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Taihoro Nukurangi

Updated habitat suitability modelling for protected corals in New Zealand waters

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Contents

Executive summary	7
1 Introduction	8
2 Methods	9
2.1 Assembly of coral presence and absence data.....	9
2.2 Selection of taxa to model	10
2.3 Environmental predictors	11
2.4 Model types	13
2.5 Model performance and outputs	15
2.6 Overlap with trawl fishing effort	16
3 Results	17
3.1 Selected taxa.....	17
3.2 Predictor variable selection	17
3.3 Model performance.....	17
3.4 Predicted coral habitat distributions	19
3.5 Overlap with trawl fishing footprint	69
4 Summary and discussion	76
4.1 Model performance.....	76
4.2 Comparison of predictions with previous models and predicted future changes in coral distribution.....	77
4.3 Relative importance of environmental predictors	78
4.4 Overlap between trawling and predicted distribution of corals	79
5 Recommendations for future research	81
6 Acknowledgements	82
7 References	83
Appendix A Environmental predictor variables	89
Appendix B Random Forest models partial dependence plots	95
Appendix C Boosted Regression Tree models partial dependence plots	101

Tables

Table 2-1:	Protected coral taxa modelled.	11
Table 2-2:	Initial set of environmental predictors considered for HSM models.	13
Table 3-1:	Performance metrics for the BRT and RF components of coral habitat suitability models.	18
Table 3-2:	Variable importance ranks by taxon and model type (RF/BRT).	19
Table 3-3:	Summary of overlap between habitat suitability and fishing footprint.	71

Figures

Figure 3-1:	Comparison of RF, BRT, and ensemble models for the predicted present habitat suitability for two representative taxa.	20
Figure 3-2:	<i>Enallopsammia rostrata</i> . Predicted habitat suitability (present).	22
Figure 3-3:	<i>Enallopsammia rostrata</i> . Predicted habitat suitability (future).	23
Figure 3-4:	<i>Enallopsammia rostrata</i> . Precision of predicted habitat suitability (present).	24
Figure 3-5:	<i>Enallopsammia rostrata</i> . Precision of predicted habitat suitability (future).	25
Figure 3-6:	<i>Solenosmilia variabilis</i> . Predicted habitat suitability (present).	26
Figure 3-7:	<i>Solenosmilia variabilis</i> . Predicted habitat suitability (future).	27
Figure 3-8:	<i>Solenosmilia variabilis</i> . Precision of predicted habitat suitability (present).	28
Figure 3-9:	<i>Solenosmilia variabilis</i> . Precision of predicted habitat suitability (future).	29
Figure 3-10:	<i>Goniocorella dumosa</i> . Predicted habitat suitability (present).	30
Figure 3-11:	<i>Goniocorella dumosa</i> . Predicted habitat suitability (future).	31
Figure 3-12:	<i>Goniocorella dumosa</i> . Precision of predicted habitat suitability (present).	32
Figure 3-13:	<i>Goniocorella dumosa</i> . Precision of predicted habitat suitability (future).	33
Figure 3-14:	<i>Madrepora oculata</i> . Predicted habitat suitability (present).	34
Figure 3-15:	<i>Madrepora oculata</i> . Predicted habitat suitability (future).	35
Figure 3-16:	<i>Madrepora oculata</i> . Precision of predicted habitat suitability (present).	36
Figure 3-17:	<i>Madrepora oculata</i> . Precision of predicted habitat suitability (future).	37
Figure 3-18:	<i>Paragorgia</i> spp. Predicted habitat suitability (present).	38
Figure 3-19:	<i>Paragorgia</i> spp. Predicted habitat suitability (future).	39
Figure 3-20:	<i>Paragorgia</i> spp. Precision of predicted habitat suitability (present).	40
Figure 3-21:	<i>Paragorgia</i> spp. Precision of predicted habitat suitability (future).	41
Figure 3-22:	<i>Primnoa</i> spp. Predicted habitat suitability (present).	42
Figure 3-23:	<i>Primnoa</i> spp. Predicted habitat suitability (future).	43
Figure 3-24:	<i>Primnoa</i> spp. Precision of predicted habitat suitability (present).	44
Figure 3-25:	<i>Primnoa</i> spp. Precision of predicted habitat suitability (future).	45
Figure 3-26:	<i>Corallium</i> spp. Predicted habitat suitability (present).	46
Figure 3-27:	<i>Corallium</i> spp. Predicted habitat suitability (future).	47
Figure 3-28:	<i>Corallium</i> spp. Precision of predicted habitat suitability (present).	48

Figure 3-29:	<i>Corallium</i> spp. Precision of predicted habitat suitability (future).	49
Figure 3-30:	<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp. Predicted habitat suitability (present).	50
Figure 3-31:	<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp. Predicted habitat suitability (future).	51
Figure 3-32:	<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp. Precision of predicted habitat suitability (present).	52
Figure 3-33:	<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp. Precision of predicted habitat suitability (future).	53
Figure 3-34:	<i>Bathypathes</i> spp. Predicted habitat suitability (present).	54
Figure 3-35:	<i>Bathypathes</i> spp. Predicted habitat suitability (future).	55
Figure 3-36:	<i>Bathypathes</i> spp. Precision of predicted habitat suitability (present).	56
Figure 3-37:	<i>Bathypathes</i> spp. Precision of predicted habitat suitability (future).	57
Figure 3-38:	<i>Leiopathes</i> spp. Predicted habitat suitability (present).	58
Figure 3-39:	<i>Leiopathes</i> spp. Predicted habitat suitability (future).	59
Figure 3-40:	<i>Leiopathes</i> spp. Precision of predicted habitat suitability (present).	60
Figure 3-41:	<i>Leiopathes</i> spp. Precision of predicted habitat suitability (future).	61
Figure 3-42:	<i>Errina</i> spp. Predicted habitat suitability (present).	62
Figure 3-43:	<i>Errina</i> spp. Predicted habitat suitability (future).	63
Figure 3-44:	<i>Errina</i> spp. Precision of predicted habitat suitability (present).	64
Figure 3-45:	<i>Errina</i> spp. Precision of predicted habitat suitability (future).	65
Figure 3-46:	<i>Stylaster</i> spp. Predicted habitat suitability (present).	66
Figure 3-47:	<i>Stylaster</i> spp. Predicted habitat suitability (future).	67
Figure 3-48:	<i>Stylaster</i> spp. Precision of predicted habitat suitability (present).	68
Figure 3-49:	<i>Stylaster</i> spp. Precision of predicted habitat suitability (future).	69
Figure 3-50:	Fishing footprint.	71
Figure 3-51:	Overlap of bottom trawl fishing effort with present habitat suitability [1].	72
Figure 3-52:	Overlap of bottom trawl fishing effort with present habitat suitability [2].	73
Figure 3-53:	Overlap of bottom trawl fishing effort with future habitat suitability [1].	74
Figure 3-54:	Overlap of bottom trawl fishing effort with future habitat suitability [2].	75
Figure A-1:	Environmental variables used in the models.	89
Figure A-2:	Environmental variables used in the models.	90
Figure A-3:	Environmental variables used in the models.	91
Figure A-4:	Environmental variables used in the models.	92
Figure A-5:	Environmental variables used in the models.	93
Figure A-6:	Environmental variables used in the models.	94
Figure B-1:	Variable marginal effects in the Random Forest models for <i>Enallopsammia rostrata</i> (top) and <i>Solenosmilia variabilis</i> (bottom).	95
Figure B-2:	Variable marginal effects in the Random Forest models for <i>Goniocorella dumosa</i> (top) and <i>Madrepora oculata</i> (bottom).	96

Figure B-3:	Variable marginal effects in the Random Forest models for <i>Paragorgia</i> spp. (top) and <i>Primnoa</i> spp. (bottom).	97
Figure B-4:	Variable marginal effects in the Random Forest models for <i>Corallium</i> spp. (top) and <i>Keratoisis</i> & <i>Lepidisis</i> spp. (bottom).	98
Figure B-5:	Variable marginal effects in the Random Forest models for <i>Bathypathes</i> spp. (top) and <i>Leiopathes</i> spp. (bottom).	99
Figure B-6:	Variable marginal effects in the Random Forest models for <i>Errina</i> spp. (top) and <i>Stylaster</i> spp. (bottom).	100
Figure C-1:	Variable marginal effects in the Boosted Regression tree models for <i>Enallopsammia rostrata</i> (top) and <i>Solenosmilia variabilis</i> (bottom).	101
Figure C-2:	Variable marginal effects in the Boosted Regression tree models for <i>Goniocorella dumosa</i> (top) and <i>Madrepora oculata</i> (bottom).	102
Figure C-3:	Variable marginal effects in the Boosted Regression tree models for <i>Paragorgia</i> spp. (top) and <i>Primnoa</i> spp. (bottom).	103
Figure C-4:	Variable marginal effects in the Boosted Regression tree models for <i>Corallium</i> spp. (top) and <i>Keratoisis</i> & <i>Lepidisis</i> spp. (bottom).	104
Figure C-5:	Variable marginal effects in the Boosted Regression tree models for <i>Bathypathes</i> spp. (top) and <i>Leiopathes</i> spp. (bottom).	105
Figure C-6:	Variable marginal effects in the Boosted Regression tree models for <i>Bathypathes</i> spp. (top) and <i>Leiopathes</i> spp. (bottom).	106

Executive summary

Many protected coral species occur as bycatch in commercial fisheries around New Zealand. To estimate the overlap between commercial fishing and corals under present and future climate conditions, and thus the potential vulnerability of these protected species, it is first necessary to predict the present and future spatial extent of corals. This work extends previous coral habitat suitability modelling studies by utilising updated modelling techniques, incorporating additional coral presence records, and by mainly using regional environmental predictor layers for the current and future climate conditions based on the New Zealand Earth System Model (NZESM).

Models were produced for all protected coral taxa considered in initial consultations with stakeholders. These comprised four separate reef-forming scleractinian coral species, *Enallopsammia rostrata*, *Solenosmilia variabilis*, *Goniocorella dumosa*, and *Madrepora oculata*; the gorgonian octocoral genera *Paragorgia* (bubblegum corals), *Primnoa* (primnoid seafans), *Corallium* (precious corals); and *Keratoisis* and *Lepidisis* (bamboo corals) combined; two antipatharian (black) coral genera, *Bathypathes* and *Leiopathes*; and two genera of stylasterid hydrocorals, *Errina* and *Stylaster*. This selection was based on the need to produce models that cover a range of the protected coral taxa and the requirement for a sufficient number and spread of presence records.

Environmental predictors were derived primarily from outputs of the NZESM, but several fixed predictors, including revised and updated sediment data layers, seafloor slope, and UTF (Underwater Topographical Feature, as a categorical variable) were also considered. Model coefficients were used to produce two sets of prediction grids for each model type; one for present-day environmental conditions (means from the period 1995 to 2014), and one for the predicted environmental conditions at the end of the 21st century (means from the period 2080 to 2099), assuming only moderate mitigation and adaptation to climate change.

Model performance was shown to be acceptable for all taxa, and although predicted taxa distributions largely agreed with previous studies, additional presence records extended the predicted distributions into new areas for some taxa. For the region as a whole, future habitat suitability ranged from somewhat less suitable (e.g. *Corallium* spp.) to somewhat more suitable overall (e.g. *Enallopsammia rostrata*), across the 12 taxa examined. For some taxa, especially the hydrocorals, predicted future habitat suitability remained largely unchanged due to the importance of temporally fixed parameters in the models. Use of a less conservative emissions pathway in the NZESM may have also provided more contrast between present and future suitability but was not possible to test due to the constraints of the project.

The risk to corals from interaction with fishing gear was assessed by comparing predicted coral distributions with the aggregated swept area from historical bottom fishing for inshore and deepwater fisheries combined. Overlaying the regions of greatest habitat suitability with the most highly fished regions (using arbitrary habitat suitability and fishing intensity thresholds) revealed considerable variability in vulnerability among taxa, both in degree and location. The greatest overlaps were seen for hydrocorals and the shallower scleractinian species, whereas the deeper scleractinians, gorgonians, and black corals were less vulnerable. Little change in overlap at the end of the century was predicted for many of the modelled taxa. However, a higher future level of overlap off the west coast of the South Island was predicted for the thicket-forming *Madrepora oculata*, the alcyonaceans *Keratoisis* and *Lepidisis* spp., and the black coral *Leiopathes* spp. A lower level of future overlap was predicted for the hydrocoral genus *Stylaster* along the east coast of the North Island.

1 Introduction

All coral species in the Orders Antipatharia and Scleractinia, gorgonian octocorals in the Order Alcyonacea, and stylasterid hydrocorals in the Order Anthoathecata, are protected in the New Zealand region under the Wildlife Act (1953) and a later (2010) amendment. This protection makes it illegal to deliberately collect or damage these coral species and all protected corals accidentally brought to the surface (for example through capture by fishing gear) must be immediately returned to the sea. Many of these protected coral species occur as bycatch in commercial fisheries in the New Zealand region (e.g., Anderson et al. 2017, Tracey & Hjørvarsdóttir 2019). In order to better understand the potential vulnerability of these protected species to trawling impacts under present and possible future climate change conditions, we need to understand the overlap between commercial fishing effort and corals, and to do so it is first necessary to predict the present and future spatial extent of corals.

This project expands on the work undertaken by Anderson et al. (2015), by carrying out improved and refined habitat suitability modelling to predict species distributions using new data. These new data include coral records collected by researchers and the Department of Conservation's (DOC) Conservation Services Programme (CSP) Observer programme during the past four years and identified by specialists (Tracey et al. 2017), coral records from shallow depths (less than 200 m), and regional environmental predictor layers for the current and future climate conditions based on the New Zealand Earth System Model (NZESM). Comparison of the predicted distributions of coral taxa with current fishing effort is made using bottom trawl footprint data compiled for recent fishing years (Baird & Mules 2020a, Baird & Mules 2020b).

The results of this project can be used to help assess the risk to protected corals from commercial fishing now and in the future, and thereby inform the management of these fragile and long-lived fauna.

The specific objectives of this project (DOC19301/POP2018-01) are:

1. To carry out improved habitat suitability modelling for protected corals in the New Zealand region.
2. To help identify areas of risk from interactions with commercial fishing gear.

2 Methods

Various techniques exist for predicting species distributions through the spatial estimation of habitat suitability, and there has been a substantial development of these in recent years, taking advantage of increased computing power, machine learning algorithms, availability of global and regional datasets of environmental variables, development of Earth System Models for predicting future oceanic conditions, the ongoing sampling of the world's oceans, and accessible species record databases (e.g., Ramiro-Sánchez et al. 2019, Burgos et al. 2020, Morato et al. 2020).

The most commonly used of the available habitat suitability modelling methods include:

- Generalised Linear Models (GLMs and GAMs) (McCullagh & Nelder 1989, Hastie & Tibshirani 1990).
- Maximum Entropy (Maxent) (Phillips et al. 2006).
- Random Forests (RF) (Breiman 2001).
- Boosted Regression Trees (BRT) (Elith et al. 2008).
- Genetic Algorithm for Rule-Set Production (GARP) (Stockwell 1999).
- Multivariate Adaptive Regression Splines (MARS) (Friedman 1991).
- Ecological Niche Factor Analysis (ENFA) (Hirzel et al. 2002).
- Artificial Neural Networks (ANNs).
- BIOCLIM (Nix 1986).

Although the approaches and underlying structures differ, each of these models essentially explores the relationship between point-sampled species occurrence records (and usually absence or background records), and spatially continuous environmental variables. These models predict the likelihood of occurrence of (or habitat suitability for) a species, or group of species, across unsampled environmental space (Reiss et al. 2015, Vierod et al. 2014). For this project we have chosen two techniques that are able to account for complex non-linear correlations between species occurrence and environmental predictors, and have proven to work well with New Zealand data (e.g., Georgian et al. 2019, Bowden et al. 2019) – Boosted Regression Trees and Random Forests.

2.1 Assembly of coral presence and absence data

A database containing records of benthic invertebrate samples from the South Pacific region is regularly updated by NIWA staff for use in various marine biodiversity research projects, including habitat suitability modelling studies. The database includes taxa which are considered Vulnerable Marine Ecosystem (VME) indicator taxa (e.g., various coral groups and sponges) and taxa that are considered indicators of VME habitat (i.e., those strongly associated with VMEs; crinoids and brisingid starfish) (Parker et al. 2009). As such the database records include all protected New Zealand coral species.

Coral presence data used in the various previous analyses of protected coral species distributions was augmented by several years of additional records. These data have come from fisheries observer sample collections, research surveys, and from records from overseas museums and research institutes. These revised and updated datasets of coral records form the basis of this new study. In

addition, we have included coral presence data from shallow waters (less than 200 m) to enable the prediction of coral distributions to the shallowest depths possible within the limits of the environmental predictor layers. Coral records were recorded at different taxonomic levels in the database (high taxonomic resolution often was not possible for records based on non-retained specimens); the focus of the current study was to produce models at the genus and species level where possible.

The coral occurrence dataset is a subset of a larger database of position records comprising all research survey stations at which all organisms in the sample were identified, including stations with no corals. This dataset, comprising over 60 000 records within the New Zealand EEZ, was used to provide the absence location data for earlier habitat suitability models, and was used again in this study, expanded as necessary to include data points from stations shallower than 200 m. For each taxon, a set of absence data was randomly selected from the coral occurrence dataset, with the number of records equal to that of the presence data (following the recommendations of Barbet-Massin et al. 2012); the presence and absence records were then combined to provide the basis for model construction.

2.2 Selection of taxa to model

The set of taxa modelled in the two previous related studies (Anderson et al. 2014, Anderson et al. 2015) were used as a starting point for taxa selection in the current study. Selection was initially guided by the coral species listed in the DOC Threatened Species List (Freeman et al. 2010) and a DOC marine invertebrate expert panel list (Freeman et al. 2013) (Table 3 1). Further details of selection criteria and rationale for species groupings can be found in Anderson et al. (2014).

Although models combining groups of taxa may be less reliable due to the conflicting effects of the differing environmental tolerances of individual species within them, this issue needed to be balanced against the lack of resources available to the current project to produce models for large numbers of individual species, and the limited number of individual species with sufficient presence data to produce robust models. The available presence data were assessed to consider additions of records of protected coral species collected since the most recent database update.

Limited resources and the greater complexity used in the present analyses restricted the final number of taxa modelled to the twelve shown in Table 2-1, one less than the thirteen taxa in the previous study. This new complexity – combining multiple independent models, calculating cross-validated model performance statistics, resampling for precision estimation, dealing with spatial auto-correlation – now represents NIWA’s standard approach to producing habitat suitability maps for VME indicator taxa in the New Zealand and wider Pacific region (e.g., Anderson et al. 2016b, Rowden et al. 2017, Georgian et al. 2019), and has been adopted internationally and specifically noted as an example of “good practice” (Winship et al. 2020). We assigned a priority ranking to each candidate taxon, with resources focussed on priority 1 and 2 taxa and models for priority 3 taxa produced only if remaining resources allowed (Table 2-1).

Table 2-1: Protected coral taxa modelled. Brief description, depth range of records, number of recorded observations available for the models (number available in the previous study, Anderson et al. (2015), in parentheses), and a priority rank. –, not modelled previously.

Order	Taxon	Description	Depth range (m)	N. records	Priority
Scleractinia	<i>Enallopsammia rostrata</i>	Reef-forming coral	186–2620	307 (130)	1
	<i>Solenosmilia variabilis</i>	Reef-forming coral	130–2620	472 (311)	1
	<i>Goniocorella dumosa</i>	Reef-forming coral	94–1595	699 (212)	1
	<i>Madrepora oculata</i>	Reef-forming coral	89–2882	251 (126)	1
Alcyonacea	<i>Paragorgia</i> spp.	Bubblegum coral (tree-like)	152–2161	221 (98)	2
	<i>Primnoa</i> spp.	Primnoid sea-fans (tree-like)	150–1611	124 (73)	2
	<i>Corallium</i> spp.	Precious coral	108–2427	99 (–)	2
	<i>Keratoisis</i> spp and <i>Lepidisis</i> spp.	Bamboo corals (tree-like)	138–2842	565 (241)	1
Antipatharia	<i>Bathypathes</i> spp.	Black coral (tree-like)	161–1831	203 (75)	1
	<i>Leiopathes</i> spp.	Black coral (tree-like)	110–1657	199 (67)	3
Anthoathecata	<i>Errina</i> spp.	Hydrocorals (small, hard)	66–2771	246 (–)	2
	<i>Stylaster</i> spp.	Hydrocorals (small, hard)	96–2094	225 (–)	3

2.3 Environmental predictors

A wide range of environmental parameters that can potentially have an impact on seafloor-dwelling invertebrates are available as outputs from Earth System Models, representing both current condition and predicted conditions at some time in the future (e.g., 2100).

The recently developed New Zealand Earth System Model (NZESM) incorporates component models of ocean biogeochemistry and other aspects of biology and chemistry that provide a highly complex model of the climate system (Behrens et al. 2019).

The model differs from the UK Earth System Model (UKESM) essentially in two respects: firstly, it includes a high-resolution regional ocean model for the seas around New Zealand. Secondly it includes a representation of the variability of solar radiation in atmospheric chemistry. Both these changes manifestly affect climate of the Southern Hemisphere (Williams et al. 2016). A preliminary evaluation shows that a cold sea surface temperature bias found in the UKESM in the New Zealand region is improved in the NZESM. Solar input drives climate variability particularly at southern high latitudes (such that when the Sun is more active, pressure over Antarctica tends to be lower than otherwise). The NZESM reproduces this association.

This NZESM can produce projections out to 200 years into the future (Williams et al. 2016), but for this analysis we focussed on predicted environmental conditions for an historical reference period (1995–2014) to represent present conditions, and a future reference period (2080–2099) to represent conditions the end of the current century. The predicted future conditions were based on the SSP2 (4.5 W/m²) pathway (RCP 4.5), which describes a future with middle-of-the-road mitigation of carbon emissions and adaptation to climate change (Fricko et al. 2017).

An initial set of potentially useful environmental parameters representing present conditions were obtained from the NZESM for the midpoint of every 1x1 km cell within the New Zealand region (see Section 2.5.3). The NZESM uses two different ocean model grids. Physical variables are available on a high-resolution 0.2° grid (~17 km around New Zealand) and on a 1° (~90 km around New Zealand), while ocean biogeochemistry is available on the 1° grid only. To be consistent between ocean physics and ocean biogeochemistry, only data from the 1° grid was used for this project. Both horizontal

grids have 75 vertical levels with a thickness of 1 m at surface and increasing with depth to about 250 m. The bottom grid cell is partially filled to allow for an improved representation of bottom topography and properties near the sea floor. The interpolation of all 2-D fields (such as seafloor temperature and benthic nitrogen) for each grid point of the 1 km target grid was done through bilinear interpolation of all surrounding model grid cells, after extrapolating ocean values onto land. This method allows for a better representation of the near-shore values. For the interpolation of 3-D seafloor variables, a similar approach was applied, but with consideration of vertical model grid and model bathymetry. Here values at the nearest vertical level of all surrounding model grid cells were used for the bilinear interpolation, except when they included land; in these cases, bottom values of the grid cell were used.

In addition to variables from the NZESM, some potentially important environmental parameters that vary only spatially (rather than temporally) were also compiled. These comprised: seabed depth, slope, underwater topographic features (UTFs) (comprising seamounts, hills, and knolls as defined in the New Zealand Standard for undersea feature names NZGBS60000), and aspects of seabed roughness and substrate composition. Spatial grids of these parameters were obtained from published research and databases, and NIWA records. Updated data layers of seafloor substrate composition for the New Zealand region have recently been produced (Bostock et al. 2018a, 2018b). The availability of these new sediment data layers (representing concentrations of sand, mud, and carbonate) for use in the habitat suitability models is important because substrate is likely to have a substantial influence on the ability of corals to settle and grow. Nonetheless, it is worth noting here that these data layers are gridded at 1 km, a spatial scale that is typically much larger than the scale at which substrate type influences sessile fauna such as corals, and their formation required a high degree of interpolation due to the uneven distribution of sediment sampling in the region. This mismatch of spatial resolution is also an issue for the NZESM-derived variables, which are on a scale such that the influence on their values from fine-scale variability in topography is not represented, and the topographic variables themselves, which can be categorised alongside substrate type in terms of the spatial scale of their influence.

The full initial set of environmental predictors is shown in Table 2-2. This set was subsequently reduced to a core set suitable for habitat suitability models because too many variables can lead to overfitting and highly correlated variables can adversely affect model performance and interpretation (e.g., Huang et al. 2011). The initial set of 19 variables was reduced in a stepwise manner by excluding the variable most highly correlated with the remainder. This procedure was done by calculating the variance inflation factor (VIF) for each variable using the R library *HH* (Heiberger, 2011), following the method described by Yesson et al. (2015). Firstly, values for each variable were determined at the unique locations of all coral presence records combined, and VIFs calculated. The variable with the highest VIF was then discarded and the process repeated with the remaining variables, continuing iteratively until all variables showed a VIF of less than 5, reflecting a low level of co-linearity (Heiberger and Holland, 2004).

Table 2-2: Initial set of environmental predictors considered for HSM models.

Variable	Description	Units	Reference
ESM variables			
Nitrogen	Benthic Nitrogen (BEN_N) [2-D]	mmol/m ²	NZESM
Detrital flux	Total detrital flux to seabed (DETFLUX3) [3-D]	mmol/m ³	NZESM
DIC	Dissolved Inorganic Carbon (DIC_C) [3-D]	mmol/m ³	NZESM
POC	Particulate Organic Carbon flux (EXPC3) [3-D]	mmol/m ³	NZESM
Calcite	Calcite saturation state (OM_CAL3) [3-D]	–	NZESM
Oxygen	Dissolved oxygen at the seafloor (OXY) [3-D]	mmol/m ³	NZESM
Pressure	Seawater pressure at seafloor (PBO) [2-D]	dbar	NZESM
Aragonite	Aragonite saturation state (SFR_OARG) [2-D]	–	NZESM
Salinity	Seafloor salinity (SO) [2-D]	psu	NZESM
Temperature	Seafloor temperature (TO) [2-D]	Degrees C	NZESM
Fixed variables			
UTF	UTF positions	–	Rowden et al. (2008), Mackay (2007)
Carbonate	Percentage of carbonate in sediment	%	Bostock et al. 2018ab
Mud	Percentage of mud in sediment	%	Bostock et al. 2018ab
Sand	Percentage of sand in sediment	%	Bostock et al. 2018ab
BPI-broad	Benthic Position Index – broad-scale	–	NIWA
BPI-fine	Benthic Position Index – fine-scale	–	NIWA
Depth	Seabed depth	m	NIWA
Slope-percent	Seabed slope in percent	%	NIWA
Stdev-slope	Standard deviation of seabed slope	–	NIWA

Following the initial reduction of predictor variables, trial BRT models were run for each taxon using the reduced set of variables to assess their predictive power and further eliminate any unsuitable predictors. This was done using the Boosted Regression Tree (BRT) *gbm.simplify* function (Elith et al. 2006), which carries out a backwards stepwise elimination of variables. This simplification process firstly assesses the relative contributions of each variable in terms of deviance explained, with the lowest contributing variables removed from the model, before the model is refitted with the remaining environmental variables. The change in deviance explained that resulted from removing the variable was then examined and the process repeated until all variables were sequentially removed. The final models were created by refitting the model with a reduced variable set that balanced the deviance explained with the number of predictor variables (after Stephenson et al. 2020) which were then used to construct final models for both BRT and Random Forest (RF) methods. This procedure aims to provide a balance between providing models with as much explanatory power as possible and minimising fitting of models to noise rather than signal.

2.4 Model types

Random Forest models

RF models are a non-parametric approach which build classification or regression trees using random subsets of the input data (Breiman 2001). The RF models were built in R (R Core Team 2018) using *randomForest*, and tuned using the train function in *caret* to select optimal values for complexity parameters *mtry* (the number of variables used in each tree node), *maxnodes* (the maximum number of terminal nodes in each trees), and *n tree* (the number of trees to grow). The RF approach to habitat suitability modelling has also been successfully applied in the past to benthic invertebrate data in the New Zealand region (Rowden et al. 2017, Georgian et al. 2019).

Boosted Regression Tree models

BRT models are an advanced form of additive regression based on decision trees, where the individual terms of the regression are simple trees, fitted in a stage-wise manner. Short trees are formed by relating a response to recursive binary splits of the data, then combined (boosted) to

improve predictive power by focussing each successive tree on model residuals. Tree-based methods such as BRT and RF have the advantage over traditional methods that they can easily handle missing data, outliers, categorical as well as continuous variables, and automatically handle interactions between predictors (Elith et al. 2008). Detailed descriptions of the BRT method are available in Ridgeway (2019) and Elith et al. (2008). The BRT method has been widely used in ecological applications and has performed well in previous studies of deep-water invertebrate and fish distributions in New Zealand (e.g., Leathwick et al. 2006, Tracey et al. 2011, Compton et al. 2013, Rowden et al. 2017, Georgian et al. 2019).

All BRT analyses were undertaken in R using the *dismo* package (Hijmans et al. 2011). Tree-complexity (number of splits) was set to 3, allowing for a level of variable interaction, and the learning rate (which determines the weight given to each successive tree in the model) was set to 0.001, but adjusted where necessary so that the number of trees in the final models exceeded 1000; a bag fraction of 0.6 was used with a random 10-fold cross evaluation method following guidelines in Elith et al. (2008).

Ensemble models

We produced an ensemble model for each taxon, to incorporate the predictions and underlying assumptions and modelling strategies of each model type. This approach limits dependence on a single model type or structural assumption and enables a more robust characterization of the predicted spatial variation and uncertainties (Robert et al. 2016). Ensemble models were constructed by taking weighted averages of the predictions from the BRT and RF models, using methods adapted from Oppel et al. (2012), Anderson et al. (2016), Rowden et al. (2017), and Georgian et al. (2019). This adapted procedure derives a two-part weighting for each component of the ensemble model, taking equal contributions from the overall model performance (cross-validated AUC values) and the uncertainty measure (coefficient of variation, CV) in each cell (see Section 2.5), as follows,

$$W_{BRT1} = \frac{MPS_{BRT}}{MPS_{BRT} + MPS_{RF}} \text{ and } W_{RF1} = \frac{MPS_{RF}}{MPS_{BRT} + MPS_{RF}}$$

$$W_{BRT2} = 1 - \frac{CV_{BRT}}{CV_{BRT} + CV_{RF}} \text{ and } W_{RF2} = 1 - \frac{CV_{RF}}{CV_{BRT} + CV_{RF}}$$

$$W_{BRT} = \frac{W_{BRT1} + W_{BRT2}}{2} \text{ and } W_{RF} = \frac{W_{RF1} + W_{RF2}}{2}$$

$$X_{ENS} = X_{BRT} * W_{BRT} + X_{RF} * W_{RF}$$

$$CV_{ENS} = \sqrt{\frac{(CV_{BRT} * X_{BRT})^2 * W_{BRT}^2 + (CV_{RF} * X_{RF})^2 * W_{RF}^2}{X_{ENS}^2}}$$

where MPS_{BRT} and MPS_{RF} are the model performance statistics; X_{BRT} and X_{RF} are the model predictions; CV_{BRT} and CV_{RF} are the bootstrap CVs; and X_{ENS} and CV_{ENS} are the weighted ensemble predictions and weighted CVs, respectively, from which maps of predicted species distribution and model uncertainty were produced.

2.5 Model performance and outputs

2.5.1 Model performance

Model performance was evaluated for the BRT and RF models primarily using the AUC metric (area under the Receiver Operating Characteristic curve), which for these types of models are defined as the area under a plot of the fraction of true positives versus the fraction of true negatives. In general, AUC scores over 0.5 indicate better than random performance, values over 0.7 indicate adequate performance, and values over 0.8 indicate excellent performance (Hosmer et al. 2013). Several additional performance metrics were also calculated; sensitivity (% of presences correctly identified), specificity (% of absences correctly identified); True Skill Statistic (TSS, which takes into account specificity and sensitivity to provide an index ranging from -1 to +1, where +1 equals perfect agreement and -1 = no better than random, Allouche et al. (2006)). Note that to “correctly identify” presences and absences, a cut-off habitat suitability value is needed. This was calculated as the value which maximises sensitivity+specificity and can also be used to predict a binary outcome from the model (i.e., presence or absence), if required.

These performance metrics were assessed for each taxon and model by a process of cross-validation, using a procedure which also considers spatial autocorrelation in the input data (Roberts et al. 2017, Valavi et al. 2019). For this procedure, model input data for each taxa was partitioned systematically into 10 spatial blocks - the size of which were based on a distance for which the residuals of a BRT model were approximately independent, as assessed by a variogram – to create training and test data sets, with 9 blocks used to construct a preliminary model which was then applied to the remaining block to measure performance. This process was repeated ten times, leaving out each of the 10 blocks in turn, for each model type, and average AUC, sensitivity, specificity, and TSS scores calculated to represent overall performance.

2.5.2 Model precision

To assess the relative confidence in predictions across the model extent, based on uncertainty stemming from the distribution of sampling data, we used a bootstrap technique to produce spatially explicit uncertainty measures, after Anderson et al. (2016) and Georgian et al. (2019). Random samples of the presence data were drawn, with replacement, from the model input datasets and to these were added an equal number of absence records, drawn randomly from the master coral occurrence dataset. Presence-absence models of each type were then constructed using the same settings as the originals, and predictions of habitat suitability made for each cell of the model extent. This process was repeated 200 times for each model type (BRT and RF) resulting in 200 estimates of abundance for each taxon in each cell. Model uncertainty in each cell was then calculated as the coefficient of variation (CV) of the bootstrap output.

Uncertainty in model predictions will also be affected by the accuracy of the predictor variables. Measures of uncertainty were not available for the environmental variables used here and although methods exist for incorporating such uncertainty (if available) into HSM models, including summarising over large numbers of models based on the spread of estimated predictor values, and input error-based models (e.g., Foster et al. (2012), Stoklosa et al. (2015)), these are not commonly used and the development of such models was beyond the available resources of this study.

2.5.3 Model outputs

Model predictions were limited to the standard New Zealand Region (CANZ 2008), extending from 157° E to 167° W and 24° to 57.5° S, an area that encompasses the New Zealand Exclusive Economic Zone (EEZ), Territorial Sea (TS), and Extended Continental Shelf (ECS). There was no upper limit to the depth range modelled, although there were few presence points for many taxa near to the shorelines and lack of environmental data points near the shore required a high degree of interpolation for some predictor variables. The maximum depth for the models was set to 2000 m, as few taxonomic records were available below this level. The resolution (cell size) of the environmental input grids and model output maps was set to 1 km². Although habitat suitability will be influenced by variability in environmental predictors at a finer scale than 1 km in many areas, the accuracy of the presence location data (mainly derived from sampling gear towed along the seafloor) along with the native resolution of the environmental predictors described above, outputs at any finer scale than this could be misleading. All resulting maps are presented using the Albers Equal Area projection centred at 175°E and 40°S (EPSG:9191), a standard format now used by DOC and Fisheries New Zealand (FNZ) (Wood et al. in prep). Maps are overlaid on a hill-shade layer to illustrate variations in bathymetry.

Because absence data used in the model were obtained randomly from a large set of sampling stations and do not represent true absence, results are presented as relative habitat suitability and not as probability of presence. To aid discussion of the model outputs, especially description and comparison of the spatial predictions of relative habitat suitability, we define “high” habitat suitability as predicted values greater than 0.5, shown in this report as areas of green or yellow in the figured maps. Maps of model precision take into account variability in the model input data, and not any other sources of error.

2.6 Overlap with trawl fishing effort

A spatial grid of the combined aggregated swept area by bottom trawling for inshore and deepwater target species, covering recent fishing years only (2007–08 to 2017–18), was compiled from annual layers calculated by Baird & Mules (2020a) and Baird & Mules (2020b) and provided by FNZ. These data are limited to the New Zealand TS and EEZ.

To compare the distribution of bottom trawl fishing effort with habitat suitability and identify the areas at greatest risk from contact with fishing gear, cells with an aggregated swept area of greater than that of the 75th percentile calculated from all cells within the TS/EEZ (i.e., the top 25%) and also in the top 25% of habitat suitability were identified for each taxon. **These “cut-off” values are not intended to define or inform any classification of fishing intensity, or to signify taxon presence/absence, but were chosen after consideration of various alternatives as they provided the best compromise for a constant value, across all taxa, at which a visual comparison was possible.** These regions of overlap were plotted and the number of overlapping 1 km² cells enumerated.

3 Results

3.1 Selected taxa

Habitat suitability models were produced for all 12 taxonomic groups listed in Table 2-1. This modelling effort was made possible due to improved efficiencies in coding and the automation of various parts of the model development. As a result, models were able to be produced for the first time for the alcyonacean genera *Primnoa* and *Corallium*, and the anthoathecatan genera *Errina* and *Stylaster*.

3.2 Predictor variable selection

The variance inflation factor procedure reduced the initial 19 potential predictor variables to a smaller set with minimal correlations among them. These comprised *Carbonate*, *Mud*, *Sand*, *BPI-fine*, *Slope-percent*, *UTF*, *Nitrogen*, *Detrital flux*, *Oxygen*, *Depth*, and *Salinity*. Despite a level of correlation with some of these variables, two additional variables were included with importance for skeletal composition in most corals; *Calcite* and *Aragonite*. Aragonite is the polymorph of calcium carbonate used in the skeletons of scleractinian and anthoathecatan corals whereas calcite is used in antipatharian and alcyonacean corals (Bostock et al. 2015). As such, only one of either *Calcite* or *Aragonite* were included in subsequent model development, depending on the taxon being modelled. Refer to Figure A-1 to Figure A-6 for maps illustrating the current and future spatial variability of each predictor used in the models.

Backwards stepwise BRT models based on these individualised sets of variables further reduced the number of variables from use in final model construction to between 4 and 8 (see Table 3-2).

3.3 Model performance

Tuning of RF models to select optimal settings did not result in clearly improved fits, based on the “out-of-bag” estimate of error rate, therefore default settings for *mtry* (square root of the number of variables), *ntree* (501), and *maxnodes* (1) were used in the models for each taxon.

Cross-validated AUC scores for the individual BRT and RF models ranged from 0.76 (*Goniocorella dumosa* - BRT) to 0.93 (*Corallium* spp. – RF), indicating adequate models (AUC > 0.7) in all cases (Table 3-1). AUC scores for most taxa, for both methods, were between 0.8 and 0.9. Only for *Goniocorella dumosa* was AUC less than 0.8 for both model types. The best fit by this measure was for *Corallium* spp. where AUC was 0.92–0.93.

Sensitivity and specificity values were also well above 0.5 in all cases. Sensitivities were over 0.9 for *Enallopsammia rostrata*, *Corallium* spp., and both black coral genera. Specificities were mostly slightly lower than Sensitivities, reaching a maximum of 0.86–0.88 for *Corallium* spp. and *Errina* spp.

True Skill Statistic (TSS) values were all at acceptable levels, all much greater than zero. The highest values were again for *Corallium* spp. with the black coral models and *Errina* spp. model also performing well by this measure. Cut-off values for presence-absence ranged from a low of 0.27 (*Leiopathes* spp. – RF) to a high of 0.52 (*Paragorgia* spp. (BRT) and *Corallium* spp. (RF)) and were in most cases slightly lower in the RF models than in the BRT models.

For most taxa most of the performance metrics were similar between the two model types, suggesting similar fits to the data. This result was more noticeable for the taxa with better fitting models, e.g., *Corallium* spp. and *Errina* spp., than for taxa with weaker performance metrics, e.g., *Stylaster* spp. and *Primnoa* spp.

Table 3-1: Performance metrics for the BRT and RF components of coral habitat suitability models.

Taxon	AUC		Sensitivity		Specificity		TSS		Cut-off	
	BRT	RF	BRT	RF	BRT	RF	BRT	RF	BRT	RF
<i>Enallopsammia rostrata</i>	0.87	0.83	0.92	0.84	0.79	0.81	0.71	0.65	0.42	0.40
<i>Solenosmilia variabilis</i>	0.84	0.82	0.88	0.78	0.78	0.82	0.66	0.60	0.43	0.40
<i>Goniocorella dumosa</i>	0.76	0.77	0.85	0.87	0.64	0.67	0.48	0.55	0.41	0.28
<i>Madrepora oculata</i>	0.79	0.85	0.83	0.86	0.80	0.83	0.63	0.69	0.43	0.36
<i>Paragorgia</i> spp.	0.80	0.77	0.80	0.82	0.82	0.73	0.62	0.55	0.52	0.38
<i>Primnoa</i> spp.	0.77	0.83	0.85	0.91	0.80	0.85	0.65	0.75	0.40	0.33
<i>Corallium</i> spp.	0.93	0.93	0.95	0.95	0.88	0.87	0.82	0.82	0.49	0.52
<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp.	0.82	0.82	0.81	0.85	0.88	0.71	0.70	0.56	0.58	0.29
<i>Bathypathes</i> spp.	0.86	0.83	0.89	0.87	0.83	0.80	0.72	0.67	0.46	0.39
<i>Leiopathes</i> spp.	0.86	0.85	0.84	0.94	0.86	0.77	0.70	0.71	0.50	0.36
<i>Errina</i> spp.	0.89	0.90	0.87	0.85	0.87	0.88	0.74	0.74	0.50	0.50
<i>Stylaster</i> spp.	0.79	0.84	0.72	0.88	0.65	0.77	0.57	0.66	0.37	0.40

Dissolved *Oxygen* was the most influential variable overall across the 12 taxa modelled, ranking first in importance in both the RF and BRT models for the bamboo corals and for both black coral models; *Oxygen* also ranked first in the RF model for the stony coral *Madrepora oculata*. The models for *Stylaster* spp. were the exception, with *Oxygen* eliminated for this taxon during the variable selection process (Table 3-2). *Nitrogen* was also strongly influential in many of the models – ranked most important for *Primnoa* spp. and *Corallium* spp. models of both types, and ranked second or third in many other models – and was eliminated only from the bamboo coral models. Seafloor *Depth* was present in only 7 of the 12 models but was ranked most important in both model types for *Goniocorella dumosa* and second most important for *Errina* spp. For the four branching scleractinian corals the key variable overall was *Aragonite*, ranking first or second in each model. For the calcite dependent taxa *Calcite* was present in all models except for *Corallium* spp. and was ranked first for *Paragorgia* spp. and second for bamboo coral models. Of the remaining variables, *Mud* was top ranked for *Errina* spp., and *BPI-fine* was top ranked for *Stylaster* spp.; the least important variables overall, with only low ranking in a few of the models, were *Salinity*, *UTF*, and *Slope-percent*. For fuller details on how the environmental variables influence habitat suitability in each model refer to the partial dependence plots in Appendix B.

Table 3-2: Variable importance ranks by taxon and model type (RF/BRT). The rank signifies the order of variable importance in each model; variables are ordered from left to right by mean overall importance across the 12 taxa.

	Oxygen	Nitrogen	Depth	Aragonite	Mud	Calcite	BPI-fine	Carbonate	Detrital flux	Salinity	UTF	Slope-percent
<i>Enallopsammia rostrata</i>	2/2	3/4	4/5	1/1	5/3					6/6		
<i>Solenosmilia variabilis</i>	5/5	2/2	3/3	1/1				4/4				
<i>Goniocorella dumosa</i>	6/3	5/6	1/1	2/2	4/8			7/4	3/5			8/7
<i>Madrepora oculata</i>	1/3	3/5	5/4	2/1				4/2				
<i>Paragorgia</i> spp.	3/2	2/3				1/1	5/5		4/4			
<i>Primnoa</i> spp.	3/2	1/1			4/4	2/3		6/5	5/6			
<i>Corallium</i> spp.	3/3	1/1	4/5				2/2		5/4		6/6	
<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp.	1/1		4/4		3/3	2/2						
<i>Bathypathes</i> spp.	1/1	2/2	5/6		6/5	3/4	4/3					
<i>Leiopathes</i> spp.	1/1	5/5	3/2			2/4	4/3			6/6		
<i>Errina</i> spp.	3/4	4/3	2/2		1/1			5/6			6/5	
<i>Stylaster</i> spp.		5/4	4/2	3/7	2/3		1/1	7/6		6/5		

3.4 Predicted coral habitat distributions

Maps of predicted habitat suitability produced by BRT and RF models showed similar overall patterns but with some subtle differences apparent in some regions for most taxa, as illustrated below for two representative genera *Paragorgia* spp. and *Leiopathes* spp. (Figure 3-1). For *Paragorgia* spp. BRT-based maps show a slightly higher level of suitability than RF-based maps in most regions, most noticeable south of the Chatham Rise. The overall level of habitat suitability is similar between models for *Leiopathes* spp. but is noticeably greater in the north for the BRT-based map. With generally similar AUC scores for most species, maps for the weighted ensemble models essentially represent an average of the BRT and RF model outputs.

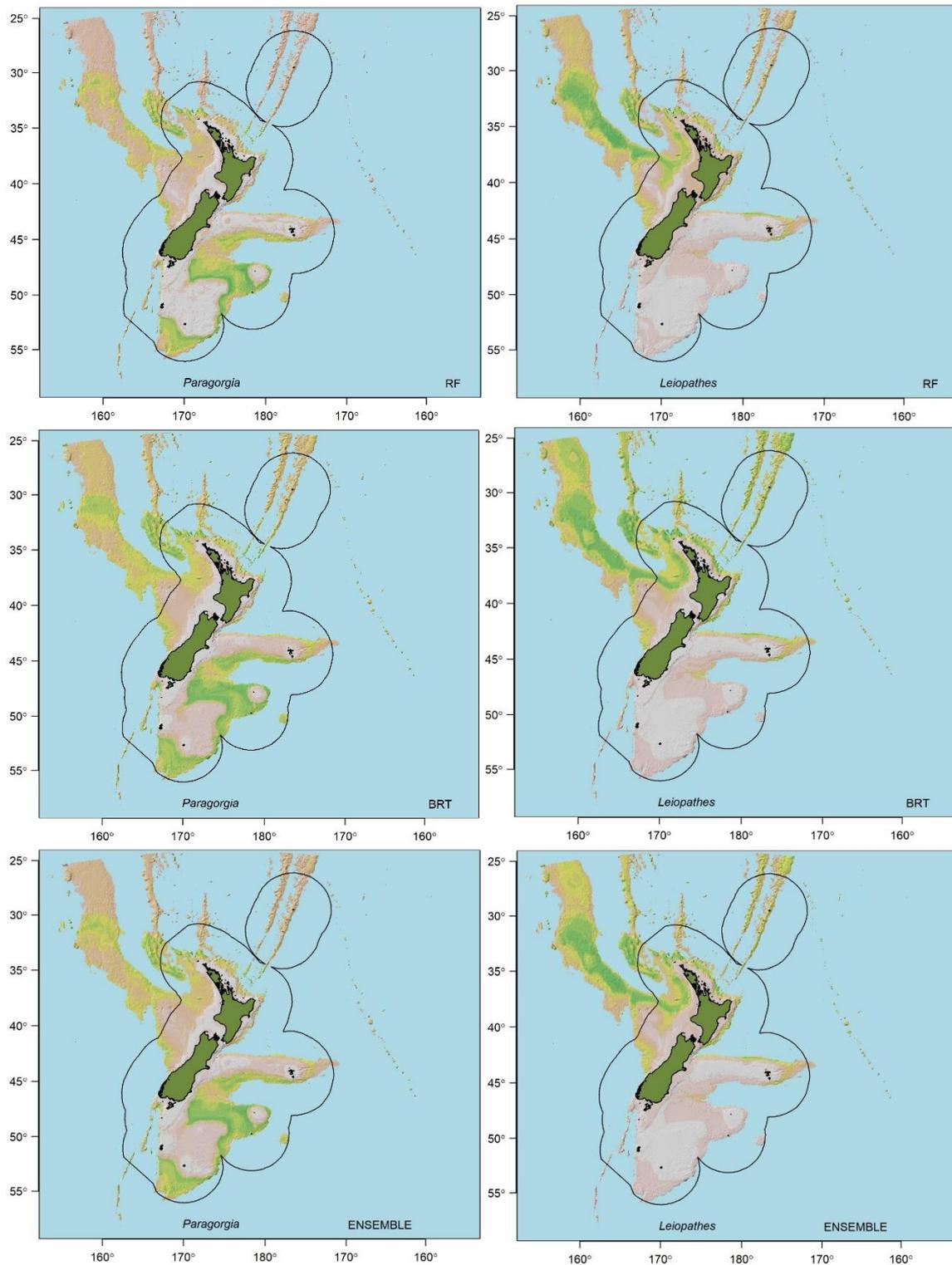


Figure 3-1: Comparison of RF, BRT, and ensemble models for the predicted present habitat suitability for two representative taxa. Left, *Paragorgia* spp.; right, *Leiopathes* spp.; top, RF; middle, BRT; bottom, ensemble models.

3.4.1 Scleractinia

Patterns of habitat suitability showed considerable variation among the four reef-forming scleractinian corals, both spatially and temporally (Figure 3-2 to Figure 3-17). Present distributions of *Enallopsammia rostrata* are focussed on deeper regions, especially on the rises and ridges north of New Zealand and around the edges of the Chatham Rise and sub-Antarctic plateaus (Figure 3-2). Predicted future distributions (Figure 3-3) are very similar in the north but indicate potentially improved habitat suitability into shallower regions of the Challenger Plateau, Chatham Rise, and sub-Antarctic plateaus. Model precision is also generally greater in southern regions, and tends to be lowest in shallower waters around the New Zealand coastline (Figure 3-4, Figure 3-5).

The present predicted distribution of *Solenosmilia variabilis* (Figure 3-6 to Figure 3-9) overlaps strongly with that of *Enallopsammia rostrata* with a focus on deeper regions in the north and around the southern rises. Future distributions are predicted to change little on the northern ridges and rises, but on the Challenger Plateau, Chatham Rise, and sub-Antarctic, are predicted to slightly increase in shallower regions and decrease in deeper regions. Model precision varies considerably for this species, both spatially and temporally, but is notably low nearer the coast and in the future in most areas.

The present predicted distribution of *Goniocorella dumosa* (Figure 3-10 to Figure 3-13) is much shallower than that of *Enallopsammia rostrata* and *Solenosmilia variabilis*, with greatest habitat suitability on shallower parts of the Chatham Rise, sub-Antarctic, and continental shelf around the North and South Islands. In the north, high levels of habitat suitability are limited to small regions of shallower seafloor. There is predicted to be only subtle changes in habitat suitability in most regions by the end of the century. Estimated model precision of these distributions is relatively high, especially in shallower parts, with CVs of less than 40% over much of the model extent and little difference between present and future patterns.

The present distribution of *Madrepora oculata* (Figure 3-14 to Figure 3-17) is predicted to be similar to that of *Enallopsammia rostrata* and *Solenosmilia variabilis*, with the highest levels of habitat suitability strongly associated with the undersea features in the north and around the margins of those in the south. As with each of the other branching coral species, predicted changes in future habitat suitability are more pronounced in southern regions than northern, with shallower water becoming slightly more suitable habitat across the main rises and plateaus around New Zealand and deeper water becoming slightly less suitable habitat in a few areas, such as eastern Campbell Plateau. Model precision around these predictions is mostly less than 40% and relatively constant across the modelled extent, and notably lower across the Challenger Plateau in the future compared to present predictions.

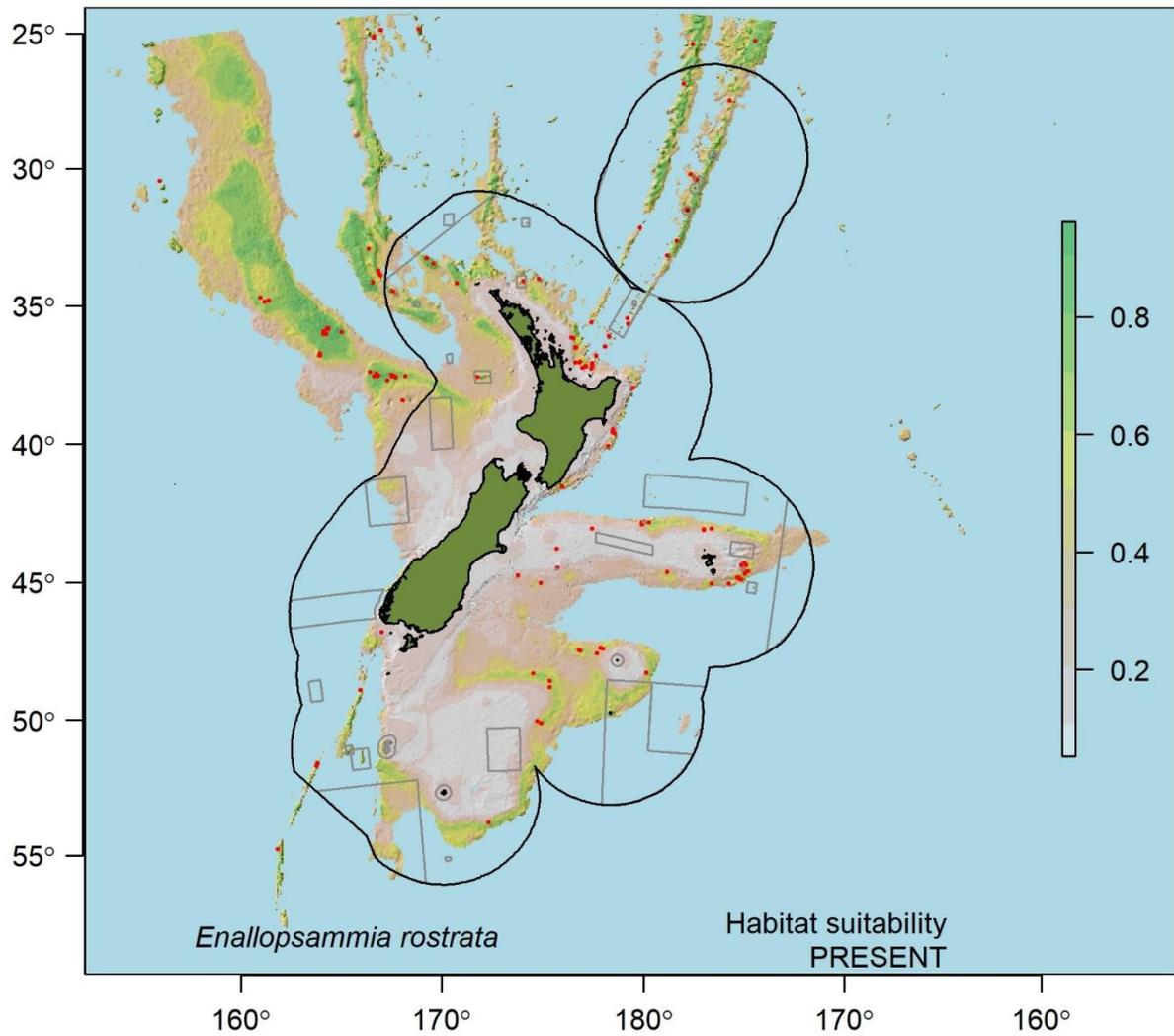


Figure 3-2: *Enallopsammia rostrata*. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1), red dots show species presence locations. The boundaries of the New Zealand EEZ (black lines) as well as Benthic Protection Areas, large Marine Reserves, and seamounts closed to bottom trawling (grey lines) are also indicated.

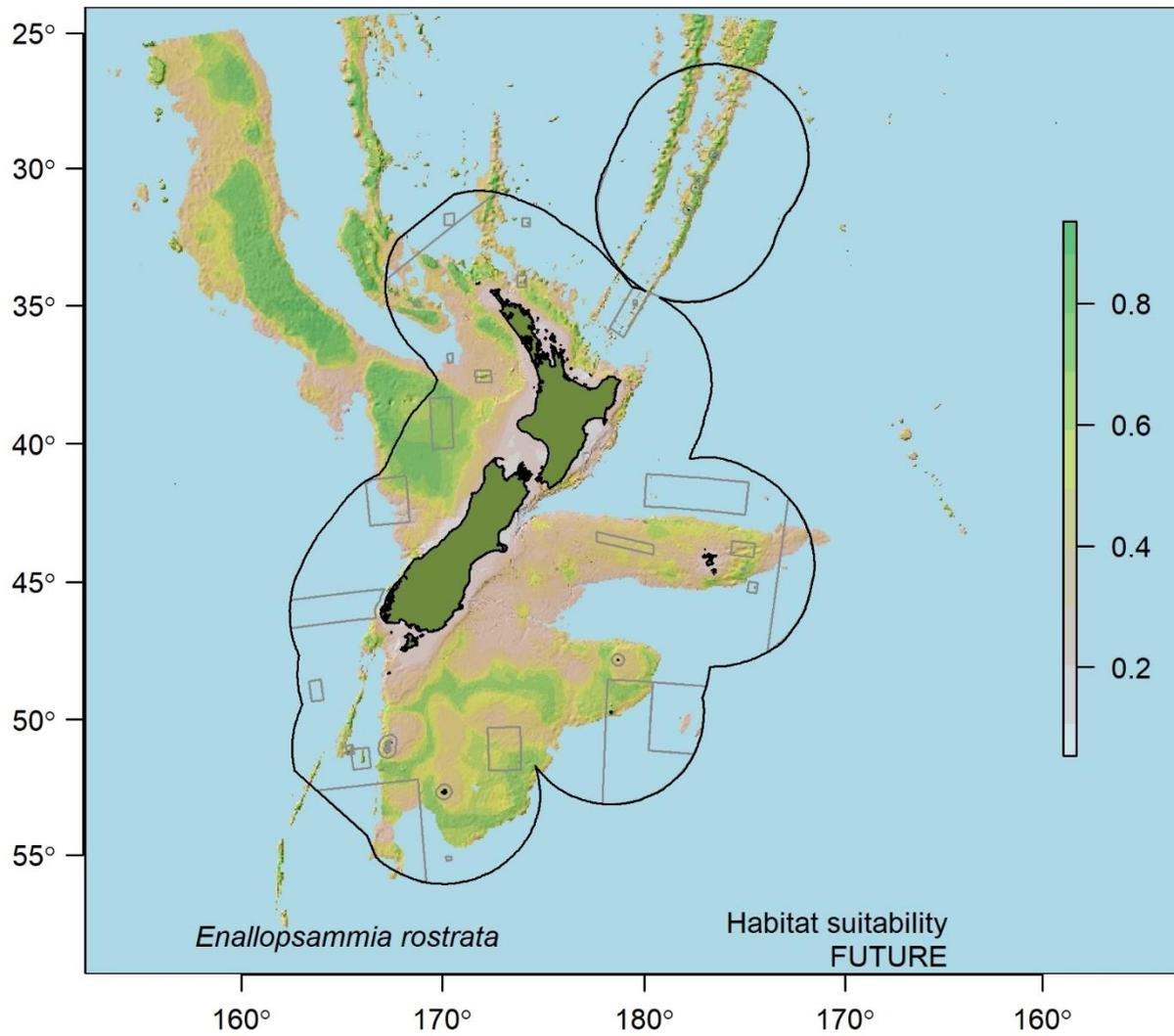


Figure 3-3: *Enallopsammia rostrata*. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

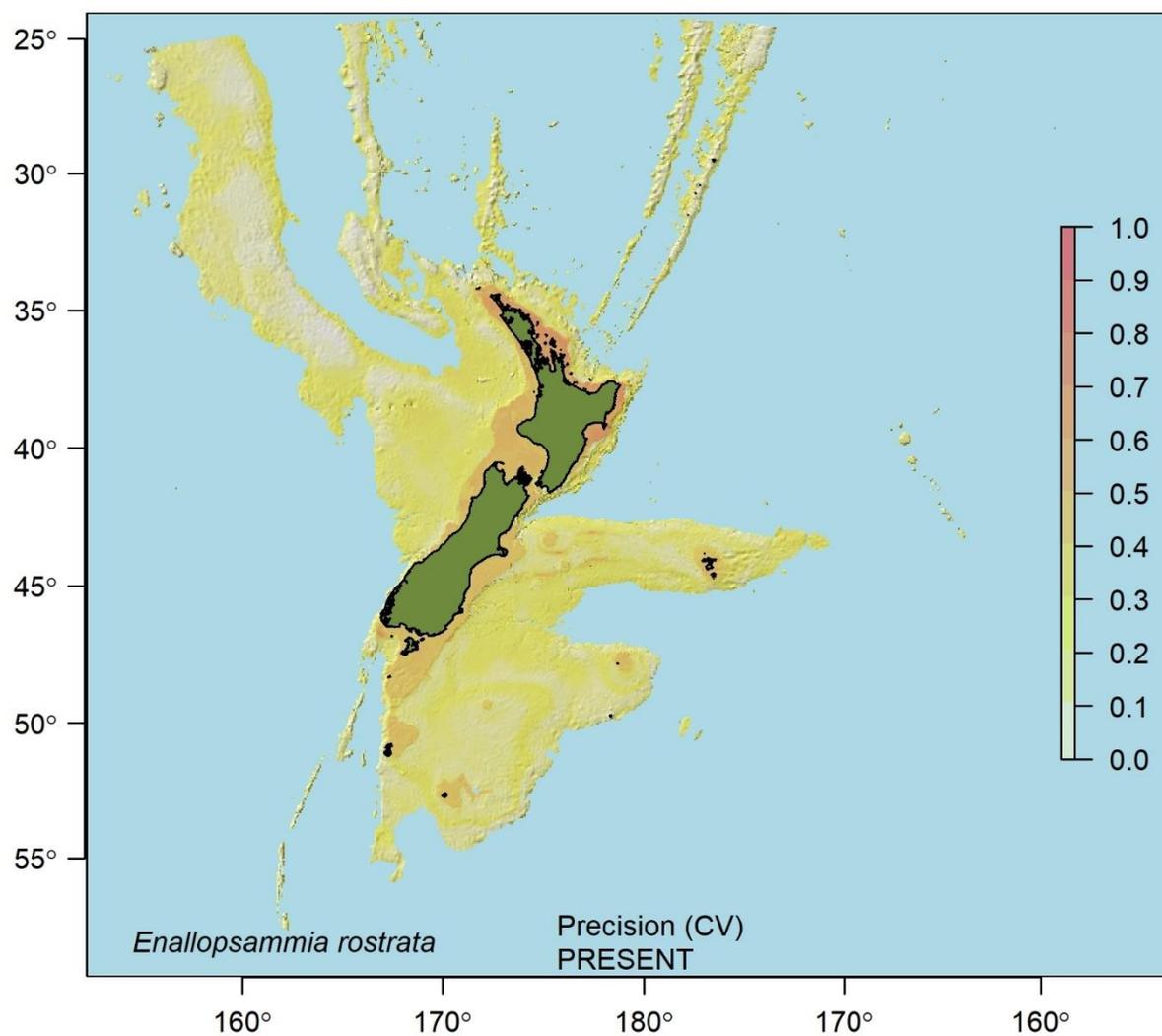


Figure 3-4: *Enallopsammia rostrata*. Precision of predicted habitat suitability (present). Precision is presented as the CV of the predicted habitat suitability, based on bootstrap resampling, and shown as a fraction (0–1).

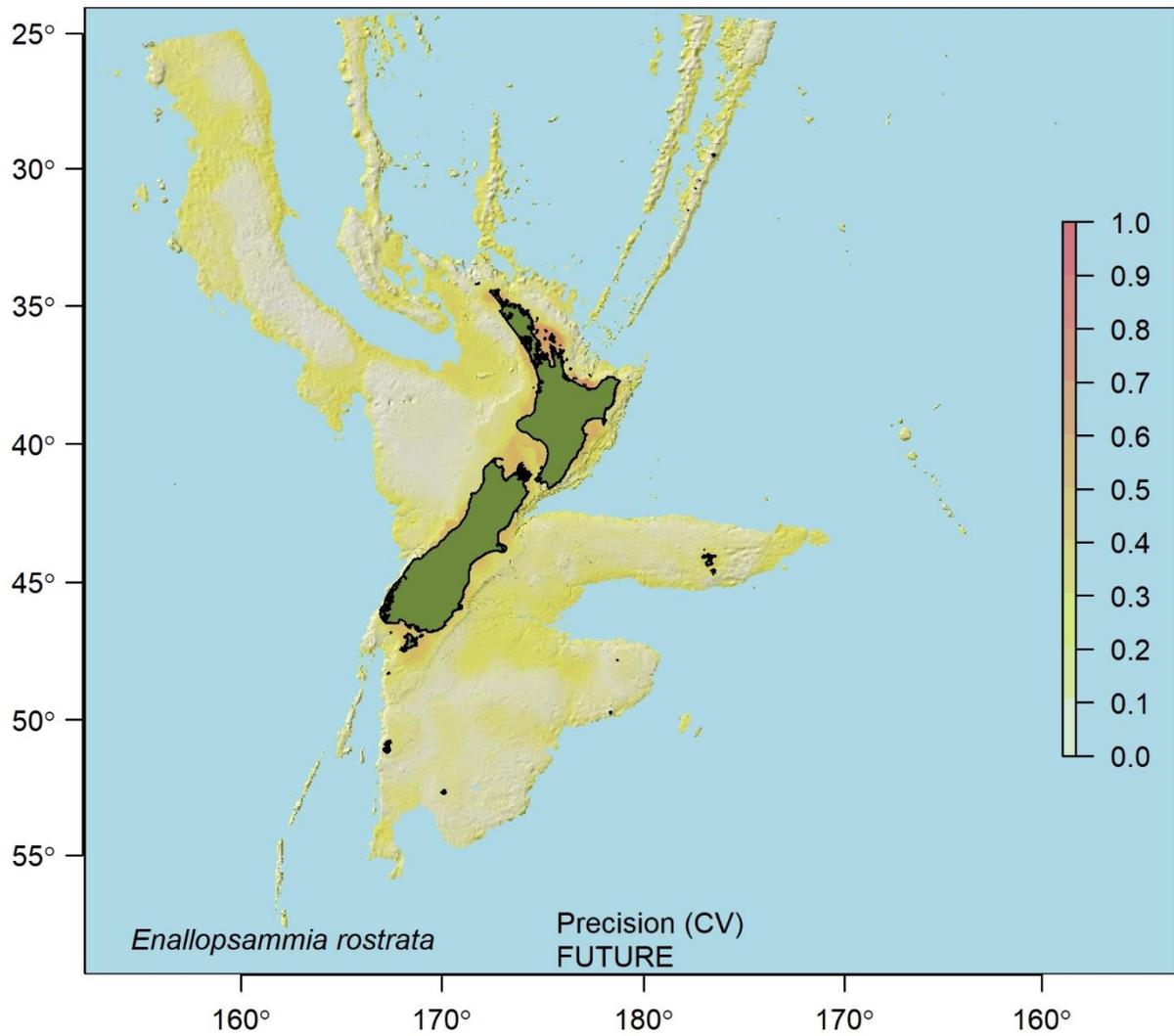


Figure 3-5: *Enallopsammia rostrata*. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

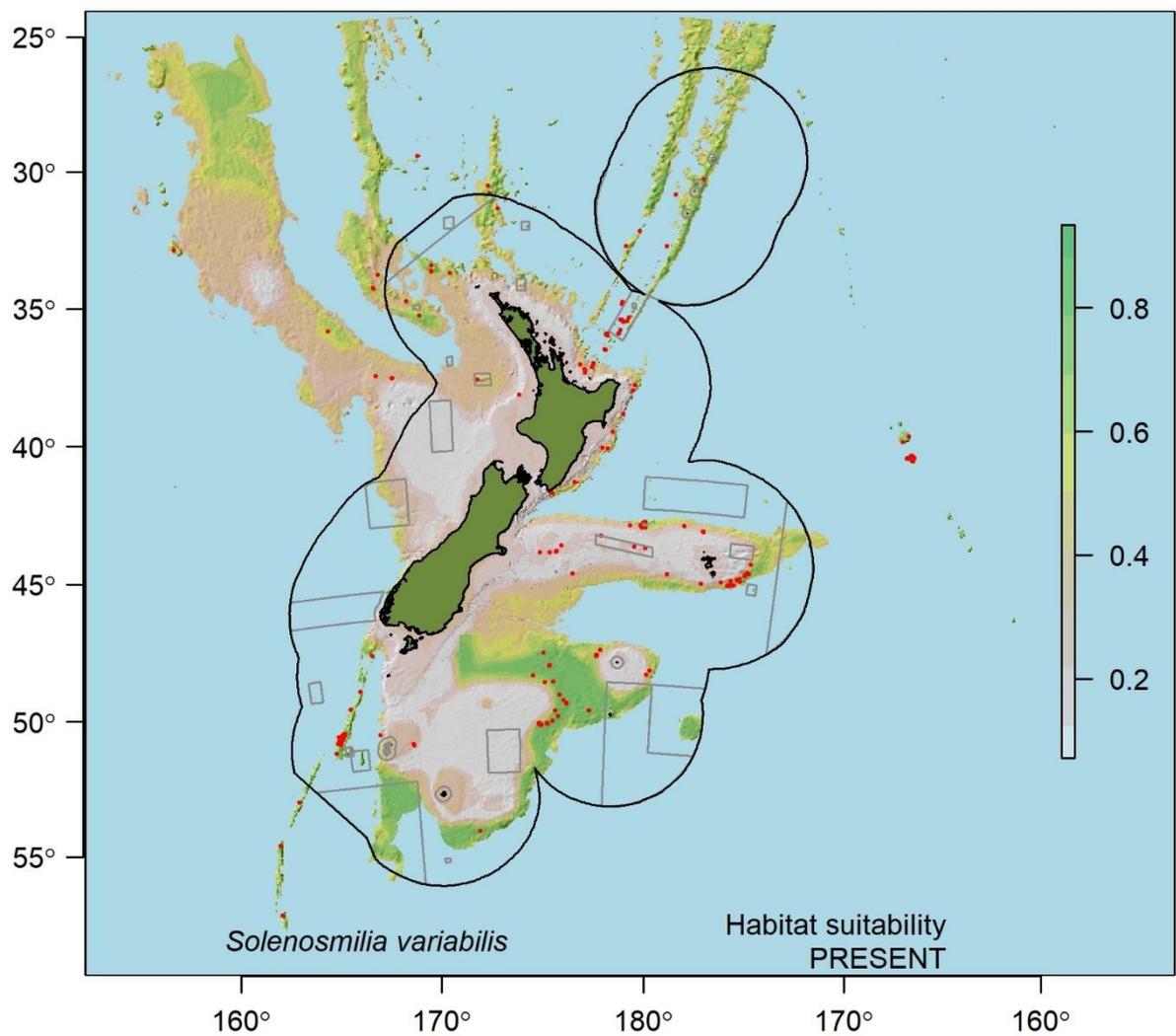


Figure 3-6: *Solenosmilia variabilis*. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

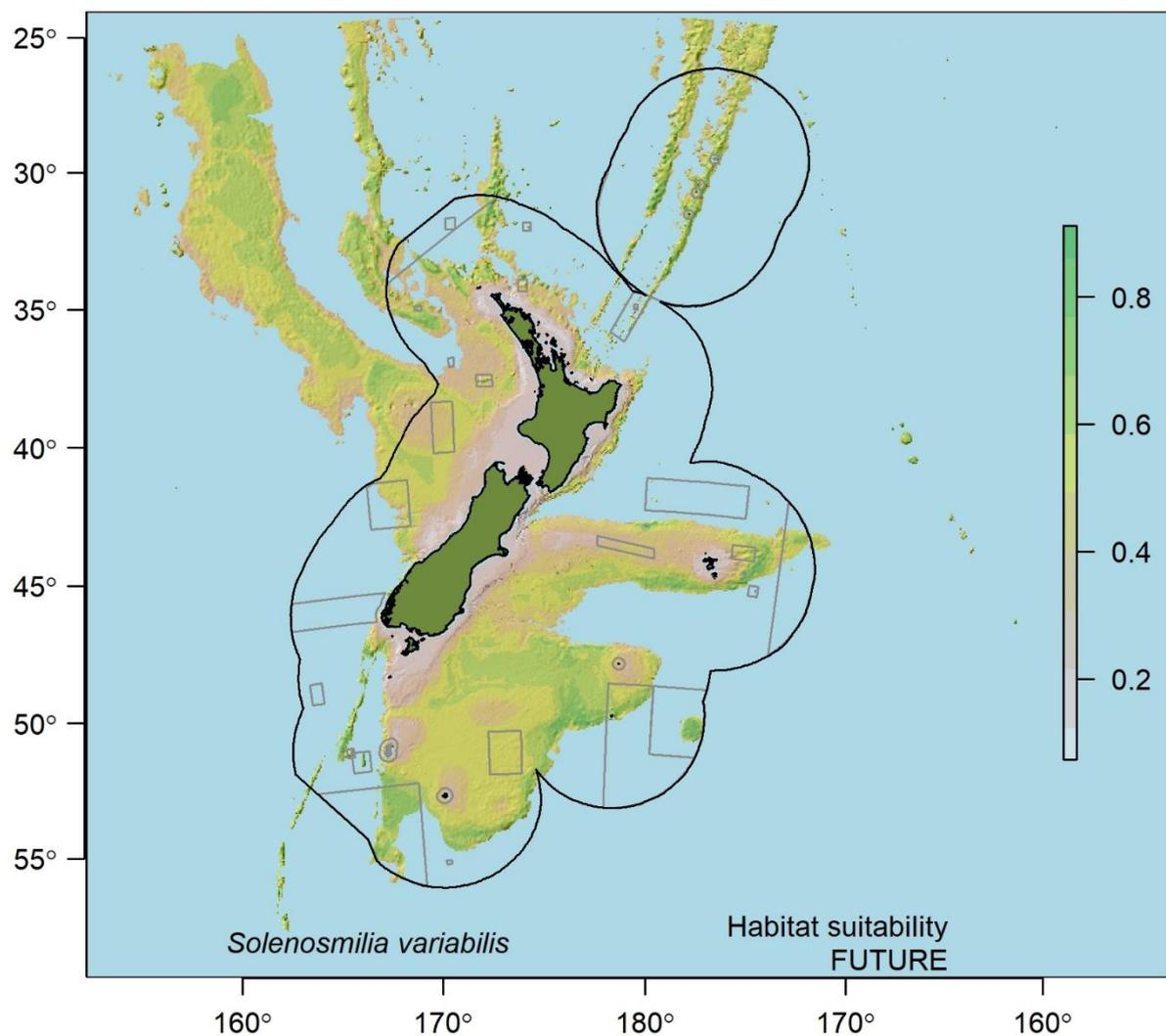


Figure 3-7: *Solenosmilia variabilis*. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

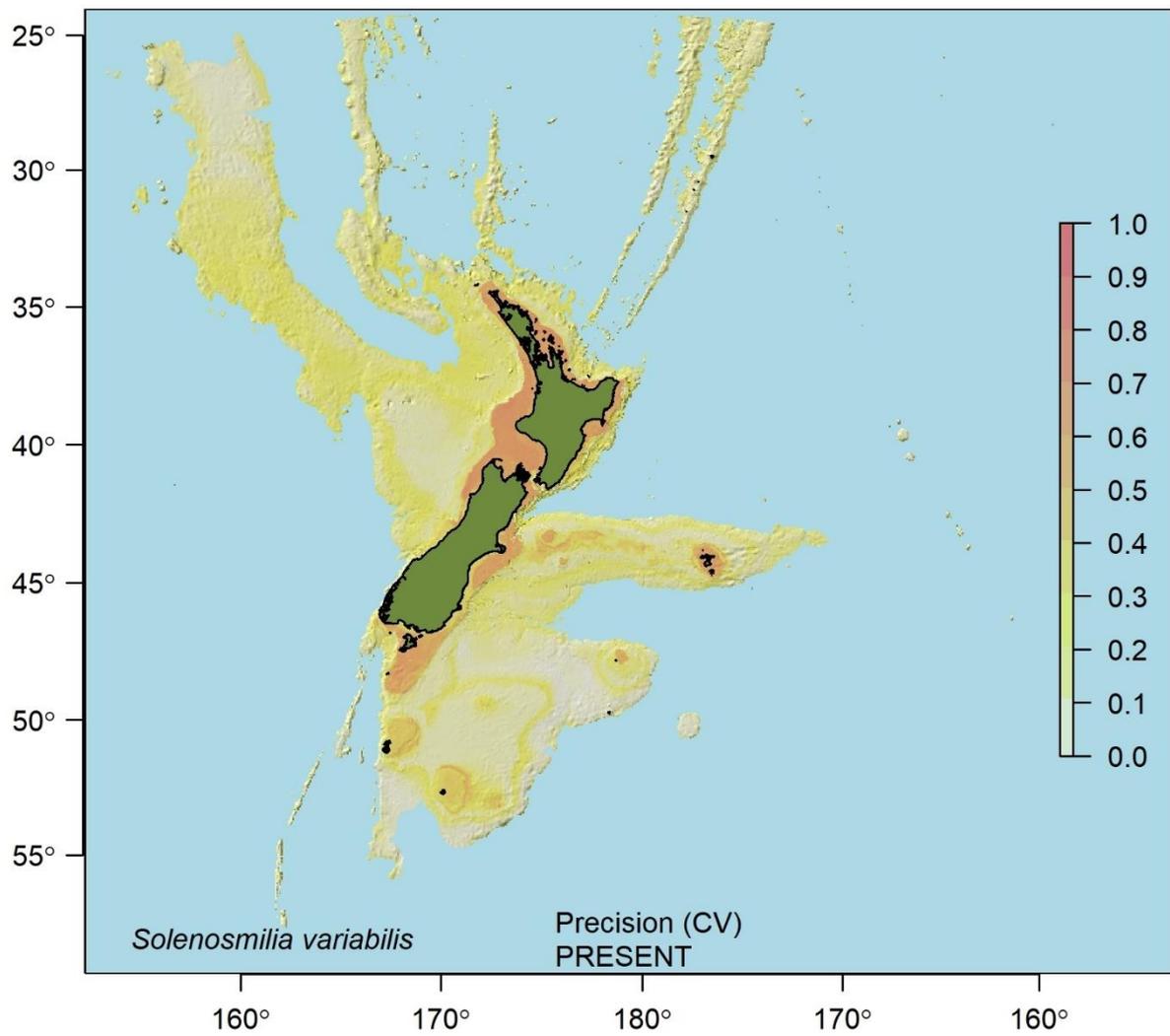


Figure 3-8: *Solenosmilia variabilis*. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

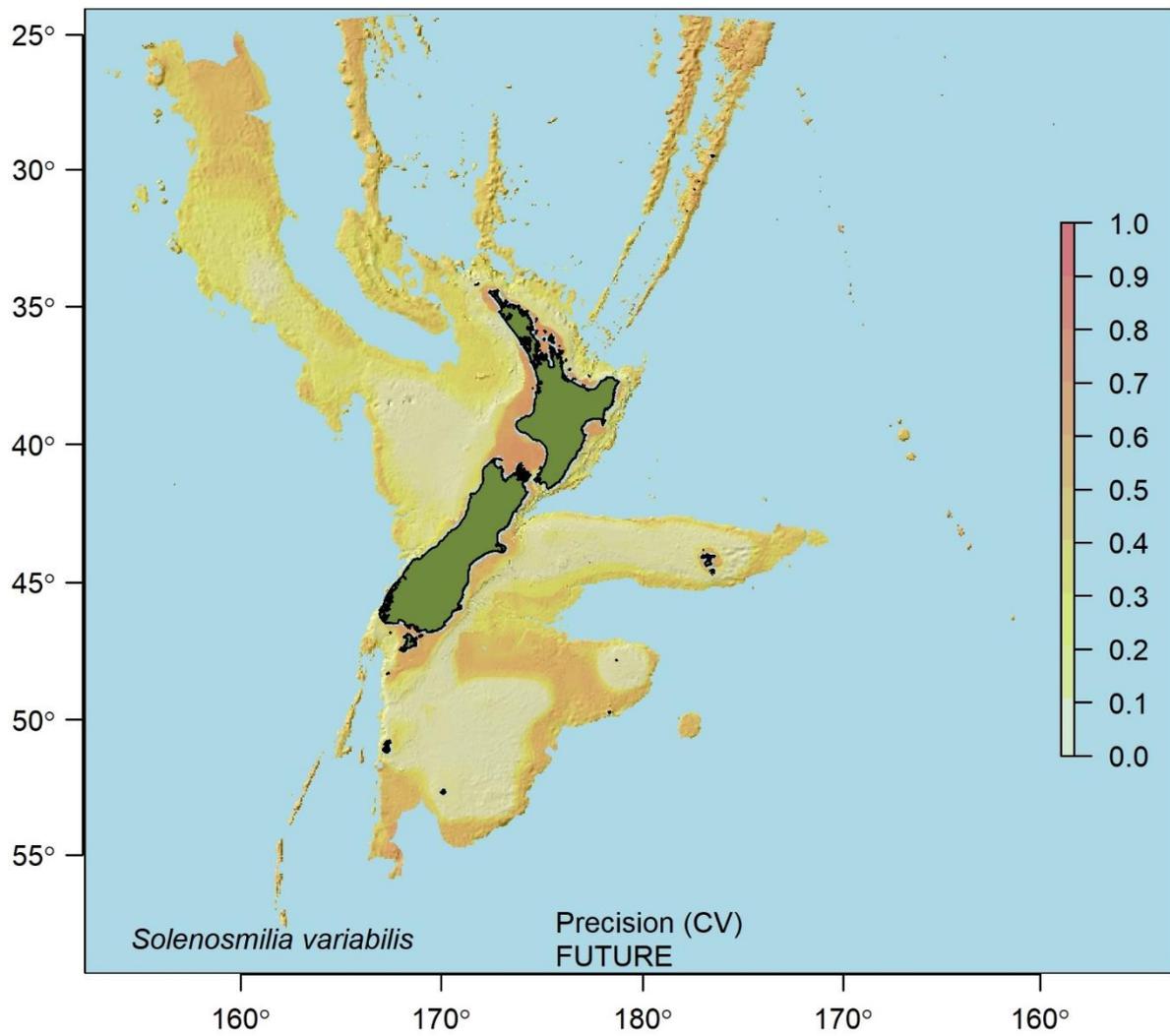


Figure 3-9: *Solenosmilia variabilis*. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

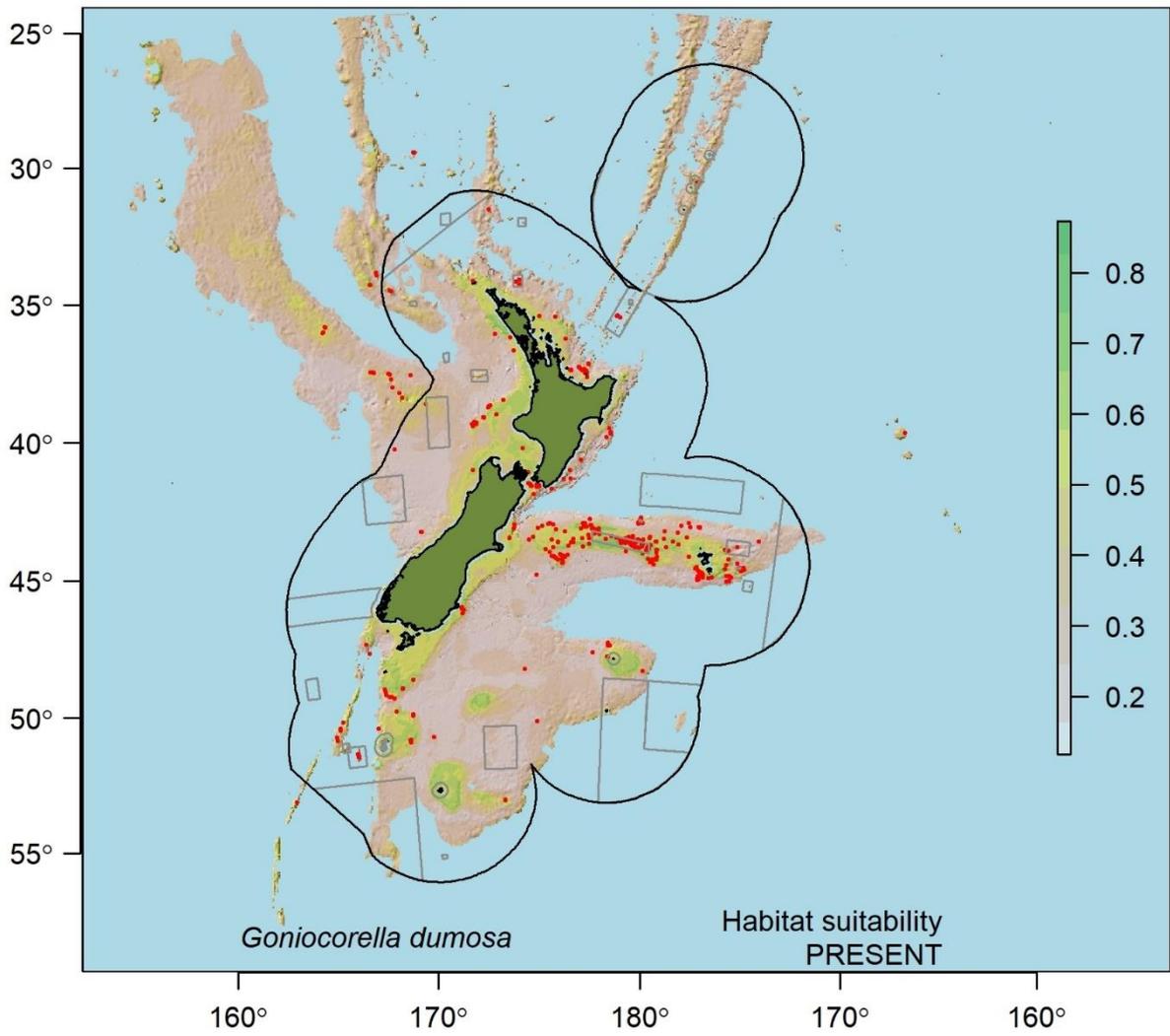


Figure 3-10: *Goniocorella dumosa*. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

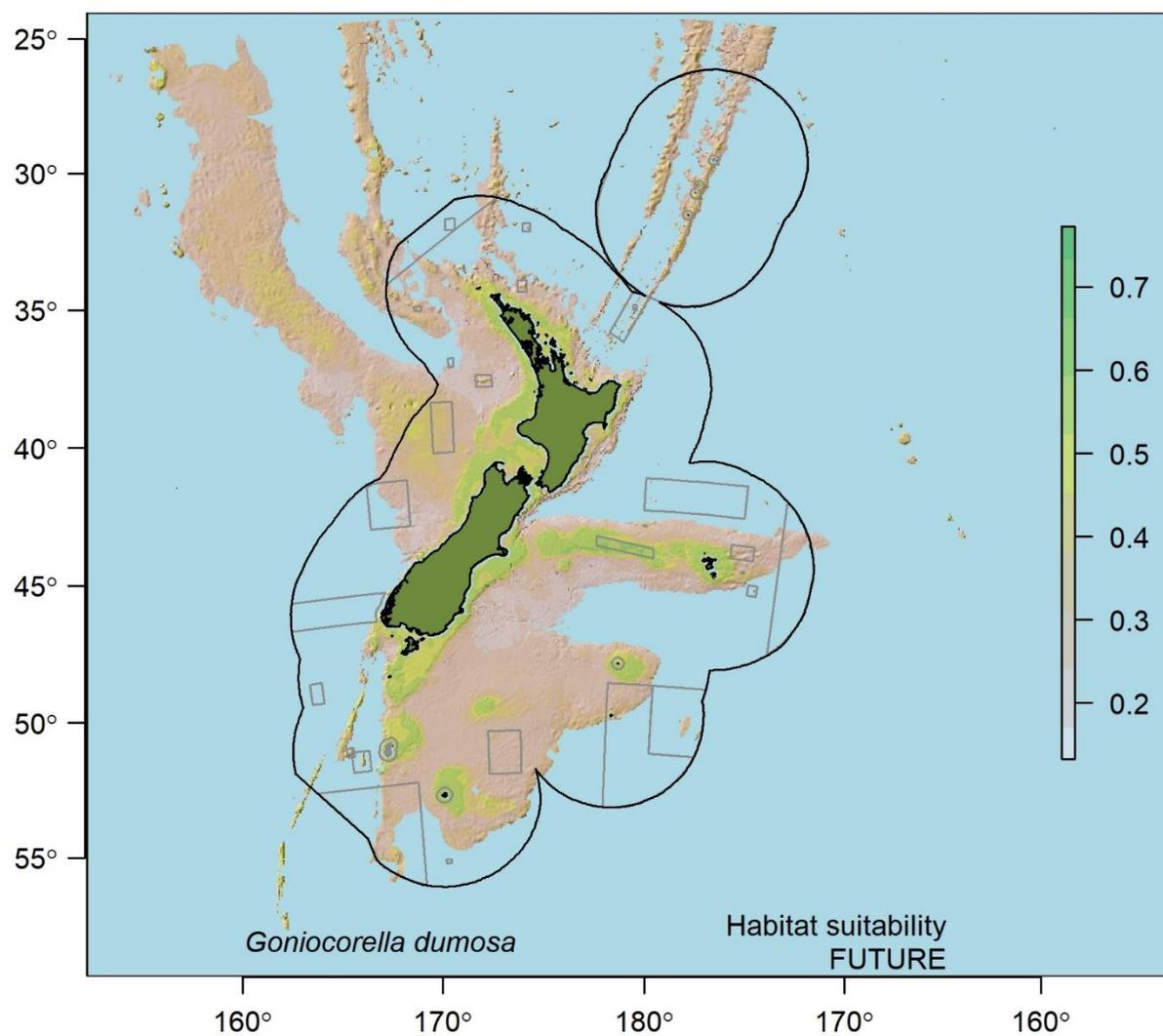


Figure 3-11: *Goniocorella dumosa*. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

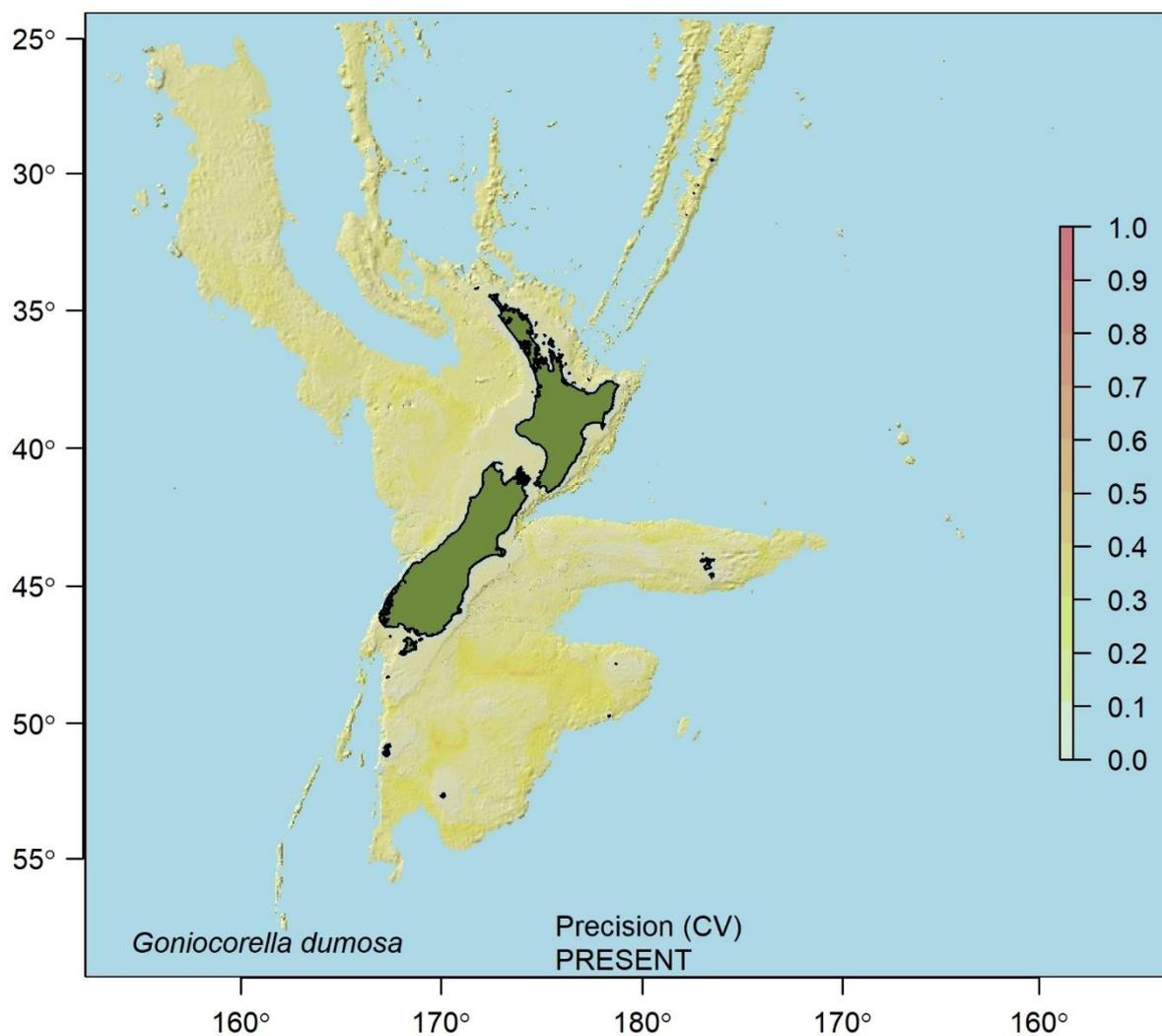


Figure 3-12: *Goniocorella dumosa*. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

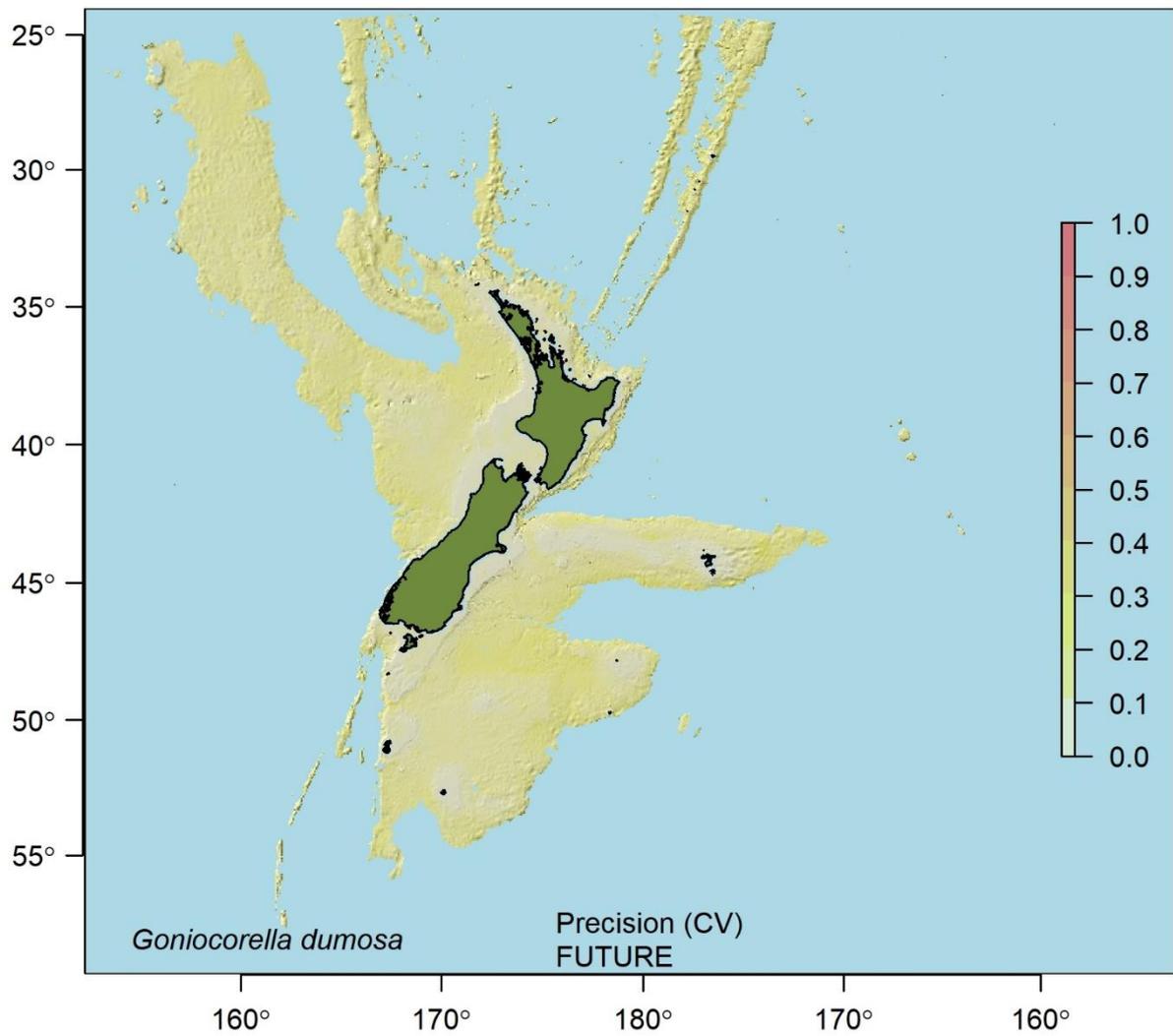


Figure 3-13: *Goniocorella dumosa*. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

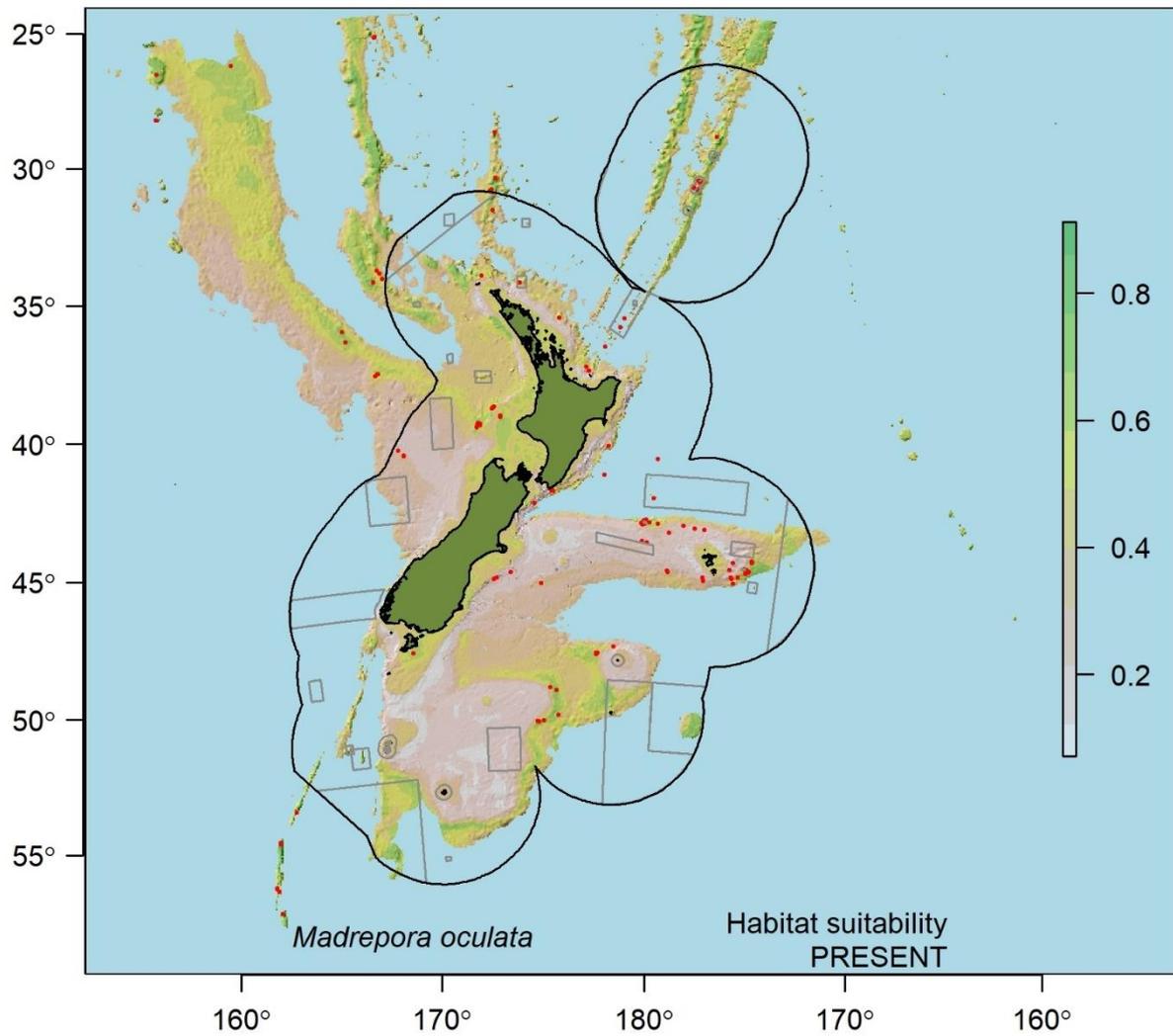


Figure 3-14: *Madrepora oculata*. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

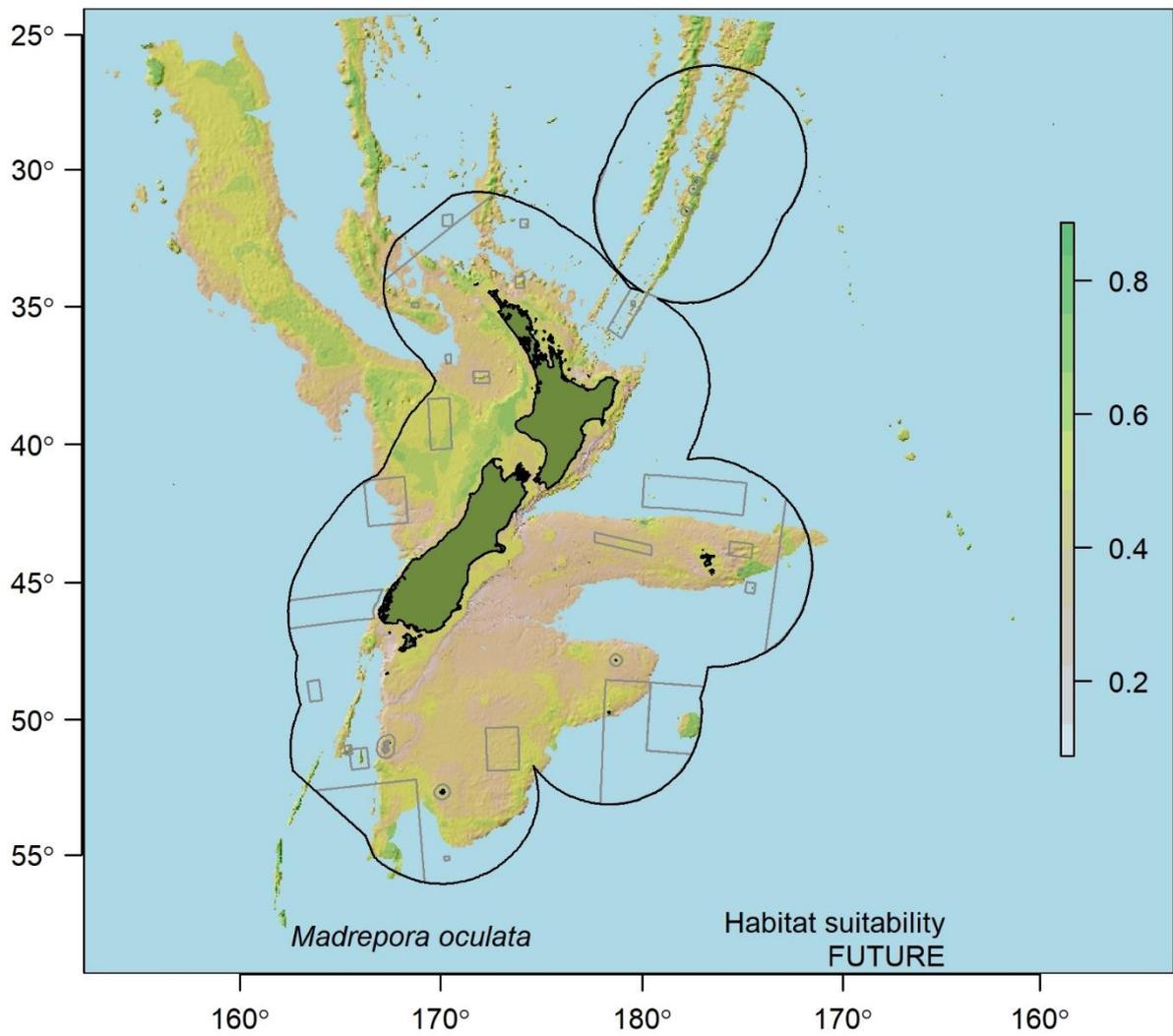


Figure 3-15: *Madrepora oculata*. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

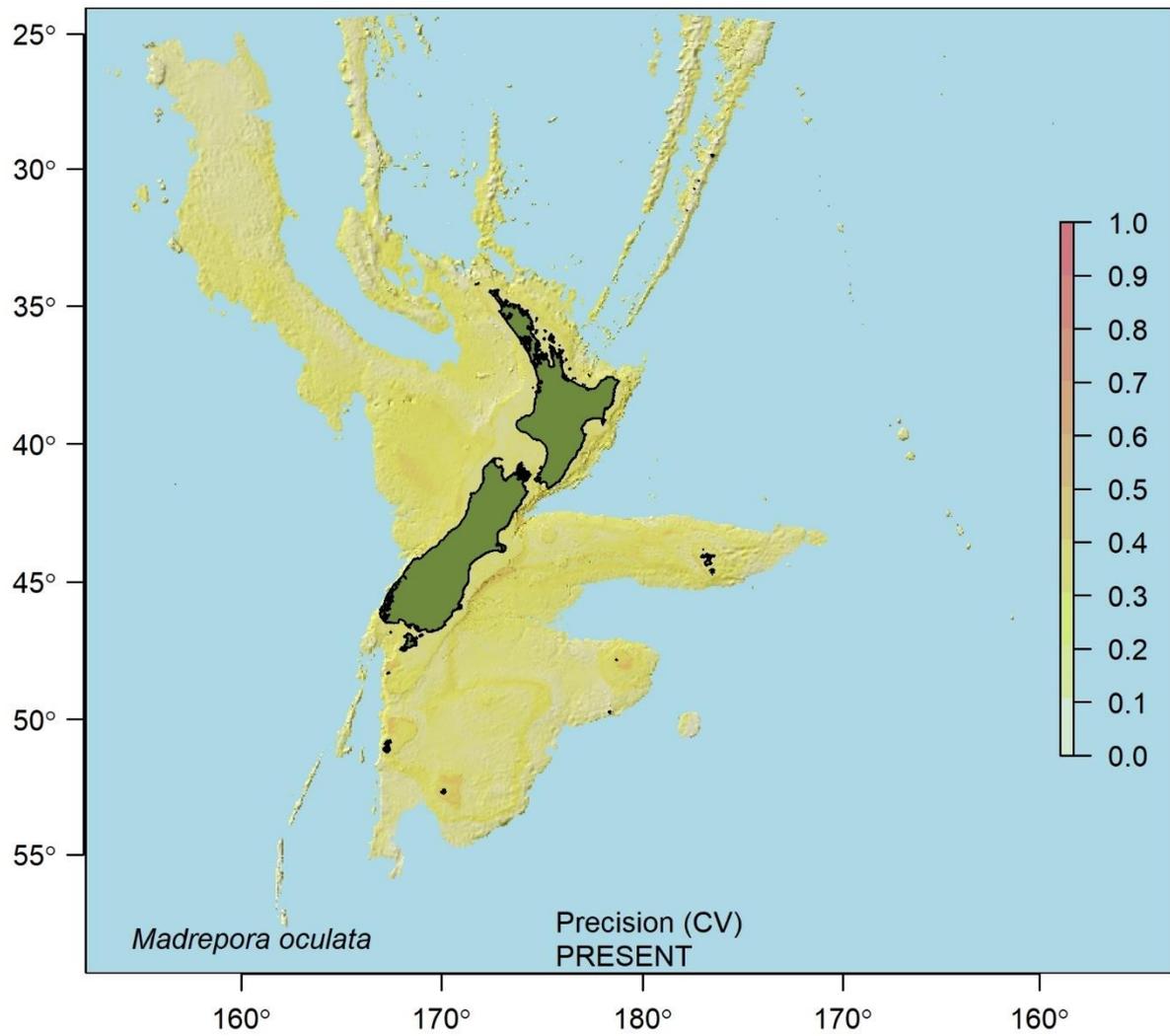


Figure 3-16: *Madrepora oculata*. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

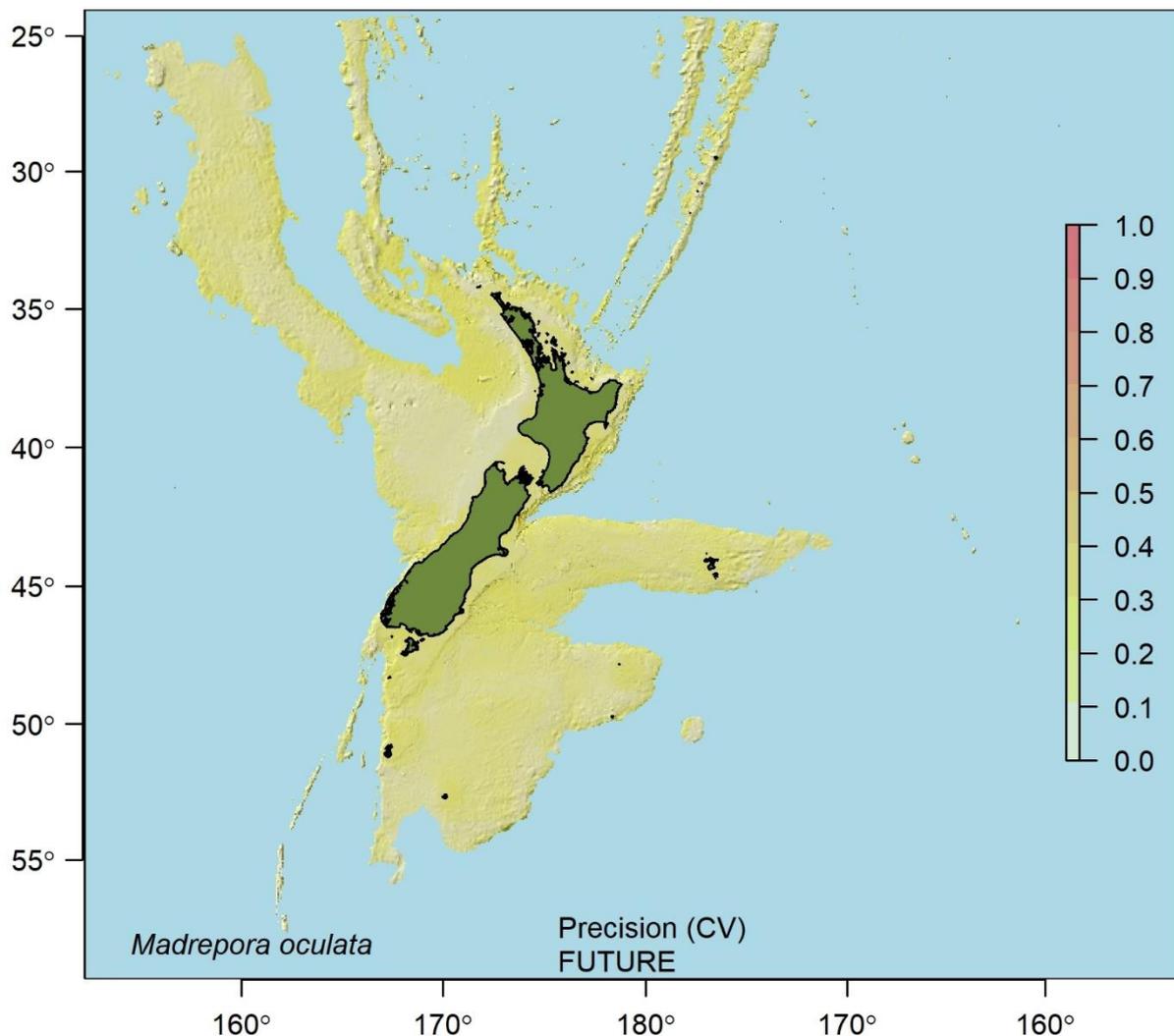


Figure 3-17: *Madrepora oculata*. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

3.4.2 Alcyonacea

Habitat suitability of *Paragorgia* spp. (Figure 3-18 to Figure 3-21) is uniformly quite low north of about 30° S, and this is not predicted to change in the future. Elsewhere, the highest suitability for this genus is predicted to currently be around the West Norfolk Ridge and deeper fringes of the southern Chatham Rise and Campbell Plateau. Habitat suitability is predicted to generally decrease in these regions in the future, with a slight shift into shallower depths indicated for the Campbell Plateau. Model precision is relatively constant across the modelled extent, although notably lower around the coastlines of the main islands.

Predicted present habitat suitability of *Primnoa* spp. (Figure 3-22 to Figure 3-25) is similar to that of *Paragorgia* spp., with high suitability around the deeper areas of the Campbell and Bounty Plateaus and low over much of the Challenger Plateau and northern Chatham Rise. A slight shift of habitat suitability into shallower depths is predicted in the future, tending towards a more even distribution of suitability, and with lower suitability in some of the deeper regions. Again, there is little change in suitability expected for this taxon in the future in regions north of about 30 °S. Model precision tends

to be greatest where habitat suitability is greater, notably increasing across the shallower reaches of the Campbell Plateau in the future.

For the *Corallium* spp. precious corals (Figure 3-26 to Figure 3-29), habitat suitability is currently greatest in the north and is uniformly high across all depth ranges encountered north of about 30° S in the west and 35° S in the east. Suitability is low over much of the rises and plateaus around New Zealand, but there are areas of higher suitability in deeper water in the easternmost Chatham Rise, and deeper reaches of the Campbell and Bounty Plateaus. Habitat suitability is predicted in the future to decrease in all the currently highly suitable areas and increase slightly in some shallower regions of the Challenger Plateau and Lord Howe Rise. Model precision tends to be greatest in areas of high habitat suitability and remains the same or increases for future predictions.

Patterns of present habitat suitability for bamboo corals *Keratoisis* spp. and *Lepidisis* spp. combined (Figure 3-30 to Figure 3-33) are similar to that for *Corallium* spp. in many areas, but differ substantially on the southern Lord Howe Rise and outer Challenger Plateau where suitability is relatively high. Habitat suitability is predicted to generally decrease in the future across the modelled region but improve slightly in shallower, currently poorly suitable, regions – especially on the Challenger Plateau. Model precision is relatively constant across the modelled region, more so and slightly lower overall for future predictions.

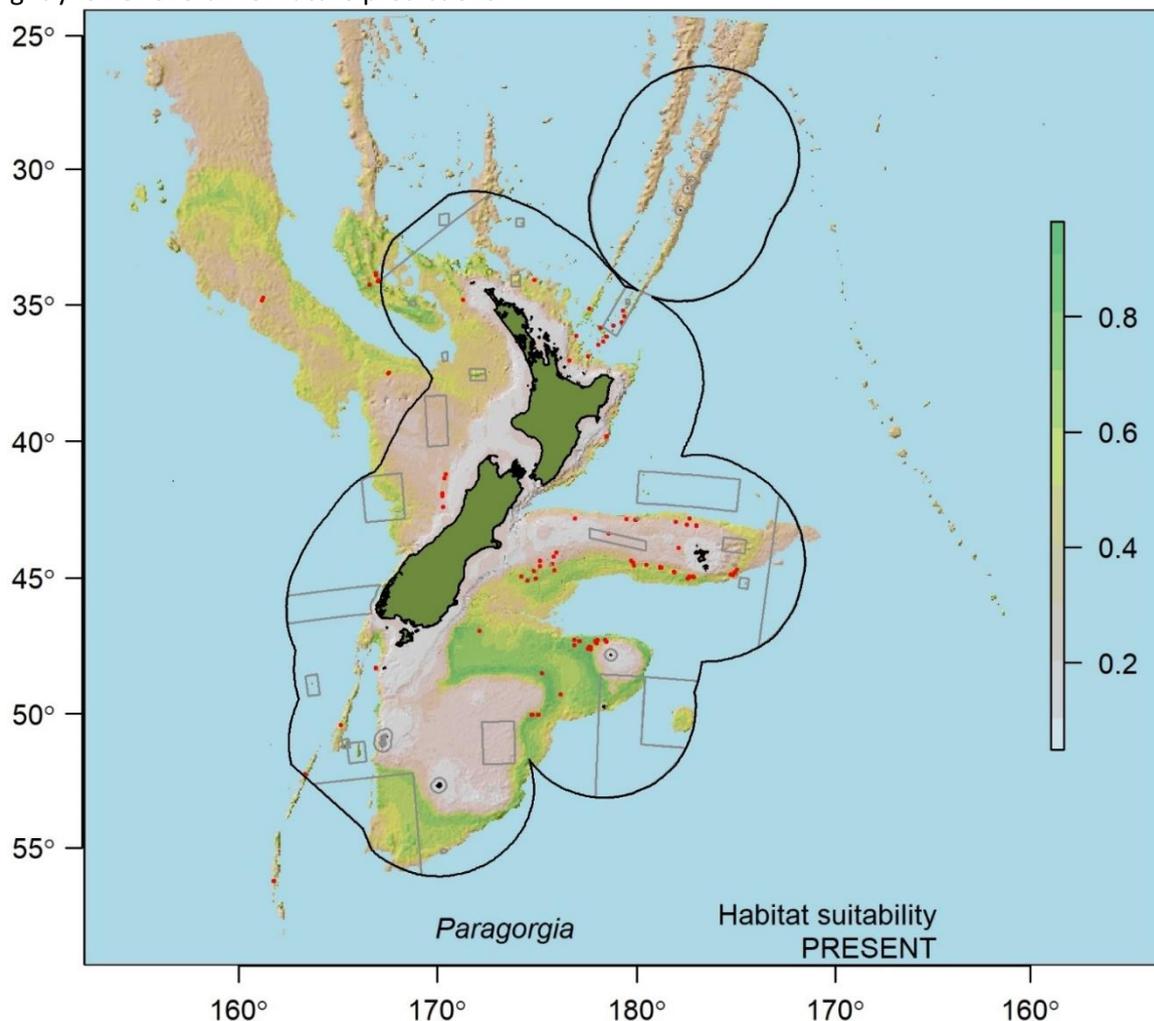


Figure 3-18: *Paragorgia* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

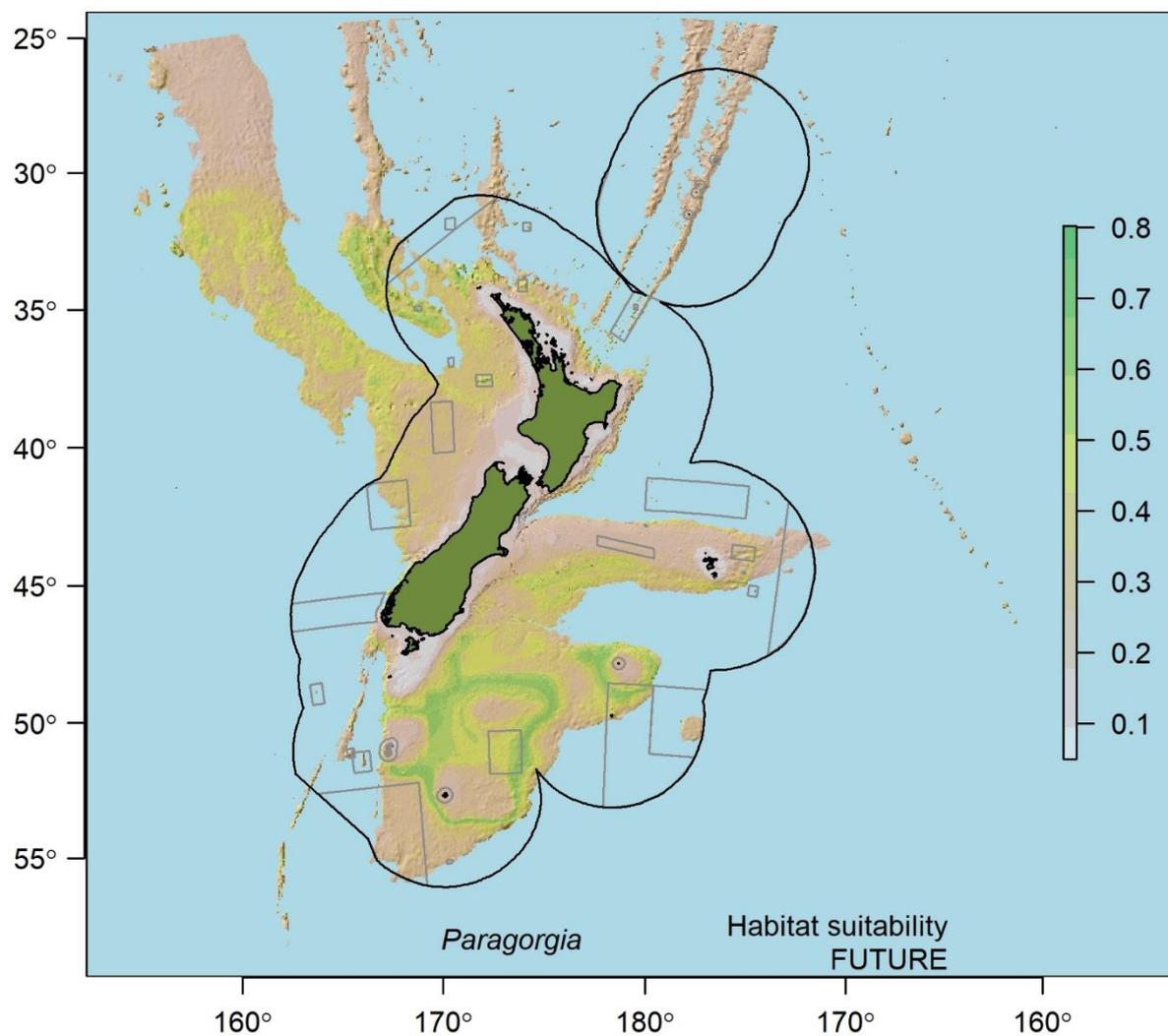


Figure 3-19: *Paragorgia* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

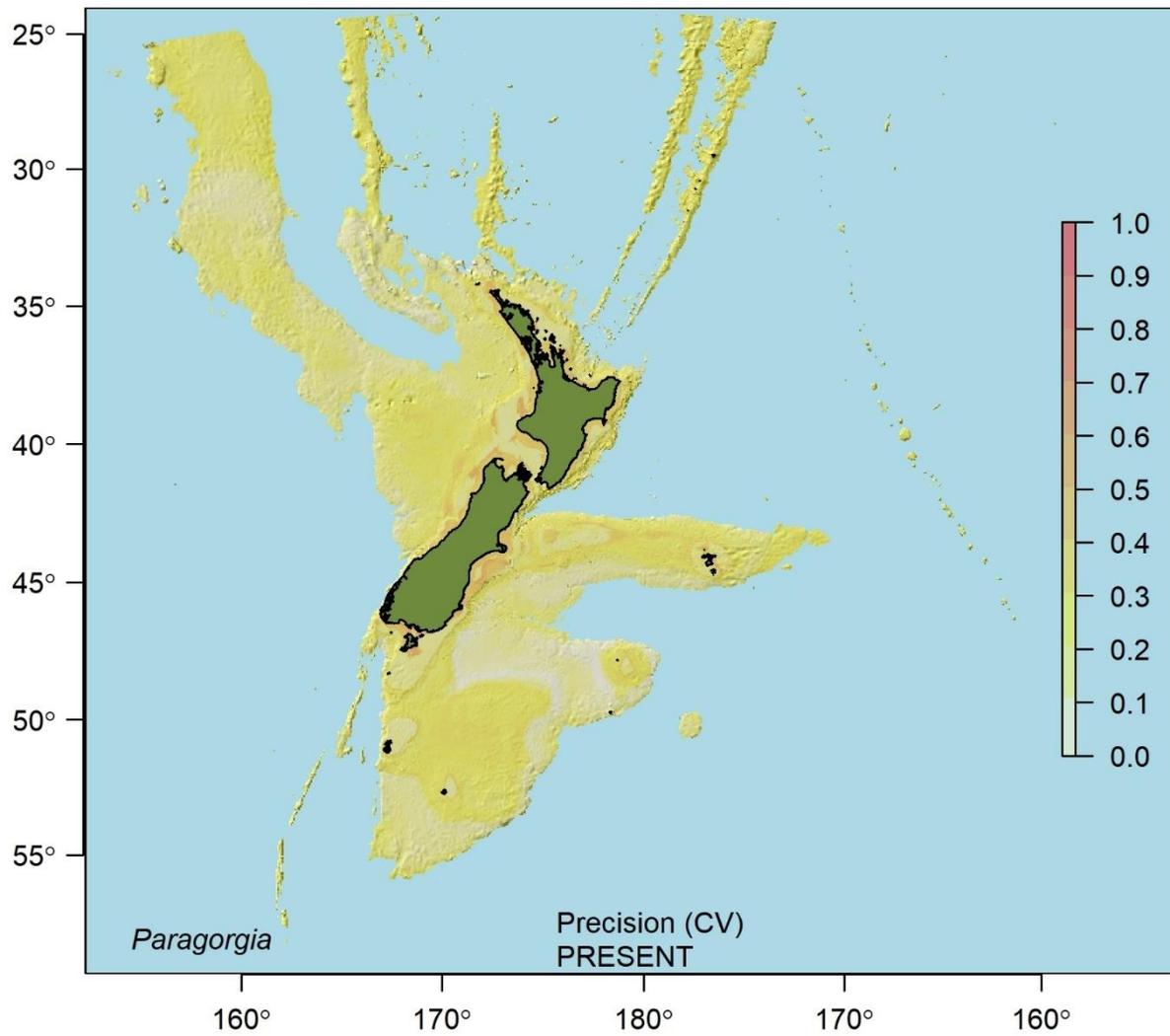


Figure 3-20: *Paragorgia* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

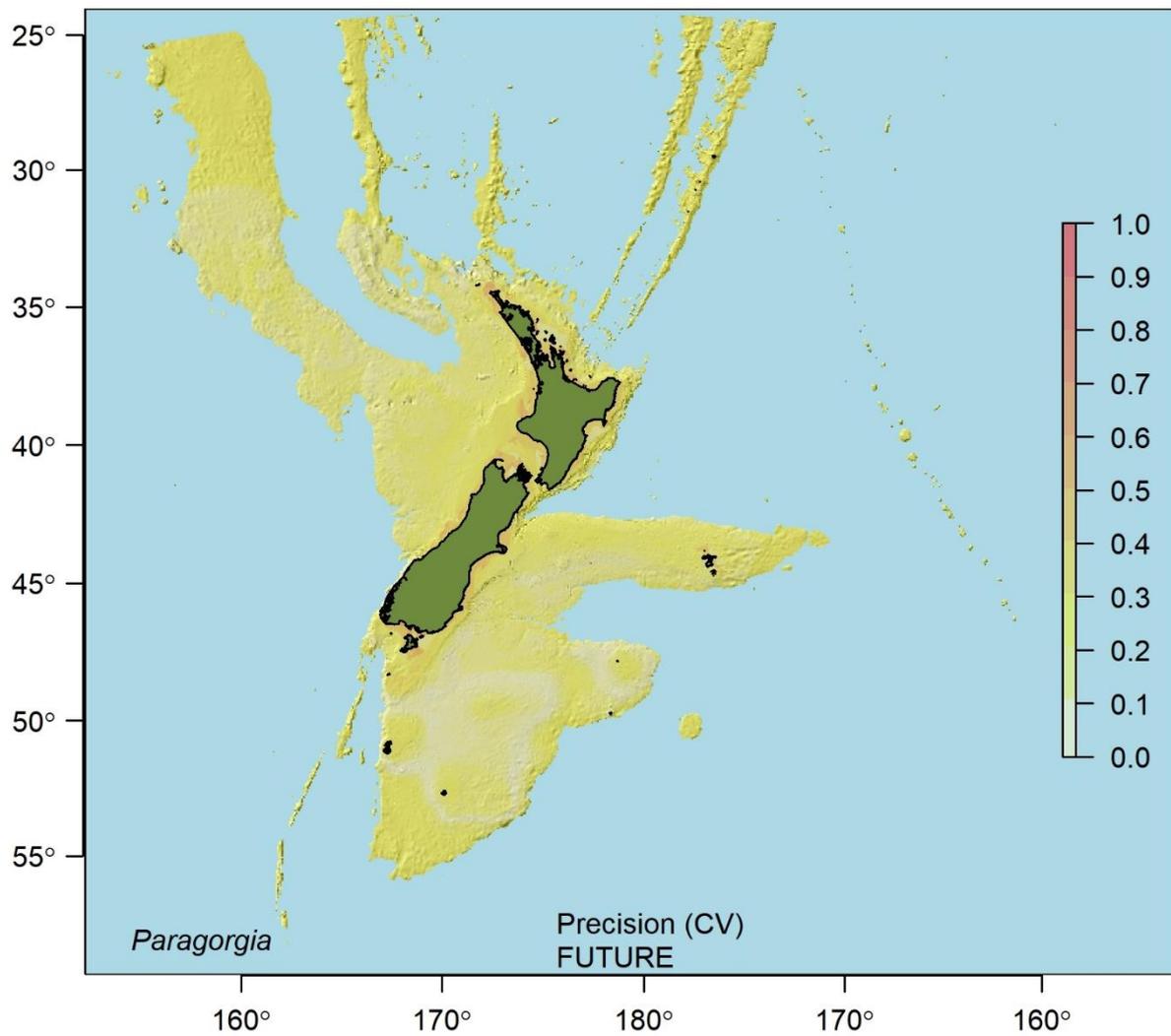


Figure 3-21: *Paragorgia* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

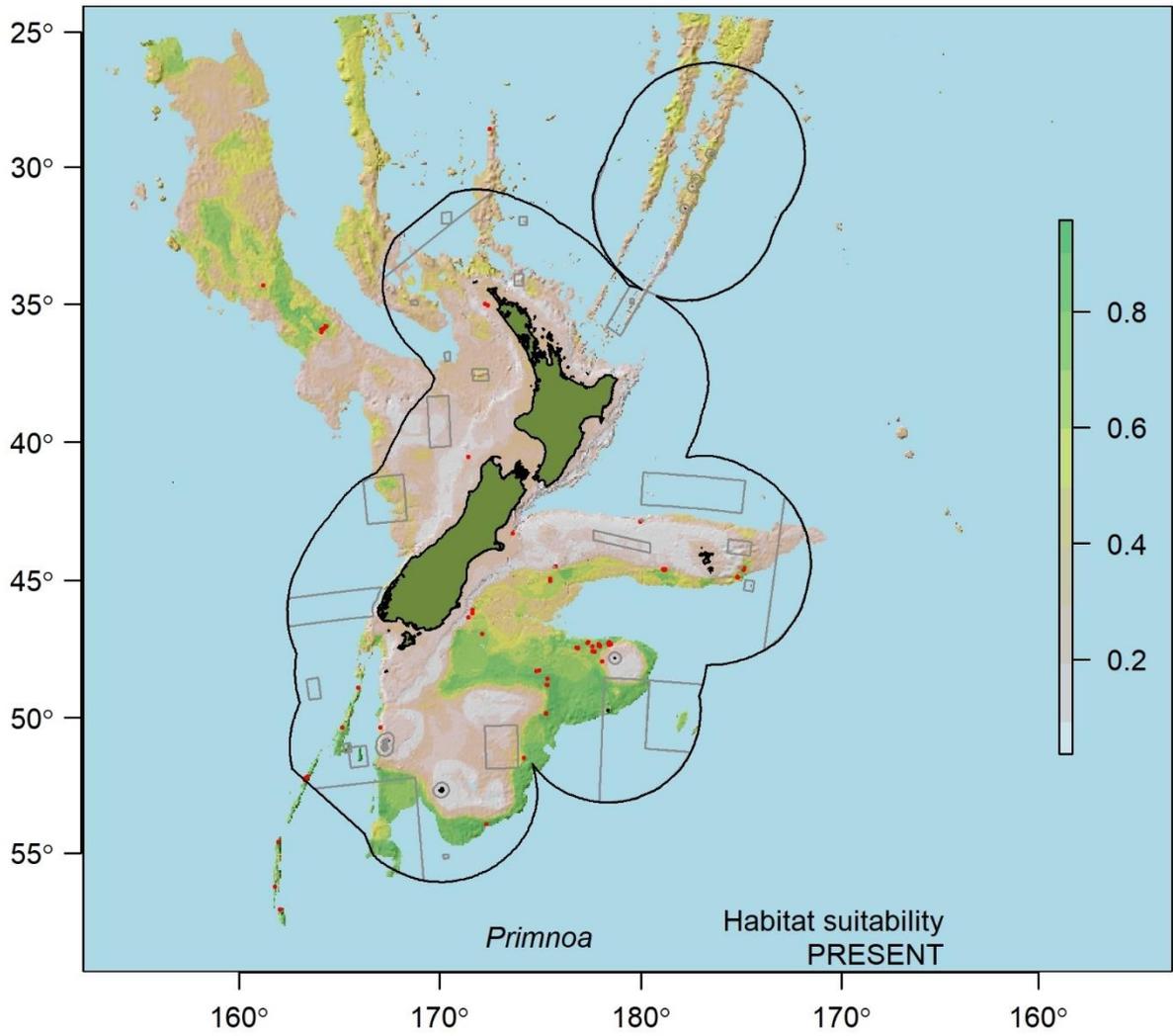


Figure 3-22: *Primnoa* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

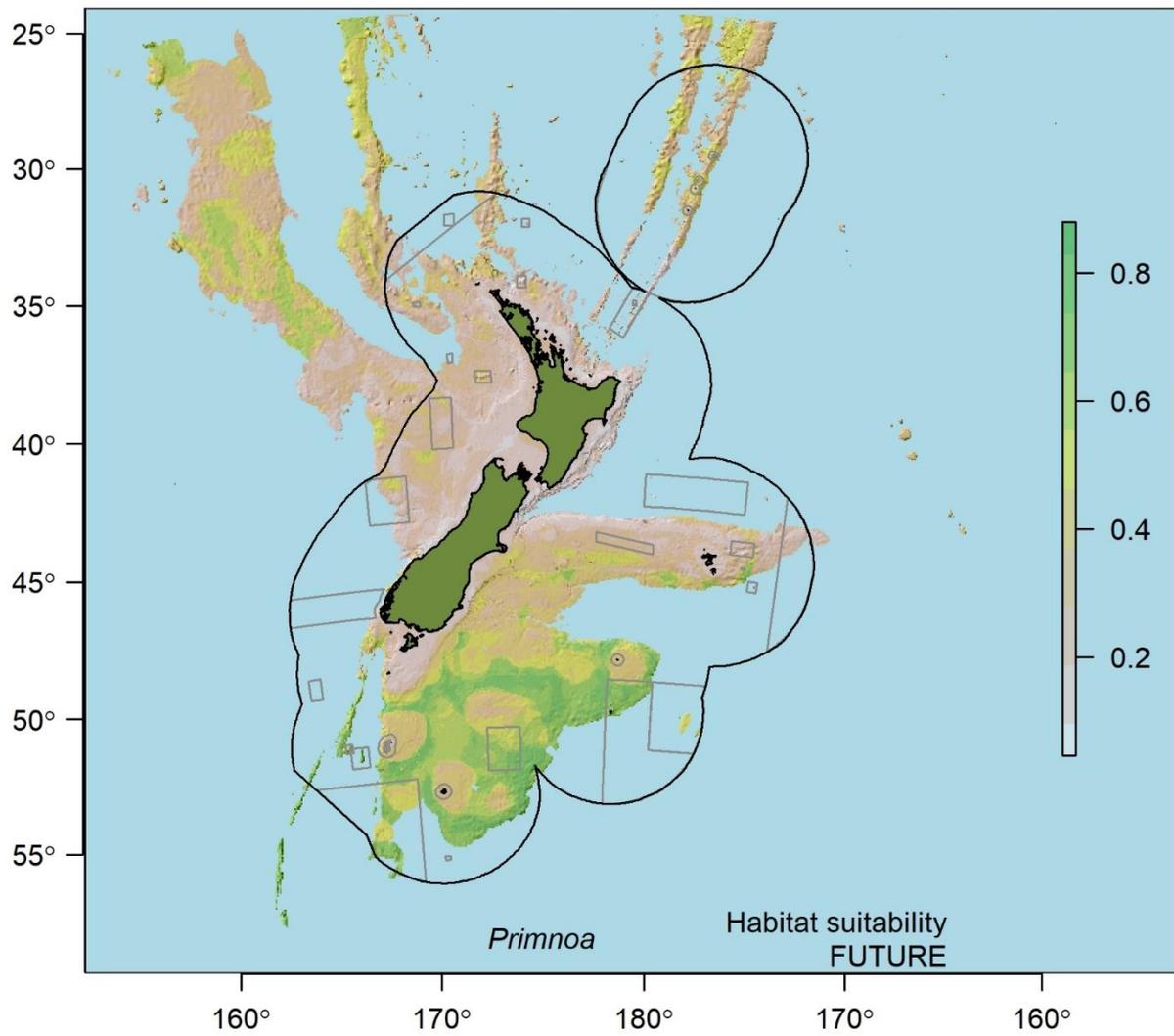


Figure 3-23: *Primnoa* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

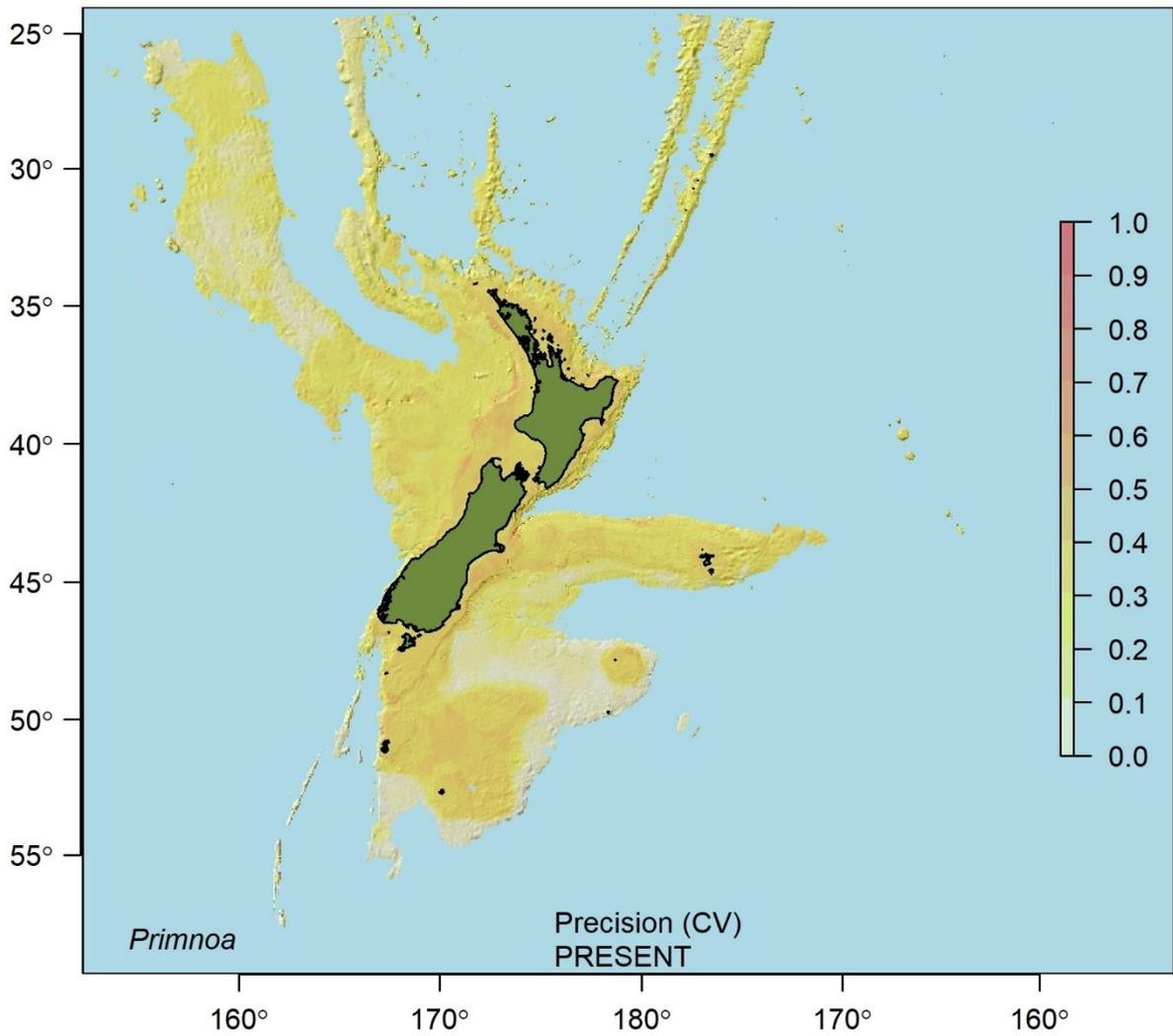


Figure 3-24: *Primnoa* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

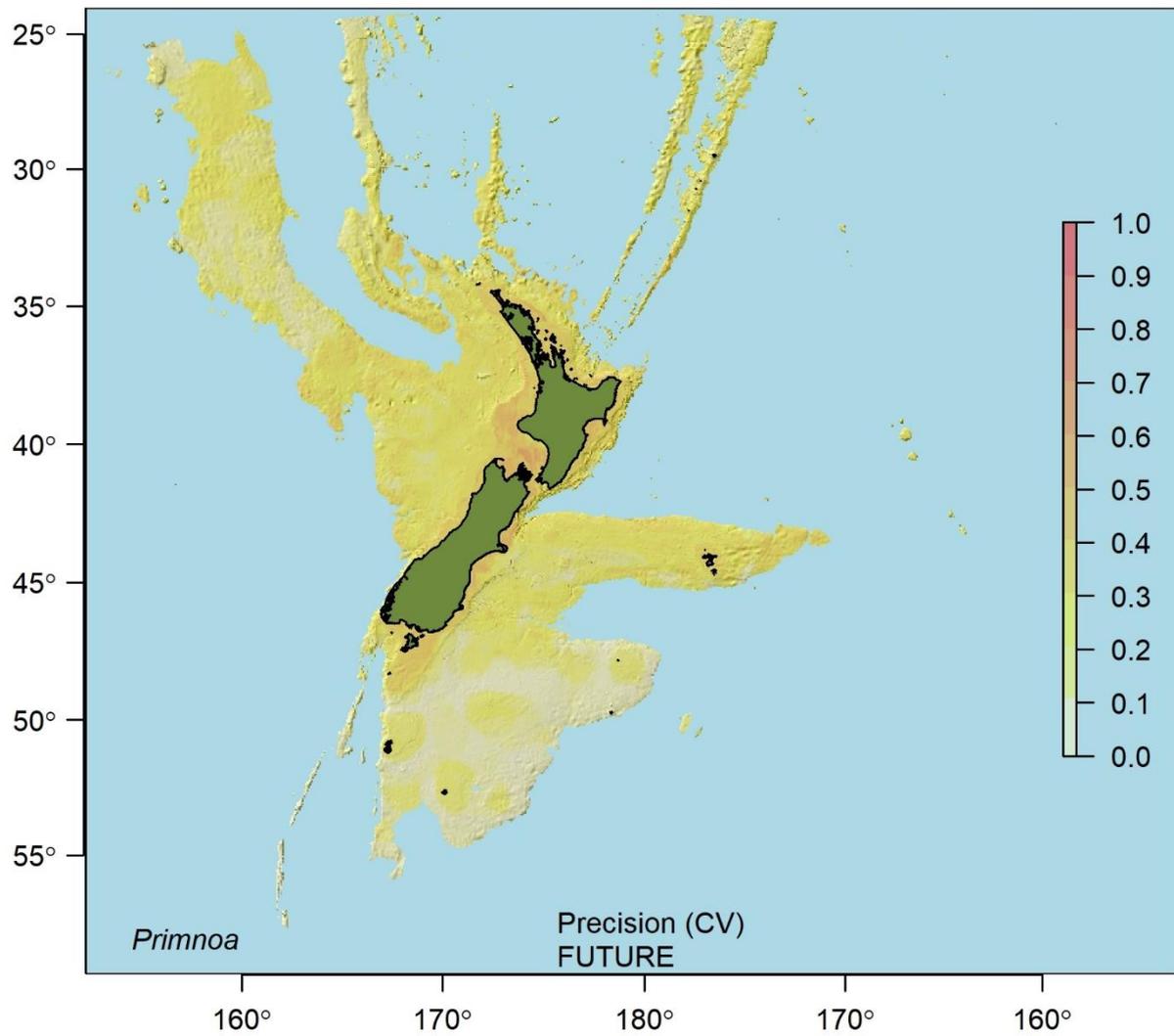


Figure 3-25: *Primnoa* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

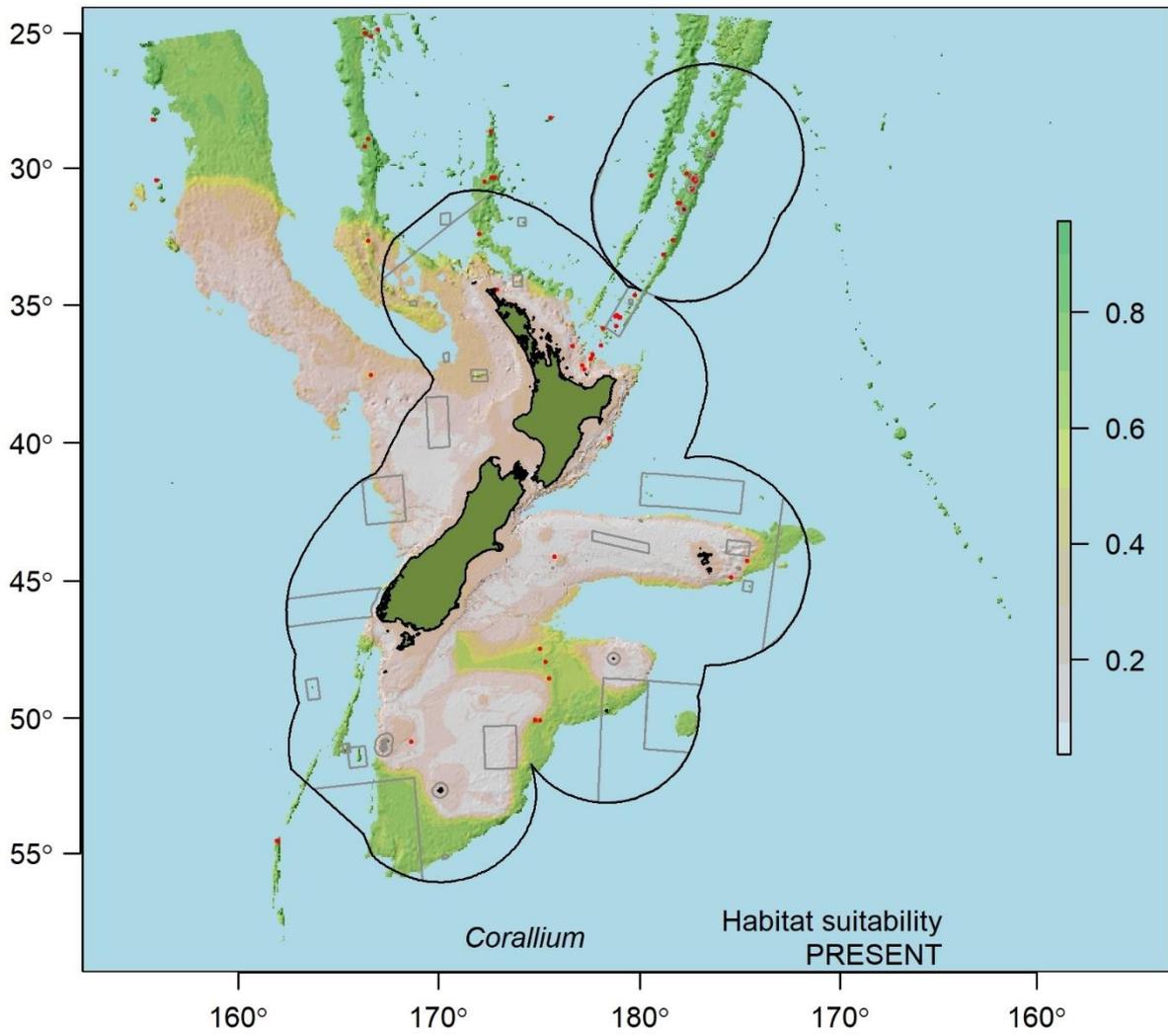


Figure 3-26: *Corallium* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

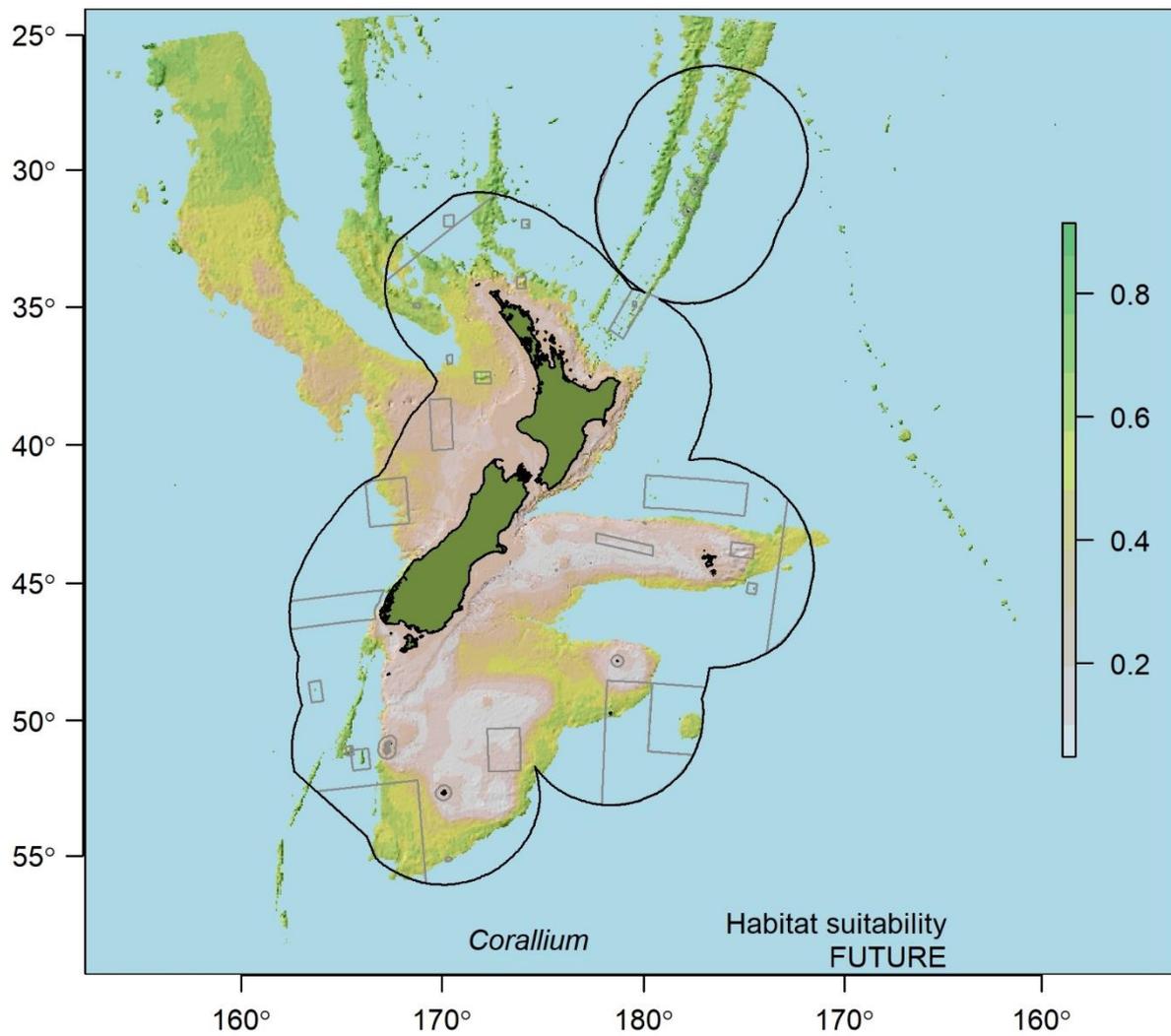


Figure 3-27: *Corallium* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

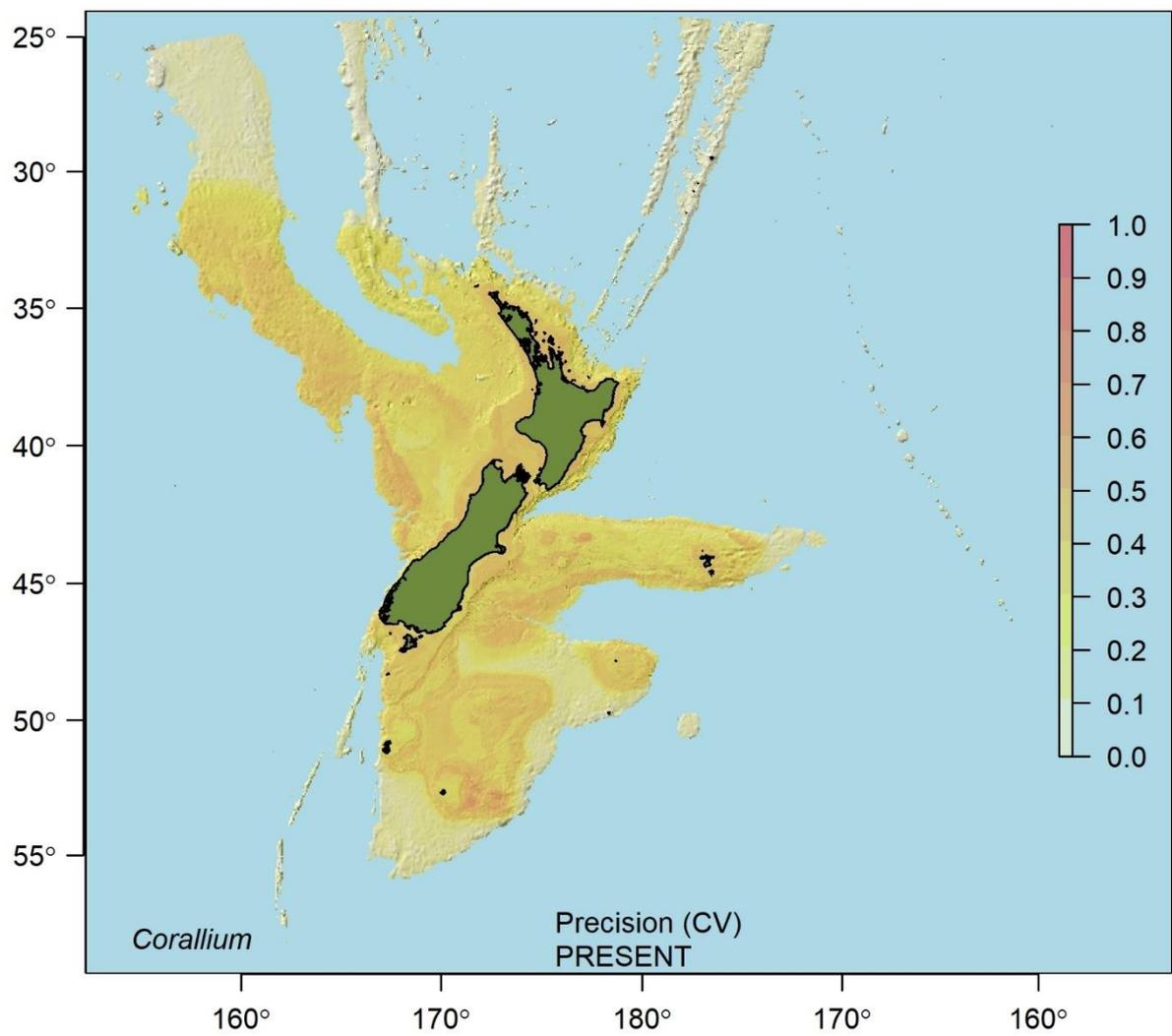


Figure 3-28: *Corallium* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

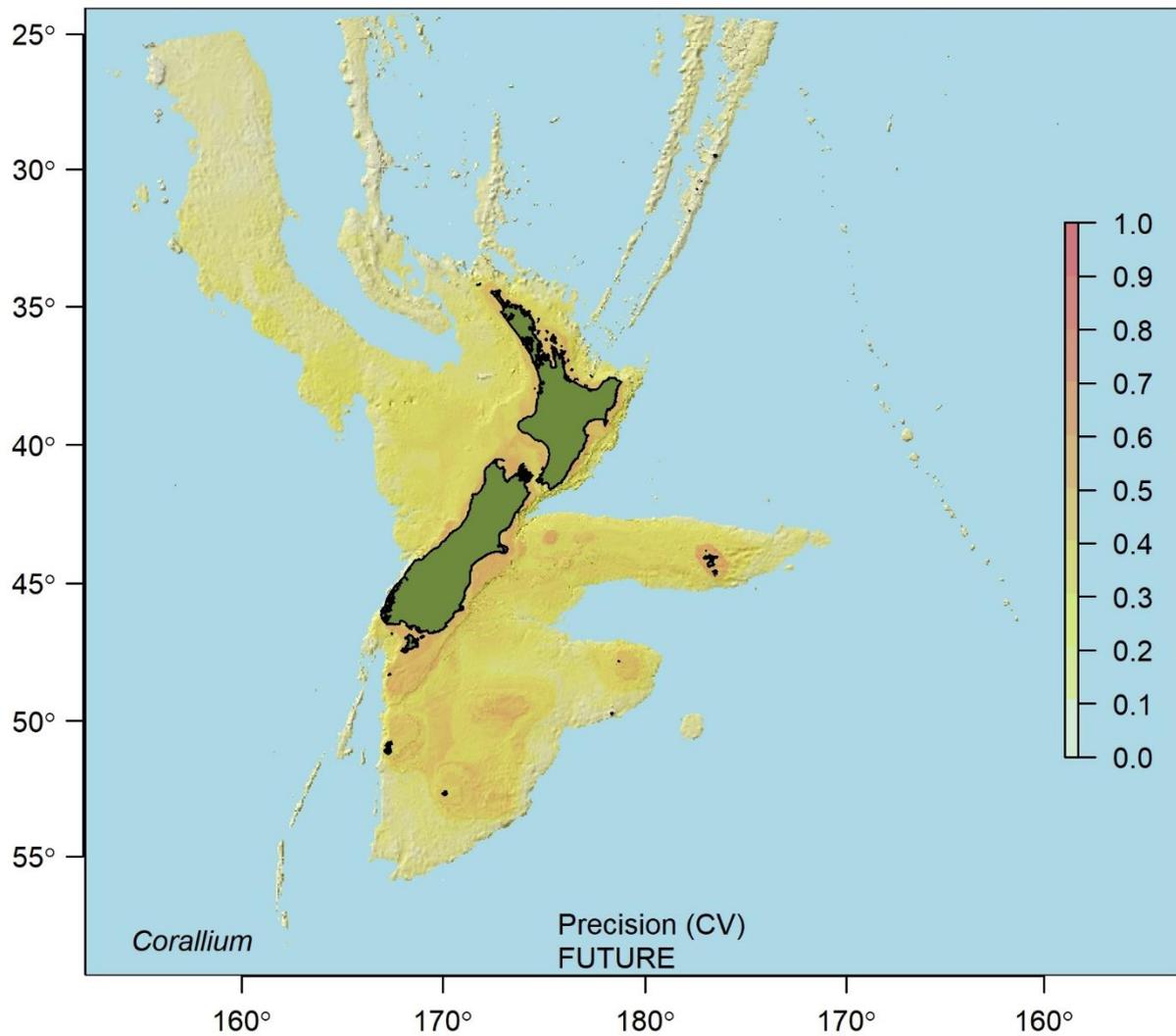


Figure 3-29: *Corallium* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

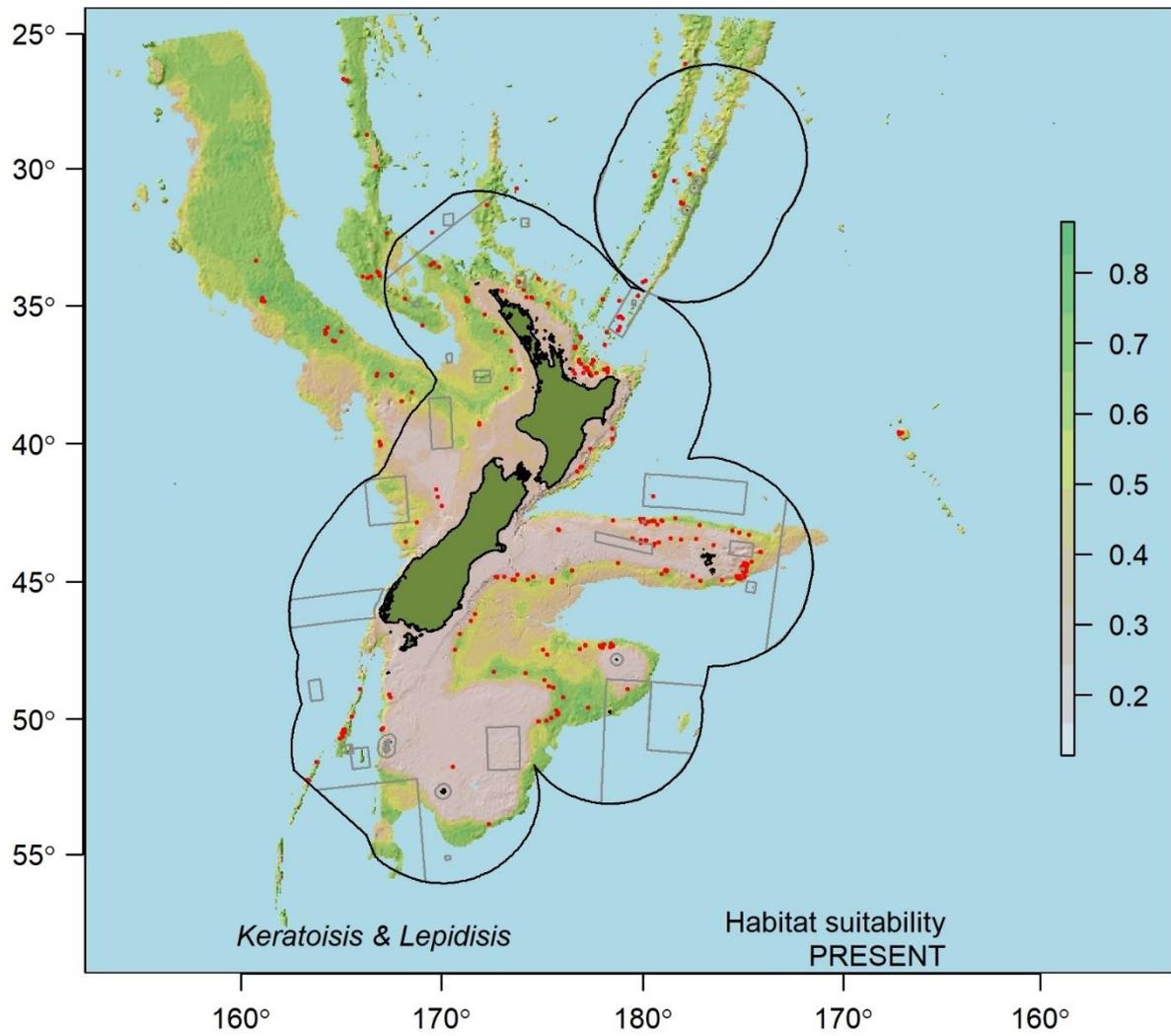


Figure 3-30: *Keratoisis* spp. and *Lepidisis* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

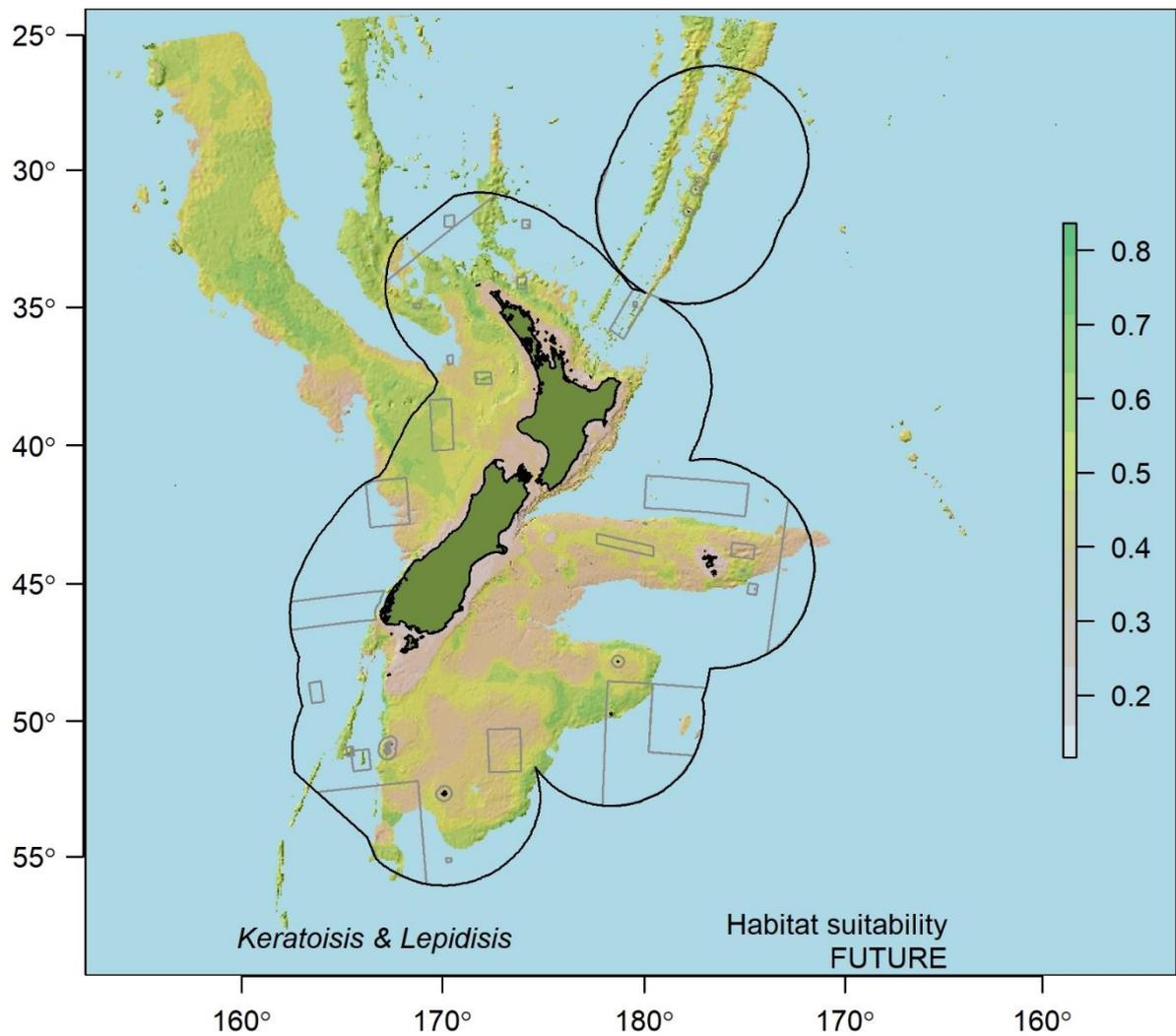


Figure 3-31: *Keratoisis* spp. and *Lepidisis* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

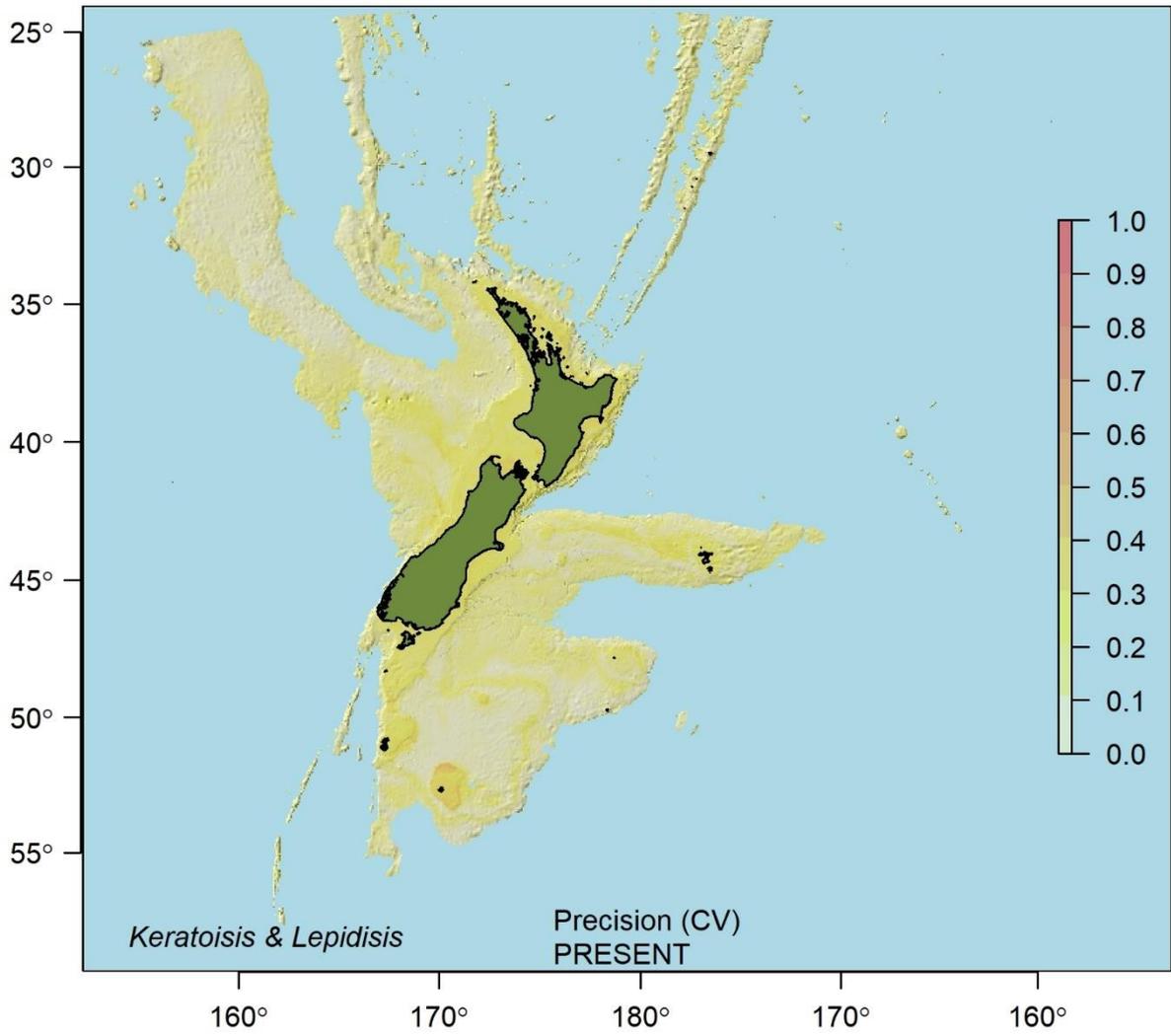


Figure 3-32: *Keratoisis* spp. and *Lepidisis* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

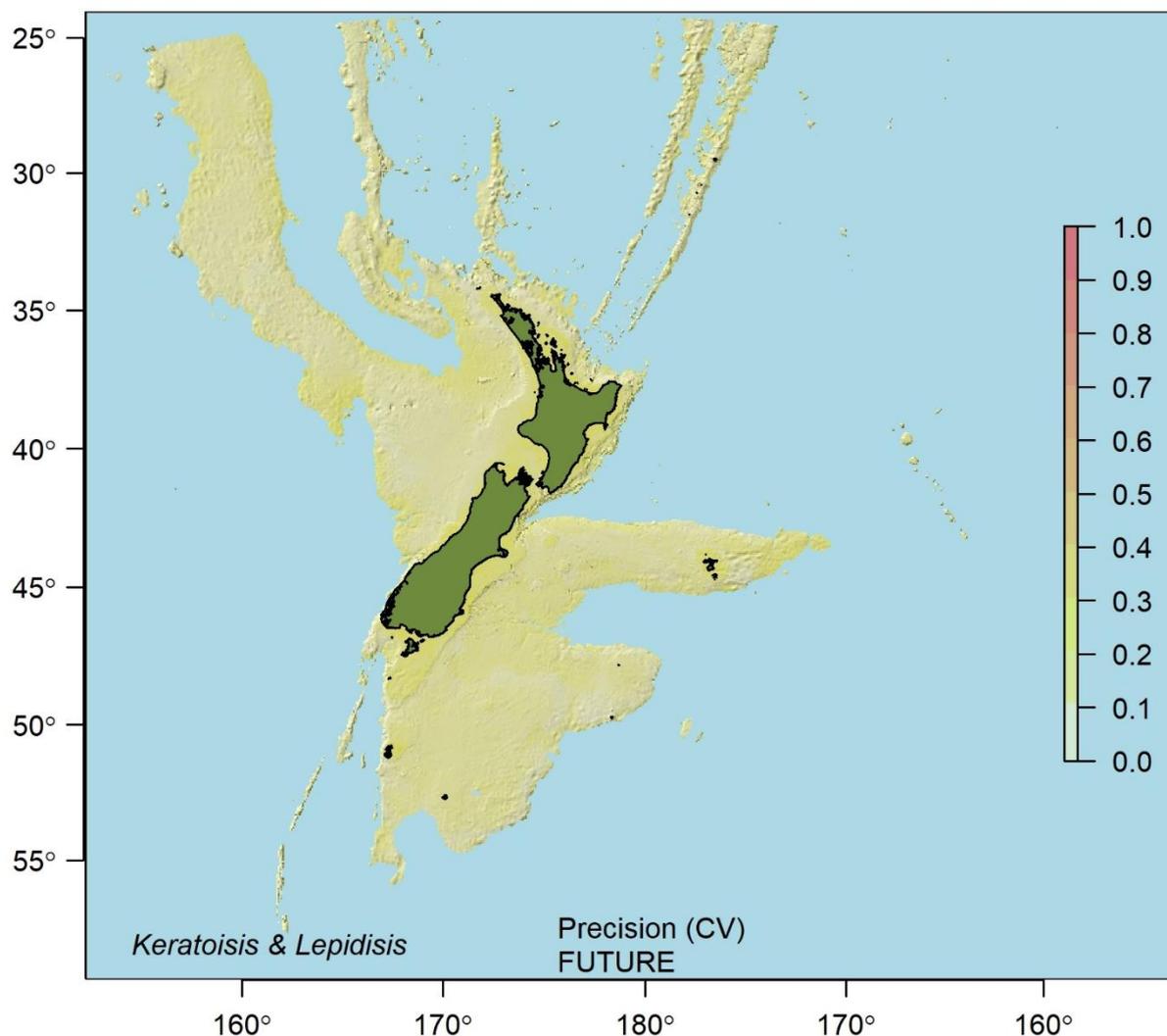


Figure 3-33: *Keratoisis* spp. and *Lepidisis* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

3.4.3 Antipatharia

The predicted present distribution of *Bathypathes* spp. (Figure 3-34 to Figure 3-37) is typical of most of the other coral groups, with highest suitability around the northern topographic features, the deeper fringes of the rises and plateaus adjacent to mainland New Zealand, and the seamount chains and ridges in the east (Louisville Seamount Chain) and south (Macquarie Ridge). This distribution is predicted to remain relatively stable in the future, with slightly decreasing suitability in the north and a subtle evening-out of suitability in the south. Model precision is greatest in the northwest and lowest in coastal regions, and is more uniform for future predictions.

Habitat suitability predicts a more limited present distribution for *Leiopathes* spp. (Figure 3-38 to Figure 3-41), with high levels of suitability centred around an area comprising the southern Lord Howe Rise, West Norfolk Ridge, and the margin of the continental shelf on northern Challenger Plateau and around the North Island. Models predict slightly lower suitability over much of this area

in the future, but slightly increased suitability notable on the western Challenger Plateau. Small areas of high habitat suitability in deeper parts of the eastern Chatham Rise become slightly less suitable in the future. Model precision, greatest in regions of highest and lowest suitability, is generally more uniform for future predictions.

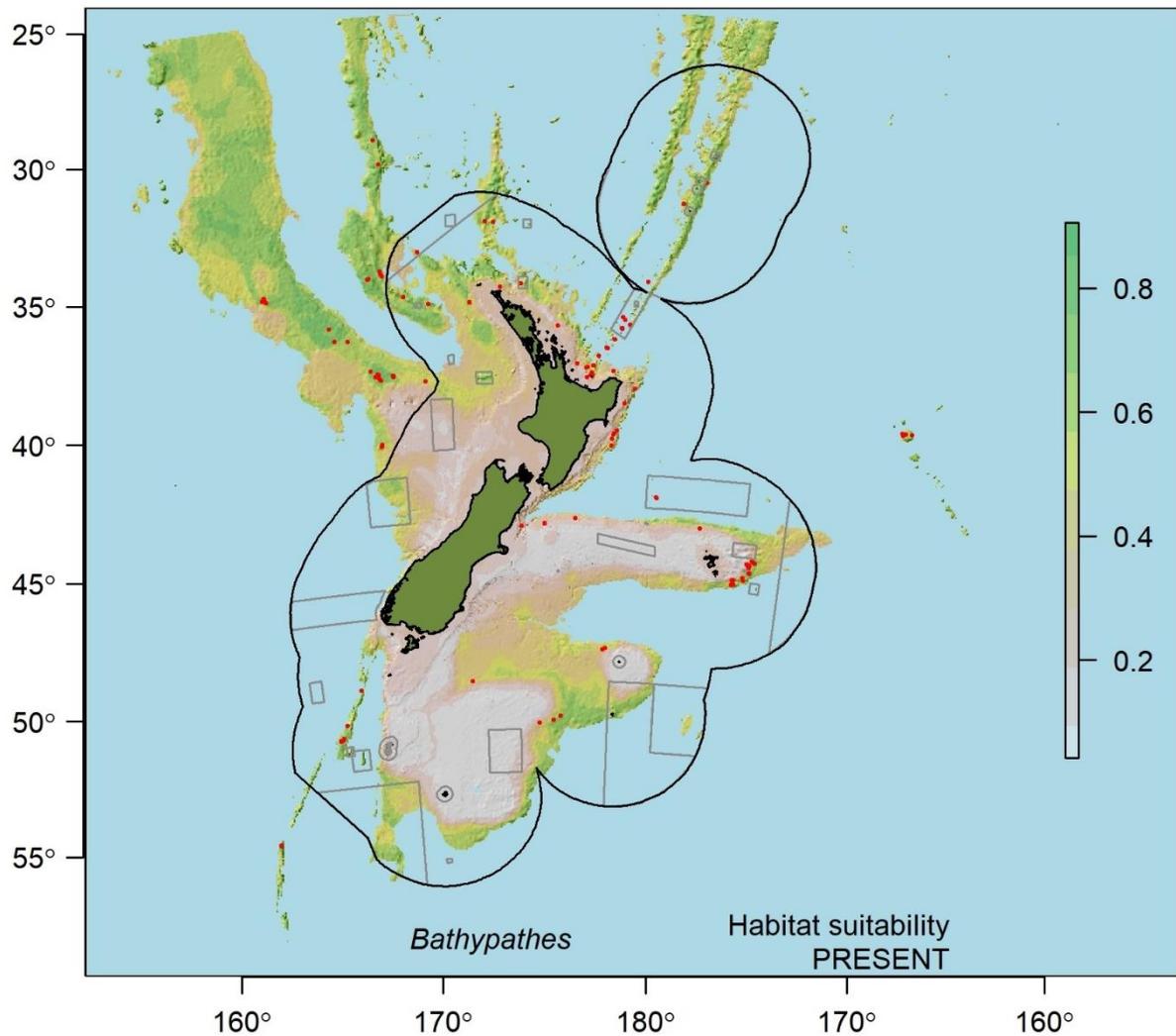


Figure 3-34: *Bathypathes* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

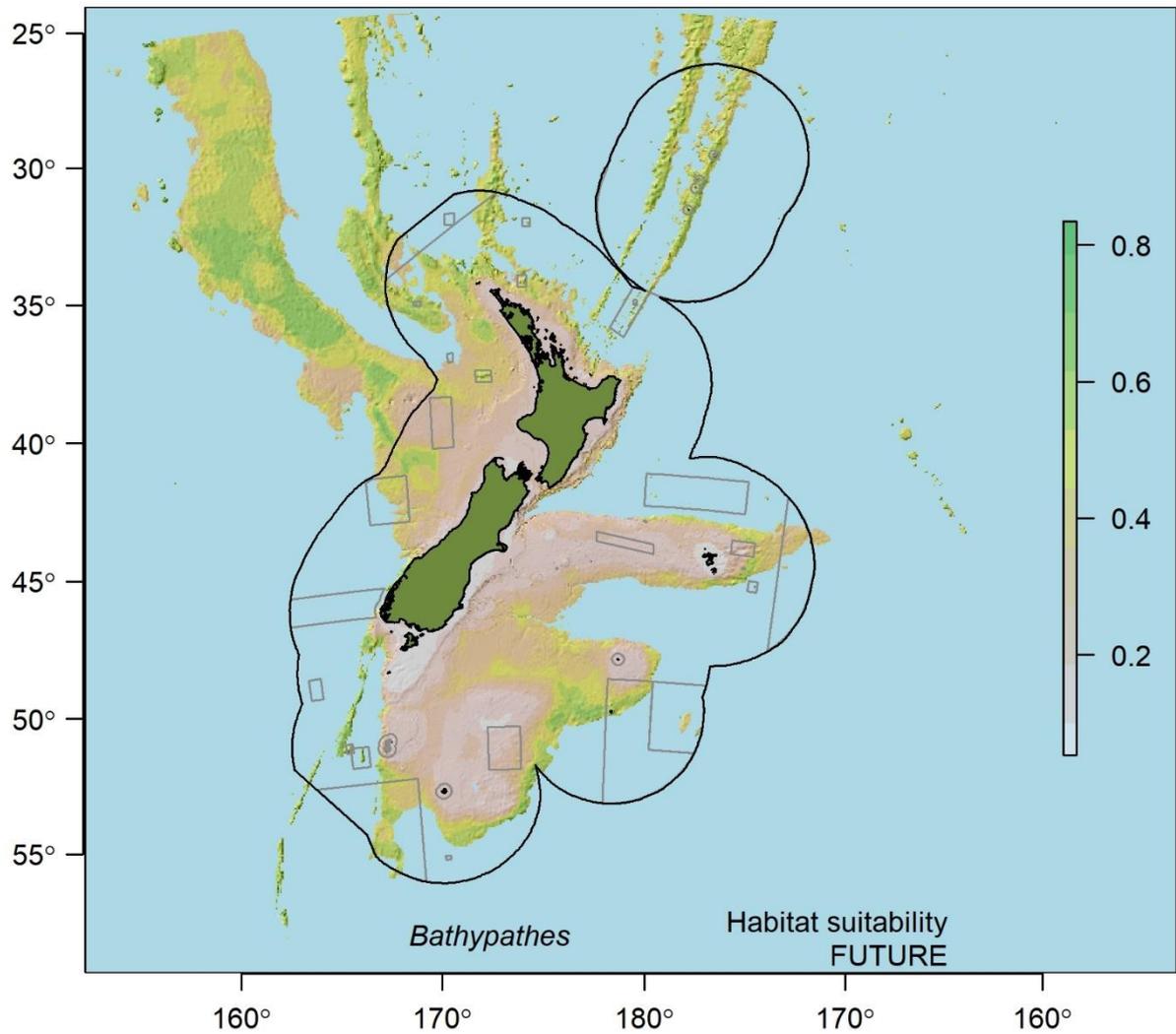


Figure 3-35: *Bathypathes* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

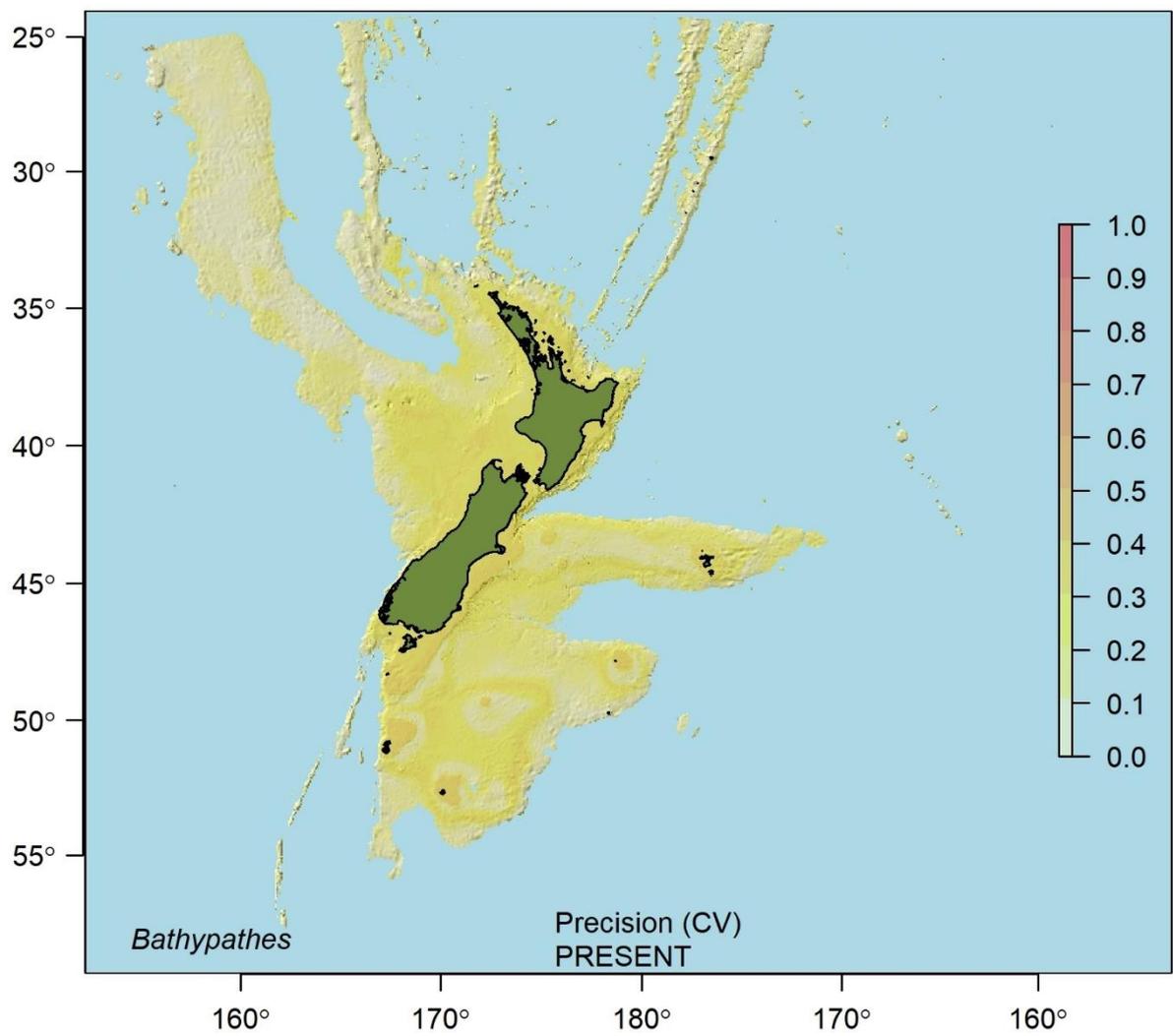


Figure 3-36: *Bathypathes* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

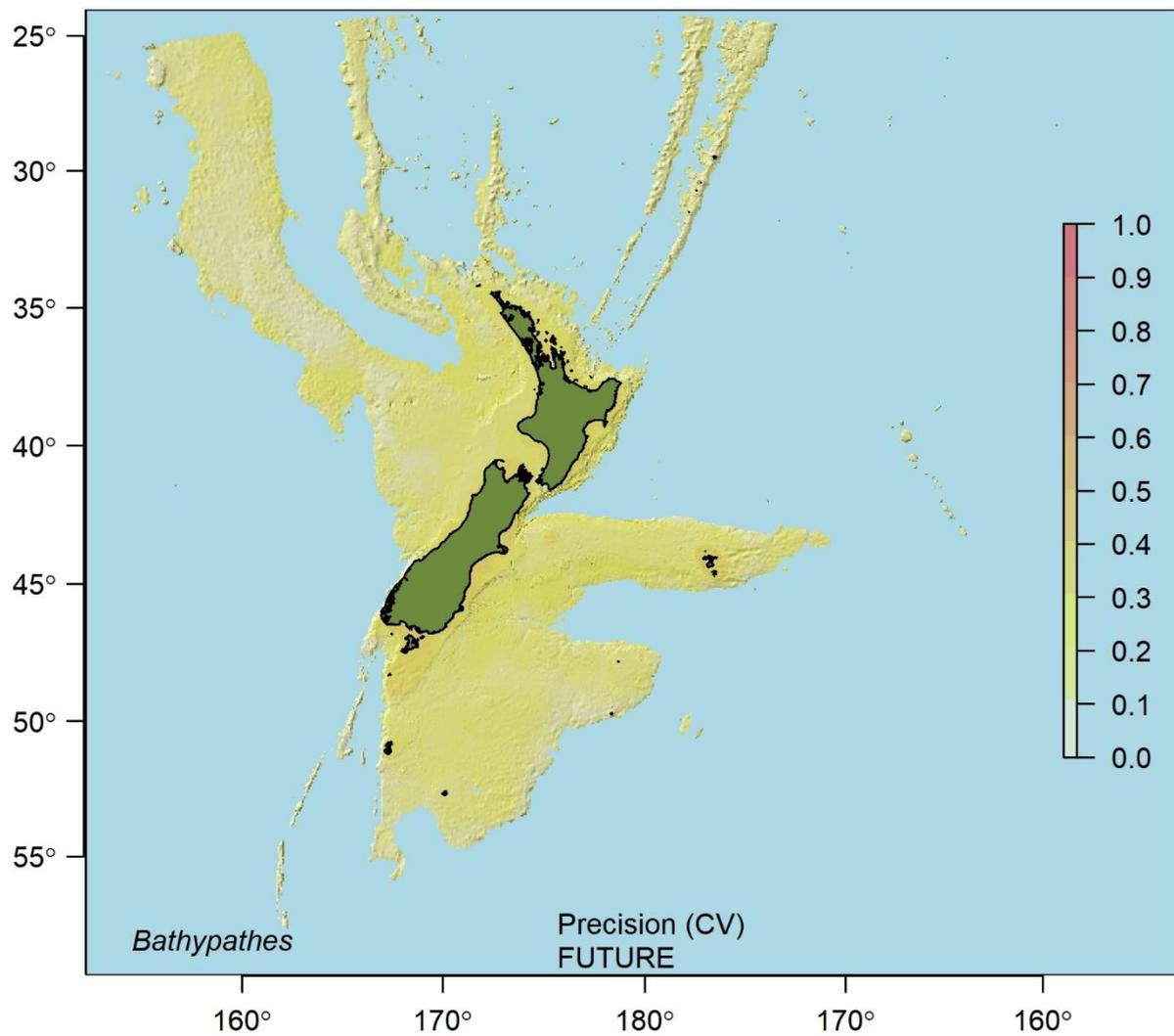


Figure 3-37: *Bathypathes* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

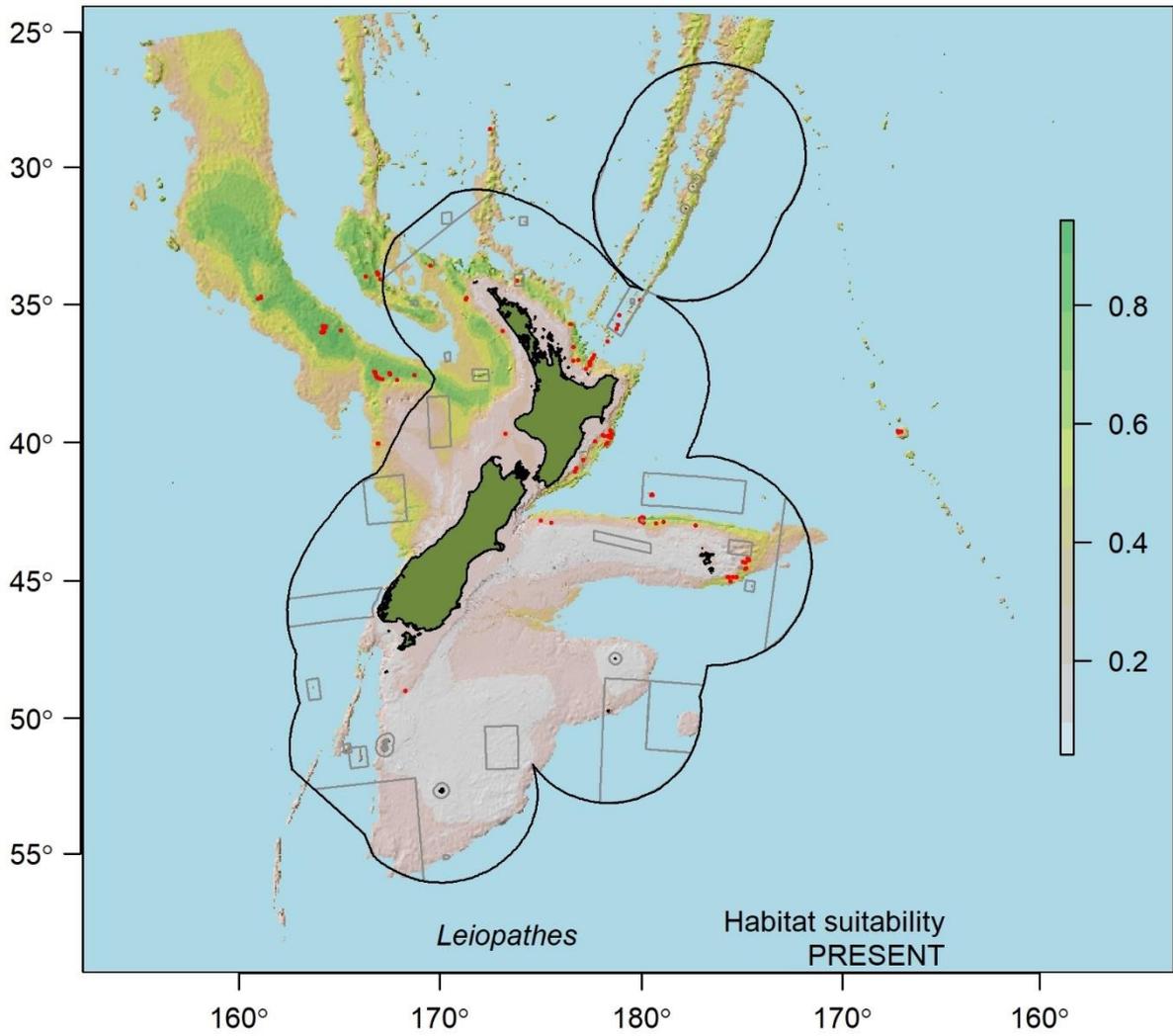


Figure 3-38: *Leiopathes* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

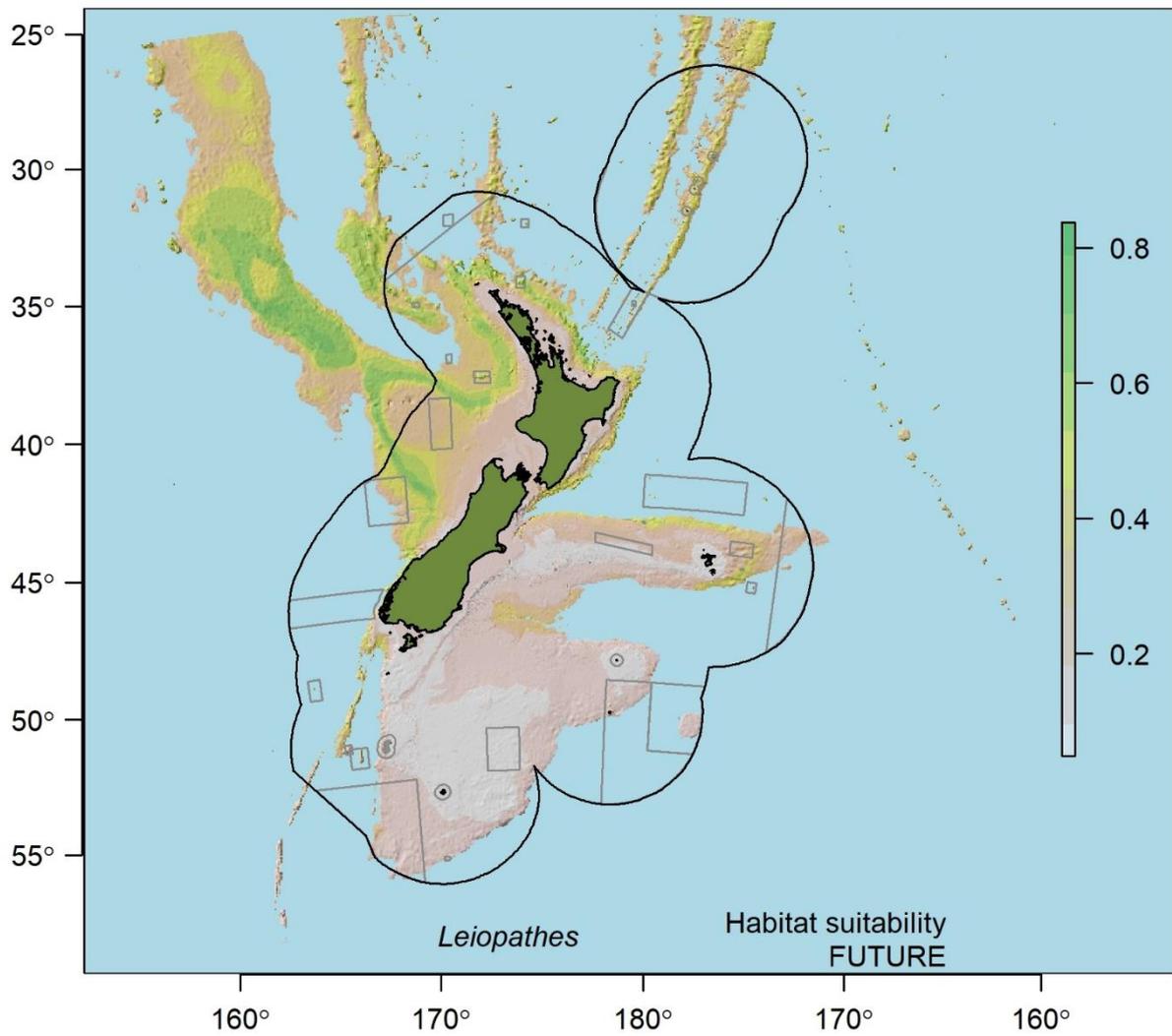


Figure 3-39: *Leiopathes* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

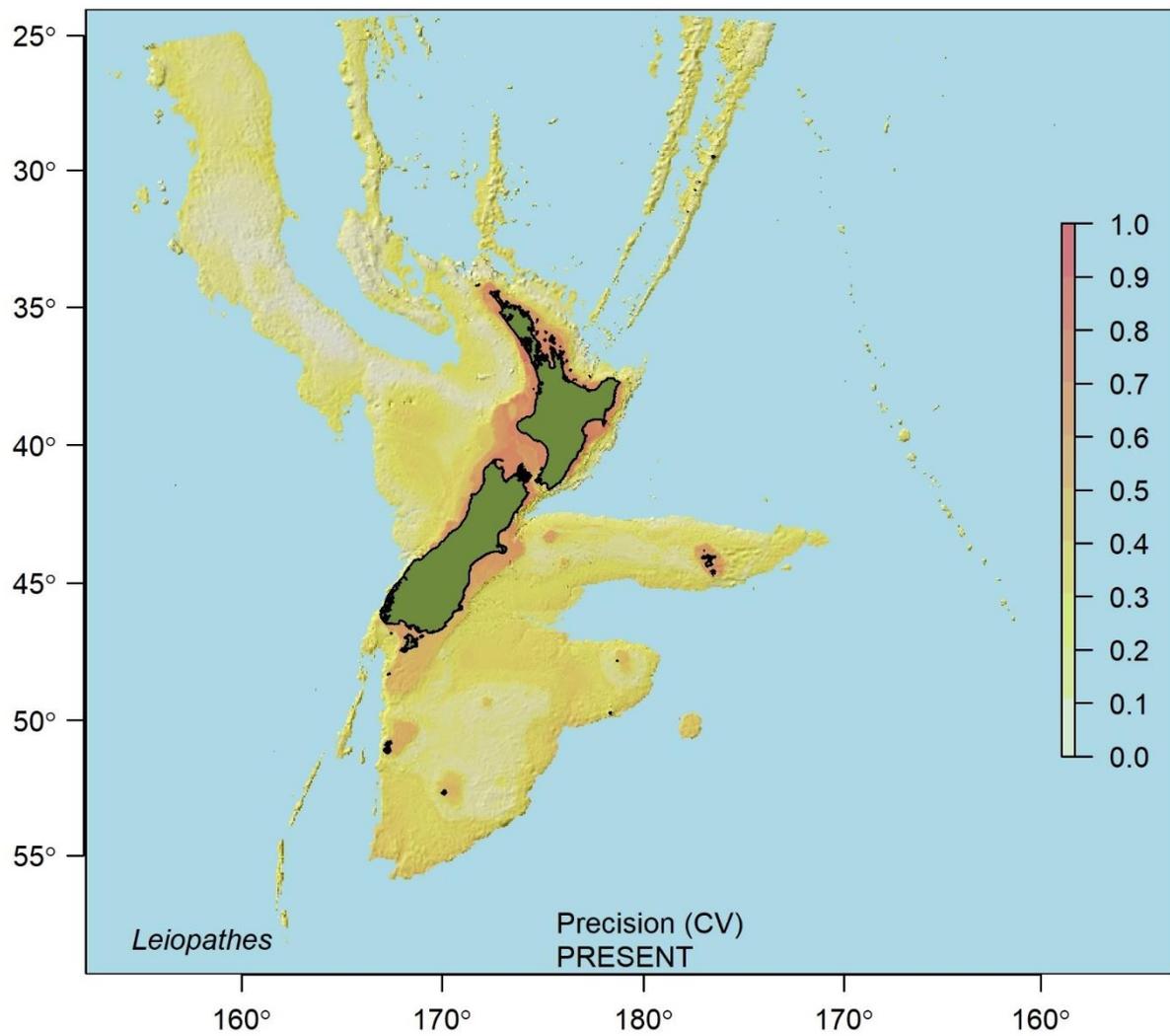


Figure 3-40: *Leiopathes* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

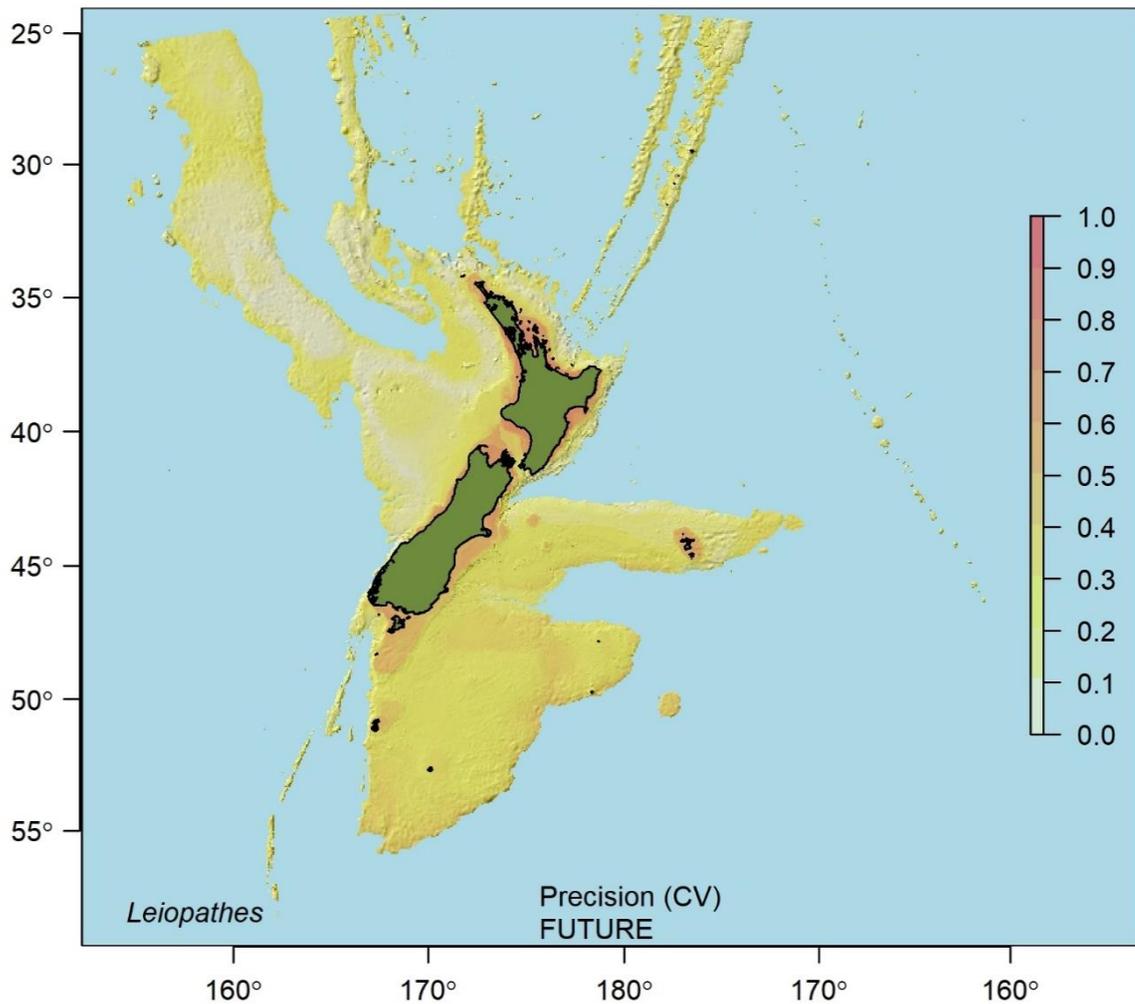


Figure 3-41: *Leiopathes* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

3.4.4 Anthoathecata

Models show a patchy present distribution for the *Errina* spp. hydrocorals (Figure 3-42 to Figure 3-45). High habitat suitability is indicated on the Stewart-Snares shelf, around all the sub-Antarctic islands, the Macquarie Ridge, eastern Campbell Plateau, and several small areas on the Chatham Rise and northern ridge features. This distribution is not predicted to alter substantially in any region in the future. Model precision is high around many of the highly suitable habitat areas, and moderate elsewhere, and differs little between the present and future model predictions.

The *Stylaster* spp. hydrocorals (Figure 3-46 to Figure 3-49) show a similar present distribution to *Errina* spp., although habitat suitability is less pronounced in southern regions. Habitat suitability is predicted to very slightly improve in southern areas in the future. High model precision is associated with high habitat suitability in many areas, and overall is slightly greater around future than the present model predictions.

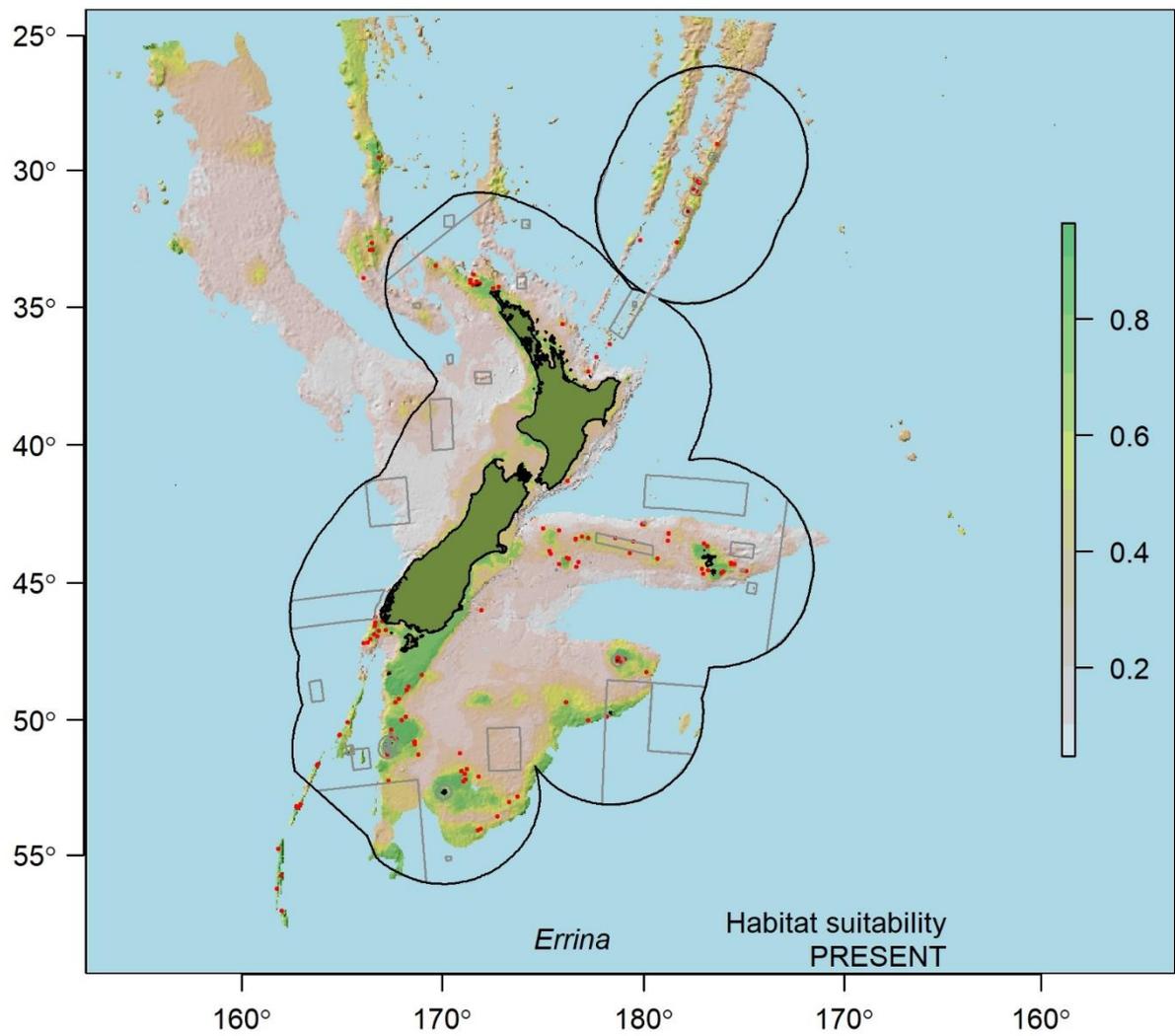


Figure 3-42: *Errina* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

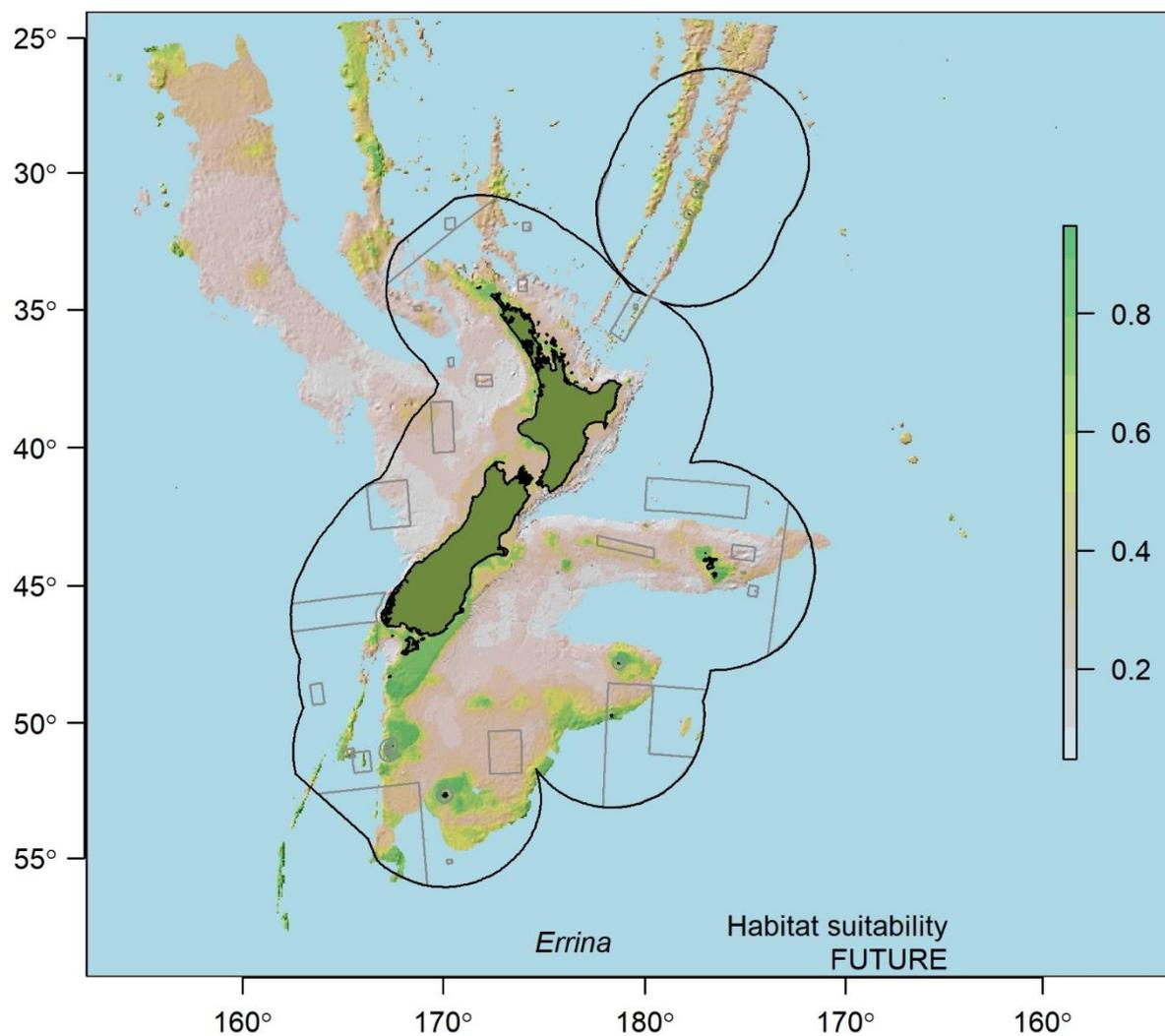


Figure 3-43: *Errina* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

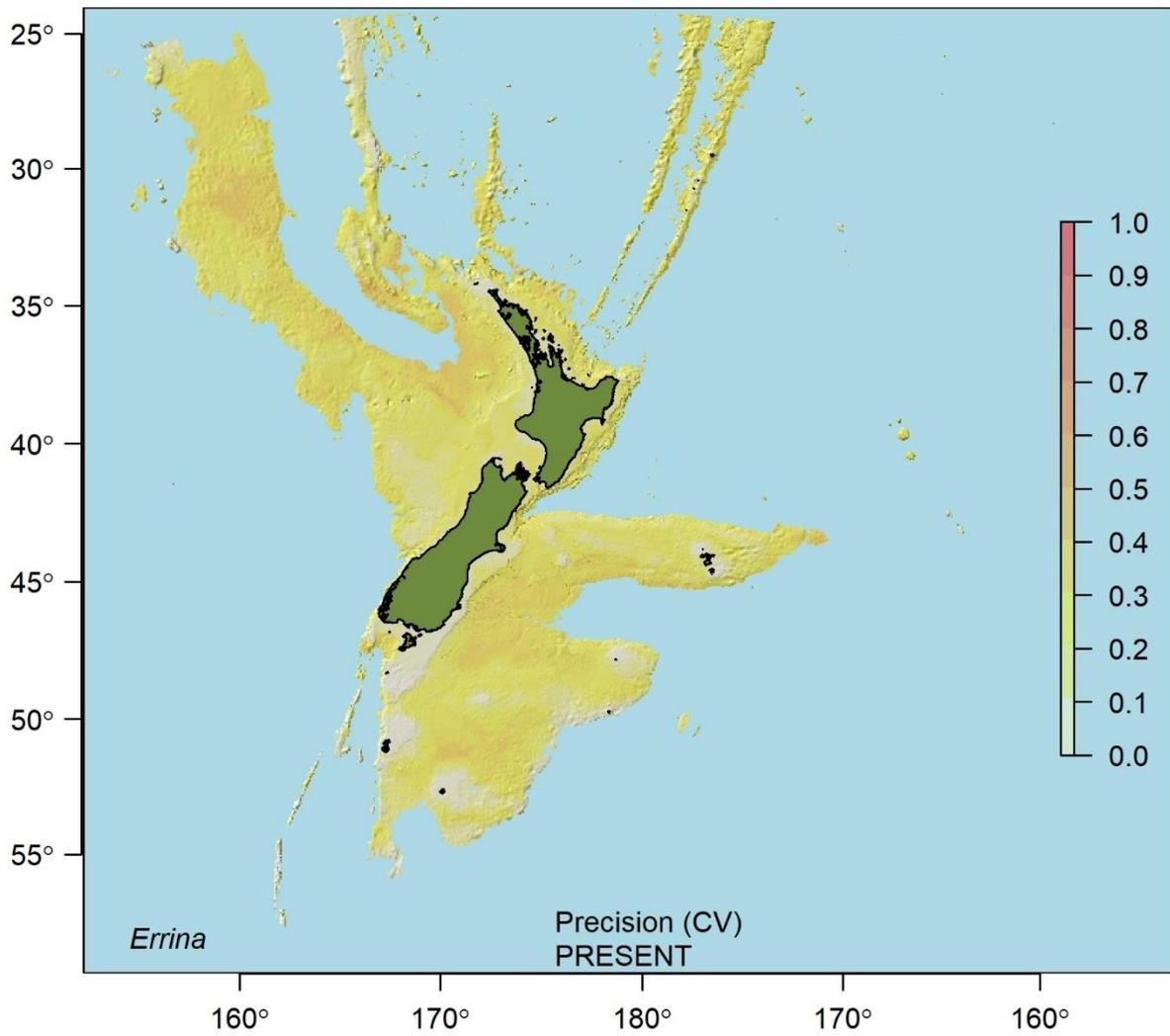


Figure 3-44: *Errina* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

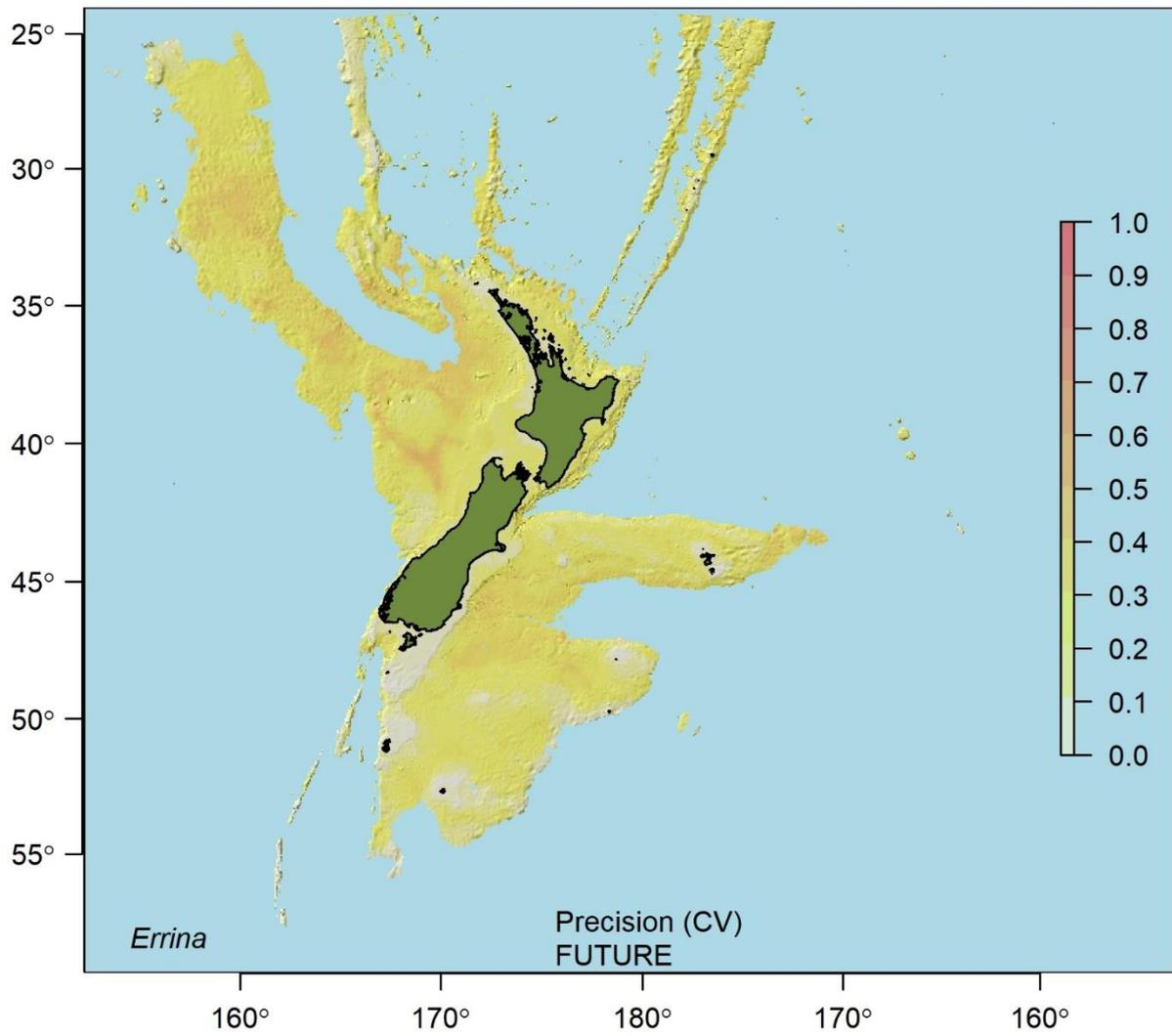


Figure 3-45: *Errina* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

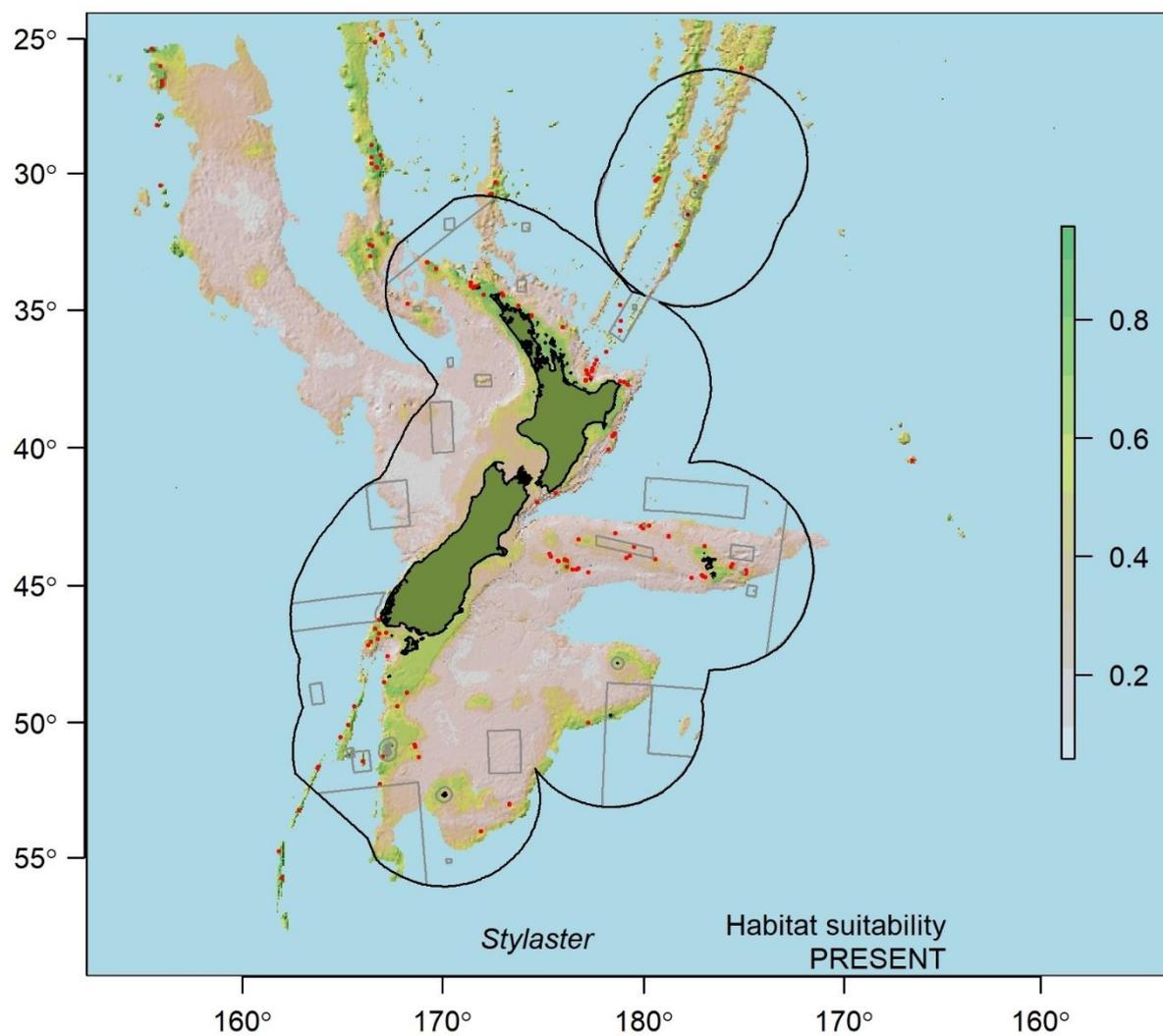


Figure 3-46: *Stylaster* spp. Predicted habitat suitability (present). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

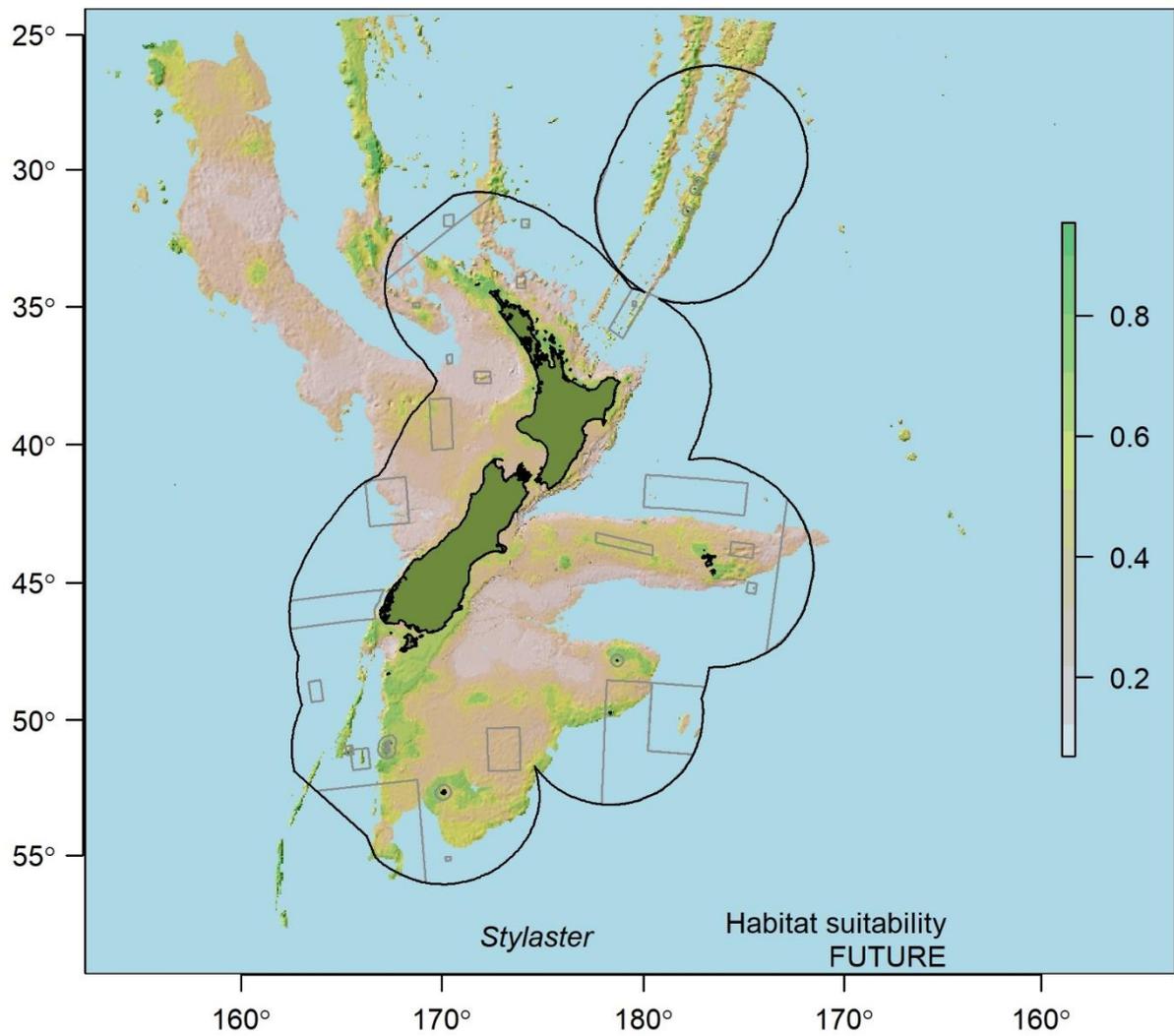


Figure 3-47: *Stylaster* spp. Predicted habitat suitability (future). Graduated colours (as shown on the scale-bar) indicate relative habitat suitability (0–1). See Figure 3-2 caption for further details.

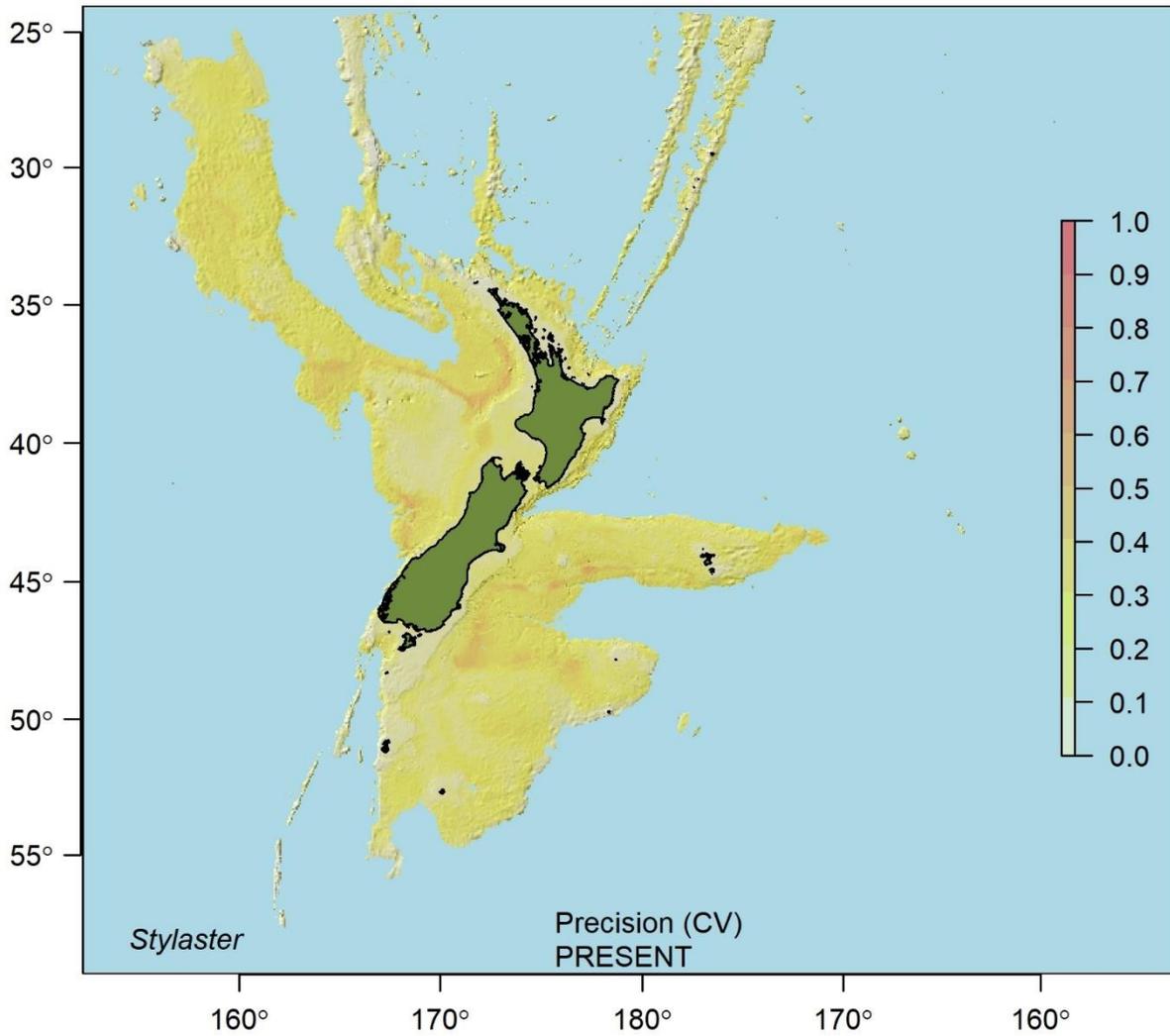


Figure 3-48: *Stylaster* spp. Precision of predicted habitat suitability (present). See Figure 3-4 caption for further details.

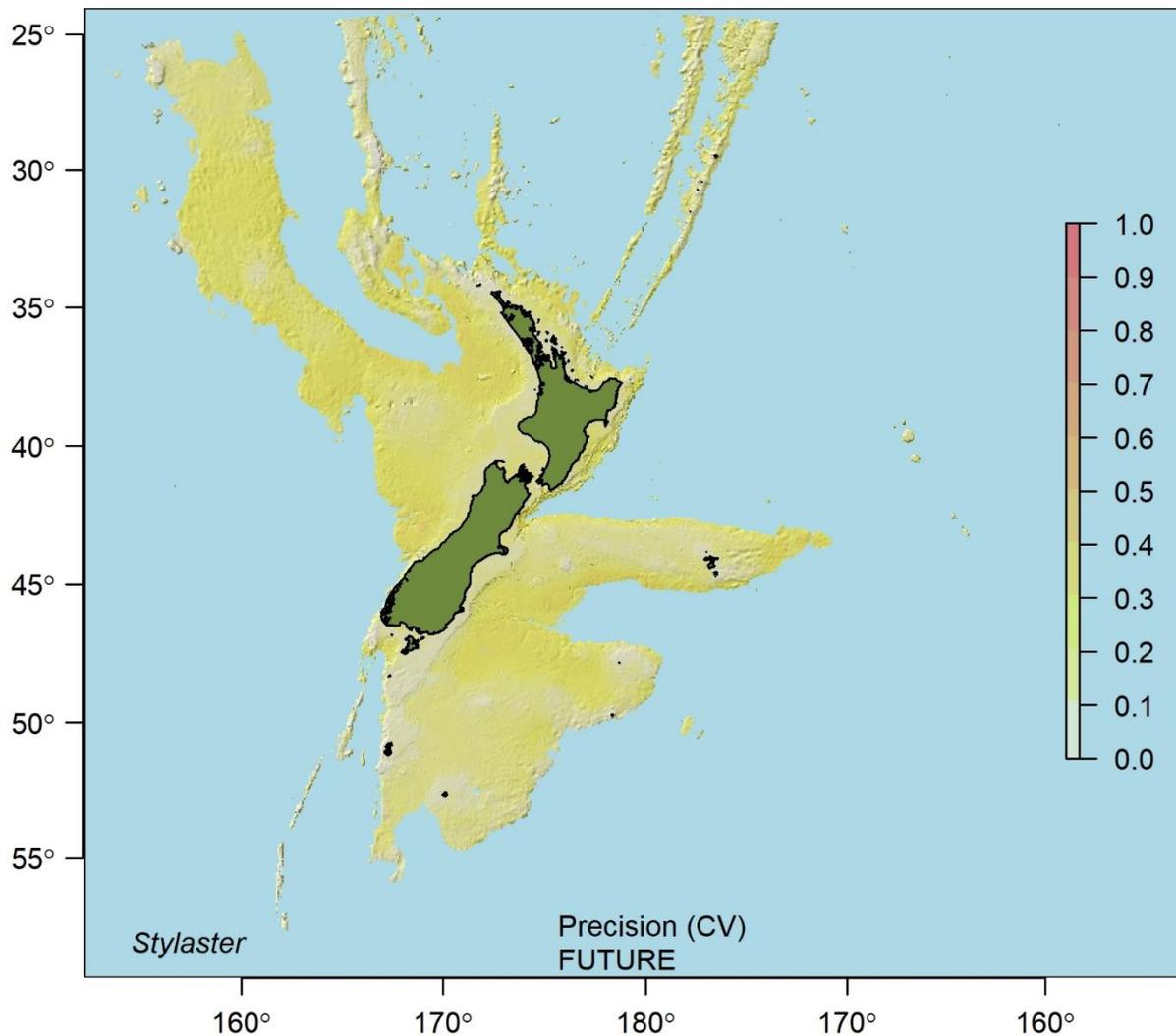


Figure 3-49: *Styaster* spp. Precision of predicted habitat suitability (future). See Figure 3-4 caption for further details.

3.5 Overlap with trawl fishing footprint

Spatial representation of the combined aggregated area swept by bottom trawling for the fishing years from 2007–08 to 2017–18 shows that the highest fishing intensity in recent years has focused on several main areas: the Chatham Rise, especially west of the Chatham Islands but excluding a shallow central region lying within a Benthic Protection Area (BPA); a contiguous region of the Stewart-Snares shelf and western Campbell Plateau extending south to below the Auckland Islands; the perimeter of the Campbell Rise, especially the eastern slopes, and perimeters of the Pukaki Rise and Bounty Plateau; the central west coast of mainland New Zealand, especially off the northern South Island; an area of the Challenger Plateau bordering the EEZ; and the shelf/slope along much of the eastern coastline of New Zealand (Figure 3-50).

The overlap of the highest levels of bottom trawling effort with the predicted present distribution of *Enallopsammia rostrata* is mainly restricted to a few locations around the deeper parts of the eastern Chatham Rise, the sub-Antarctic Plateau, Puysegur Shelf, and the central east coast of the North Island (Figure 3-51); this overlap increases slightly for the predicted future distribution of this species, notably off the South Island west coast (Figure 3-53, Table 3-3). The overlap is less for the

predicted present distribution of *Solenosmilia variabilis*, and is limited to a few small areas on the Chatham Rise, the southern plateaus, and the North Island east coast; the overlap is slightly greater for the predicted future habitat suitability, notably in a small region northeast of the Auckland Islands. The shallower present distribution of *Goniocorella dumosa* leads to a much greater overlap with bottom trawling than these other two branching corals, at about 23–24% (Table 3-3). Areas of overlap exist around the perimeter of the Chatham Rise, the Stewart-Snares and Auckland Islands shelves, and around much of mainland New Zealand; the pattern of overlap changes little for the predicted future distribution. Bottom trawling overlaps with the present *Madrepora oculata* distribution mainly off the central east coast of the South Island, and around much of the North Island; the total number of overlapping cells isn't predicted to change much in the future, but an increase is suggested off the South Island west coast.

For the alcyonaceans modelled, the similar present habitat suitability of *Paragorgia* spp., *Primnoa* spp., and *Keratoisis* spp. and *Lepidisis* spp. translates to similar overlaps with bottom trawling, with just a few small regions of overlap along the Chatham Rise and in the sub-Antarctic (Figure 3-51, Figure 3-52). In the future, the overlaps for *Paragorgia* spp. and *Primnoa* spp. are predicted to be more focussed around the northern slopes of the Auckland Islands shelf, and for *Primnoa* spp. also across parts of the central Chatham Rise (Figure 3-53). For *Keratoisis* spp. and *Lepidisis* spp. combined, future overlap is predicted to be greatest off the South Island west coast (Figure 3-54). For *Corallium* spp. the overlap between trawling and habitat is relatively low – both for the present and future predicted suitability for this genus – and focussed on the Puysegur Bank and a few small areas around the sub-Antarctic and east of the Chatham Islands.

For black corals, fishing overlap with the present predicted habitat suitability for *Bathypathes* spp. is seen off the North Island east coast, east of the Chatham Islands, the Puysegur Bank and a few small areas around the sub-Antarctic; this overlap is not predicted to change appreciably in the future. For the predicted present distribution of *Leiopathes* spp., overlaps with fishing are mainly seen on the northern Chatham Rise and around the North Island; in the future overlap is predicted to increase off the South Island west coast and decrease on the Chatham Rise.

For the anthoathecatan genera *Errina* and *Stylaster*, which show similar present distributions, overlap with trawling is evident around the Stewart-Snares Shelf, Auckland Islands shelf, South Island east coast, the Chatham Rise, and around much of the North Island (particularly, for *Stylaster* spp., on the east coast). These areas of overlap decrease in the future, especially along the North Island east coast, and especially for *Stylaster* spp.

Table 3-3: Summary of overlap between habitat suitability and fishing footprint. Calculated as the percentage of cells in the top 25% of habitat suitability (for present and future predictions separately) that lie within the area defined by the top 25% of historical total swept area.

Order	Taxon	Percentage of top 25% habitat overlapping with top 25% fishing footprint	
		Present	Future
Scleractinia	<i>Enallopsammia rostrata</i>	0.4	1.6
	<i>Solenosmilia variabilis</i>	0.2	0.6
	<i>Goniocorella dumosa</i>	23.0	24.0
	<i>Madrepora oculata</i>	13.2	13.3
Alcyonacea	<i>Paragorgia</i> spp.	0.2	2.2
	<i>Primnoa</i> spp.	0.2	1.4
	<i>Corallium</i> spp.	0.1	0.3
	<i>Keratoisis</i> spp. and <i>Lepidisis</i> spp.	0.2	1.8
Antipatharia	<i>Bathypathes</i> spp.	0.2	0.4
	<i>Leiopathes</i> spp.	1.2	1.4
Anthoathecata	<i>Errina</i> spp.	15.3	14.8
	<i>Stylaster</i> spp.	17.2	14.4

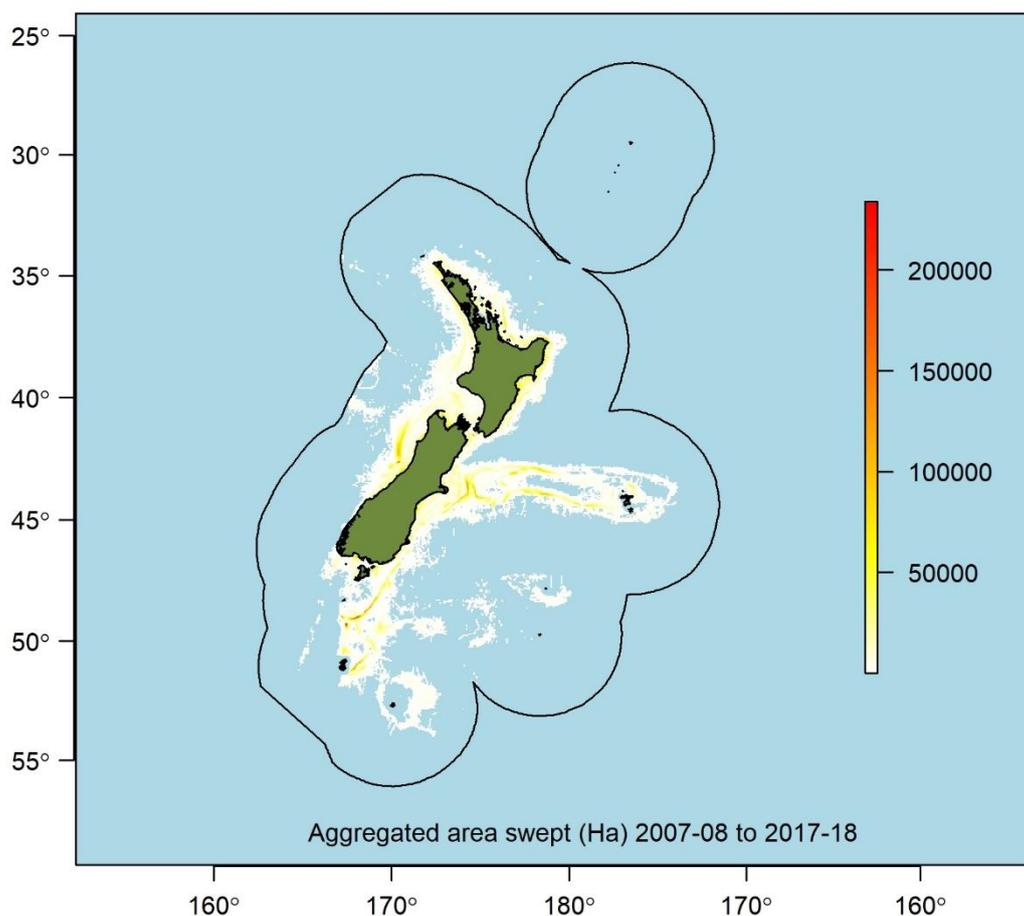


Figure 3-50: Fishing footprint. Aggregated area swept (hectares) per cell by bottom trawling for inshore and deepwater target species for the fishing years 2007–08 to 2017–18.

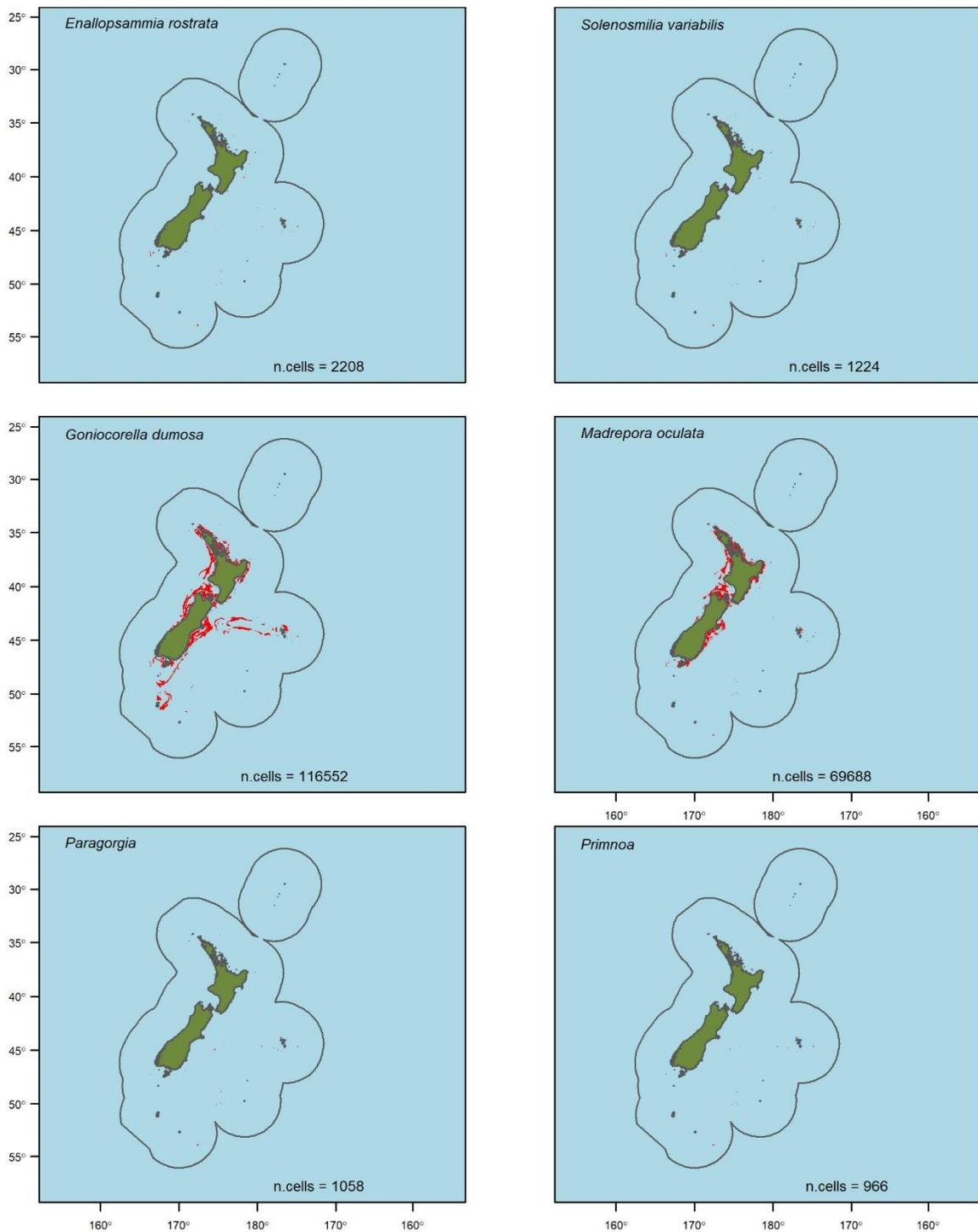


Figure 3-51: Overlap of bottom trawl fishing effort with present habitat suitability [1]. Red coloured cells signify areas with both the greatest 25% aggregated swept area (inshore and deepwater target fisheries combined, 2007–08 to 2017–18) and the greatest 25% habitat suitability. N.cells = the number of overlapping 1x1 km cells.

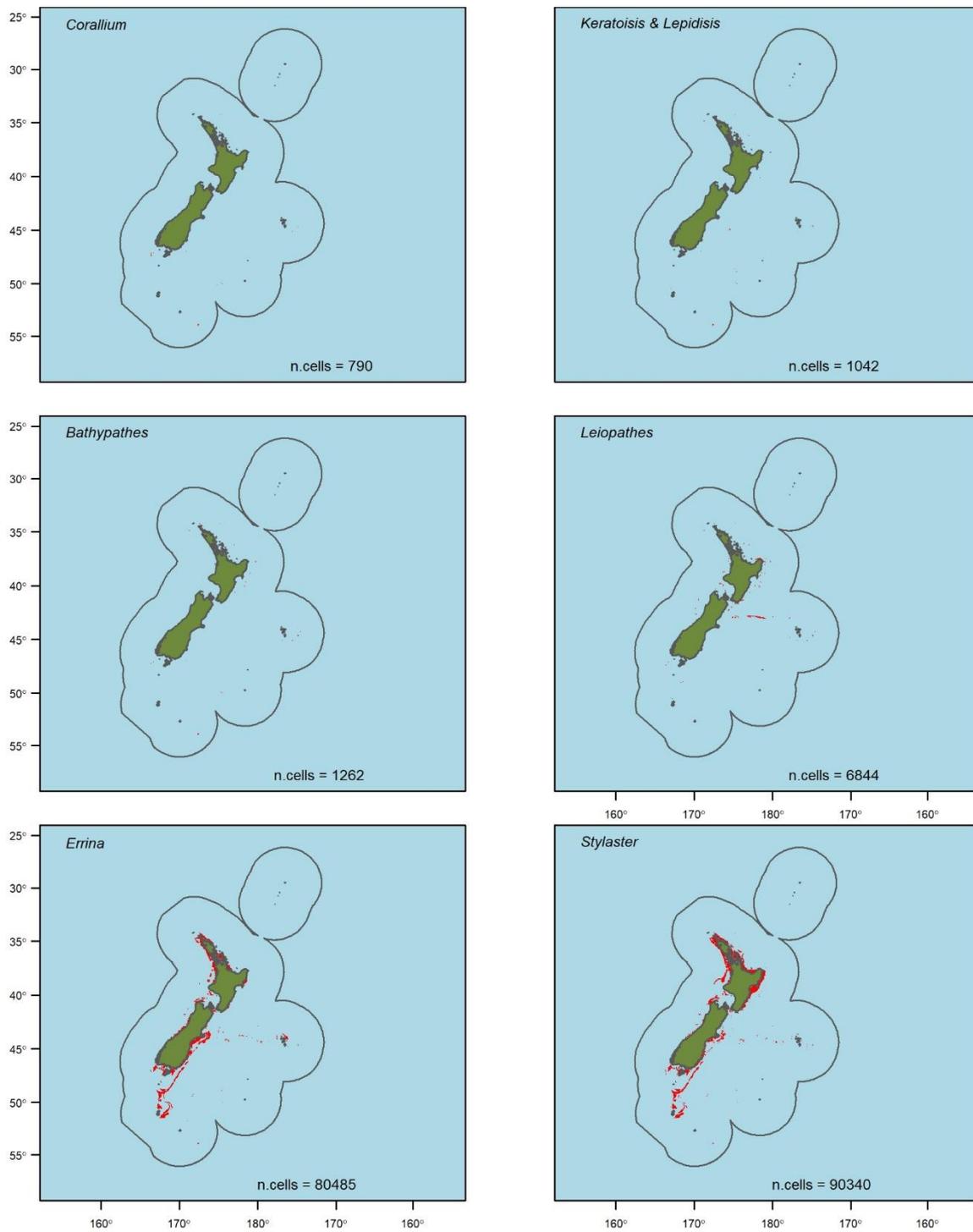


Figure 3-52: Overlap of bottom trawl fishing effort with present habitat suitability [2]. See Figure 3-51 for further details.

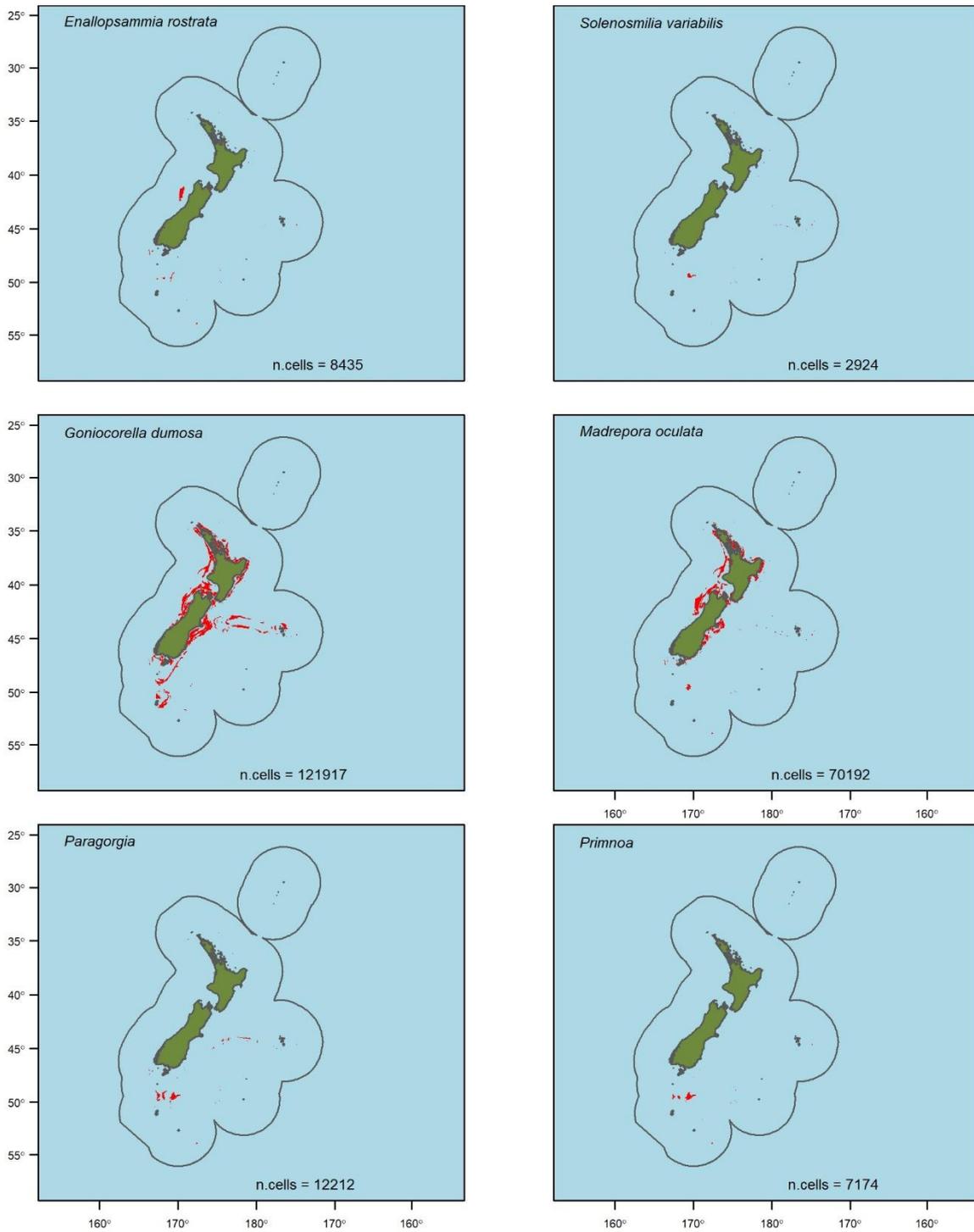


Figure 3-53: Overlap of bottom trawl fishing effort with future habitat suitability [1]. See Figure 3-51 for further details.

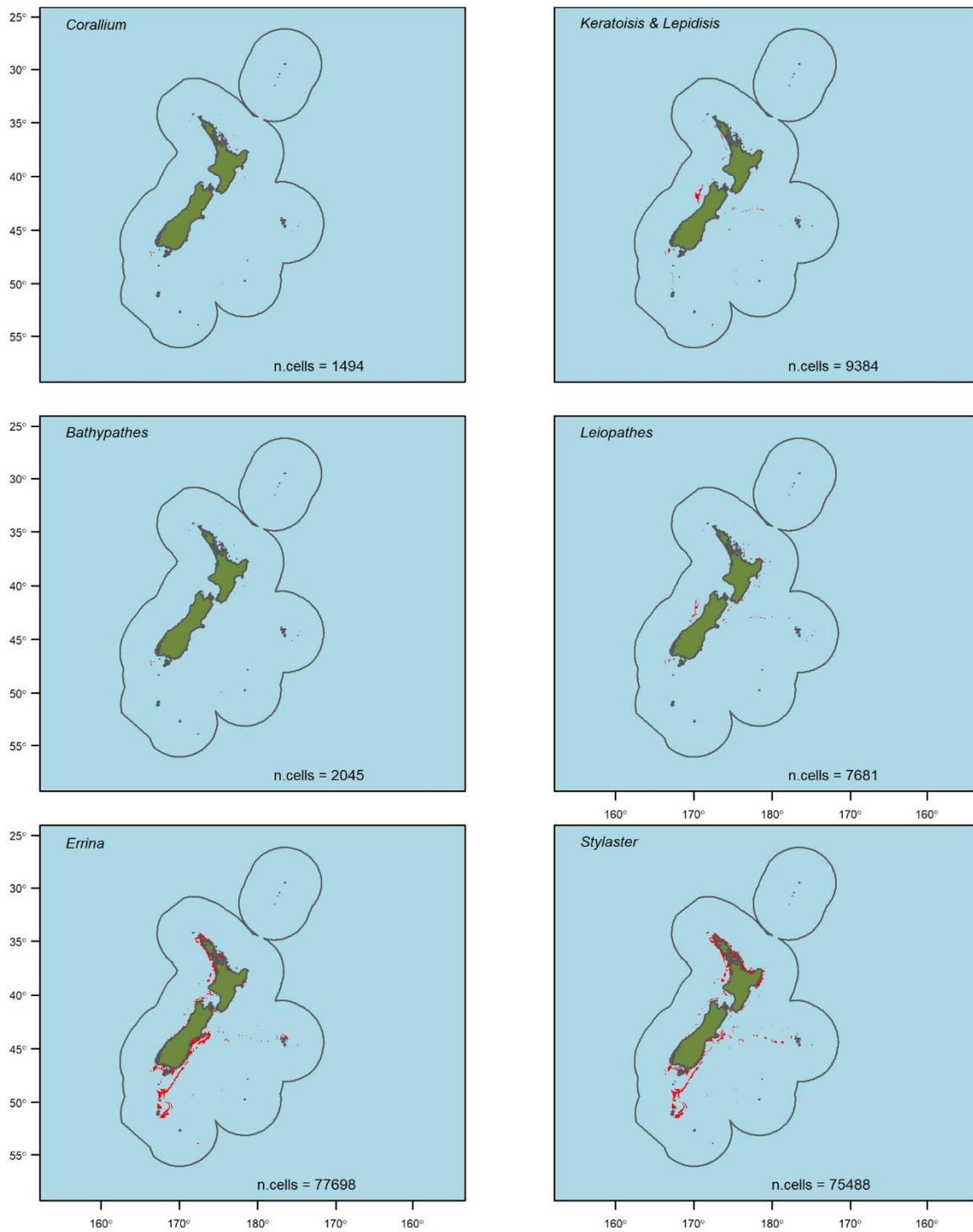


Figure 3-54: Overlap of bottom trawl fishing effort with future habitat suitability [2]. See Figure 3-51 for further details.

4 Summary and discussion

This analysis represents the first use of the New Zealand Earth System Model (NZESM) to predict the future suitability of seafloor environmental conditions for supporting protected corals in the region. Forecasts from the NZESM tuned to local oceanic and atmospheric conditions, along with substantial additions to species occurrence records and developments in habitat suitability modelling in recent years, has made it possible to provide some advancements in predictive models for several protected coral taxa, and produce models for several taxa for the first time. These models were used to predict the present and future distribution of protected corals and, combined with updated data for the spatial distribution of historical bottom trawling, have allowed for an assessment of the potential risk faced by these vulnerable animals now and in a climate changed future.

4.1 Model performance

Model accuracy was not tested with fully independent data, but the cross-validation procedure provided a useful test of model reliability by setting aside portions of the input data for comparison with model predictions. The AUC values generated by this method indicated more than adequate performance (>0.7) for all models and excellent performance (>0.8) for 18 of the 24 individual models; an AUC of over 0.9 was achieved in both models for one taxon, *Corallium* spp. Rates of correct identification of presence (sensitivity) and absence (specificity) were mostly high, falling below 0.7 in only one case (*Goniocorella dumosa*).

Direct comparison of these AUC values with those from models for the same taxa in earlier studies of protected corals (i.e., Anderson et al. 2014, Anderson et al. 2015) is not possible due to the different approaches taken for assigning absence records. In general, however, the AUC values were similar or slightly lower in the current study. The use of equal numbers of presence and absence records in the models will have reduced the calculated AUC compared with the approach of using all records in the database of research survey stations (as described in Section 2.1) as absences in the earlier studies.

The wide bathymetric spread of *Goniocorella dumosa*, noted in previous studies (e.g. Tracey et al. 2011), suggests a wide tolerance for a range of depth-related environmental factors and therefore a less well-defined niche, and is likely to have contributed to the poorer model fits. Model prediction bias for most taxa, and both models, tended to be in the direction of high sensitivity/low specificity. In this aspect the two model types sometimes differed, with specificity higher in one and sensitivity higher in the other for *Solenosmilia variabilis*., *Paragorgia* spp., and *Keratoisis* spp. and *Leiopathes* spp. combined.

There remains a level of uncertainty in model predictions, for several reasons. A key reason is that NZESM simulations are based on a spatial resolution that is very coarse (0.2° or 1°) compared to the scale at which environmental conditions are known to affect benthic marine invertebrates, although this was partially ameliorated by upscaling predictor variables to a 1 km resolution where possible. Grids of some environmental data are available from other sources at a higher resolution, but a trade-off is necessary when predicting to future conditions, as current and future data layers need to have matching provenance to be sure that changing conditions are the sole driver of any changing habitat suitability over time. Uncertainty in predictions may also come from the influence of any important explanatory variables not available to the models, from variability in catchability among the different sampling methods used, errors in recording or specimen identification, and model inadequacies (Barry and Elith 2006).

4.2 Comparison of predictions with previous models and predicted future changes in coral distribution

Visual assessment of the spatial predictions indicates that the new model predictions are generally in good agreement with earlier models for the same taxa. Predicted distributions for *Enallopsammia rostrata* are similar to those of Anderson et al. (2015) and Anderson et al. (2014), which also showed higher habitat suitability in northern regions, and similar patterns around the Chatham Rise and sub-Antarctic. As in the current study, future predictions from Anderson et al. (2015) also showed an increase in habitat suitability on parts of the Chatham Rise and less change in the North, but overall predicted lower future suitability for the species. The distribution predicted for this species by Georgian et al. (2019) highlighted the hotspots and these, showing highest suitability on the southeast Chatham Rise, southern Bounty Plateau, and the ridge systems to the north and south of New Zealand, are in general agreement with our study.

Both this study and that of Anderson et al. (2015) show a higher level of future habitat suitability for *Solenosmilia variabilis* in the easternmost Chatham Rise compared with the present, and little change in the north. The biggest difference between models is in the greater habitat suitability predicted for the future in shallow areas in the current study. The predictions of Anderson et al. (2014) show some differences with the results of Anderson et al. (2015) and this study; with higher habitat suitability in parts of the sub-Antarctic and Challenger Plateau not seen in the more recent studies. The models of Georgian et al. (2019) show broad agreement with the present distribution of corals predicted in this study, although they don't mirror the higher level of habitat suitability seen in the easternmost Chatham Rise or northern Lord Howe Rise compared to surrounding areas.

Because of no shallow depth cut-off was used in our models (in contrast to the 200 m or 300 m limit imposed in the models of Anderson et al. (2014), Anderson et al. (2015), and Georgian et al. 2019), predictions of high habitat suitability (>0.5, see Section 2.5.3) for *Goniocorella dumosa* are shown for some near-coast areas where predictions were previously unavailable. In other areas the new models gave very similar results to Anderson et al. (2015) and Anderson et al. (2014), with a focus of the predicted distribution on the shallow crest region of the Chatham Rise and a few small areas on the shallower shelves around the sub-Antarctic islands. For future predictions of habitat suitability, Anderson et al. (2015) indicated a general increase in habitat suitability across the Chatham Rise and sub-Antarctic plateaus but no change elsewhere; our models predict no appreciable change in the location of areas of highest relative habitat suitability for *Goniocorella dumosa* from the present to the future. The Georgian et al. 2019 models agree well with our models for the present distribution of this species but, with their deeper maximum model extent, show some additional areas of more suitable habitat in deeper water to the northwest of New Zealand.

The new models show some areas with relatively high habitat suitability for *Madrepora oculata* on the Lord Howe Rise and West Norfolk Ridge that Anderson et al. (2015) did not predict. This difference may be due to the influence in the model of several new presence records for the species in that area. In other areas predicted distributions were mostly similar between these studies and that of Anderson et al. (2014). Changes in habitat suitability for this species between the present and future predicted by Anderson et al. (2015) were minor in northern regions but lower everywhere, whereas habitat suitability levels were predicted to slightly increase in a few areas in the new models. Predictions for *Madrepora oculata* are also consistent with those of Georgian et al. (2019), although that study indicated a more definitive band of high suitability around the slopes of the Chatham Rise, and additional small areas of higher suitability on the western Challenger Plateau.

A substantial and widespread increase in habitat suitability levels for *Paragorgia* spp. was predicted by Anderson et al. (2015) but this unusual result was not reinforced by our study. Otherwise, the key areas for the present habitat suitability for this genus were predicted by both studies to be around the Campbell and Bounty plateaus. The Anderson et al. (2014) predictions for present habitat suitability were similar to this study, although that study indicated some areas of high suitable habitat on the sub-Antarctic plateaus that were not predicted by the later studies.

Several new records of *Primnoa* spp. in northern regions led to some areas of predicted high habitat suitability on the Lord Howe Rise and West Norfolk Ridge that were not identified by Anderson et al. (2015). Otherwise the predictions of this study were very similar to those of both Anderson et al. (2015) and Anderson et al. (2014), where most high habitat suitability is predicted to be south of the Chatham Rise. Changes in habitat suitability in the future were not predicted to be substantial in either study.

The present predicted habitat suitability for *Keratoisis* spp. and *Lepidisis* spp. combined was very similar to that shown by Anderson et al. (2015), although some shallower areas on the Chatham Rise and Challenger Plateau that were predicted by Anderson et al. (2014) to have high habitat suitability were not seen to be so in newer models. Both this study and Anderson et al. (2015) predict little change in the future distribution of suitable habitat in northern regions, but increased levels of habitat suitability on the Chatham Rise (especially along the crest) is a prediction common to both future models.

Some new presence records from northern regions have probably led to higher habitat suitability for the two black coral genera in some areas (especially for *Leiopathes* spp.) compared to previous models, but otherwise the predictions of Anderson et al. (2015) and Anderson et al. (2014) are very similar to those presented here. The new predictions for *Bathypathes* spp. and *Leiopathes* spp. correspond to those of Anderson et al. (2015) in predicting little change between present and future distributions in any area, although notably both models show a general increase in the level of habitat suitability on the southern Challenger Plateau.

4.3 Relative importance of environmental predictors

Models for *Enallopsammia rostrata* and *Solenosmilia variabilis* (and to a lesser extent the other two scleractinian genera modelled) are strongly driven by *Aragonite* concentration (see Appendix B and Appendix C). Concentration of *Aragonite* is positively correlated with prevalence for these species for values between slightly undersaturated and slightly oversaturated, but for higher concentrations the correlation becomes negative. This relationship suggests that once seawater is fully saturated with *Aragonite* other factors may come into play to limit habitat suitability, with *Aragonite* potentially acting as a proxy for other, unknown, parameters. Seafloor *Aragonite* (and *Calcite*) concentrations are predicted to decrease substantially over the study area by the end of the century (Appendix A), hence the notable changes in habitat suitability between present and future shown for these species. Other key environmental variables in the models for these species, *Oxygen* and *Nitrogen* in particular, have previously been shown to be important drivers of habitat suitability for them (e.g. Anderson et al. 2015). The influence of these predictors on altered future habitat suitability is relatively minor however as, under the middle-of-the-road-mitigation SSP2 emission pathway selected, benthic *Nitrogen* is predicted to increase only moderately, and dissolved *Oxygen* decrease only moderately, by the end of the century (Appendix A). The *UTF* variable was not selected for use in any of these models and was only of minor importance in models for other taxa. Although these branching corals, and many species among the other taxa modelled which require hard substrate for

settlement, are expected to have a strong association with UTFs, the rather coarse definition of this variable (the area within the deepest continuous contour around the feature) is likely to be limiting its usefulness in these models.

Just as *Aragonite* is important for scleractinians, the *Calcite* polymorph of CaCO_3 is a key predictor in the models for alcyonacean corals, especially *Paragorgia* spp., for which also a peak in habitat suitability occurs at a level above full saturation, followed by decreasing suitability at higher concentrations. Benthic *Nitrogen* is also an important predictor for the alcyonacean taxa modelled, overall showing a negative correlation with habitat suitability.

For the two black coral genera modelled, dissolved *Oxygen* was the key driver of habitat suitability. Peaks in suitability occur near the lower end of the range of values experienced by the sampled populations, with higher values of oxygen not improving habitat suitability; again, this result may indicate that other factors not accounted for in the models may be coming into play with these species.

Habitat suitability for the two anthoathecatan taxa is driven in the models mainly by fixed parameters (*Mud* and *Depth* for *Errina* spp.; *BPI-fine*, *Mud*, and *Depth* for *Stylaster* spp.). The strong negative correlation with mud shown for these two taxa (see Appendix B and Appendix C) is unsurprising given their known affinity with hard, rocky substrates. Because of the dominant influence of fixed parameters, changes in predicted future habitat suitability for these species are very minor. Although the other taxa modelled generally showed more change in habitat suitability over time than these anthoathecatan taxa, this was less obvious for *Corallium* and the two black coral genera as the non-fixed variables that models for these species were driven by (primarily benthic *Nitrogen* and dissolved *Oxygen*) were not predicted to change greatly in the future (Appendix A).

4.4 Overlap between trawling and predicted distribution of corals

It is worth noting here that the definition used for the spatial overlap of predicted coral habitat with historical bottom trawling (identifying model cells that were within the top 25% of aggregated trawl-swept and also within the top 25% of habitat suitability) was made for convenience. Other values were considered, but 25% was chosen because it provided a measure that allowed a visual comparison of the overlap for all taxa. Thus, these overlap thresholds are arbitrary and should not be taken as the levels of fishing intensity that is likely to significantly impact the presence of a benthic taxon. Also worth noting, is that the level and spatial extent of bottom trawling effort has declined substantially in many fisheries in recent years (Fisheries New Zealand 2019, Baird & Mules 2020a, Baird & Mules 2020b), and no attempt was made here to estimate likely future levels/spatial extent of effort. Therefore, the overlaps presented for trawling and the predicted future distribution of corals should be considered only as an indication of the *potential* areas of vulnerability of protected corals to future bottom trawling, based on the location of fisheries that have been important in the past.

That said, there is considerable variability among coral taxa in the overlap of predicted distributions with bottom trawling. The taxa currently most vulnerable to trawling are the thicket-forming corals *Goniocorella dumosa* and *Madrepora oculata*, and the hydrocorals *Errina* spp. and *Stylaster* spp. These taxa have present distributions extending into shallower depths, and into key fishery areas on the South Island northern west coast and central east coast, the Chatham Rise, and western regions of the sub-Antarctic. Predicted future overlaps are not substantially different for *Goniocorella dumosa* and *Errina* spp. but for *Madrepora oculata* the higher levels of habitat suitability predicted

for the future on the west coast South Island overlap with the major middle-depth fisheries currently operating in this region, and the decreasing levels of habitat suitability for *Stylaster* spp. predicted in the future along the east coast of the North Island substantially decrease the overlap with bottom trawling in this region, and overall.

The present overlap with bottom trawling for the two other thicket-forming coral species, *Solenosmilia variabilis* and *Enallopsammia rostrata*, is much lower than for the generally shallower *Goniocorella dumosa* and *Madrepora oculata*, although an future increase in this overlap is predicted for the west coast South Island (for *Enallopsammia rostrata*) and for the north-western Campbell Plateau (*Solenosmilia variabilis*) as a result of the predicted increase in habitat suitability in these areas for these species.

Present overlaps with fishing for the six alcyonacean and antipatharian genera are generally low, although there is a noticeable overlap for the black coral genus *Leiopathes* on the north-western Chatham Rise. A predicted future change in the areas of greatest habitat suitability for *Leiopathes* indicates a potential increase in overlap developing on the west coast South Island, with the Chatham Rise overlap decreasing. Similarly, an increased overlap is predicted for *Keratoisis* spp. and *Lepidisis* spp. combined on the west coast South Island in the future, with higher levels of habitat suitability predicted in that region for these corals.

5 Recommendations for future research

Further improvements in habitat suitability models for predicting the present distribution of protected corals will be possible with the continued expansion of the area around New Zealand surveyed by towed camera and multibeam echosounders. Towed camera surveys (ideally coupled with targeted direct sampling using grabs/sleds) provide reliable determinations of coral abundance and habitat associations (Bowden et al. 2019), while multibeam data provide for the determination of topographic derivatives (e.g., ruggedness) at scales (e.g. 25 x 25 m) more commensurate with the settlement, growth, and survival of corals, and which together have been shown to produce accurate habitat suitability models (Rowden et al. 2017, Ramiro-Sánchez et al. 2019). Substantial improvements in the prediction of the future distribution of corals will, however, require advancements in the precision of NZESM model outputs, with resolution much finer than the 1° or 0.2° currently available. Assessment of the impact of alternative emissions pathways would also be a useful extension of this work, particularly applying a less conservative “business-as-usual or “worst-case-scenario” future that may provide more contrast with present distributions. Furthermore, it will be ideal to incorporate measures of uncertainty in the environmental predictors used in future habitat suitability modelling efforts (Foster et al. 2012, Stoklosa et al. 2015) and, if utilising species presence data from multiple sampling gears, gains could be made by incorporating a gear catchability parameter into the model structure.

To further improve the estimation of risk to protected corals from commercial fishing, and to assist the development of measures to protect representative areas of protected coral habitat we recommend working towards a quantitative Level-3 Ecological Risk Assessment for the Effects of Fishing (ERAEF) on protected deep-sea corals (*after* Hobday et al. 2011). This level of assessment would be a natural extension of the Level-2 Productivity-Susceptibility-Analysis (PSA) undertaken for DOC several years ago focussing on the Chatham Rise (Clark et. al 2014). The PSA method is a non-quantitative method reliant on expert opinion in addition to published data, useful for the initial identification of significant risk but not typically informative for spatial management of susceptible benthic habitats and commercial resources.

A useful input to a Level-3 assessment would be the combination of spatial estimates of predicted habitat suitability with estimates of the historical impact from fishing. Several methods are available for producing impact estimates and these are currently being evaluated and applied to bottom fishing effort data from New Zealand and the wider South Pacific region under two projects currently being carried out by NIWA and associates. These spatial data sets could be considered alongside other spatial environmental classifications and existing spatial protection measures for benthic habitats in an objective manner using spatial priority ranking software approaches (e.g. Zonation, Marxan) and the development of clearly defined management objectives. To extend such an analysis into the future, it will be necessary to also predict the future distribution of bottom trawling effort, potentially based on habitat suitability model-based predictions of the future distribution of commercial fish species.

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7 References

- Allouche, O., Tsoar, A., Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43: 1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x
- Anderson O.F., Guinotte, J.M., Rowden, A.A., Tracey, D.M., Mackay, K.A., Clark, M.R. (2016b) Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 115: 265-92.
- Anderson, O., Mikaloff Fletcher, S., Bostock, H. (2015) Development of models for predicting future distributions of protected coral species in the New Zealand Region. *NIWA Client Report* prepared for Department of Conservation WLG2015-65.
- Anderson, O., Tracey, D., Bostock, H., Williams, M., Clark, M. (2014) Refined habitat suitability modelling for protected coral species in the New Zealand EEZ. *NIWA Client Report* prepared for Department of Conservation WLG2014-69.
- Anderson, O.F., Ballara, S.L., Edwards, C.T.T. (2017) Fish and invertebrate bycatch and discards in New Zealand orange roughy and oreo trawl fisheries from 2001–02 until 2014–15. *New Zealand Aquatic Environment and Biodiversity Report*, No. 190: 216.
- Baird, S. J., Mules, R. (2020b) Extent of bottom contact by commercial trawling for deepwater fishstocks in New Zealand waters, and the combined inshore and deepwater footprint for 2008–18. *Draft New Zealand Aquatic Environment and Biodiversity Report* held by Fisheries New Zealand.
- Baird, S. J., Mules, R. (2020a) Extent of bottom contact by commercial fishing in New Zealand inshore waters, 2008 to 2018. *Draft New Zealand Aquatic Environment and Biodiversity Report* held by Fisheries New Zealand.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W. (2012) Selecting pseudoabsences for species distribution models: how, where and how many. *Methods in Ecology and Evolution*, 3: 327–338.
- Barry, S., Elith, J. (2006) Error and uncertainty in habitat models. *Journal of Applied Ecology*, 43(3): 413–423.
- Behrens, E., Williams, J., Morgenstern, O., Sutton, P., Rickard, G., Williams, M. (2019). Local Grid Refinement in New Zealand's Earth System Model: Tasman Sea Ocean Circulation Improvements and Super-Gyre Circulation Implications. *Earth and Space Science Open Archive*.
- Bostock, B., Jenkins, C., Mackay, K., Carter, L., Nodder, S., Orpin, A., Pallentin, A., Wysoczanski, R. (2018a) Distribution of surficial sediments in the ocean around New Zealand/Aotearoa. Part A: continental slope and deep ocean. *New Zealand Journal of Geology and Geophysics*. DOI:10.1080/00288306.2018.1523198

- Bostock, B., Jenkins, C., Mackay, K., Carter, L., Nodder, S., Orpin, A., Pallentin, A., Wysoczanski, R. (2018b) Distribution of surficial sediments in the ocean around New Zealand/Aotearoa. Part B: continental shelf. *New Zealand Journal of Geology and Geophysics*. DOI:10.1080/00288306.2018.1523199
- Bostock, H.C., Tracey, D.M., Currie, K.I., Dunbar, G.B., Handler, M.R., Mikaloff-Fletcher, S.E., Smith, A.M., Williams, M.J.M. (2015) The carbonate mineralogy and distribution of habitat-forming deep-sea corals in the southwest pacific region. *Deep-Sea Research Part II*, 100: 88–104.
- Bowden, D.A., Anderson, O.A., Escobar-Flores, P., Rowden, A.A., Clark, M.R. (2019) Quantifying benthic biodiversity: using seafloor image data to build single-taxon and community distribution models for Chatham Rise, New Zealand. *New Zealand Aquatic Environment and Biodiversity Report*, No. 235: 65.
- Breiman, L. (2001) Random forests. *Machine learning*. 45(1): 5-32.
- Burgos, J.M., Buhl-Mortensen, L., Buhl-Mortensen, P., Ólafsdóttir, S.H., Steingrund, P., Ragnarsson, S.Á., Skagseth, Ø. (2020) Predicting the Distribution of Indicator Taxa of Vulnerable Marine Ecosystems in the Arctic and Sub-arctic Waters of the Nordic Seas. *Frontiers in Marine Science*, 7(131). doi: 10.3389/fmars.2020.00131
- CANZ (2008) New Zealand Region Bathymetry. *NIWA Chart*, Miscellaneous Series No. 85, National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Clark, M., Tracey, D., Anderson, O., Parker, S. (2014) Pilot ecological risk assessment for protected corals. *NIWA Client Report* prepared for Department of Conservation WLG2014-70.
- Compton, T.J., Bowden, D.A., Pitcher, R.C., Hewitt, J.E., Ellis, N. (2013) Biophysical patterns in benthic assemblage composition across contrasting continental margins off New Zealand. *Journal of Biogeography*, 40(1): 75-89. <http://dx.doi.org/10.1111/j.1365-2699.2012.02761.x>
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Townsend, P., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29: 129-151.
- Elith, J., Leathwick, J. (2011) Boosted regression trees for ecological modelling. r-project.org. <http://dx.doi.org/http://cran.r-project.org/web/packages/dismo/vignettes/brt.pdf>. 22 p
- Elith, J., Leathwick, J.R., Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77(4): 802-13.
- Fisheries New Zealand (2019) Fisheries Assessment Plenary, May 2019: stock assessments and stock status. Compiled by the *Fisheries Science and Information Group*, Fisheries New Zealand, Wellington, New Zealand: 1641.

- Foster, S.D., Shimadzu, H., Darnell, R. (2012) Uncertainty in spatially predicted covariates: is it ignorable? *Applied Statistics*, 61(4): 637–652.
- Freeman, D.J., Marshall, B.A., Ah Yong, S.T., Wing, S.R., Hitchmough, R.A. (2010) Conservation status of New Zealand marine invertebrates, 2009. *New Zealand Journal of Marine and Freshwater Research*, Vol. 44(3): 129-148.
- Freeman, D.J., Schnabel, K., Marshall, B.A., Gordon, D., Wing, S.R., Tracey, D., Hitchmough, R.A. (2013) Conservation status of New Zealand marine invertebrates, 2013. *Department of Conservation Report: 25*.
- Fricko, O. et al. (2017) The marker quantification of the Shared Socioeconomic Pathway 2: A middle-of-the-road scenario for the 21st century. *Global Environmental Change*, 42: 251-267. <https://doi.org/10.1016/j.gloenvcha.2016.06.004>
- Friedman, J.H. (1991) Multivariate Adaptive Regression Splines. *Annals of Statistics*, 19 (1): 1-67. doi:10.1214/aos/1176347963. <https://projecteuclid.org/euclid.aos/1176347963>
- Georgian, S.E., Anderson, O.F., Rowden, A.A. (2019) Ensemble habitat suitability modeling of vulnerable marine ecosystem indicator taxa to inform deep-sea fisheries management in the South Pacific Ocean. *Fisheries Research*, 211: 256-274.
- Hastie, T., Tibshirani, R. (1990) *Generalized Additive Models*. London: Chapman and Hall.
- Heiberger, R., Holland, B. (2004) *Statistical analysis and data display: an intermediate course with examples in S-PLUS R and SAS (Springer texts in statistics)*. Springer.
- Heiberger, R.M., (2011) *HH: Statistical Analysis and Data Display: Heiberger and Holland. R. Package version 2: 2–23* <http://CRAN.R-project.org/package=HH>
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. (2011) Package ‘dismo’. Available online at: <http://cran.r-project.org/web/packages/dismo/index.html>
- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N. (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology*, 2002(83): 2027-2036.
- Hobday, A.J., Smith, A.D.M., Stobutzki, I.C., Bulman, C., Daley, R., Dambacher, J.M., Deng, R.A., Dowdney, J., Fuller, M. Furlani, D., Griffiths, S.P., Johnson, D., Kenyon, R., Knuckey, A., Ling, S.D., Pitcher, R., Sainsbury, K.J., Sporcic, M., Zhou, S. (2011) Ecological risk assessment for the effects of fishing. *Fisheries Research*, 108 (2–3): 372-384. <https://doi.org/10.1016/j.fishres.2011.01.013>
- Hosmer, D.W.J., Lemeshow, S., Sturdivant, R.X. (2013). *Applied Logistic Regression*, Third Edition. John Wiley and Sons: 528.
- Huang, Z., Brooke, B., Li, J. (2011) Performance of predictive models in the marine benthic environments based on predictions of sponge distribution on the Australian continental shelf. *Ecological Informatics*, 6 (3-4): 205-216.

- Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T., Taylor, P. (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series*, 321: 267–281.
- Mackay, K.A. (2007) Database documentation: SEAMOUNT. *NIWA Internal Report*: 42.
- McCullagh, P., Nelder, J.A. (1989) *Generalized Linear Models*. Chapman and Hall, London.
- Morato, T., González-Irusta, J-M., et al. (2020) Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. *Global Change Biology* 2020, 00: 1–22. DOI: 10.1111/gcb.14996
- Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. In: R. Longmore (ed) *Atlas of elapid snakes of Australia: Australian flora and fauna*, series 7. Bureau of Flora and Fauna, Canberra: 4–15.
- Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I., Louzao, M., (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation*, 156: 94–104.
- Parker, S.J., Penney, A.J., Clark, M.R. (2009) Detection criteria for managing trawl impacts on vulnerable marine ecosystems in high seas fisheries of the South Pacific Ocean. *Marine Ecology Progress Series*, 397: 309-17.
- Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3-4): 231-59.
- R Core Team (2018) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ramiro-Sánchez, B., González-Irusta, J.M., Henry, L-A., Cleland, J., Yeo, I., Xavier, J.R., Carreiro-Silva, M., Sampaio, Í., Spearman, J., Victorero, L., Messing, C.G., Kazanidis, G., Roberts, J.M., Murton, B. (2019) Characterization and Mapping of a Deep-Sea Sponge Ground on the Tropic Seamount (Northeast Tropical Atlantic): Implications for Spatial Management in the High Seas. *Frontiers in Marine Science*, 6: 278. doi: 10.3389/fmars.2019.00278
- Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., van Hoey, G., Zettler, M.L., Degraer, S. (2015) Benthos distribution modelling and its relevance for marine ecosystem management. *Ices Journal of Marine Science*, 72(2): 297-315. <http://dx.doi.org/10.1093/icesjms/fsu107>
- Ridgeway, G. (2019). *Generalized Boosted Models: A guide to the gbm package*. https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=2&cad=rja&uact=8&ved=2ahUKewijkdH3icvnAhVi7HMBHbg1B34QFjABegQIAhAB&url=https%3A%2F%2Fcran.r-project.org%2Fweb%2Fpackages%2Fgbm%2Fvignettes%2Fgbm.pdf&usq=AOvVaw3G_GwG3t2iypBBrtj4mFyt

- Robert, K., Jones, D.O.B., Roberts, J.M., Huvenne, V.A.I. (2016) Improving predictive mapping of deep-water habitats: Considering multiple model outputs and ensemble techniques. *Deep-Sea Research Part I-Oceanographic Research Papers*, 113: 80-89. <http://dx.doi.org/10.1016/j.dsr.2016.04.008>
- Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F. and Dormann, C.F. (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, 40: 913-929. <https://doi.org/10.1111/ecog.02881>
- Rowden, A.A., Oliver, M., Clark, M.R., Mackay, K. (2008) New Zealand's "SEAMOUNT" database: recent updates and its potential use for ecological risk assessment. *New Zealand Aquatic Environment and Biodiversity Report*, 27: 49.
- Rowden, A.A., Anderson, O.F., Georgian, S.E., Bowden, D.A., Clark, M.R., Pallentin, A., Miller, A. (2017) High-resolution habitat suitability models for the conservation and management of vulnerable marine ecosystems on the Louisville Seamount Chain, South Pacific Ocean. *Frontiers in Marine Science*, 4: 335. doi: 10.3389/fmars.2017.00335
- Stephenson, F., Goetz, K., Sharp, B.R., Mouton, T.L., Beets, F.L., Roberts, J., MacDiarmid, A.B., Constantine, R., Lundquist, C.J. (2020) Modelling the spatial distribution of cetaceans in New Zealand waters. *Diversity and Distributions*, 2020;00: 1–22. <https://doi.org/10.1111/ddi.13035>
- Stockwell, D.R.B. (1999) Genetic algorithms II. In: A.H. Fielding (ed) Machine learning methods for ecological applications. Kluwer Academic Publishers, Boston: 123–144
- Stoklosa, J., Daly, C., Foster, S.D., Ashcroft, M.B., Warton, D.I. (2015) A climate of uncertainty: accounting for error in climate variables for species distribution models. *Methods in Ecology and Evolution*, 2015(6): 412–423. doi: 10.1111/2041-210X.12217
- Tracey, D., Mills S., Macpherson, D., Thomas, H. (2017) Identification and storage of cold-water coral bycatch specimens. Final Report prepared by NIWA for the Conservation Services Programme, Department of Conservation. INT2015-03. *NIWA Client Report* 2017349WN: 38. <https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-conservation-services/reports/coral-id-final-annual-report-december-2017-web.pdf>
- Tracey, D.M., Hjørvarsdóttir, F. (2019) The State of Knowledge of Deep-Sea Corals in the New Zealand Region. *NIWA Science and Technology Series*, Number 84: 140.
- Tracey, D.M., Rowden, A.A., Mackay, K.A., Compton, T. (2011) Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. *Marine Ecology-Progress Series*, 430: 1-U59. <http://dx.doi.org/10.3354/meps09164>
- Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G. (2019) blockCV: An r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution*, 10: 225–232. <https://doi.org/10.1111/2041-210X.13107>

- Vierod, A.D.T., Guinotte, J.M., Davies, A.J. (2014) Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 99: 6-18.
<http://dx.doi.org/10.1016/j.dsr2.2013.06.010>
- Williams, J., Morgenstern, O., Varma, V., Behrens, E., Hayek, W., Oliver, H., Dean, S., Mullan, B., Frame, D. (2016) Development of the New Zealand Earth System Model: NZESM. *Weather and Climate*, 36: 25-44.
- Winship, A.J., Thorson, J.T., Clarke, M.E., Coleman, H.M., Costa, B., Georgian, S.E., Gillett, D., Grüss, A., Henderson, M.J., Hourigan, T.F., Huff, D.D., Kreidler, N., Pirtle, J.L., Olson, J.V., Poti, M., Rooper, C.N., Sigler, M.F., Viehman, S., Whitmire, C.E. (2020) Good Practices for Species Distribution Modeling of Deep-Sea Corals and Sponges for Resource Management: Data Collection, Analysis, Validation, and Communication. *Frontiers in Marine Science*, 7(303). doi:10.3389/fmars.2020.00303
- Wood, B., Finucci, B., Black, J. (in prep) A standardised approach for creating spatial grids for analysing (binning) New Zealand fisheries data.
- Yesson, C., Bedford, F., Rogers, A.D., Taylor, M. (2015). The global distribution of deep-water Antipatharia habitat. *Deep-Sea Research part II*.
<http://dx.doi.org/10.1016/j.dsr2.2015.12.004i>

Appendix A Environmental predictor variables

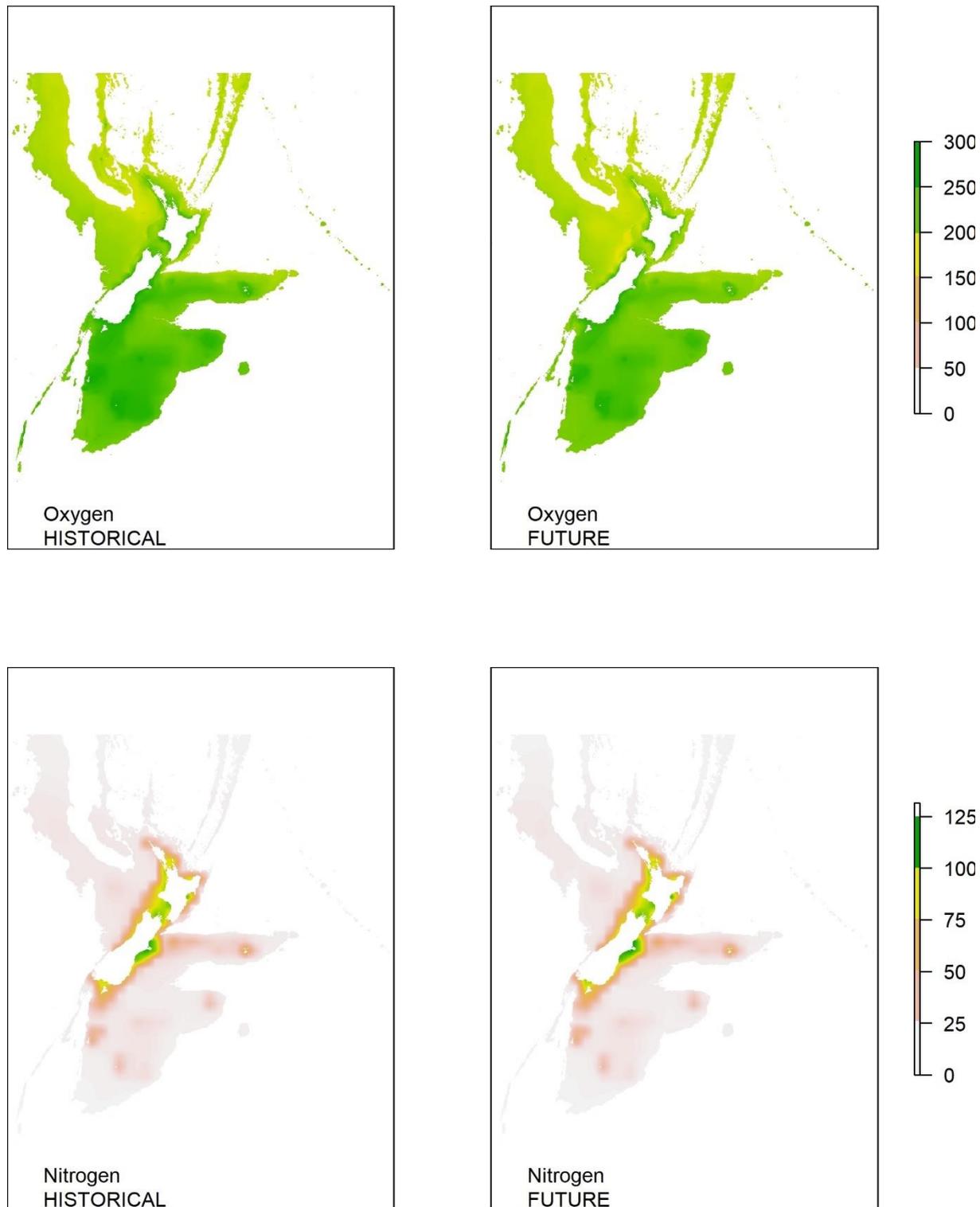


Figure A-1: Environmental variables used in the models. Top, Dissolved Oxygen (mmol/m²); bottom, Benthic Nitrogen (mmol/m³).

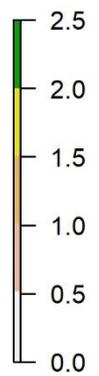
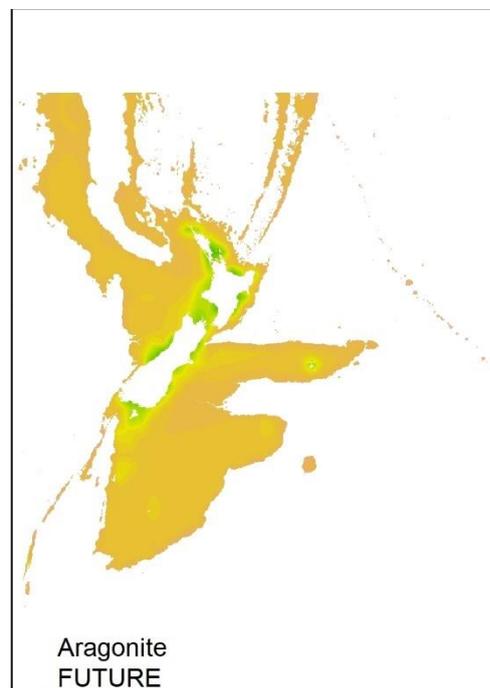
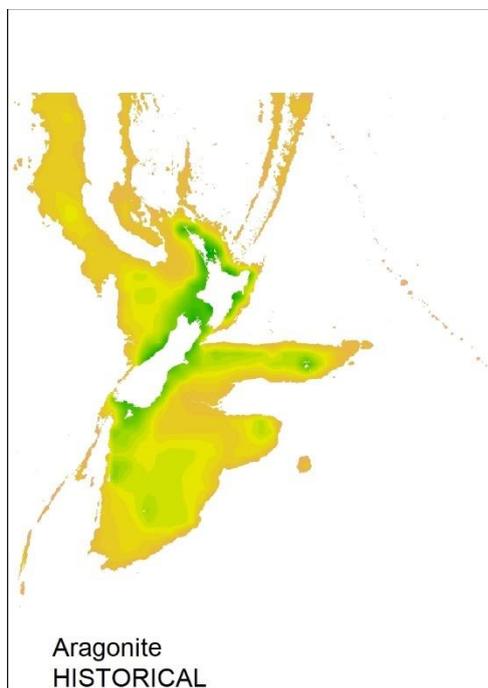
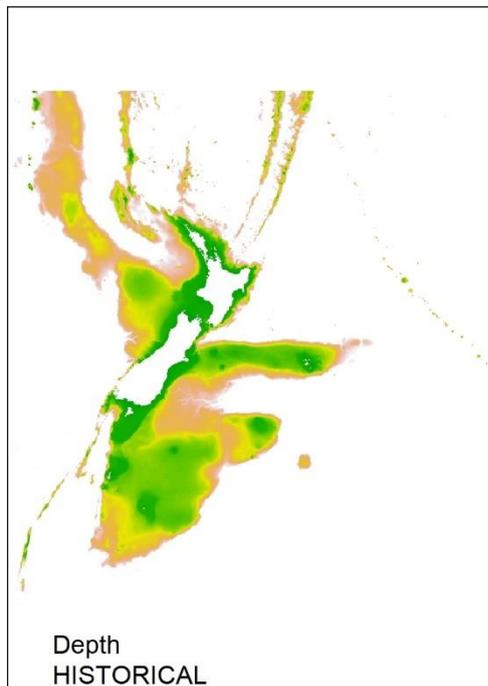


Figure A-2: Environmental variables used in the models. Top, Depth (m); bottom, Aragonite saturation.

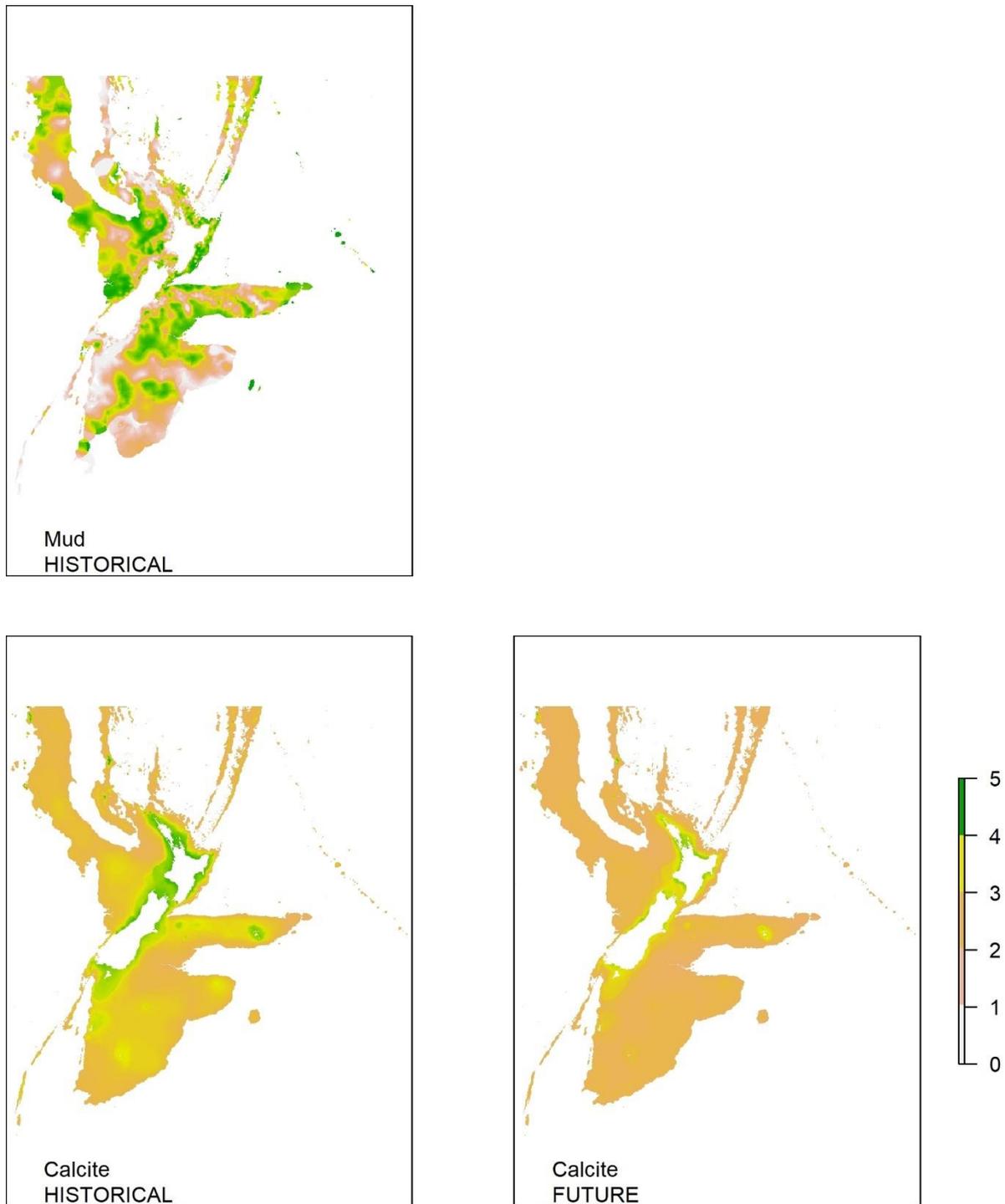


Figure A-3: Environmental variables used in the models. Top, Mud (%); bottom, Calcite saturation.

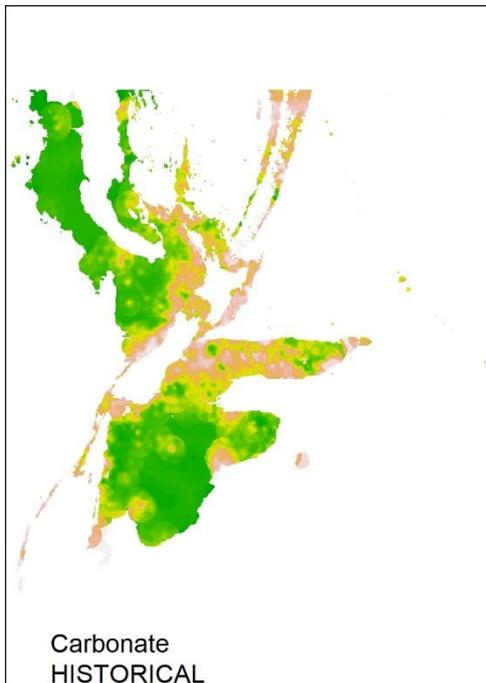
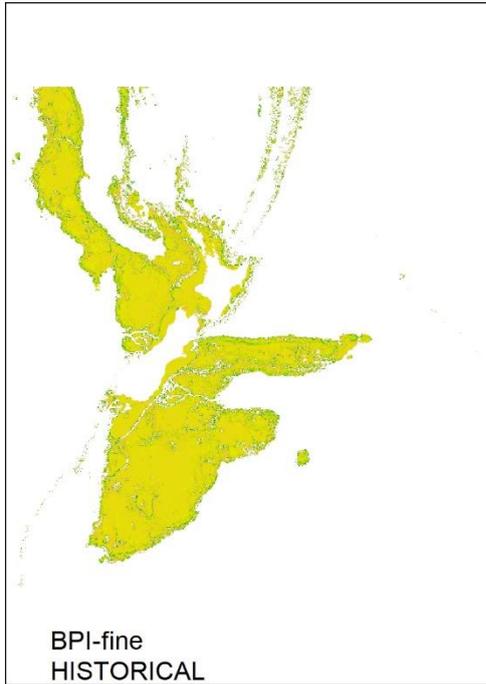


Figure A-4: Environmental variables used in the models. Top, BPI-fine; bottom, Carbonate (%).

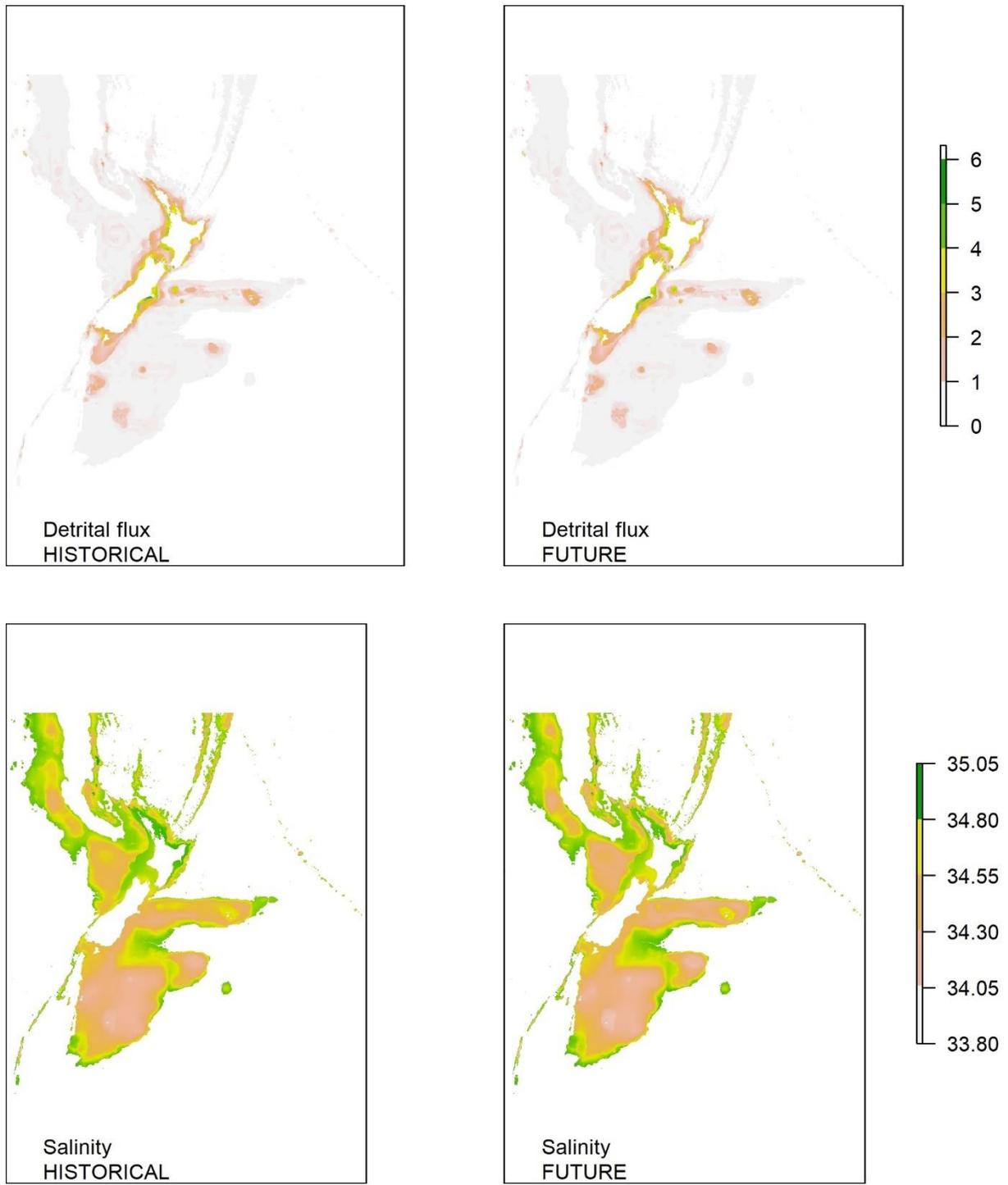


Figure A-5: Environmental variables used in the models. Top, detrital flux to seabed (mmol/m³); bottom, Salinity (Psu).

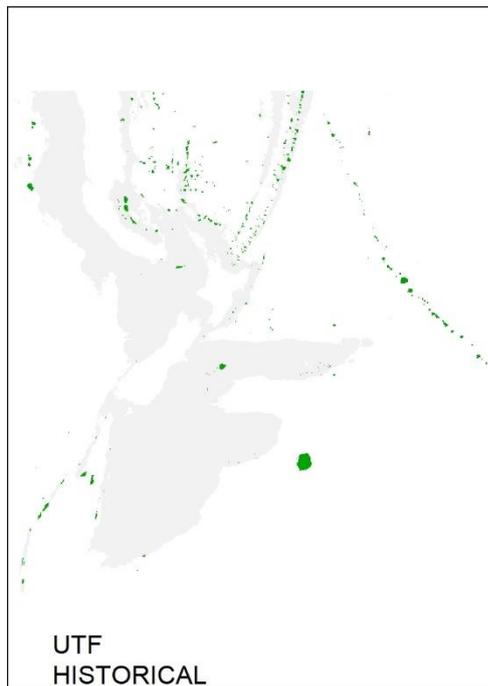


Figure A-6: Environmental variables used in the models. Top, UTF (note: many UTFs with small basal areas, or outside the modelled depth range, are not visible in this plot); bottom, Slope-percent.

Appendix B Random Forest models partial dependence plots

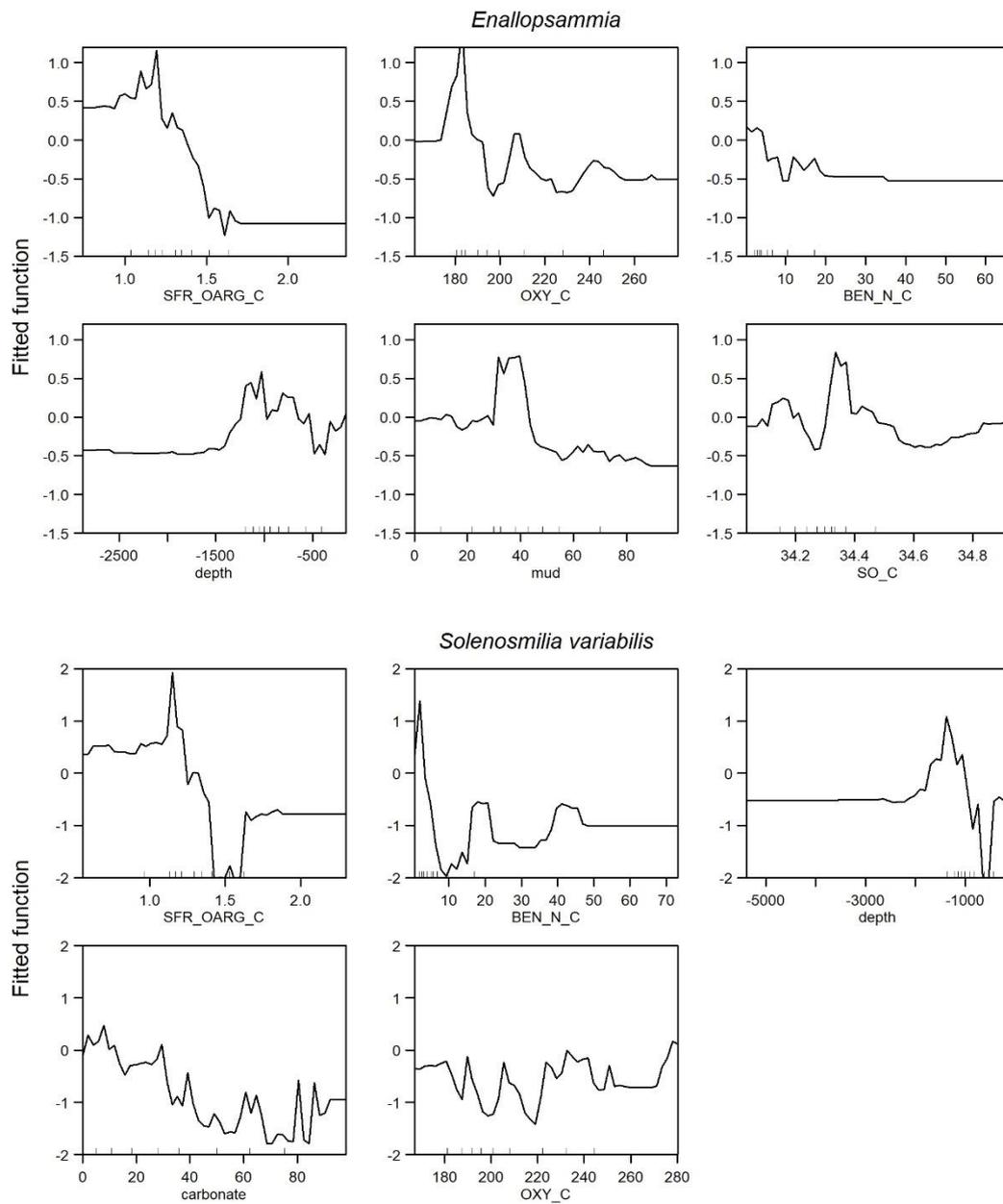


Figure B-1: Variable marginal effects in the Random Forest models for *Enallopsammia rostrata* (top) and *Solenosmilia variabilis* (bottom). See Table 2-2 for an explanation of the variables.

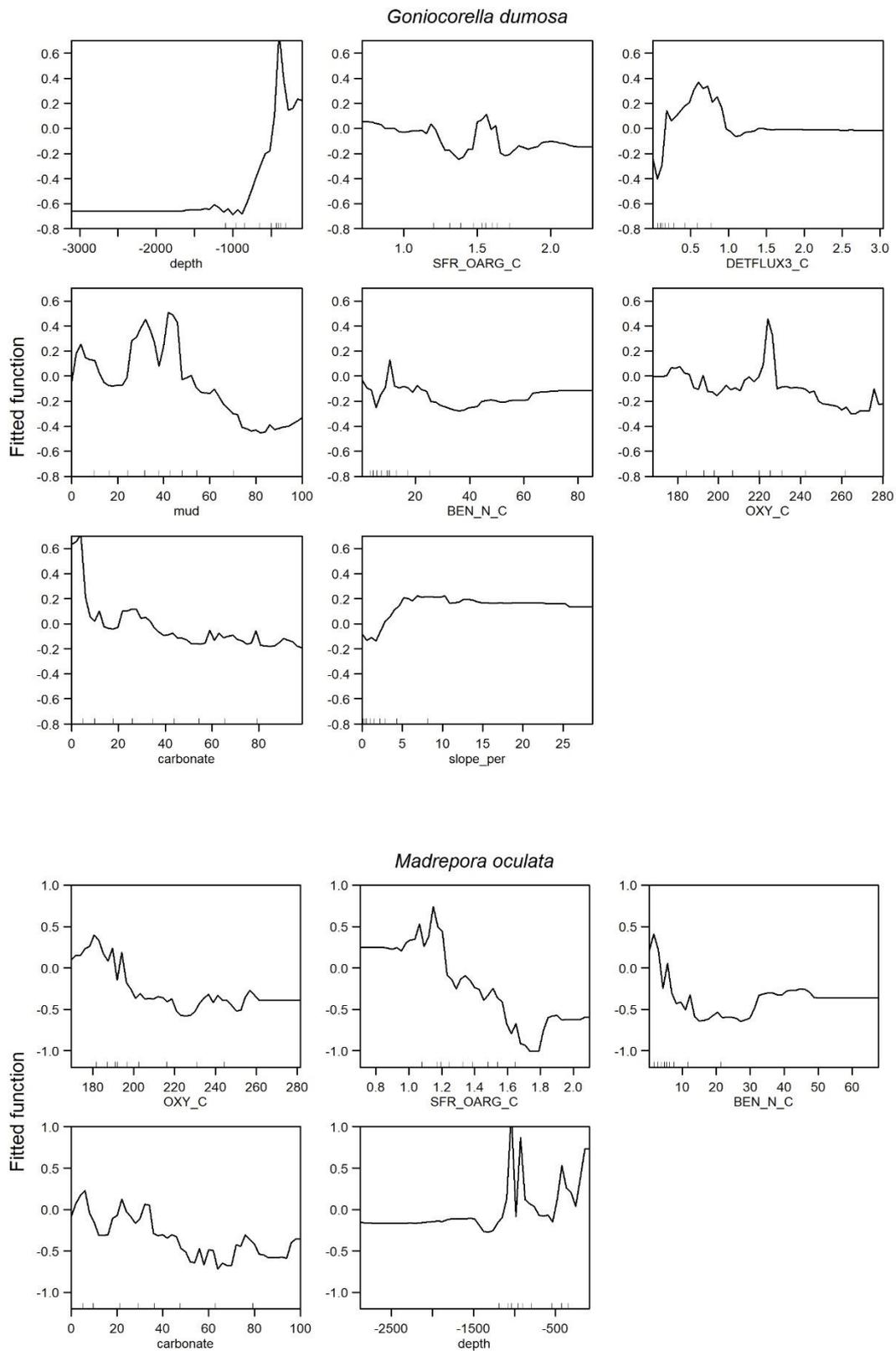


Figure B-2: Variable marginal effects in the Random Forest models for *Goniocorella dumosa* (top) and *Madrepora oculata* (bottom). See Table 2-2 for an explanation of the variables.

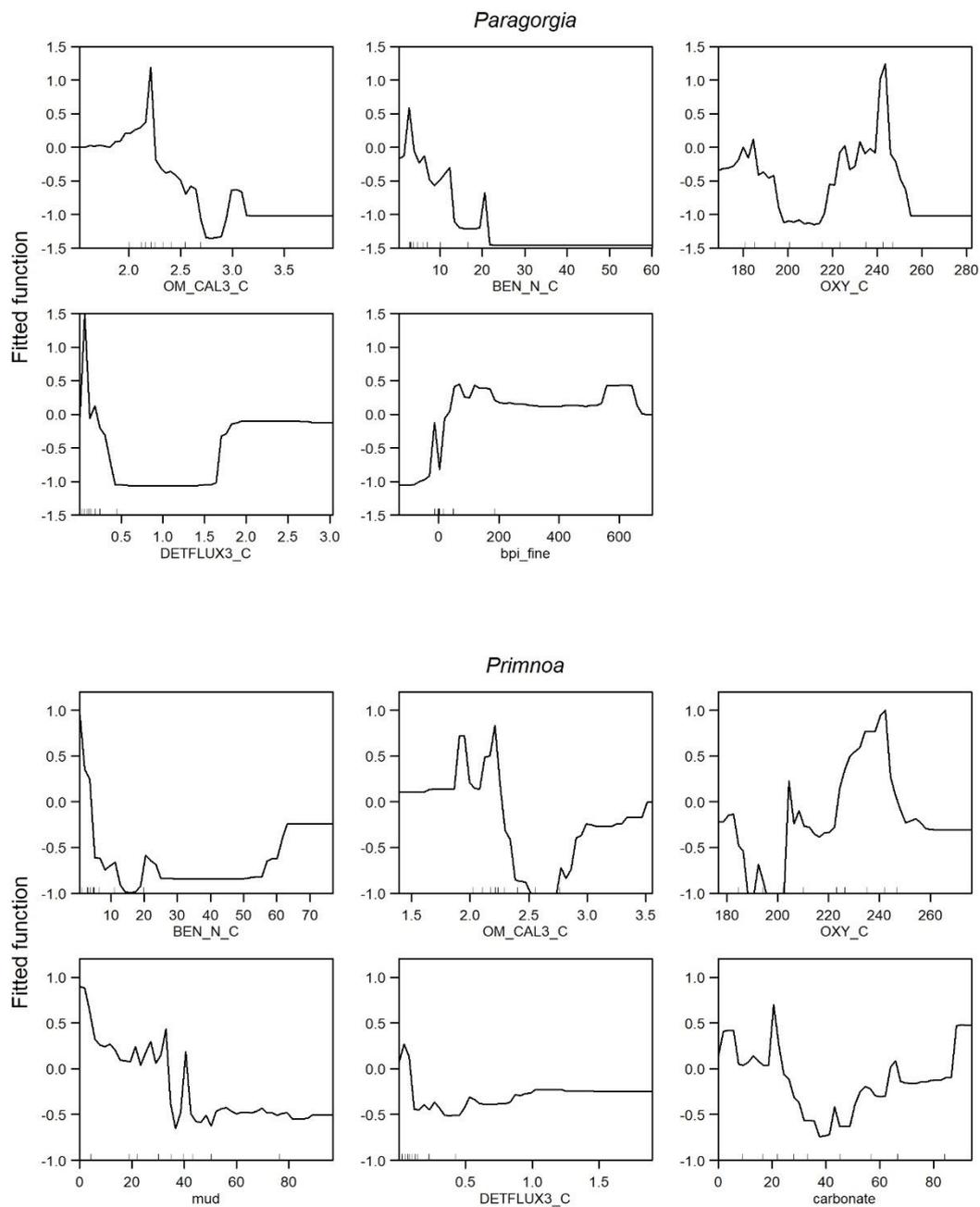


Figure B-3: Variable marginal effects in the Random Forest models for *Paragorgia* spp. (top) and *Primnoa* spp. (bottom). See Table 2-2 for an explanation of the variables.

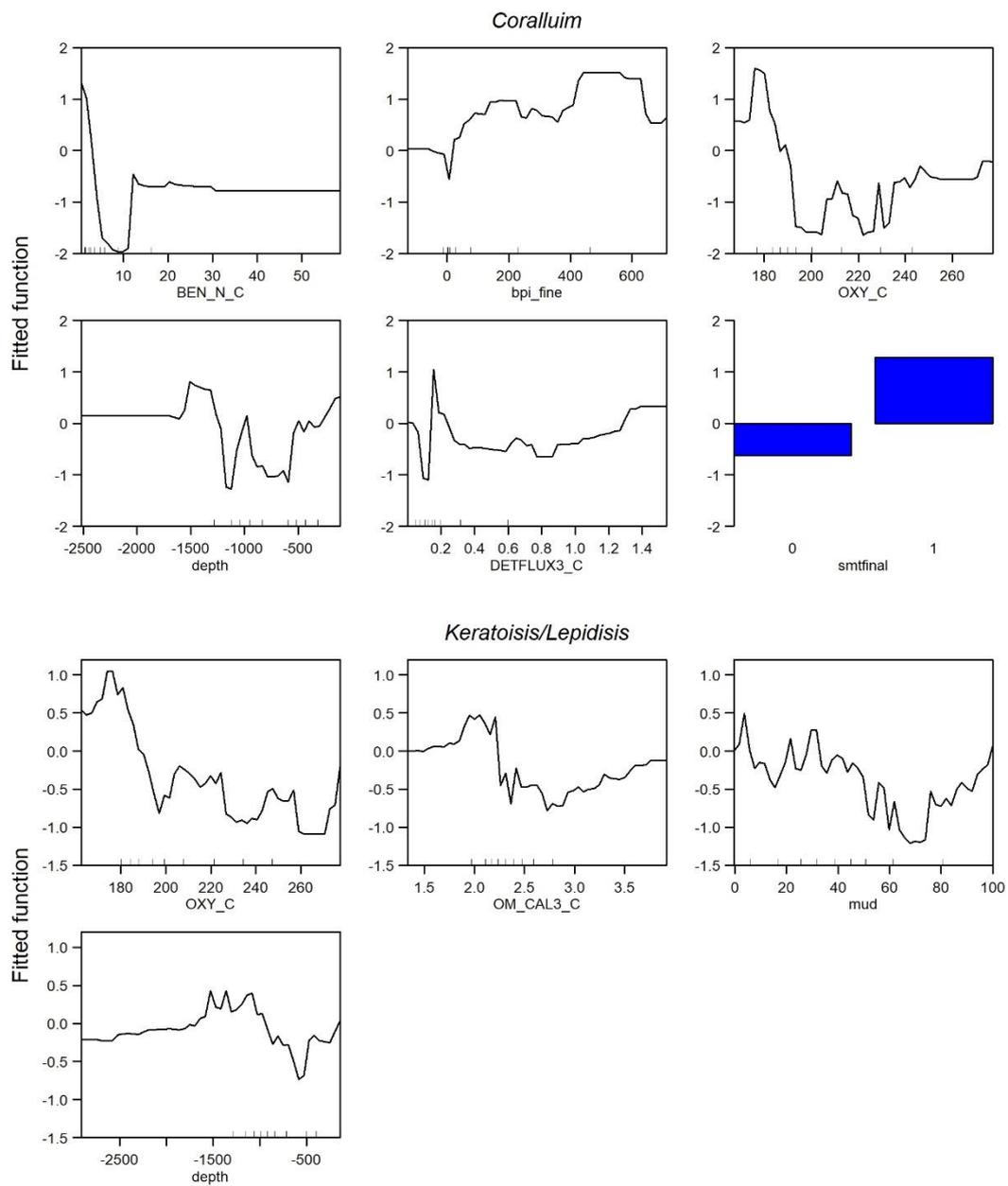


Figure B-4: Variable marginal effects in the Random Forest models for *Corallium* spp. (top) and *Keratoisis* & *Lepidisis* spp. (bottom). See Table 2-2 for an explanation of the variables.

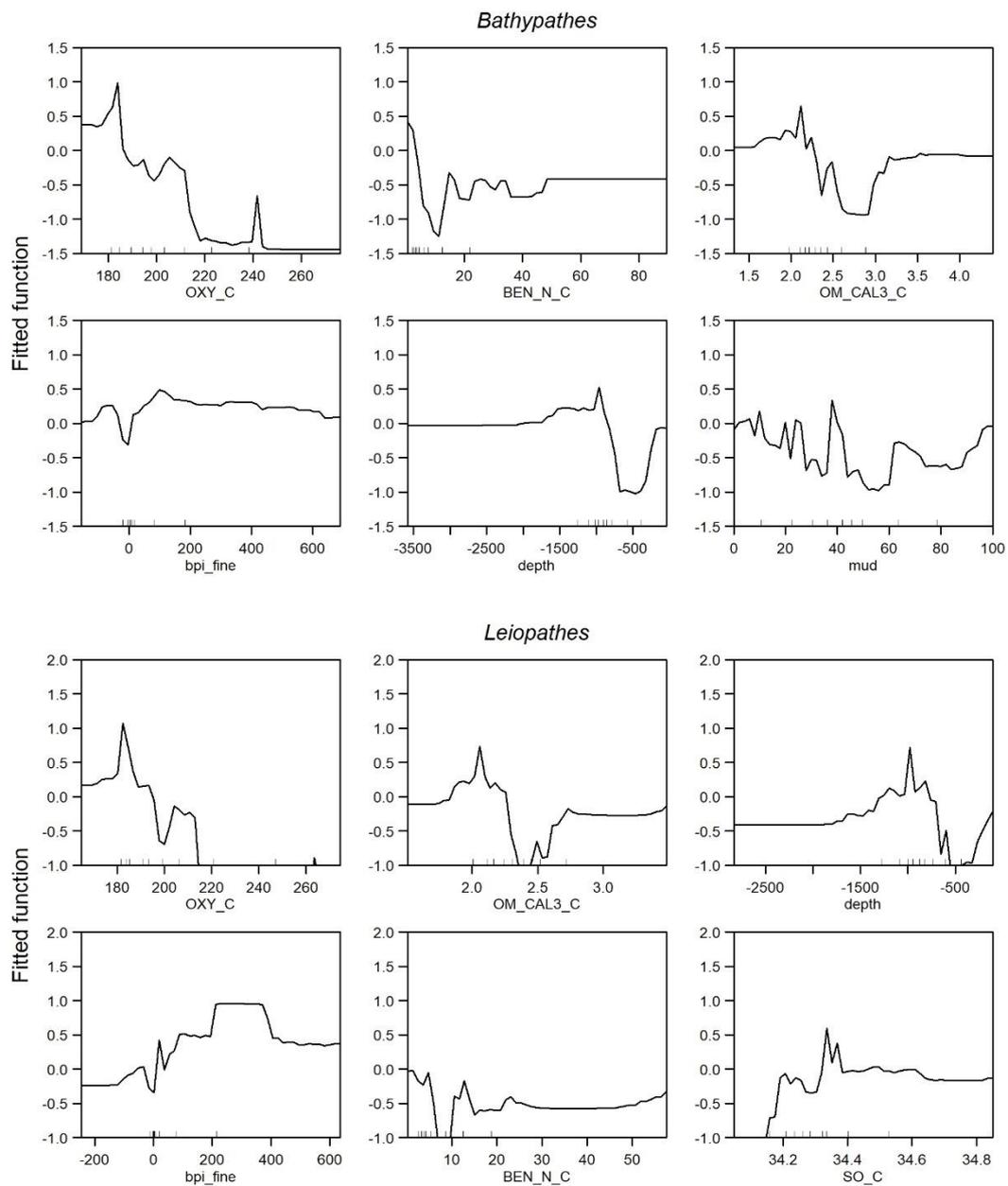


Figure B-5: Variable marginal effects in the Random Forest models for *Bathypathes* spp. (top) and *Leiopathes* spp. (bottom). See Table 2-2 for an explanation of the variables.

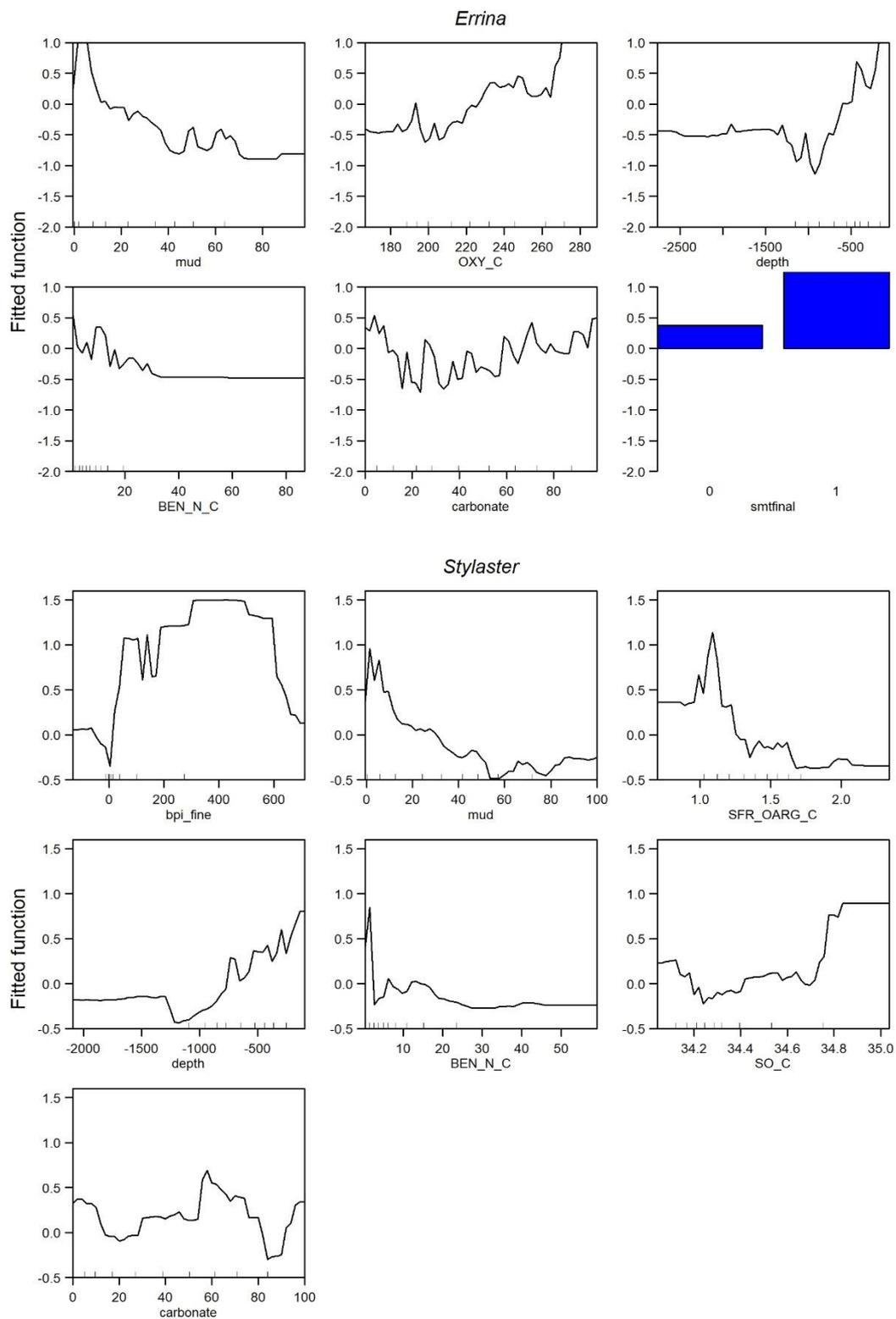
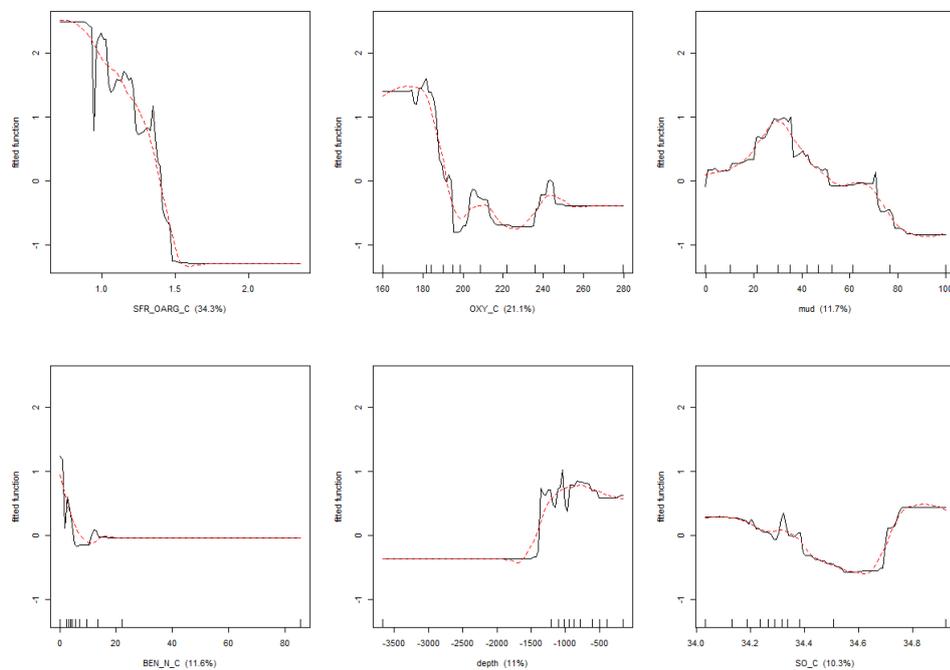


Figure B-6: Variable marginal effects in the Random Forest models for *Errina* spp. (top) and *Stylaster* spp. (bottom). See Table 2-2 for an explanation of the variables.

Appendix C Boosted Regression Tree models partial dependence plots

Enallopsammia rostrata



Solenosmilia variabilis

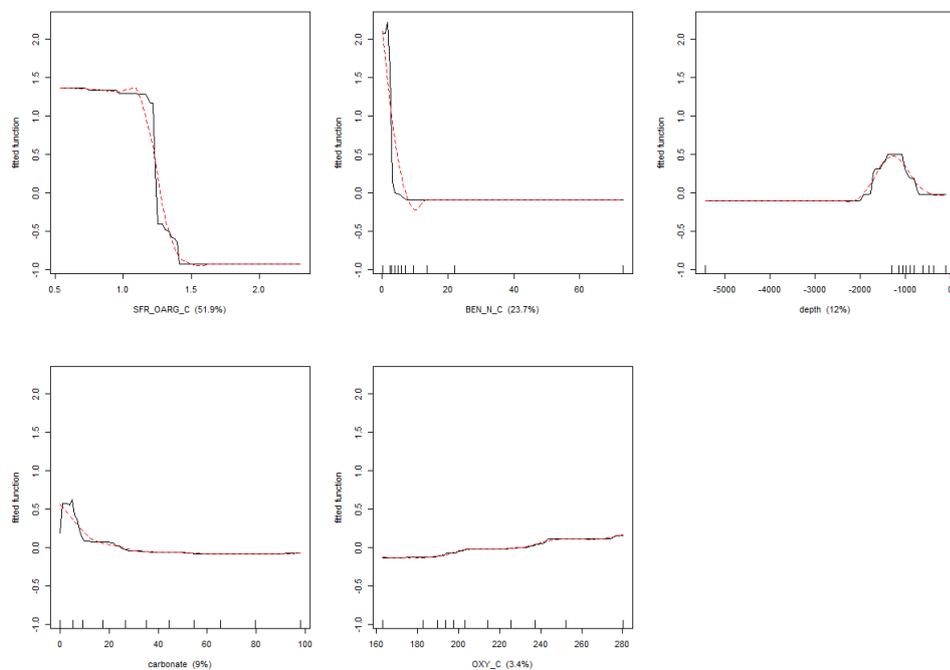
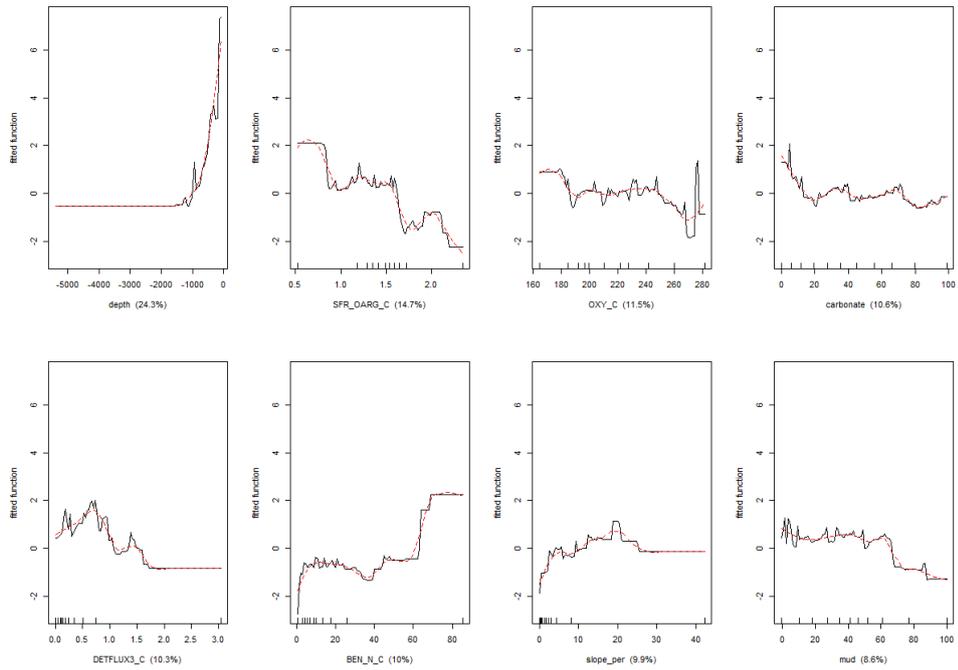


Figure C-1: Variable marginal effects in the Boosted Regression tree models for *Enallopsammia rostrata* (top) and *Solenosmilia variabilis* (bottom). See Table 2-2 for an explanation of the variables.

Goniocorella dumosa



Madrepora oculata

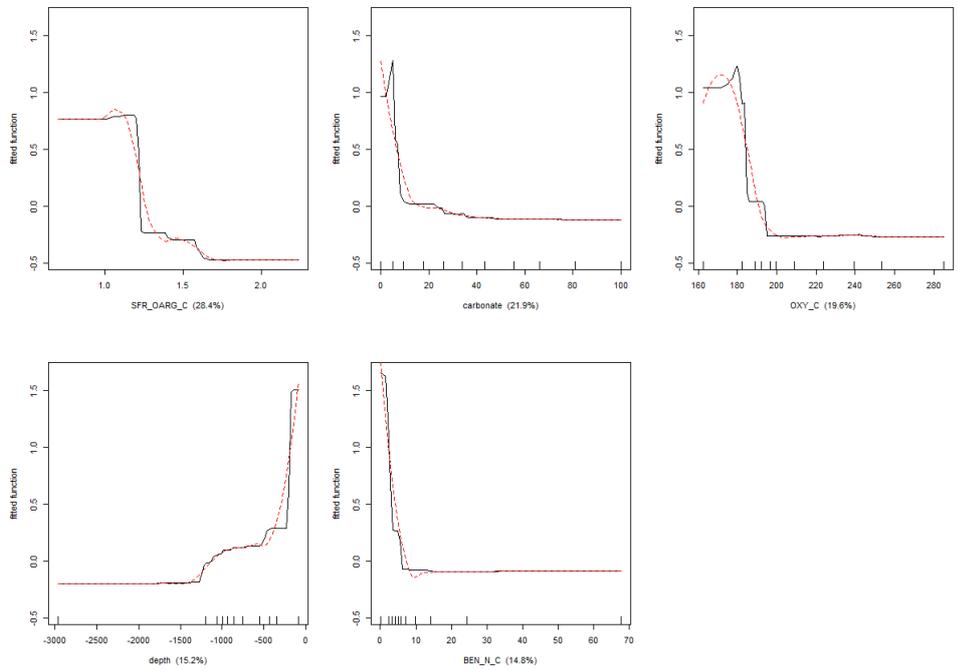
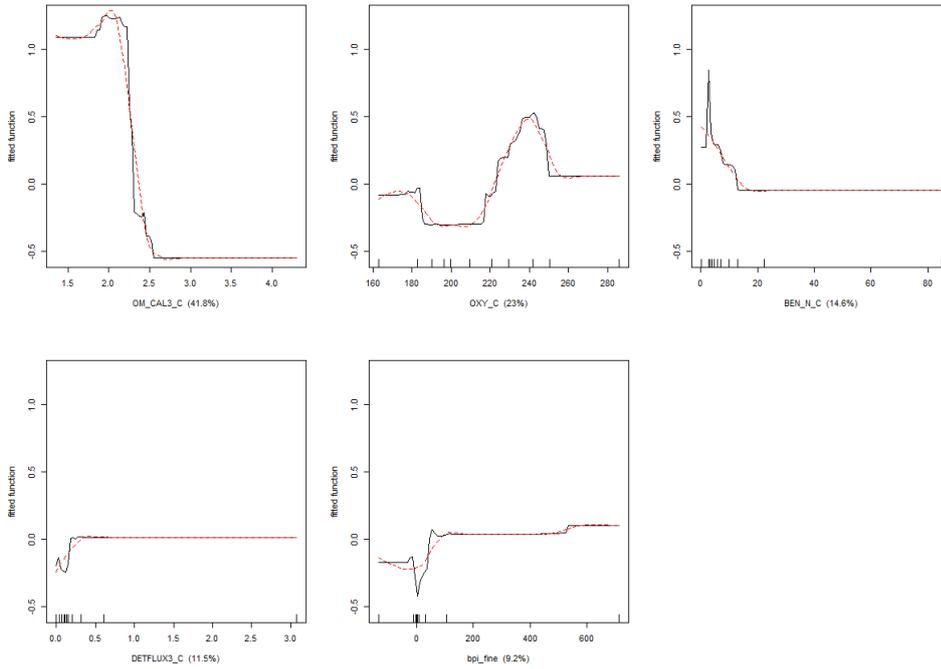


Figure C-2: Variable marginal effects in the Boosted Regression tree models for *Goniocorella dumosa* (top) and *Madrepora oculata* (bottom). See Table 2-2 for an explanation of the variables.

Paragorgia spp.



Primnoa spp.

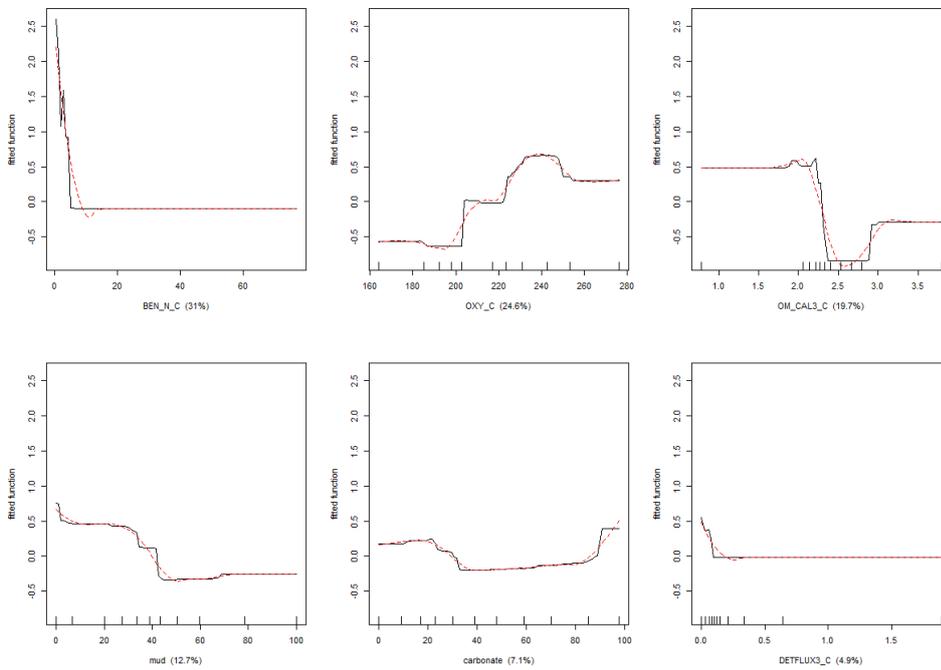
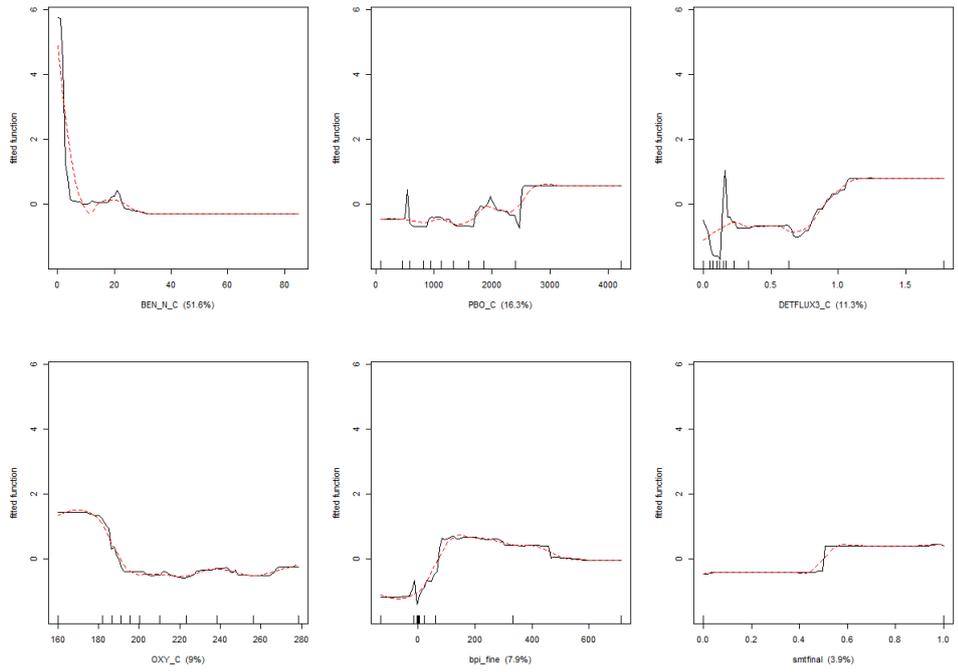


Figure C-3: Variable marginal effects in the Boosted Regression tree models for *Paragorgia spp.* (top) and *Primnoa spp.* (bottom). See Table 2-2 for an explanation of the variables.

Corallium spp.



Keratoisis & Lepidisis spp.

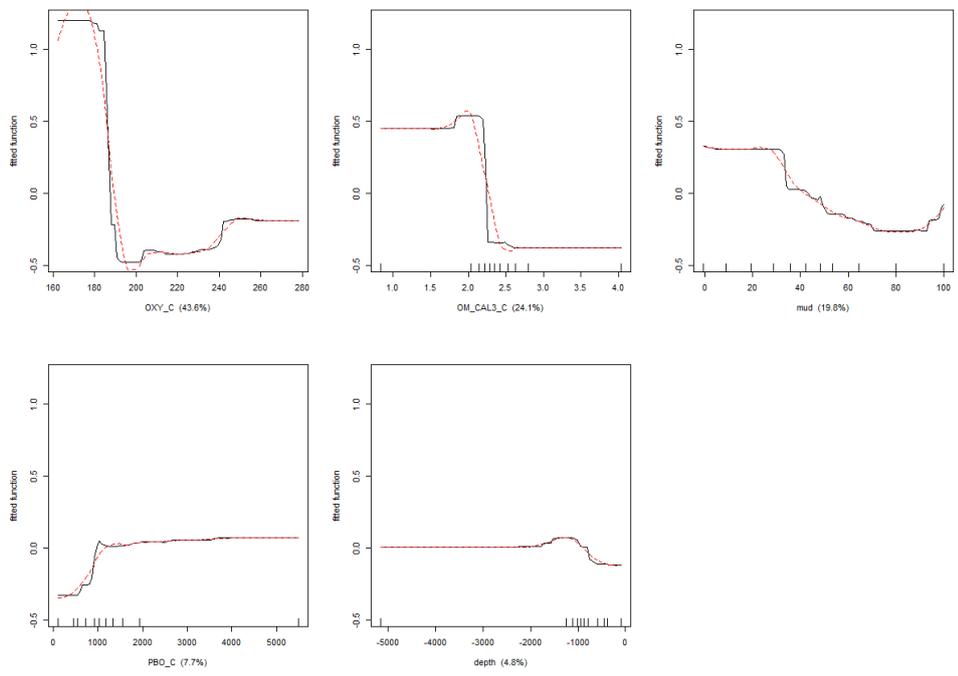
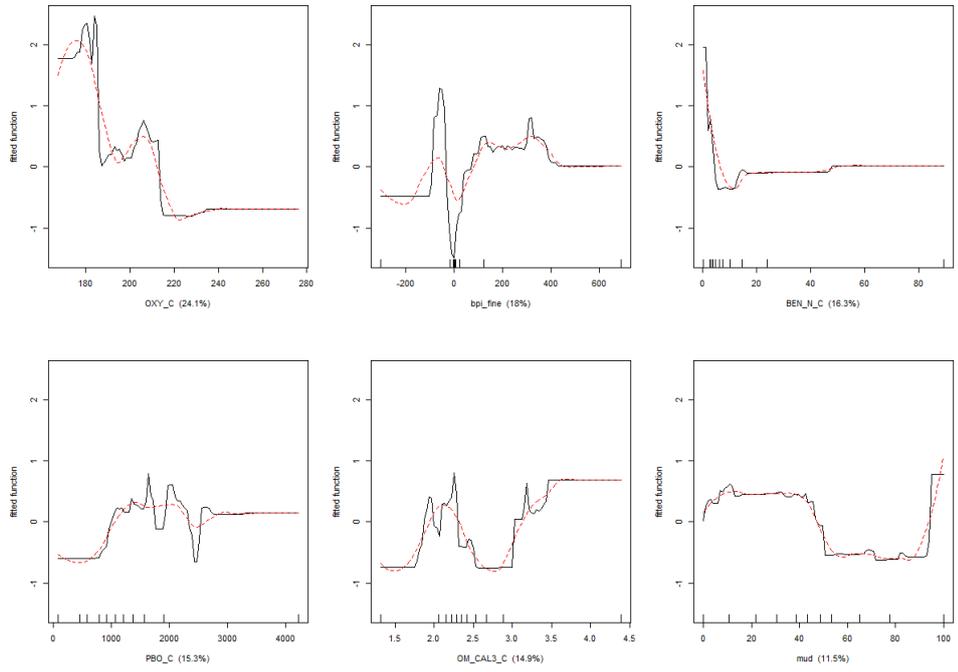


Figure C-4: Variable marginal effects in the Boosted Regression tree models for *Corallium* spp. (top) and *Keratoisis & Lepidisis* spp. (bottom). See Table 2-2 for an explanation of the variables.

Bathypathes spp.



Leiopathes spp.

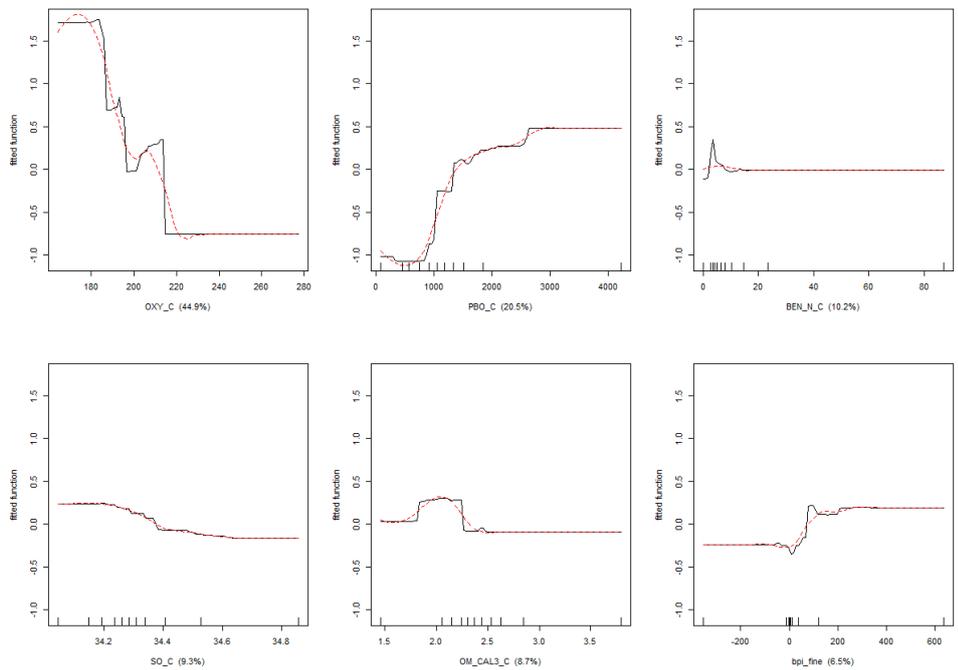
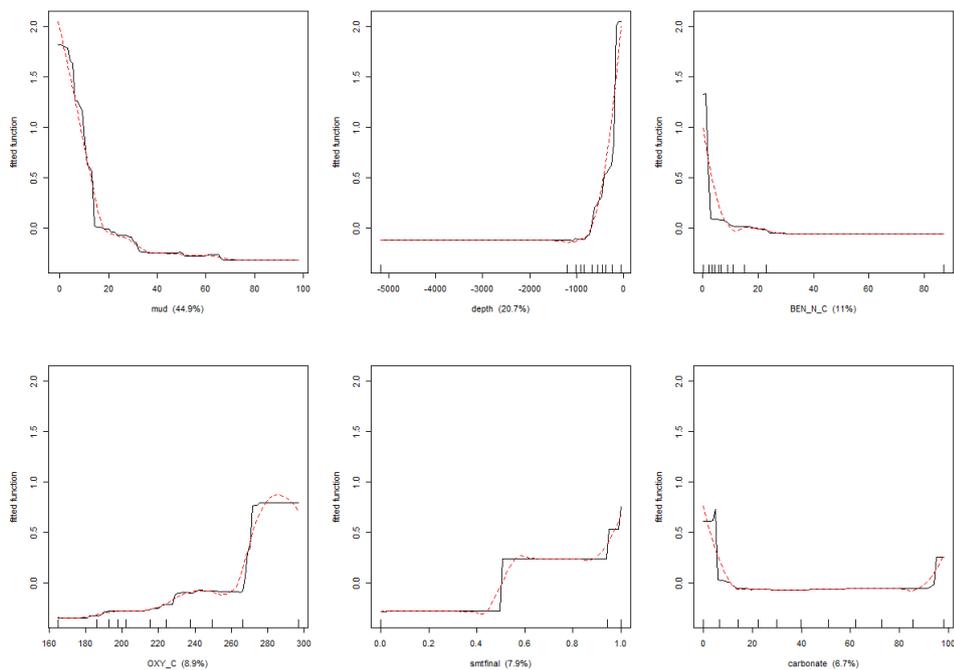


Figure C-5: Variable marginal effects in the Boosted Regression tree models for *Bathypathes* spp. (top) and *Leiopathes* spp. (bottom). See Table 2-2 for an explanation of the variables.

Errina spp.



Stylaster spp.

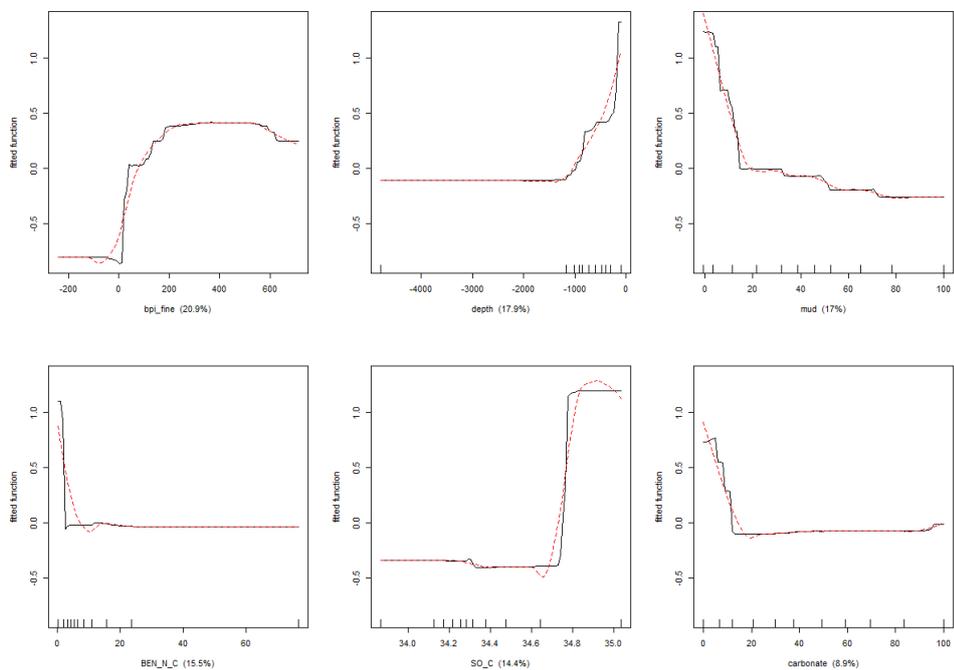


Figure C-6: Variable marginal effects in the Boosted Regression tree models for Bathypathes spp. (top) and Leiopathes spp. (bottom). See Table 2 2 for an explanation of the variables.