% posterior probability, or higher) of both positive and negative relationships between explanatory variables and taxon occurrence (Figure 11, left) and abundance (Figure 11, right). The variance explained by each explanatory variable and by the random spatial effect are shown in Appendix 3). The *intercept* provides information on relative rarity; blue cells indicate rare taxa (in the context of the dataset) and red cells indicate common or abundant taxa (Figure 11). Relationships with environmental explanatory variables varied by taxon but there were general patterns for both taxon occurrence and abundance to be negatively related to increasing depth and decreasing salinity, and positively related to increasing profile curvature of the seabed (*profcurv*) and primary productivity (*epp_mean*) (Figure 11). Trawl history (*trawl*) was negatively associated with the occurrence of *Goniocorella dumosa* and REEF), Demospongiae, Hexactinellida, hydroids, Brachiopoda, and hydrocorals (Stylasteridae) but positively associated with occurrence of Buccinidae+Ranellidae, *Hyalinoecia* sp., Paguridae, Pennatulacea, and Volutidae (Figure 11).



Figure 11: Relationships between benthic taxa (y-axis) and explanatory variables (x-axis) that have at least 95% posterior probability of being positive (red) or negative (blue) in the HSMC model using presence-absence data (left) and abundance data (right). Taxa codes used in the figure: ASR (Asteroidea), BPD (Brachiopoda), BUCC (Whelks), CID (Cidaroida), COR (Stylasteridae), COZ (Bryozoa), DEM (Demospongiae), EUE (Euechinoida), GDU (G. dumosa), HYD (Hydroids), HEX (Hexactinellida), HTH (Holothuroidea), HTU (Hyalinoecia sp.), PAG (Paguridae), PTU (Pennatulacea), branching corals (REEF), SCI (M. challenger), SPT (Spatangidae), VOL (Volutidae), ZFR (Xenophyophoroidea).

Traits and environment

Relationships between the occurrence of functional traits and predictor variables were mostly weak but there was evidence of moderately strong (at least 75% posterior probability) positive association for some traits when using both presence-absence (Figure 12, left) and abundance data (Figure 12, right). The strongest association was a positive relationship between salinity and traits representing maximum adult body size (medium, large) and longevity (long-lived) for both presence-absence and abundance

models (Figure 12). Despite the strong relationship between trawl history and taxa occurrence and abundance, the only association between traits and trawl history was a negative relationship with the abundance of large taxa (Figure 12, right).



Figure 12: Association of taxa traits and species niches with at least 75% posterior probability of being positive (red) or negative (blue) for the HSMC model using presence-absence data (left) and abundance data (right).

Biotic interactions

Three broad groups of pairwise taxon associations were observed when using presence-absence data (Figure 13). Holothuroidea and *M. challengeri* had a strong positive association (i.e., co-occurrence when accounting for the environmental niche as described by taxon traits and explanatory variables) and a negative association with most other taxa except Euechinoidea, Paguridae, Volutidae, and Pennatulacea (Figure 13), for which there were no strong associations (white cells in Figure 13). There was also strong support for positive association among a large number of other taxa: Brachiopoda, Demospongiae, *Goniocorella dumosa*, REEF, hydroids, Cidaroida, Spatangidae, Bryozoa, Stylasteridae, Hexactinellida, Xenophyophoroidea, Asteroidea, and Buccinidae+Ranellidae.

There was also strong evidence of positive associations in the abundances of several, primarily epifaunal, taxa (Figure 13): Bryozoa, Hexactinellida, Demospongiae, Asteroidea, hydroids, Stylasteridae, Cidaroida, *Goniocorella dumosa*, and REEF). Paguridae abundance was also positively associated with the above group, except for *Goniocorella dumosa* and REEF, whereas *M. challengeri* was negatively associated with most of the above taxa (Figure 13).



Figure 13: Taxon-to-taxon association matrix identifying taxon pairs that show a positive (red) or negative (blue) association with at least a 95% posterior probability for the HSMC model using presence-absence data (left) and abundance data (right). Taxa codes used in the figure: ASR (Asteroidea), BPD (Brachiopoda), BUCC (Whelks), CID (Cidaroida), COR (Stylasteridae), COZ (Bryozoa), DEM (Demospongiae), EUE (Euechinoida), GDU (G. dumosa), HYD (Hydroids), HEX (Hexactinellida), HTH (Holothuroidea), HTU (Hyalinoecia sp.), PAG (Paguridae), PTU (Pennatulacea), branching corals (REEF), SCI (M. challenger), SPT (Spatangidae), VOL (Volutidae), ZFR (Xenophyophoroidea).

Spatial predictions

Probability of occurrence, predicted abundance, and model certainty estimates (as coefficient of variation, CV) for all taxa are reported in Appendix 2 (Figures 2.29–2.58). As in section 3.1 (single-taxon models), example spatial predictions from the jSDMs distribution models are shown here for four taxa: *Metanephrops challengeri*, Buccinidae+Ranellidae, Hexatinellida, and *Goniocorella dumosa*.

Across all taxa, the majority of spatial patterns predicted using the jSDMs were broadly similar to those predicted from the single-taxon models for both presence-absence and abundance models (Figures 14 to 21). However, for some taxa this was not the case, e.g., the abundance of *Goniocorella dumosa* was predicted to be highest in shallower parts of the study area when using the jSDM compared with deeper parts of the study area (Bounty Trough) in the single-taxon model (compare Figure 19 A to Figure 8 A). As would be expected, the distribution of uncertainty also differed between the two model types (compare Figure 19 B to Figure 8 B).

Overall, uncertainty predictions tended to be higher and cover larger areas for predictions made using the jSDM when compared with the uncertainty estimates predicted using the single-taxon models (e.g., compare Figure 17 B with Figure 7 B). In addition, there were marked localised differences between jSDM and single-taxon model predictions for those taxa predicted to be affected by trawling history with larger, more obvious, changes to predicted distributions in parts of the study area with high intensity of trawling (e.g., edge of the continental shelf, see low predicted abundance of *Goniocorella dumosa* in Figure 19 A and high predicted abundance for Buccinidae+Ranellidae in Figure 17 A).



Figure 14: *Metanephrops challengeri*. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.

Figure 15: *Metanephrops challengeri*. Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.

Figure 16: Buccindae+Ranellidae. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.

Figure 17: Buccinidae+Ranellidae. Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.

Figure 18: *Goniocorella dumosa*. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.

Figure 19: Goniocorella dumosa. Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.


Figure 20: Hexactinellida. Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 21: Hexactinellida. Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.

3.3 Community models

Community data from joint species distribution models

Richness estimates

Richness estimates from the jSDM using 66 taxa were highest along the shelf break of the South Island from Cook Strait to Kaikōura Canyon and south of Banks Peninsula, with high values extending around the western, northwestern, and southwestern flanks of Chatham Rise in depths of approximately 500 to 1000 m (Figure 22). Richness was predicted to be lowest on the shallower areas of the Stewart-Snares and Auckland Islands shelves, around the Chatham Islands, and on Mernoo Bank (Figure 22). Highest uncertainty in richness estimates was in deep waters (1000 to 1500 m depth) north and south of the Chatham Rise and along the South Island shelf break, spanning the areas of highest predicted richness,

and in the bight west of Stewart Island. Lowest uncertainty in richness estimates was for areas with low predicted richness (Figure 22).



Figure 22: Taxonomic richness (left) and associated uncertainty (standard deviation, right) estimated from occurrence predictions of the joint species distribution model using 66 taxa.

Regions of common profile

The interpretation of the classification strength of the grouped community abundance predictions from the jSDMs was similar between assessment methods (elbow method and silhouette method, Figure 23). The largest differences between groups were observed for low classification levels for both methods. Following a very rapid decline, the elbow method started to plateau with a classification detail (group number) of eight (Figure 23) coinciding with the highest average silhouette width (Figure 23). There were further smaller declines in the strength of inter-group differences although very little was observed past 25 groups (Figure 23). RCP estimates were therefore based on 8 and 25 with an intermediate number of groups at 16 groups. Broad patterns in RCP predictions were similar across classification levels (Figure 24).



Figure 23: Results of the elbow (left) and silhouette (right) methods for selection of optimal class number in the Regions of Common Profile (RCP) classification. Dashed lines represent values at classifications with 8 groups, 16 groups, and 25 groups.



Figure 24: Regions of Common Profile (RCP) classification developed from abundance predictions of the joint species distribution model using 66 taxa, showing three classification levels: 8 (top left), 16 (top right), and 25 (bottom left).

Gradient Forest

Of the 66 taxa available in the faunal dataset, 54 were represented adequately (R^2 greater than 0) in the GF models, with a median value R^2 of 0.38 and values per taxon ranging from 0.65 for Galatheidae/Chirostylidae (squat lobsters) to less than 0.01 for Corallimorpharia (a group of anemones), *Enallopsammia* sp. (a stony coral), and *Enypniastes eximia* (a swimming sea cucumber) (Figure 25). The most influential predictor variables for both the accuracy of the GF model and the R^2 correlations with observed faunal distributions were profile curvature of the seabed (*profcurv*), trawl history (*trawl*), primary productivity (*cbpm_mean*), and dynamic oceanography (*dynoc*) (Figure 26).

Classifications at all levels from 5 to 75 classes produced generally coherent, well-defined spatial classes, with little evidence of fragmentation into multiple instances of a given class or blurring of class boundaries, other than areas of complex seafloor topography, including the steep southeastern flank of Chatham Rise and the canyon-incised shelf break off the Otago coast (Figure 27).



Figure 25: Strength of correlations between faunal occurrence and transformed predictor variables in the Gradient Forest community analysis, showing the 54 taxa with correlations greater than zero.

There was adequate representation of faunal survey data points (at least five sites per class) for more than 70% of all classes in classifications up to 25-class level (Figure 28 and Table 7), decreasing to less than 50%, for classifications with more than 40 classes, and less than 40% at 75 classes (Table 7). Global ANOSIM-R values for all class levels were significant at the 1% level, indicating that at least some of the pairwise comparisons between classes were significant. Global ANOSIM-R values tended to increase as the classification detail was increased, with a rapid increase in global ANOSIM-R values from 5 to 20 classes, followed by a plateau from 25 classes until another, more gradual increase occurred from 50 classes, rising to a maximum of 0.87 at 70 to 75 classes (Figure 28).

Although maximum ANOSIM-R values occurred at the highest class levels, the overall classification was progressively less well-informed by survey data as class level increased, with only 30 of 75 classes being represented by at least five survey sites at the highest class level. This pattern illustrates a trade-off between data availability and classification detail, in which increasing detail comes at the cost of decreasing credibility. From this analysis of the GF results, the point of intersection between increasing ANOSIM-R values and decreasing values for the proportion of classes supported by survey data (Figure 28) presents as a potential criterion by which optimal trade-off in class level might be selected. By this criterion, the class level indicated for the GF would be 25 classes (Figure 28).



Figure 26: Importance of predictor variables in the Gradient Forest community model.



Figure 27: Gradient Forest classification developed using quantitative benthic invertebrate observation data from Chatham Rise and Campbell Plateau, showing 5, 10, 15, 50, and 25 class levels.



Figure 28: Gradient Forest classification: mean significant global ANOSIM R-statistic (black line) in relation to the proportion of classes represented by at least 5 survey sites (blue line) at levels of classification detail from 5 to 75 classes.

Table 7: Results of the pairwise ANOSIM-R	analysis for the Gradient	Forest model at class	levels from 5
to 75 classes.			

Classification detail (number of classes)	Proportion of classes ≥ 5 unique occurrences	Proportion of significant inter-class differences	Mean significant ANOSIM R-statistic
5	1.00	1.00	0.22
10	0.90	0.92	0.34
15	0.87	0.91	0.36
20	0.80	0.93	0.42
25	0.72	0.88	0.44
30	0.60	0.88	0.44
35	0.57	0.87	0.44
40	0.50	0.87	0.44
45	0.47	0.87	0.43
50	0.46	0.90	0.47
55	0.44	0.92	0.49
60	0.43	0.89	0.51
65	0.43	0.87	0.51
70	0.41	0.87	0.52
75	0.39	0.83	0.52

4. DISCUSSION

Progressing species distribution modelling for benthic fauna in the New Zealand region

The model predictions presented here are the most recent stage in a process that began with development of an independent quantitative dataset of benthic invertebrate distributions from seafloor photographic surveys (Bowden et al. 2019b) to evaluate the usefulness of predictions from published SDMs for Chatham Rise (Bowden et al. 2021). Having used the novel dataset in this assessment, it was then used to inform new models for Chatham Rise that differed from all existing models of comparable spatial scale in the New Zealand region by being based on observations of taxon abundances (numbers of individuals per unit area of seabed), rather than just their presence at a given location (Bowden et al. 2019a). The general reliance on presence-only data in existing SDM studies of seafloor taxa is not restricted to New Zealand; a recent review of 328 published studies worldwide finding that less than 10% used abundance, density, or biomass data, most of which were modelling commercially exploited fish taxa (Melo-Merino et al. 2020). The lack of abundance-based models for seafloor invertebrate taxa is a consequence of the paucity of spatially consistent abundance data for non-commercial marine taxa. The lack of such data is a major limitation for use of SDM predictions to inform environmental management because patterns of occurrence (presence) alone cannot indicate the range of environmental conditions under which a species is likely to thrive, rather than just survive (Rullens et al. 2019). SDMs derived from abundance data (quantitative models), by contrast, can provide more ecologically nuanced information that is more useful for informing spatial management decisions (Dedman et al. 2015).

The quantitative multivariate benthic dataset developed for this project and used here to generate new model predictions of distributions is novel in the context of marine ecological research in New Zealand because it is the first to enable use of abundance data recorded in a robust and consistent way across a large geographical area and spanning broad environmental gradients of ecological relevance. The initial formulation of this dataset, spanning Chatham Rise, was used to develop the first quantitative distribution models (as opposed to the predictions of suitable habitat derived from presence-only data) for marine benthos yet to be attempted at these spatial scales in the New Zealand region (Bowden et al. 2019a). Here, the incorporation of quantitative observation data from Campbell Plateau enables expansion of these predictions to encompass much of the southeastern sector of New Zealand's EEZ; a region that is of importance for fisheries, encompasses areas of oil and gas exploration, and is of potential future interest for extraction of seabed minerals. In the following sections, these predictions and the methods used to generate them are critically appraised.

Single-taxon predictions

In addition to the novelty of using abundance data to inform SDM predictions, the single-taxon model predictions here are also based on methods that represent the latest and most advanced techniques in the field. The ensemble predictions combine estimates from three modelling techniques, each of which has been shown to perform well for predicting the distribution of benthic taxa in New Zealand, and the combination of their predictions limits the dependence on a single model type or structural assumption, thus providing more robust characterisation of predicted spatial variation and uncertainties (Robert et al. 2016). Moreover, a weighted approach was used to combine model outputs, which accounts for the predicted uncertainty from each modelling method in a spatially explicit manner (Anderson et al. 2020b). These ensemble model outputs are, therefore, likely to be the most reliable predictions of distributions for these taxa currently available across this region of New Zealand's EEZ that can be achieved using established methods and available data. Results from earlier stages of this project suggest that the robustness of the predictions is likely to be more closely linked to the quality and quantity of the input data than to the modelling methods used (Bowden et al. 2021). However, application here of the recently developed jSDM methods to predict distributions for the same set of twenty taxa, using exactly the same data, provides a further opportunity to assess the influence of different modelling methods on the credibility of predictions.

The jSDM approach is of interest because it can incorporate interactions among taxa, environmental covariates, species traits, and phylogenetic relationships in a hierarchical Bayesian structure (Ovaskainen & Abrego 2020) and shows considerable promise in the ability to account for biotic interactions in community data. jSDMs have been shown to have higher predictive and explanatory power than many commonly used SDM methods (Norberg et al. 2019), with methodological advantages compared to other single taxon SDM methods including the capacity to provide simultaneous inferences at the species and community levels and thus allowing generation of individual species predictions and community predictions without having to rely on 'stacking' as would be needed for single-taxon SDM models (e.g., Calabrese et al. 2014). Furthermore, through its Bayesian approach, it can overcome (at least in part) some of the problems of modelling communities with sparse data (although GF-a form of stacking of single-taxon SDM models—also seems to be able to account for rare species in the way that it predicts turnover (Stephenson et al. 2021) (Stephenson et al. in review). jSDM overcomes the long-standing challenge in species distribution modelling of how to account for species interactions in explaining and predicting species occurrences or abundances. jSDM also provides functionality to easily investigate the partitioning of variation in species occurrence or abundance attributable to environmental variation in measured versus random (unmeasured) processes at different spatial scales, both at species level and community level, and can be applied to many kinds of study designs and data (presence-absence, abundance, counts, etc). Finally, jSDM can generate predictions of species, community, or traits whilst propagating uncertainty in the predicted parameter values. The latter is likely to be of particular importance for management applications.

Although a formal comparison between the ensemble model and jSDM predictions was not conducted here, some specific and general points of interest are evident in the example taxa shown. As a general observation, estimates of prediction uncertainty are higher in the jSDM outputs than in the corresponding ensemble model outputs. This result is likely to be because, as described above, jSDM propagates uncertainty across all components of the input data simultaneously and is, thus, likely to present a more realistic estimate of the actual uncertainty in predictions by comparison with the ensemble methods that consider only the target taxon, resulting in potential underestimation of uncertainty. At the level of individual taxa, although most predictions are broadly comparable between the two modelling approaches, predictions for the stony coral G. dumosa appear to be more credible in the jSDM outputs than the ensemble model outputs in that its jSDM predictions do not show the improbable areas of high predicted abundance in deep waters of the Bounty Trough, and that their predictions of abundance align with their predictions of presence. Although this comparison is only for one taxon, it suggests that the general level of credibility of the jSDM predictions may be higher than that of the ensemble models. Once again, however, the actual reliability of the different models can only be estimated here based on the input data themselves; full evaluation of the predictions will come only with availability of sufficient independent survey data.

Community methods

The ability to predict community composition across space is important for input to conservation and spatial management of impacts (Compton et al. 2013, Stephenson et al. 2018a), but use of community level predictions and spatial classifications developed from them is hindered by the same questions about credibility as are single-taxon predictions. Using two independent methods (RCP and GF) to generate classifications from the same source data here provides an opportunity to assess how similar their predictions are and, thus, how useful they are for planning purposes (i.e., if both showed the same patterns, it would indicate an encouraging consensus, whereas if patterns differ markedly, there would be no way to determine which is more realistic without validation against independent data). Although both methods are environment-based, in terms of the outputs of their spatial predictions, the classifications can be understood as spatial summaries of variation in seafloor community composition (Stephenson et al. 2020).

Defining the optimal level of detail at which to use a hierarchical community classification is challenging because ecological communities are rarely delimited by clear and consistent spatial boundaries. Nonetheless, it is useful from a spatial management perspective to produce classifications

with 'hard' community boundaries to enable allocation of protected areas among representative community types. However, because methods vary as to how to define an optimal level classification level, there is likely to be no single definitively correct answer. This study assessed optimal class level using three methods, two of which assess the dissimilarity in groups based on the differences in transformed environmental space (elbow and silhouette methods), whereas the third (ANOSIM) assesses class distinctions based on community measures from the biological data. Despite the different approaches, results from all three methods and for both classifications provided similar ranges of indicative class levels, spanning a range from 8 to 25 classes. While the agreement between class level assessment methods is to be expected, given that the underlying input data are the same for both models, it both indicates that there is some spatial structuring in community composition that can be represented in hard-boundary classes and provides support for direct comparison between the RCP and GF classifications at the same class levels. In terms of which class level assessment approach is to be preferred, the ANOSIM method has advantages in that it can also be applied to assess classification strength using independent faunal occurrence data, and thus provide objective tests of the credibility of the environmental classification (Bowden et al. in press). The silhouette and elbow methods, while providing results that are apparently equally valid, are less useful for assessing classification strength against new data because they are based on the transformed environmental data generated by the community models themselves.

In both the RCP and GF classifications, predicted classes reflected broadscale patterns in environmental variables linked to well-defined oceanographic patterns. For example, there were distinct classes between the north and the south of the Chatham Rise, which are likely to be differentiated by the Sub-Tropical Front (a highly productive zone of mixing between high salinity, nutrient poor, warm, northern waters, and colder, southern waters) and distinct groups on the Campbell Plateau likely driven by the low salinity, nutrient rich, cold, southern waters associated with the Sub-Antarctic Front. In terms of how these classifications might be interpreted, an 8-class representation might be viewed as a bioregionalisation, whereas the greater detail in the 25-class representation could be used to define communities at finer spatial scales.

At the 25-class level, there were some similarities between the RCP and GF classifications but many points of difference (Figure 29). Similarities are most evident around western and southern flanks of Chatham Rise, extending into Bounty Trough, and in the grouping of Campbell Island Shelf, Pukaki Rise, and Bounty Islands shelf in the same class. Obvious differences are present on Campbell Plateau, however; the GF classification assigned fewer classes across central areas, particularly in the area spanning Campbell Island and Pukaki Rise, and the RCP delineated more depth-associated class boundaries. Because both classifications are based on the same input sample data, the differences between them result from the modelling methods. Without independent observations against which to test the two classifications, it is not possible to say which is the more reliable. In earlier analyses in this project, however, a GF classification developed from Chatham Rise data predicted community composition across Campbell Plateau more reliably than did the comparable RCP model developed for Chatham Rise, when tested against the TAN2004 survey data (Bowden et al. in press). Although this result suggests that GF may be the more reliable approach, the implementation of RCP in the current project is both more fully-developed and better-informed by data than was the case for Chatham Rise and, thus, is likely to be more reliable than the earlier iterations.



Figure 29: Comparison between the Regions of Common Profile (RCP) and Gradient Forest (GF) community classifications at 25-class level.

5. MANAGEMENT IMPLICATIONS

Failure to acknowledge sources of uncertainty can lead to poor management decisions (Regan et al. 2005). Whilst uncertainty can readily be incorporated into single-taxon models, for example by quantifying the error around estimates as done here, incorporation of uncertainty into multi-taxa models or for ecosystem-based management is more challenging. The Bayesian inference used in the jSDMs does allow meaningful multi-taxa model uncertainty to be generated. That is, uncertainty for individual taxa is generated accounting for the occurrence or abundance of other taxa in the community. However, model uncertainty is only a portion of the uncertainty in the real world (Marcot 2020); much of the true underlying uncertainty remains unquantified because it stems from factors including the lack of predictor variables that are known to be of fundamental importance to benthic faunal distributions (notably substrate composition) and the reliability of the available input predictor variables (see Bowden et al. 2021). By comparison with existing SDMs that are based on relatively high densities of occurrence data accumulated from multiple sources over decades, the models presented here are informed by a lower density of sample data collected using consistent methods and over a shorter period. Although the lower spatial density of data is likely to have some influence on the reliability of the predictions, this must be weighed against the advantages that are conferred by the overall reliability of the new image-derived data and the capability for modelling relative abundance that they confer. In the results presented here, for instance, it is likely that the use of reliable abundance data enables a more nuanced picture of the influence of trawling on faunal distributions, and the shorter period over which the survey data were collected provides a more accurate picture of what current distributions actually look like in the present, rather than a composite representation of occurrences over several decades, some of which will pre-date any impacts from trawling. This latter point is particularly important in relation to environmental factors that vary in their influence over time. The relative intensity of trawling is the most immediate example of this, but the principle applies equally to any ecologically important variable that responds to global warming.

In the results presented here, spatial variation in trawling history emerged as a key predictor of distributions for nine out of twenty taxa in the ensemble models and for twelve out of twenty taxa in the jSDM models and was the third most important variable in the GF community model. The jSDM results also showed that the influence of trawl fishing varies across taxa, with most taxa, particularly larger-bodied ones, being negatively affected (e.g., the relatively large and fragile stony coral *Goniocorella dumosa*) but smaller predatory or scavenging taxa positively affected (e.g., hermit crabs

and whelks); positive and negative responses to trawling impacts that have been observed consistently elsewhere (Sciberras et al. 2018). Bottom-contacting trawling has been a factor in the marine environment of New Zealand for many years and these results, and previous studies, indicate that it has influenced the distributions of benthic invertebrate taxa across broad spatial scales (Thrush et al. 1998, Cryer et al. 2002). Given this, trawl history should be included routinely as a candidate predictor variable in species distribution models designed to predict the distributions of benthic taxa in the region. The use of trawl history data in the present study is simplistic, in that the cumulative swept area over the full time-span of the available fisheries records was used. In future analyses, however, it would be instructive to examine correlations between species distributions and trawl history summaries spanning a range of periods (e.g., 1, 5, 10, 20, or 30 years before the date of the first faunal occurrence data). This approach could provide information about the duration of trawl impact effects on the benthos and thus help to inform estimates of recovery potential or resilience, which are key inputs to benthic risk assessment initiatives (e.g., Kaiser et al. 2016, Hiddink et al. 2017, Pitcher et al. 2017).

Uncertainty of predictions is not unique to species distribution models; examples of this are seen in daily life (e.g., weather forecasts, insurance premiums, stock markets, interest rates, gambling odds). The level of uncertainty can be reduced to some extent by improvements in the sophistication of statistical methods, but the strongest advances will come only with increasing data density (in the same way that, for instance, weather forecasts improved dramatically with the advent of satellite remote sensing data). Although it is easy to focus only on the uncertainties associated with data-limited predictions, a more constructive perspective is to accept that the knowledge is incomplete but proceed on the basis that the most recent analyses are likely to provide the most reliable predictions. From this perspective, all predictive distribution maps can be viewed as hypotheses to be tested against new knowledge generated by future exploration. The maps and understanding of the world are not static; they develop through a continuing process in which speculation, exploration, data assimilation, and testing interact to inform the current 'model' of the global environment.

In the context of the present work, the study has developed models that provide the best currently available predictions of benthic faunal distributions across a sector of the New Zealand EEZ encompassing two major fisheries areas: Chatham Rise and Campbell Plateau. These predictions are certain to be imperfect in some respects, but they can serve two key roles: first, to inform environmental management decisions for scenarios in which seafloor impacts are likely in the modelled regions and, second, to propagate predictions into other areas of the ECS that have comparable environmental ranges. The latter role is key to improving overall knowledge of the distributions of seafloor habitats and fauna in New Zealand waters because it generates hypotheses about distributions in unsampled areas that can be tested by subsequent surveys structured to assess the reliability of the extended predictions. Given the environmental characteristics of the combined Chatham Rise-Campbell Plateau region and the distributions of commercial deepwater fisheries around New Zealand, an obvious candidate area for the next iteration of this prediction-surveying-testing cycle would be Challenger Plateau, to the east of central New Zealand. This feature is one of three major offshore plateaux in the ECS (together with Chatham Rise and Campbell Plateau) and is of interest for management of fisheries impacts both within New Zealand's EEZ and in high-seas areas in which New Zealand vessels operate. Challenger Plateau also has existing photographic survey data from the inaugural Ocean Survey 20/20 initiative (Bowden 2011). Although relatively sparse, these data have already been incorporated into earlier SDM initiatives for the region (Compton et al. 2013) and thus would provide an immediate extension of the current photographic dataset, when merged using appropriate procedures, and basis on which to develop expanded model predictions.

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APPENDIX 1

Table 1.1: Biological traits used in the Joint Species Distribution Model. Traits assignments are based on those developed by Lundquist et al. (2018). A fuzzy coding approach is used, in which each taxon may be assigned to more than one trait, in proportions summing to 1 for each category of trait (Adult size, Feeding mode, etc.). Trait categories for which only a single trait level is shown are assumed here to be represented by only two levels; e.g., Growth form is either 'erect' or 'not erect' and Longevity is either 'long-lived'.

Taxon	Traits										
	Growth form	Motility	Feeding mode Adult size			Longevity					
	erect	sessile	mobile	filter	suspension	deposit	predscav	small	medium	large	long-lived
Asteroidea	0	0	1	0	0.05	0.2	0.75	0	0.1	0.9	0.2
Brachiopoda	0.5	1	0	1	1	0	0	0	0.86	0.14	1
Whelks	0	0	1	0	0	0	1	0.25	0.75	0	0.2
Hydroids	1	1	0	0	1	0	0	0.5	0.5	0	0.53
Stylasteridae	1	1	0	0	1	0	0	0	0.7	0.3	1
Bryozoa	0.8	1	0	1	1	0	0	0	1	0	1
Demospongiae	1	1	0	1	1	0	0	0	0.9	0.1	1
Cidaroida	0	0	0.8	0	0	1	0	0	1	0	0.2
Euechinoida	0	0	0.8	0	0.1	0.9	0	0	0.75	0.25	0.2
Goniocorella dumosa	1	1	0	0	1	0	0	1	0	1	1
Hexactinellida	1	1	0	1	1	0	0	0	0.5	0.5	1
Holothuroidea	0	0	0.8	0	0	1	0	0	0.5	0.5	0.2
Hyalinoecia tubicola	0	0	1	0	0	0.25	0.75	0.5	0.5	0	0.2
Paguridae	0	0	1	0	0	0.25	0.75	1	0	0	0.2
Pennatulacea	1	1	0	0	1	0	0	0	0	1	1
REEF corals	1	1	0	0	1	0	0	0	0	1	1
Scampi	0	0	1	0	0	0	1	0	1	0	1
Spatangidae	0	0	0.7	0	0	1	0	0	0.75	0.25	0.2
Volutidae	0	0	1	0	0	0	1	0	1	0	0.2
Xenophyophoroidea	0	1	0	0	0.25	0.75	0	0	0.9	0.1	1

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APPENDIX 2 Single-taxon models



Figure 2.1: Brachiopoda (lamp shells, BPD) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.2: Brachiopoda (lamp shells, BPD) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.3: Bryozoa (COZ) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.4: Bryozoa (COZ) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.5: Branching stony corals (REEF) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.6: Branching stony corals (REEF) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.7: Pennatulacea (sea pens, PTU) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



 $\label{eq:Figure 2.8: Pennatulacea (sea pens, PTU) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.$



Figure 2.9: Stylasteridae (hydrocorals, COR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.10: Stylasteridae (hydrocorals, COR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.11: Euchinoida (regular urchins, EUE) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.12: Euchinoida (regular urchins, EUE) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.13: Spatangidae (burrowing urchins, SPT) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.14: Spatangidae (burrowing urchins, SPT) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.15: Cidaroida (pencil urchins, CID) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.16: Cidaroida (pencil urchins, CID) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.17: Holothuroidea (sea cucumbers, HTH) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.18: Holothuroidea (sea cucumbers, HTH) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.19: Xenophyophoroidea (giant foraminiferans, ZFR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.20: Xenophyophoroidea (giant foraminiferans, ZFR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.21: Hydrozoa (hydroids, HDR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.22: Hydrozoa (hydroids, HDR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.23: Volutidae (volute snails, VOL) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.24: Volutidae (volute snails, VOL) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.25: Demospongiae (common sponges, DEM) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from ensemble modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.26: Demospongiae (common sponges, DEM) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.27: Asteroidea (sea stars, ASR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.



Figure 2.28: Paguridae (hermit crabs, PAG) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from ensemble modelling.

Joint Species Distribution Models



Figure 2.29: Brachiopoda (lamp shells, BPD) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.30: Brachiopoda (lamp shells, BPD) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.31: Bryozoa (COZ) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.32: Bryozoa (COZ) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.


Figure 2.33: Branching stony corals (REEF) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.34: Branching stony corals (REEF) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.35: Pennatulacea (sea pens, PTU) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.36: Pennatulacea (sea pens, PTU) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.37: Stylasteridae (hydrocorals, COR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.38: Stylasteridae (hydrocorals, COR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.39: Euchinoida (regular urchins, EUE) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.40: Eucchinoida (regular urchins, EUE) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.41: Spatangidae (burrowing urchins, SPT) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.42: Spatangidae (burrowing urchins, SPT) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.43: Cidaroida (pencil urchins, CID) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.44: Cidaroida (pencil urchins, CID) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.45: Holothuroidea (sea cucumbers, HTH) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.46: Holothuroidea (sea cucumbers, HTH) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.47: Xenophyophoroidea (giant foraminiferans, ZFR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.48: Xenophyophoroidea (giant foraminiferans, ZFR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.49: Hydrozoa (hydroids, HDR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset



Figure 2.50: Hydrozoa (hydroids, HDR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.51: Volutidae (volute snails, VOL) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.52: Volutidae (volute snails, VOL) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.53: Demospongiae (common sponges, DEM) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.54: Demospongiae (common sponges, DEM) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.55: Asteroidea (sea stars, ASR) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.56: Asteroidea (sea stars, ASR) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.



Figure 2.57: Paguridae (hermit crabs, PAG) - Predicted probability of occurrence (A) and associated uncertainty (B, coefficient of variation) from jSDM modelling. Black dots show sites at which the taxon was present in the photographic survey dataset.



Figure 2.58: Paguridae (hermit crabs, PAG) - Predicted abundance (A) and associated uncertainty (B, standard deviation) from jSDM modelling.

APPENDIX 3



Figure 3.1: Variance partitioning of the explanatory variables and a random spatial effect for models fitted with presence / absence (left, units Tjur R^2) and abundance data (right, units R^2) for each taxon.