Received: 4 April 2022 | Revised: 29 July 2022 | Accepted: 31 July 2022

DOI: 10.1111/gcb.16389

Global Change Biology WILEY

RESEARCH ARTICLE

Predicting the effects of climate change on deep-water coral distribution around New Zealand—Will there be suitable refuges for protection at the end of the 21st century?

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Funding information
Fisheries New Zealand; New Zealand Department of Conservation, Conservation Services Programme, Grant/Award Number: POP202801; New Zealand Ministry of Business, Innovation and Employment, Grant/Award Number: C01X1901

Abstract

Deep-water corals are protected in the seas around New Zealand by legislation that prohibits intentional damage and removal, and by marine protected areas where bottom trawling is prohibited. However, these measures do not protect them from the impacts of a changing climate and ocean acidification. To enable adequate future protection from these threats we require knowledge of the present distribution of corals and the environmental conditions that determine their preferred habitat, as well as the likely future changes in these conditions, so that we can identify areas for potential refugia. In this study, we built habitat suitability models for 12 taxa of deep-water corals using a comprehensive set of sample data and predicted present and future seafloor environmental conditions from an earth system model specifically tailored for the South Pacific. These models predicted that for most taxa there will be substantial shifts in the location of the most suitable habitat and decreases in the area of such habitat by the end of the 21st century, driven primarily by decreases in seafloor oxygen concentrations, shoaling of aragonite and calcite saturation horizons, and increases in nitrogen concentrations. The current network of protected areas in the region appear to provide little protection for most coral taxa, as there is little overlap with areas of highest habitat suitability, either in the present or the future. We recommend an urgent re-examination of the spatial distribution of protected areas for deep-water corals in the region, utilising spatial planning software that can balance protection requirements against value from fishing and mineral resources, take into account the current status of the coral habitats after decades of bottom trawling, and consider connectivity pathways for colonisation of corals into potential refugia.

KEYWORDS
boosted regression trees, climate change, earth system models, habitat suitability models, marine protected areas, random forest, refugia

1 | INTRODUCTION

Corals are found from shallow to deep waters and are key species in highly biodiverse and productive ecosystems (Roberts et al., 2009). The effects of climate change on shallow-water (zooxanthellate) coral taxa have been the focus of much research (see review by Hoegh-Guldberg et al. (2017)) and recent studies have predicted the impact of climate change on suitable future habitat for some such corals (e.g., de Oliveira et al., 2019; Principe et al., 2021). Deep-water (azooxanthellate) corals (i.e., those predominately found at depths deeper 200 m) are also thought to be under significant threat from climate-related stressors, through ocean warming and ocean acidification, and their associated changes in the chemical and physical properties of waters in the deep sea (see review by Hebbeln et al. (2019), and recent historical meta-analysis by Portilho-Ramos et al. (2022)). However, few studies have explored how these stressors could affect spatial distribution patterns of deep-water corals.

Water temperature is known to be a critical factor in determining the distribution of deep-water corals (e.g., Davies & Guinotte, 2011; Dullo et al., 2008; Morato et al., 2020; Roberts et al., 2009), and experimental and in situ studies have shown that while corals can tolerate a relatively wide range of temperatures, their maximum temperature tolerances could influence distribution patterns under future climate change scenarios (e.g., Brooke et al., 2013). Ocean warming is predicted to cause deoxygenation of large portions of the deep sea (Oschlies, 2021), which threatens the metabolic viability of deep-water corals and thereby their distribution patterns which have been shown to be influenced by oxygen availability (Tittensor et al., 2009). Changes in temperature and oxygen are also likely to interact to further influence the distribution patterns of deep-water corals, although few studies have explored these interactions (e.g., Dodds et al., 2007).

Many deep-water corals, notably the scleractinian or stony corals that often provide the structural foundations for diverse deep-sea benthic communities (e.g., Henry & Roberts, 2007), are reliant on high concentrations of dissolved calcium carbonate ($CaCO_3$) to build and maintain their skeletal structures, and levels of carbonate minerals in the water influence the distribution of these corals (Flögel et al., 2014). Ocean acidification lowers these concentrations and has been steadily raising the saturation horizons for $CaCO_3$ (the depths above which the aragonite and calcite polymorphs of $CaCO_3$ are fully saturated in seawater) in the 21st century (Orr et al., 2005; Turley et al., 2007). The depths of these horizons have been strongly linked to coral distributions, with over 95% of deep-water aragonitic coral reefs found above the aragonite saturation horizon (Guinotte et al., 2006).

Combined, changes in the depth of carbonate saturation horizons and other properties of bottom seawater, such as temperature and oxygen, are predicted to result in unsuitable conditions for the settlement and growth of deep-water corals across vast ocean areas (Morato et al., 2020). Conversely, deep-water corals in some ocean regions may be less affected by changes in these environmental variables, and conditions in some areas may remain unaltered or even become more suitable for deep-water corals with climate change. Given the ecological importance of deep-water corals, notably due to the complex biogenic habitat provided to other species by scleractinian coral reefs and octocoral/stylasterid gardens (Roberts et al., 2016), it will be crucial to identify locations where these corals may persist under future climate change conditions to inform conservation planning. It has been predicted that human-induced changes in seawater chemistry may alter the distribution of deep-water stony corals, with only 30% of coral locations remaining in carbonate-supersaturated waters by the end of the 21st century; the vast majority of these locations are in the North Atlantic, where the Aragonite saturation horizon is predicted to remain relatively deep (Guinotte et al., 2006). A global study focussing on the impact of ocean acidification on stony corals on seamounts in the North Atlantic found that while projected changes in ocean chemistry reduced habitat suitability, seamount summits could act as potential refugia from the effects of ocean acidification because they lie in shallower waters with a higher aragonite saturation state (Tittensor et al., 2010). A later study examining changes in habitat suitability in the North Atlantic for six species of deep-water corals predicted a decrease of 28%–100% in suitable habitat and only limited climate change refugia for these species (Morato et al., 2020). However, no studies to date have investigated in such detail the potential impacts of climate change on deep-water coral distributions in other regions of the globe.

The waters around New Zealand are a global hotspot of biodiversity for deep-water corals; approximately a sixth of the worlds' deep-water coral species have been described in the seas surrounding these islands (approximately 110 species), including the world's deepest reef-forming coral species, *Solenosmilia variabilis* (Tracey & Hjorvarsdottir, 2019). In the New Zealand region, all deep-water corals in the orders Antipatharia and Scleractinia, the gorgonian octocorals in the order Alcyonacea, and stylasterid hydrocorals in the order Anthoathecata, are protected from deliberate harm by law (New Zealand Wildlife Act 1953/2010). Nonetheless, protected corals are frequently caught in commercial fisheries (Anderson & Finucci, 2022), and the impact of trawling on deep-water corals has led to the inclusion of many taxa in New Zealand's threatened species classification (Freeman et al., 2013) and to the introduction of marine protected areas to mitigate the impact of trawling (Brodie & Clark, 2004; Helson et al., 2010). However, the latter do not currently account for the vulnerability of deep-water corals to future climatic conditions. That is, to ensure the conservation of these important organisms, in addition to understanding impacts from fishing, distribution of deep-water corals under future climate conditions must be understood.

The starting point for this understanding relies upon predicting the distribution of coral taxa, but physical records of such taxa in the deep seas around New Zealand are too sparse on their own to enable an adequate representation of their distribution. Modelling of species distributions using correlative species distribution models, also known as habitat suitability models, are one tool that aim to address this shortfall (Reiss et al., 2015; Ross & Howell, 2012). Many

techniques for predicting species distributions through spatial estimation of habitat suitability have been developed over the last several decades, taking advantage of increased computing power, machine learning algorithms, availability of global and regional datasets of environmental variables, the ongoing sampling of the world's oceans, and accessible species record databases (e.g., Burgos et al., 2020; Morato et al., 2020; Ramiro-Sánchez et al., 2019). These models attempt to predict species distributions by correlating occurrence/abundance and absence/background data with a set of spatial environmental predictors (Guisan et al., 2017; Reiss et al., 2015; Vierod et al., 2014). Ensemble models, combining outputs from multiple independent individual species distribution models, are increasingly used because they have the benefit of incorporating the variation in predictions, underlying assumptions, and modelling strategies of each model type. This approach limits the risk from acceptance of any deficiencies specific to a single model type or structural assumption and can enable a more robust characterization of the predicted spatial variation and uncertainties (Robert et al., 2016).

Numerous studies have been undertaken to predict the distribution of deep-water coral taxa in the New Zealand region, especially habitat-forming taxa (e.g., Anderson et al., 2014, 2015; Anderson, Guinotte, Rowden, Clark, et al., 2016; Baird et al., 2013; Compton et al., 2013; Tracey et al., 2011), and several that have used an ensemble modelling approach (Anderson, Guinotte, Rowden, Tracey, et al., 2016; Georgian et al., 2019; Rowden et al., 2017; Stephenson et al., 2021). These studies found that the more important drivers of cold-water coral distributions were temperature, dissolved oxygen, aragonite/calcite (for the scleractinian and stylasterid corals in particular that are dependent on dissolved $CaCO_3$ for skeletal growth and maintenance), and seabed slope and roughness (particularly as many taxa require hard substrate for settlement; Freiwald, 2002; Rogers, 1999; Rowden et al., 2010) on and benefit from the increased food supply offered by such environments (Davies et al., 2009; Duineveld et al., 2004). Depth was also often a key predictor as it is proxy for environmental variables with which it is highly correlated, for example, temperature, salinity, carbonate ion concentration, and nutrient supply, but which are not always available at the required resolution or precision for a specific model.

Variables that represent the chemical or physical properties of bottom water are typically incorporated into models as long-term annual or seasonal means and are therefore temporally static. The use of such variables, therefore, ultimately limits the applicability of model predictions in the face of changing climatic conditions and creates uncertainty for spatial management of damaging human activities that may overlap with the distribution of deep-water corals. However, the rapidly developing field of Earth System Modelling (ESM) provides one way to estimate past, present and future environmental conditions (Kawamiya et al., 2020). Recently, a regional model has been developed—the New Zealand ESM (NZESM)—which incorporates component models of ocean biogeochemistry and other aspects of biology and chemistry, and now provides a highly complex model of the climate system tuned to the New Zealand region (Behrens et al., 2020a). The NZESM is expected to be superior to other ESMs for local conditions, as it incorporates a high-resolution regional ocean model for the seas around New Zealand as well as a representation of the variability of solar radiation in atmospheric chemistry that manifestly affects the climate of the Southern Hemisphere (Dennison et al., 2019; Williams et al., 2016). These refinements have led to smaller surface model biases around New Zealand compared with its parent model, United Kingdom ESM (Behrens et al., 2020b; Sellar et al., 2019). Other environmental parameters that may influence deep-water coral growth and survival in the New Zealand region include those that vary only spatially. Many of these parameters, for example, seabed depth, slope, aspect, roughness, can be derived from bathymetric grids compiled from long-term accumulation of depth records. Others, such as spatial representations of underwater topographic features (seamounts, hills, and knolls) and grids of seafloor substrate composition are available from published research and databases (Bostock et al., 2018a, 2018b; Rowden et al., 2008; Yesson et al., 2011).

Given the importance of the New Zealand region as a global biodiversity hotspot for deep-water corals and the presence of a substantial deep-water trawl fishery, it is crucial that informed conservation efforts are made to ensure the long-term persistence of these important taxa in the face of climate change (Brock et al., 2012; Santos et al., 2020). Here we use the latest predictions from the NZESM in combination with fixed variables and a comprehensive set of deep-water coral sampling data to produce ensemble models trained on present conditions to predict future distributions of 12 taxa in the New Zealand region, using both optimistic and pessimistic future emissions scenarios. Our expectation was that shifts in seafloor environmental conditions due to climate change, including decreases in oxygen levels and food supply, and increased ocean acidity, would act to reduce the future amount of suitable habitat for deep-water corals, and alter its location. We use the outputs from these models to identify potential climate change refugia for deep-water corals and discuss whether current spatial conservation measures will likely provide sufficient protection for the primary habitat of these corals in the future.

2 | METHODS

2.1 | Study area

The spatial extent of the habitat suitability models for deep-water corals comprised the New Zealand region (Mackay et al., 2015) extended eastward to incorporate most of the Louisville Seamount Chain, the whole of which encompasses the area bounded by 24° S, 57.5° S, 157° E, and 160° W (Figure 1). This area includes the entire Territorial Sea, Exclusive Economic Zone and Extended Continental Shelf of New Zealand. Model outputs were constrained to a maximum water depth of 2000 m, as this represents the approximate maximum depth of the sample sites, but no minimum depth limit was imposed as some deep-water corals have a very broad bathymetric

tolerance in the region, for example, *Antipathella* spp. which have been found in depths ranging from a few metres to over 500 m (Tracey & Hjorvarsdottir, 2019).

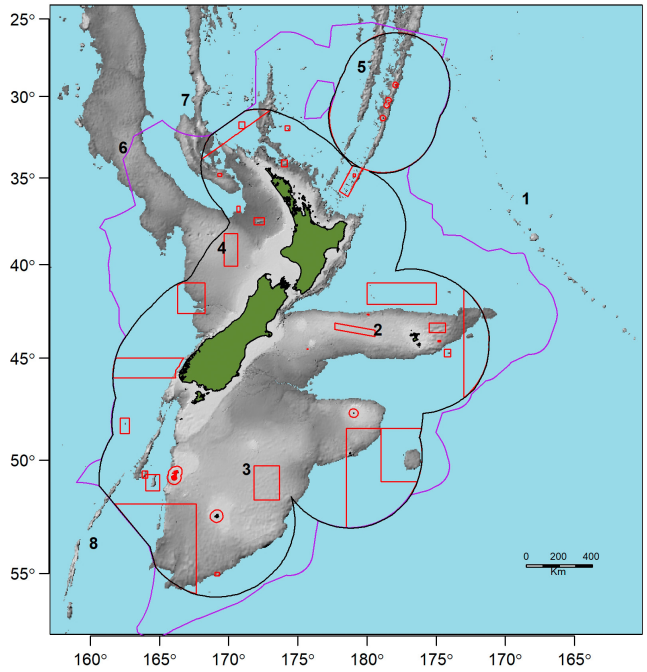

FIGURE 1 The New Zealand region, showing the main marine geographical features: 1, Louisville Seamount Chain; 2, Chatham Rise; 3, Campbell Plateau; 4, Challenger Plateau; 5, Colville and Kermadec Ridges; 6, Lord Howe Rise; 7, Norfolk Ridge; 8, Macquarie Ridge. Bathymetry shown in grey (clipped, as in the model outputs, to 2000 m); benthic protection areas, seamount closures, and large marine reserves shown in red outline; the New Zealand exclusive economic zone is shown as a black line and the extended continental shelf as a purple line.

2.2 | Sampling data and taxon selection

The deep-water coral taxa selected for the study were guided by three considerations: (a) New Zealand threatened species rankings (Freeman et al., 2010, 2013), (b) the importance of the taxon in providing the structural basis for habitat for other organisms (i.e., satisfying at least one criteria for a Vulnerable Marine Ecosystem indicator taxon, FAO, 2009), and (c) the level and distribution of the available sampling data. Records of a wide range of benthic invertebrates in the New Zealand region have been compiled from various sources including fisheries trawl survey catch records, government fisheries observer records, biodiversity research surveys, museum records, and online databases, and are held in a National Institute of Marine and Freshwater Research database, which is regularly updated. Records were extracted from this database to form the deep-water coral occurrence dataset.

Coral observations were recorded at varying taxonomic levels, with high taxonomic resolution often not possible for records based on non-retained specimens. Although models combining groups of species may be considered less reliable due to the conflicting effects of the differing environmental tolerances of individual species within them, closely related species may be expected to retain ancestral traits and therefore have somewhat similar patterns of occurrence, an effect known as phylogenetic niche conservatism (Losos, 2008); additionally, there are a few species with sufficient presence data to produce robust single-species models. Based on these considerations we selected 12 taxa for modelling, including four reef-forming scleractinian species, five gorgonian alcyonacean genera (two bamboo coral genera were combined), two black coral genera, and two stylasterid hydrocoral genera (Table 1).

Absence data was assembled from "target-group background" sampling locations (Phillips et al., 2009), that is, sampling locations for

TABLE 1 Deep-water coral taxa modelled along with the observed depth range from the samples collected within the study area, and the number of records used in the models

Order	Taxon	Description	Depth range (m)	N. Records
Scleractinia	*Enallopsammia rostrata*	Reef-forming coral	186–2620	307
	Solenosmilia variabilis	Reef-forming coral	130–2620	472
	Goniocorella dumosa	Reef-forming coral	94–1595	699
	Madrepora oculata	Reef-forming coral	89–2882	251
Alcyonacea (gorgonians)	*Paragorgia* spp.	Bubblegum coral (tree-like)	152–2161	221
	Primnoa spp.	Primnoid sea-fans (tree-like)	150–1611	124
	Corallium spp.	Precious coral	108–2427	99
	Keratoisis spp. and *Lepidisis* spp.[a]	Bamboo corals (tree-like)	138–2842	565
Antipatharia	*Bathypathes* spp.	Black coral (tree-like)	161–1831	203
	Leiopathes spp.	Black coral (tree-like)	110–1657	199
Anthoathecata (Stylasteridae)	*Errina* spp.	Hydrocorals (small, hard)	66–2771	246
	Stylaster spp.	Hydrocorals (small, hard)	96–2094	225

Note: Colours differentiate broad taxonomic groups.

[a]But note a recent revision of these genera Saucier et al. (2021) and Watling and France (2021).

taxa not being modelled. The use of target-group background data has been shown to improve average performance for regression-based models compared to using random pseudo-absences (Phillips et al., 2009). This improvement is especially the case when the target-group is part of the same broad biological group as the modelled taxon and records have been collected using similar methods with the same sampling biases (Phillips et al., 2009), as was the case here. Locations were derived from a database of over 60,000 records comprising all research survey stations at which all organisms in the sample were identified and did not include any of the deep-water coral taxa used in this study. For each deep-water coral taxon, a set of absence data was randomly selected from this database, 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 for each taxon were then combined to provide the basis for model construction.

2.3 | Environmental predictors

The NZESM can produce projections of environmental conditions from 1850 to 2100 and beyond. For this analysis we have focussed on predicted conditions for two periods: a historical period (1995–2014) representing present conditions, and a future period (2080–2099) representing conditions at the end of the 21st century. The predicted future conditions were based on two greenhouse gas concentration trajectories following: (1) the SSP2-4.5 (4.5 W/m^2) "Moderate" increase trajectory, which describes a future with modest mitigation of carbon emissions and adaptation to climate change, and (2) the SSP3-7.0 (7.0 W/m^2) "Strong" increase trajectory, in which much more limited emissions mitigation leads to increased geographical and social inequalities (Fricko et al., 2017; O'Neill et al., 2016).

An initial set of potentially useful environmental parameters representing present conditions were obtained from 1° resolution NZESM grids for the midpoint of every 1 × 1 km cell within the New Zealand region, by interpolation and upscaling of 3D parameters using a 1 km bathymetry grid (derived from Mitchell et al., 2012; see Davies & Guinotte, 2011 for upscaling methodology).

Spatial grids for the following additional parameters that vary only spatially were also compiled: seabed depth, slope, underwater topographic features (UTFs; seamounts, hills, and knolls), and aspects of seabed shape (fine-scale and broad-scale benthic position index, and roughness [standard deviation of slope]) as well as substrate composition. Although most of these variables were based on extensive sampling data, the available information on substrate composition required a high degree of interpolation due to the uneven distribution of sediment sampling in the region (Bostock et al., 2018a, 2018b). Precision of the UTF layers was limited by the variability in spatial resolution of the bathymetry data, and with similar coarseness in current/tidal data from the NZESM, parameters such as the probability of Taylor Cone formation (Rogers, 1994) that may influence production around UTFs were not able to be considered in the models. The complete set of predictor variables made available to the models are listed in Table 2.

Too many variables can lead to model overfitting and highly correlated variables can negatively impact model performance and interpretation (Huang et al., 2011). Therefore, the number of variables offered to the final models was reduced, in a two-step process. Firstly, highly correlated variables were removed by calculating the variance inflation factor (VIF) for each variable (Heiberger & Holland, 2015; Yesson et al., 2015). Variables with a VIF of less than 5 were retained, reflecting a low level of co-linearity (Heiberger & Holland, 2004). This step also helps to address issues that can arise due to the use of highly correlated dynamic/static variable combinations in the models. In cases where this occurs, the structure of interactions or dependencies between a pair of such variables (e.g., depth (constant over time) and bottom temperature (changing over time)) may change with future changes in values of the dynamic variable (Stanton et al., 2012). Our approach does not eliminate this issue, and we have chosen to include static variables alongside dynamic variables in part to avoid producing models that might be over-sensitive to climate change if these were not considered (Iverson & Prasad, 1998). Secondly, trial models were fitted for each taxon using this reduced set of variables and the Boosted Regression Tree *gbm.simplify* function in R (Elith et al., 2006), a process which removes uninformative predictors by backward stepwise elimination in which the least contributing variable (in terms of deviance explained) is removed at each step. This process allows models to be fitted to a core set of variables that balances the level of deviance explained against the number of predictor variables used (after Stephenson et al., 2020). The final, taxon specific, sets of predictor variables were used in both Boosted Regression Tree and Random Forest models.

2.4 | Habitat suitability modelling

Two modelling methods were used, Random Forests (RF; Breiman, 2001) and Boosted Regression Trees (BRT; Elith et al., 2006; Ridgeway, 2020). While both methods are based on the creation of large numbers of decision trees, the underlying strategies that the two approaches take for model building are quite different. RF models build large numbers of fully grown (even over-fitted) classification or regression trees using random subsets of input data and average out the results. BRT models are a form of additive regression where the individual terms of the regression are simple, short, decision trees, fitted in a stage-wise manner. Trees formed from recursive binary splits of the data are combined (boosted) to improve predictive power by growing successive trees using model residuals from each step. Other model types, for example, Generalised Additive Models or Maximum Entropy models were not considered as, although these methods have often been used for habitat suitability modelling of benthic fauna for New Zealand and elsewhere, we have found that results have not differed considerably from those of tree-based methods and wished to minimise overall model complexity. Furthermore, using similar data, RF and BRT performed

TABLE 2 Initial set of environmental predictors considered for habitat suitability 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]	°C	NZESM
Fixed variables			
UTF	UTF positions	—	Rowden et al. (2008)
Carbonate	Percentage of carbonate in sediment	%	Bostock et al. (2018a, 2018b)
Mud	Percentage of mud in sediment	%	Bostock et al. (2018a, 2018b)
Sand	Percentage of sand in sediment	%	Bostock et al. (2018a, 2018b)
BPI-broad	Benthic Position Index—broad-scale (25 × 25 window)	—	NIWA
BPI-fine	Benthic Position Index—fine-scale (5 × 5 window)	—	NIWA
Depth	Seabed depth	m	NIWA
Slope-percent	Seabed slope in percent	%	NIWA
Stdev-slope	Standard deviation of seabed slope (3 × 3 window)	—	NIWA

Note: See Table 3 for the taxon-specific set of variables used in final models.

better than other model types (as assessed by independent evaluation data; Stephenson et al., 2021).

We built RF models using the *randomForest* function in R, tuned to select optimal values for complexity parameters *mtry* (the number of variables used in each tree node), *maxnodes* (the maximum number of terminal nodes), and *ntree* (the number of trees to grow).

BRT models were built using functions in the *dismo* package (Hijmans et al., 2020) in R, with parameters *tc* (tree-complexity) set to 3 and *lr* (learning rate) set to a value allowing the number of trees to exceed 1000. A bag fraction of 0.6 was used with a standard random 10-fold cross evaluation method. All data preparation, modelling, and analysis of results was carried out using functions available in R (R Core Team, 2020).

2.5 | Model performance

Model performance was evaluated primarily using AUC, the Area Under the receiver operating characteristic Curve—presented as the fraction of true positives versus the fraction of true negatives. An AUC score of 0.5 indicates a model with predictions no better than random, whereas values over 0.7 indicate "adequate" performance, and values over 0.8 indicate "excellent" performance (Hosmer et al., 2013). Other performance metrics were also calculated; sensitivity (% of presences correctly identified), specificity (% of absences correctly identified) and True Skill Statistic (TSS, a combination of specificity and sensitivity giving an index from −1 to +1, where +1 equals perfect agreement and −1 = no better than random, Allouche et al., 2006). A cut-off habitat suitability value for presence/absence was calculated as that which maximises sensitivity and specificity, useful for creating binary model output.

These performance metrics were derived from a process of spatial cross-validation, taking into account the level of spatial autocorrelation in the input data (Roberts et al., 2017; Valavi et al., 2018). Model input data were partitioned systematically into many spatial blocks which were assigned a value from 1–10 to create training and test data sets. Nine of the ten sets were used to construct a preliminary model which was then compared to observations in the remaining set to measure performance. The ideal block dimensions to account for the effects of spatial autocorrelation was based on the length for which the residuals of a BRT model were approximately independent, as assessed by a variogram. The cross-validation process was repeated 10 times for each model type, leaving out each of the 10 data sets in turn, and average AUC, sensitivity, specificity, and TTS scores calculated to represent overall performance.

2.6 | Model outputs and estimation of uncertainty

Each BRT and RF model, for each taxon, was fitted to spatial grids of the predictor variables to estimate a habitat suitability value for each

TABLE 3 Variable inclusion and importance ranks by deep-water coral taxon and model type (random Forest/boosted regression tree)

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

Note: 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. Asterisks denote fixed variables; colours differentiate broad taxonomic groups (see Table 1), with the two key variables highlighted for each taxon model, blanks indicate the variable was not used in the model.

cell of the model extent. Model outputs are presented as relative habitat suitability rather than true probability of presence, as the absence data used do not accurately represent true absence locations due to the unknown and variable catchability associated with the range of sampling gear used.

To incorporate uncertainty stemming from the distribution of sampling data, we used a bootstrap technique to produce spatially explicit uncertainty measures, after Anderson, Guinotte, Rowden, Tracey, et al. (2016). A random sample of the presence data were drawn, with replacement, from the sample presence data and combined with an equal number of absence records, drawn randomly from the entire coral occurrence dataset. A new model was then constructed using these data and 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 resulting in 200 estimates of habitat suitability in each cell, from which uncertainty (measured as the coefficient of variation [CV]) was calculated.

The unevenness of sampling across the modelled environmental space (i.e., the multidimensional space formed from the combination of each of the environmental variables) will result in predictions for some areas being based on few samples and predictions for others based on many samples, leading to spatial variability in the reliability of model predictions. To assess this variability, we estimated the "coverage of the environmental space" (Smith et al., 2013; Stephenson et al., 2020) by modelling variation in sampling density within the environmental space by combining presence records for all taxa into a model dataset with an equal number of absence values sampled randomly from the model extent. We then used a BRT model to model the relationship between these presence/absence samples for the environmental variables used to train the ensemble models. The model used a Bernoulli error distribution, a learning rate that yielded over 5000 trees, and an interaction depth of 2 (i.e., considering only pair-wise combinations of the environmental variables). In this way we could estimate, for all coral taxa combined, the probability of a sample occurring in each part of the environmental space (Stephenson et al., 2020). Finally, predictions using this model were applied to environmental variables under future climatic conditions (SSP3-7.0).

2.7 | Model ensembling

Outputs from the BRT and RF models were combined to produce an ensemble model for each taxon. The ensembling procedure followed methods adapted from Oppel et al. (2012) by Georgian et al. (2019) and Stephenson et al. (2021) by taking weighted averages of the predictions from the BRT and RF models in each cell. This procedure incorporates a two-part weighting for each component of the ensemble model, comprising equal contributions from the overall model performance (spatially cross-validated AUC values) and the uncertainty measure (coefficient of variation, CV) in each cell. Combination of the ensembled taxon models into an overall model

representing habitat suitability for all protected coral taxa could also be considered, but interpretation may be difficult when distributions are markedly different among taxa, and individual taxa may require specific protection strategies.

2.8 | Changes in primary coral habitat

Examining climate change induced changes in habitat suitability for the region as a whole can be misleading as there are typically broad areas where habitat suitability is predicted to be relatively low and may also be poorly estimated due to sparse/uneven coverage of the associated environmental variables (Stephenson et al., 2021). To better examine predicted changes in habitat suitability in areas most likely to be currently occupied by coral taxa it is more informative to focus in on areas of high present habitat suitability.

To examine such changes in a consistent manner across all taxa, we set a threshold at the 95th percentile of present habitat suitability to represent present "primary habitat." This value was chosen to be consistent across all taxa and is considerably higher than model-derived cut-off values for presence-absence. We then assessed the change in suitability over time in those cells classified as primary habitat and measured the future gain or loss of habitat area, defined as the percentage increase or decrease in the area in which habitat suitability is predicted to be above the minimum habitat suitability of present primary habitat. We also identified future primary habitat, areas of the study region with values of future habitat suitability above their 95th percentile. We conducted these analyses for both moderate and strong greenhouse gas concentration increase scenarios, but for brevity report here only the results for the strong (SSP3-7.0) scenario to allow a more useful level of contrast (see Appendix S1 for SSP2-4.5 results).

3 | RESULTS

3.1 | Model performance

Spatial cross-validated AUC scores for the BRT and RF models created for the 12 taxa ranged from 0.76 (*Goniocorella dumosa*—BRT) to 0.93 (*Corallium* spp.—RF), indicating better than "adequate" performance (AUC > 0.7) in all cases and "excellent" performance (AUC > 0.8) for 18/24 models. Sensitivity and specificity values were all well above 0.5, with sensitivities of over 0.9 for *Enallopsammia rostrata* (BRT), *Corallium* spp. (BRT and RF), and *Leiopathes* spp. (RF). True Skill Statistic (TSS) values were all much greater than zero, ranging from 0.48 for *G. dumosa* (BRT) to 0.82 (*Corallium* spp., BRT and RF). Performance metrics were generally similar between the two model types, particularly for taxa with better fitting models, for example, *Corallium* spp. And *Errina* spp. (see Appendix S1 for full details of model performance).

3.2 | Environmental drivers of present and future distributions

Models for each of the four branching scleractinian taxa were strongly influenced by aragonite concentration (Table 3). For example, in the *S. variabilis* model partial dependence plots (Figure 2) indicate that saturation of aragonite is positively correlated with occurrence of this coral in both BRT and RF for values up to about 1.3, with the correlation becoming negative as saturation levels exceed the median value across all sample locations. Occurrence decreases at higher aragonite saturations, strongly correlated to increasingly shallower depths nearing the bathymetric limit for the taxon. Similar peaks in the partial dependence plots for aragonite can be seen in models for the other scleractinians, and a similar pattern can be seen in the plots of calcite saturation from models for the gorgonian taxa, which build skeletal structure with this alternative polymorph of $CaCO_3$ (see Appendix S1). These consistent patterns suggest a general relationship for these taxa between habitat suitability and carbonate ion concentration up to the point where other factors come into play toward the shallower end of their depth range. This relationship results in a predicted increase in future habitat suitability in generally shallower areas where concentrations of aragonite are currently well above fully saturated but are predicted to fall below about 1.3 in the future, as evidenced for *S. variabilis* across broad areas of the Campbell and Challenger Plateaus, and Lord Howe Rise (Figure 3).

Seafloor dissolved oxygen concentration is a key variable in models for most taxa, especially bamboo and black corals, and is the most important variable overall (Table 3). Oxygen concentration is mostly positively correlated with occurrence in both models for *Bathypathes* spp. For levels up to about 215 μmol/m^3, but becomes abruptly negative at higher concentrations, as occurrence of *Bathypathes* becomes increasingly lower (Figure 4). The relationship between seafloor oxygen levels and depth is more complex than for aragonite/calcite but generally concentrations are lower in the north and predicted to generally decrease across the region over time. This relationship, as for aragonite, again contributes to predictions of broad shallow regions becoming more suitable for *Bathypathes*, where oxygen levels reduce closer to optimum levels for the taxon. At the same time, areas currently with relatively low oxygen concentration (in deeper or northern regions) are predicted to have similar or lowered future habitat suitability for *Bathypathes*, as concentrations fall below optimum levels (Figure 5). (See Appendix S1 for partial dependence plots and habitat suitability maps for the complete set of modelled taxa).

3.3 | Changes in regions of primary habitat

Future habitat suitability for most taxa (but especially the gorgonians *Paragorgia*, *Keratoisis* and *Lepidisis*, and *Primnoa*, and the black corals *Leiopathes* and *Bathypathes*) was lower in most cells within the area of present primary habitat (Figure 6). This is in strong contrast

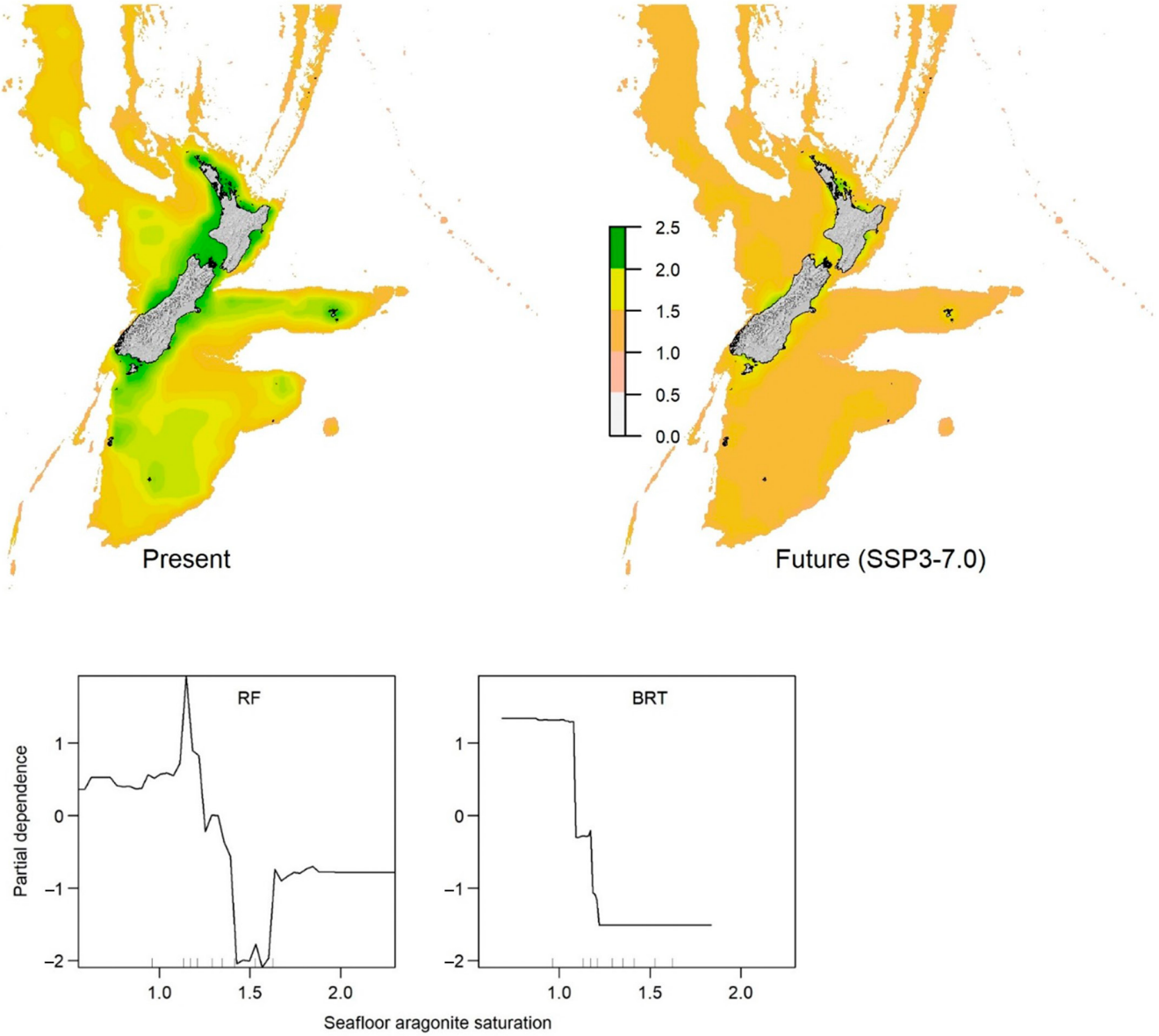

FIGURE 2 NZESM predicted distribution of present and future (under a strong greenhouse gas concentration trajectory; SSP3-7.0) seafloor aragonite saturation state (top), and partial dependence plots for aragonite saturation from the random Forest (left) and boosted regression tree (right) habitat suitability models for *Solenosmilia variabilis*. Marks on the *x*-axis in the lower figures indicate the deciles of the variable values at the locations of the sample data.

to all cells of the study region, where many cells with very low suitability show a slight increase, for the reasons explained above. In addition, for some taxa, models predicted a broader range of future habitat suitability, with more extreme values. This situation resulted in gains in habitat area, as we have defined it (the area where habitat suitability is above the minimum of that in present primary habitat), for some taxa for which there was little change in mean habitat suitability (e.g., *E. rostrata* and *Stylaster* for which habitat was predicted to increase by 100% or more; Table 4).

Mean habitat suitability within the region of present primary habitat of *S. variabilis* drops from 0.81 to 0.72 and is only slightly higher (0.74) in the recalculated region of future primary habitat, with an associated 81% loss in habitat (Table 4). Of the other branching scleractinians, *G. dumosa* is predicted to experience a similar drop in habitat suitability within present primary habitat while *E. rostrata* and *Madrepora oculata* will experience little change, with gains in habitat area for each species. However, the greatest changes in habitat suitability within present primary habitat are predicted among the gorgonian taxa, especially *Paragorgia* for which mean habitat suitability within present primary habitat drops from 0.82 to 0.48, and remains substantially lower (0.65) when the region of future primary habitat is recalculated (Table 4; Figure 7). Habitat loss is 99%–100% for three of the four gorgonians, with a 40% increase for *Corallium*, and the two black coral taxa (*Leiopathes* and *Bathypathes*) also show substantial reductions in mean habitat suitability within both present and future regions of

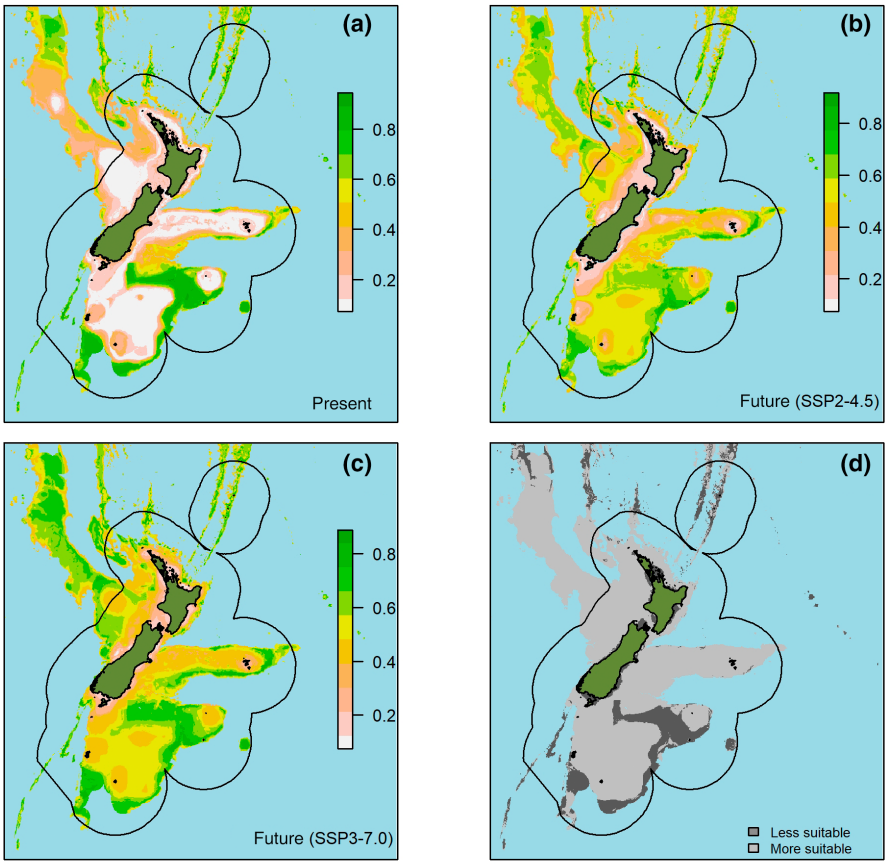

FIGURE 3 Predicted relative habitat suitability (0–1) for the stony coral *Solenosmilia variabilis*. (a) Present distribution based on climatic conditions from the 1995–2014 reference period; (b) Future distribution based on conditions at the end of the 21st century (2080–2099) under a moderate greenhouse gas concentration trajectory (SSP2-4.5); (c) Future distributions under a strong greenhouse gas concentration trajectory (SSP3-7.0); (d) Areas of less/more future habitat suitability under SSP3-7.0 (c – a).

primary habitat at this strong level of predicted future greenhouse gas concentration, and near total loss of habitat. In contrast to other taxa, the stylasterids *Errina* spp. and *Stylaster* spp. Are predicted to experience negligible change in mean habitat suitability within the region of present primary habitat, as the modelled distributions for these taxa were driven mainly by temporally fixed variables (such as percentage of mud, fine-scale Bathymetric Position Index, depth [Table 3]), and habitat loss is low or positive.

The predicted changes in overall levels of habitat suitability described above, between the present and future climate change modelled predictions, often correspond to distinct changes in the spatial distribution of primary habitat for deep-water corals in the New Zealand region. Among the stony corals, future *S. variabilis* primary habitat includes new areas on the ridge and rise features north of New Zealand and the southeast Chatham Rise and reduced regions on the southern plateaus (Figure 7); both *G. dumosa* and *M. oculata* see reduced areas of primary habitat in sub-Antarctic regions and more subtle changes elsewhere; while future primary habitat for *E. rostrata* moves away from ridge features in the northwest to include fringes of the Challenger Plateau. Among the gorgonians, *Paragorgia* sees a loss of the fragmented northern distribution of primary habitat and a shift of the southern distribution of this habitat toward the southwest (Figure 7); *Primnoa* primary habitat shifts into shallower regions in the south; *Keratoisis* and *Lepidisis* primary habitat show a northward shift, while *Corallium* primary habitat remains little changed. For both the antipatharian taxa, distributions of primary habitat become more restricted on Lord Howe Rise and extend more onto the Challenger Plateau. Distribution of primary habitat of the two stylasterid genera remain relatively constant. Overall, mean depths for primary habitat generally become shallower (especially for *Paragorgia* and *Primnoa*) but become deeper for *Errina*, *Keratoisis* and *Lepidisis*, and *S. variabilis* (Table 4). There is no indication of an overall net latitudinal shift in the areas of primary habitat, with half the taxa models showing a northern shift and the remainder a southern shift in primary habitat location. (See Appendix S1 for plots similar to Figure 7 for all other taxa).

3.4 | Coverage of the environmental space

Environmental coverage values based on sample locations for all taxa and present environmental conditions were highest on the Chatham Rise, in near-coastal regions around much of the North Island and southwest of the South Island, on some of the major northern offshore features such as the Kermadec Ridge and Louisville Seamount Chain, and around the fringes of the southern Plateaus; in contrast, low values of environmental coverage (less than about 0.2) were shown for large parts of the interior of the Campbell Plateau, the northern Lord Howe Rise, and many deeper parts of the study region (Figure 8). The overall spatial patterns of

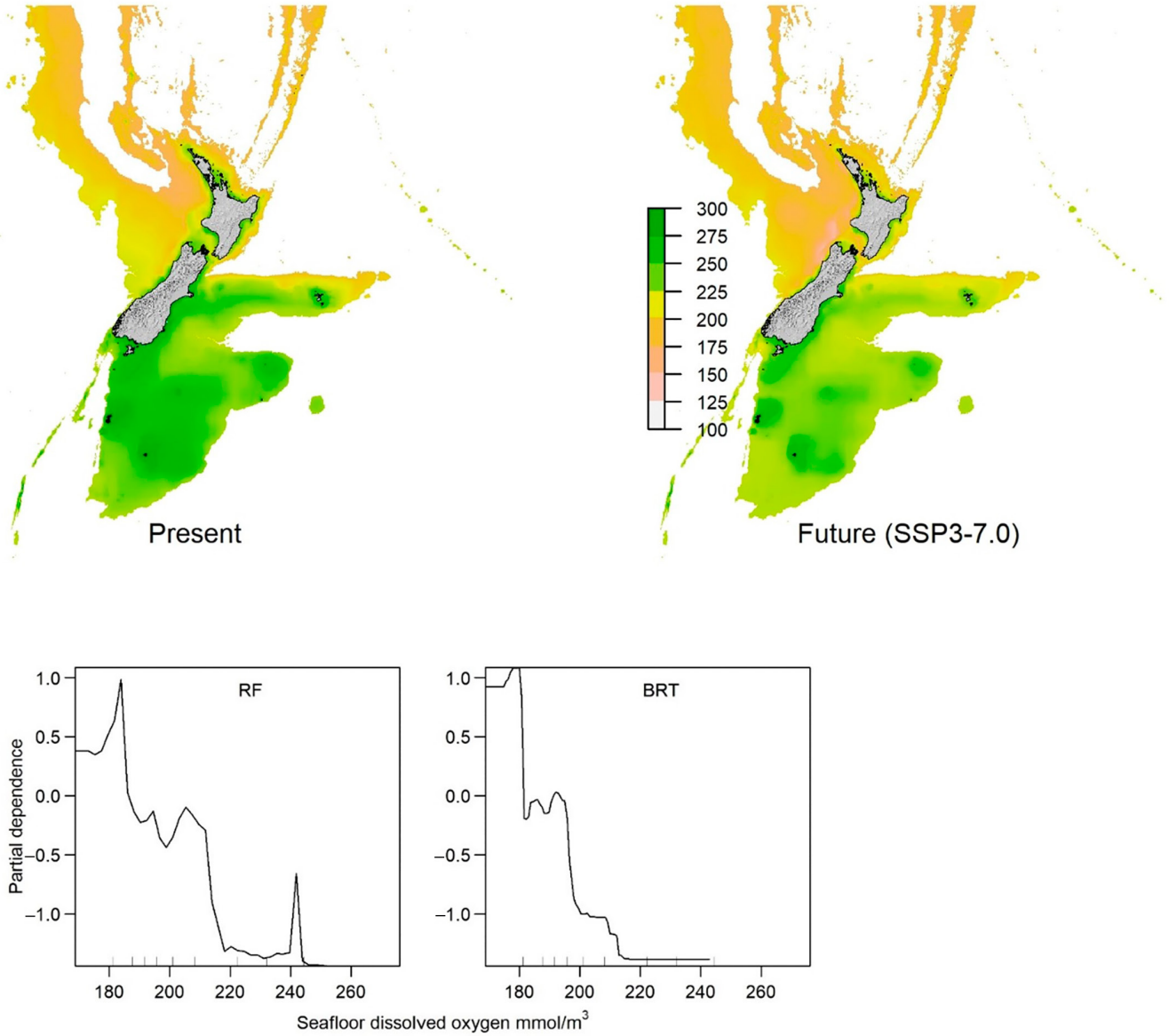

FIGURE 4 NZESM predicted distribution of present and future (under a strong greenhouse gas concentration trajectory; SSP3-7.0) seafloor dissolved oxygen concentration (μmol/m^3, top), and partial dependence plots for the random Forest (left) and boosted regression tree (right) habitat suitability models for *Bathypathes* spp. Marks on the *x*-axis in the lower figures indicate the deciles of the variable values at the locations of the sample data.

environmental coverage were similar when considering future environmental conditions but were generally lower, particularly in the areas of highest environmental coverage under present conditions. Predicted primary habitat for most taxa (both under present and future conditions) was mostly located within areas of moderate to high environmental coverage (see Figure 7; Appendix S1).

4 | DISCUSSION

The results of this study add to recent demonstrations of the value of combining outputs from complex models of climate change in the world's oceans with those from habitat suitability modelling of deep-sea benthic invertebrates at risk from this change (e.g., for sponges, Beazley et al., 2021; Liu et al., 2021), to provide insights into potential future refuges for these species and inform spatial management planning. The models produced here for deep-water corals predict that by the end of the 21st century, there will be substantial changes in the location and degree of suitable primary habitat for many species of these vulnerable taxa in New Zealand waters for which current protections may not be sufficient for providing ongoing protection from climate change and anthropogenic impacts. Looking ahead in this way is crucial, as the complex process of setting aside areas for protection based on predicted or observed present distributions of corals is still taking place, and risks being made redundant if shifts in distribution caused by climate change are not taken into account.

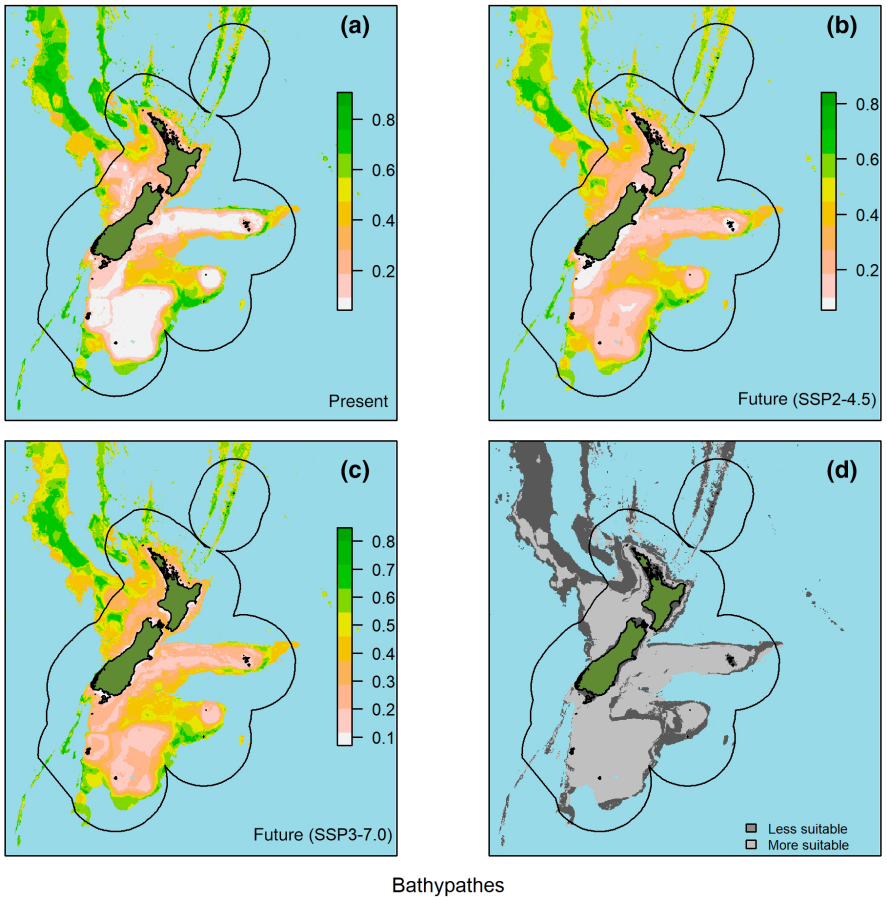

FIGURE 5 Predicted relative habitat suitability (0–1) for the black coral genus *Bathypathes*. (a) Present distribution based on climatic conditions from the 1995–2014 reference period; (b) Future distribution based on conditions at the end of the 21st century (2080–2099) under a moderate greenhouse gas concentration trajectory (SSP2-4.5); (c) Future distributions under a strong greenhouse gas concentration trajectory (SSP3-7.0); (d) Areas of less/more future habitat suitability under SSP3-7.0 (c – a).

4.1 | Changes in suitable habitat for deep-water corals because of climate change

Our expectation that models would indicate an overall deterioration of suitable conditions where deep-water corals are found in the seas around New Zealand over the course of the 21st century, due to factors such as decreasing oxygen levels and food supply, and increasing temperature and acidity of near-bottom waters of the deep sea (Byrne et al., 2010; Purkey & Johnson, 2010; Stramma et al., 2010), was largely confirmed by model results. We found that the main drivers of the predicted changes in suitable habitat for deep-water corals were future decreases in the seafloor concentrations of dissolved oxygen, carbonate ion saturation levels (aragonite or calcite, depending on the taxon), and an increase in nitrogen concentration. Hydrocoral species appeared to be more robust to environmental changes, at least to those represented in the models, with the distributions of both genera modelled (*Errina* and *Corallium*) driven primarily by fixed rather than dynamic variables, and showing therefore little predicted change in future suitable habitat.

To help our understanding of the predicted spatial changes in habitat suitability and their implications, we examined specifically the changes in primary habitat for the deep-water corals studied. These regions of primary habitat were found to differ greatly among taxa, and habitat suitability within them was predicted to decline substantially over time for most taxa. Moreover, for many species the most highly suitable areas at the end of the 21st century are predicted to have shifted considerably from their current locations. Overall decreases in habitat suitability in present primary habitat for coral taxa, ranging from 1% to 34%, were predicted to occur for 11 of the 12 modelled taxa in the future; but changes were slight (2% or less) for four taxa, including the two hydrocoral genera. For some taxa, habitat conditions were predicted to improve across broad regions where habitat suitability is currently very low, but only to levels still well short of that at which corals are currently found. Although the prediction of more extreme values of future habitat suitability for some taxa led to predicted increases in habitat area, our results align well with predictions of reduction in suitable habitat for deep-water corals in the North Atlantic (Morato et al., 2020). In that study, suitable habitat was projected to decline between 28% and 100% overall but increase in some regions for scleractinian corals, under a more severe future climate scenario (SSP5-8.5). The habitat-forming scleractinian *M. oculata* occurs in the north Atlantic as well as the Pacific, and was modelled in both studies. In our study, areas of primary habitat for this species were predicted to shift (with a 62.5% overlap between present and future locations) but mean habitat suitability in these areas remained constant. Prediction of more extreme habitat suitability values resulted in a 30% gain in primary habitat in our study, compared with a predicted reduction in suitable habitat of 30%–55% in the north Atlantic. Additionally, there was no evidence in our study of a poleward shift in distribution or a shift toward deeper water, as

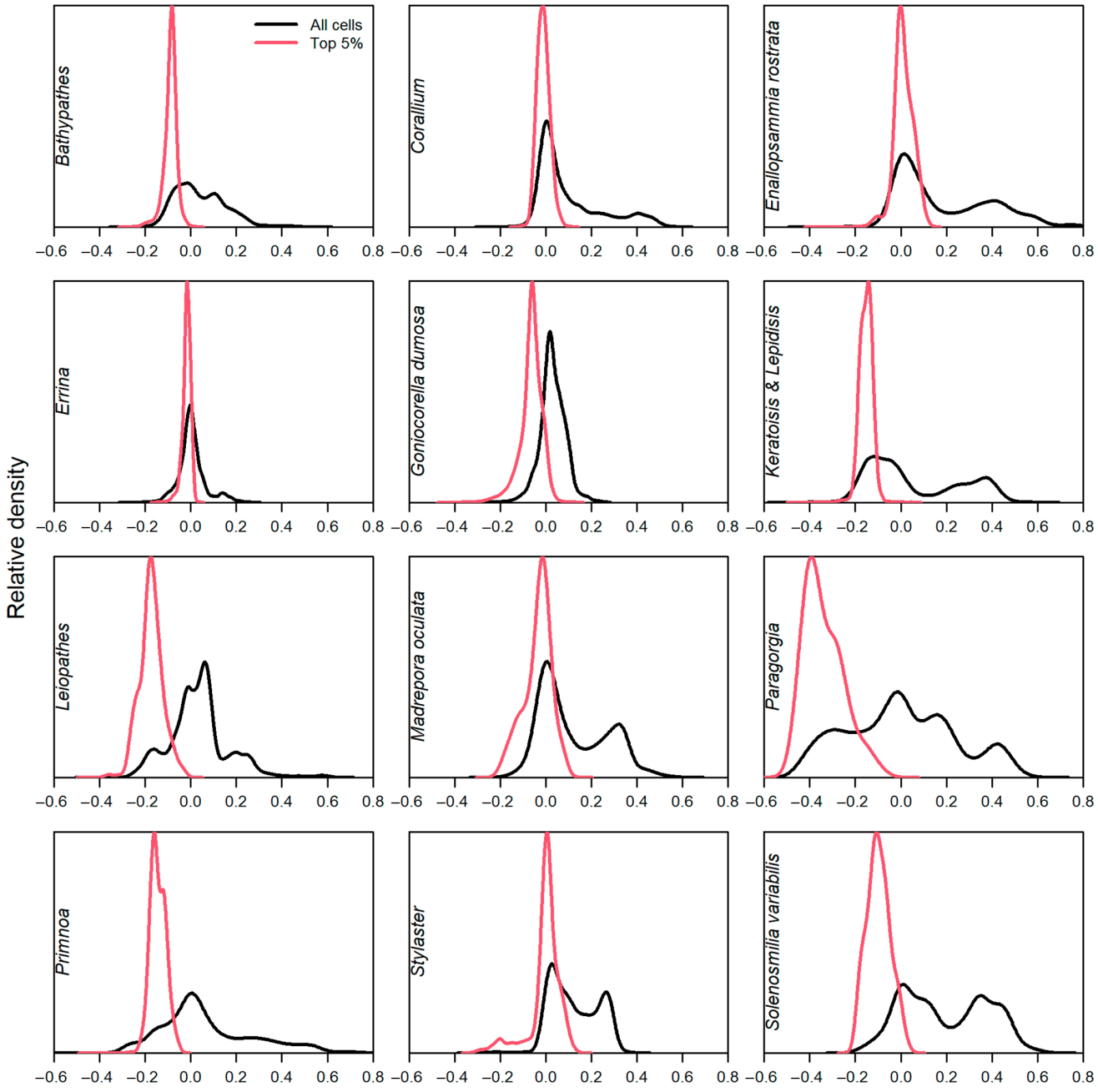

FIGURE 6 Density plots showing the change in relative habitat suitability over time (future − present habitat suitability) for the 12 modelled taxa under a strong greenhouse gas concentration trajectory (SSP3-7.0) and differing areal extents. Black lines, all cells; red lines, cells within present primary habitat (top 5% of habitat suitability).

predicted for this species by Morato et al. (2020). We are unsure of the reasons for these differences between studies, but these results strongly suggest that patterns observed for a species in one ocean basin cannot be assumed to hold true in another.

For some taxa, for example, the scleractinian *G. dumosa* and the stylasterid *Errina*, much of the predicted future primary habitat either overlaps with, is adjacent to, or is an extension/contraction of present primary habitat. Therefore, a transition for these taxa to these areas under future climate change scenarios may be achievable, even for species with limited larval dispersal capability. But this is not the case for all taxa. For the other scleractinians modelled, a large area of future primary habitat predicted for *E. rostrata* on the southern Challenger Plateau is well away from the main present concentration of primary habitat predicted for this species further north on the Lord Howe Rise and West Norfolk Ridge. And new areas of primary habitat for the scleractinian *S. variabilis* on the south Chatham Rise and in the northwest, and for *M. oculata* on the southern plateaus, are also isolated from present primary habitat for these species. Future regions of primary habitat for the bamboo corals *Keratoisis* & *Lepidisis* are predicted to become more fragmented

TABLE 4 Mean habitat suitability, depth, and latitude of present and future (under a strong greenhouse gas concentration trajectory; SSP3-7.0) deep-water coral taxon distributions, based on the 95th percentile of suitability (i.e., primary habitat)

	Mean habitat suitability				Mean depth		Mean latitude		
Taxon	Present	Future (at present dist.)	Future	Percent overlap	Present	Future	Present	Future	Habitat gain/loss
Enallopsammia rostrata	0.85	0.86	0.89	57.4	991	967	−32.0	−34.1	+106
Solenosmilia variabilis	0.86	0.76	0.81	42.5	1178	1230	−49.2	−45.3	−81
Goniocorella dumosa	0.68	0.61	0.64	40.9	281	201	−46.1	−42.9	+39
Madrepora oculata	0.74	0.70	0.74	62.5	924	823	−38.9	−37.1	+30
Paragorgia spp.	0.82	0.48	0.65	19.2	1061	743	−47.3	−49.1	−100
Primnoa spp.	0.90	0.76	0.81	22.7	1064	779	−51.1	−50.8	−100
Corallium spp.	0.86	0.85	0.87	55.4	1239	1113	−28.9	−30.7	+41
Keratoisis and *Lepidisis* spp.	0.81	0.65	0.69	18.9	1152	1404	−38.4	−34.6	−99
Bathypathes spp.	0.81	0.72	0.74	53.9	1177	1124	−32.8	−37.2	−97
Leiopathes spp.	0.83	0.65	0.71	47.2	1141	1019	−34.2	−36.4	−98
Errina spp.	0.88	0.86	0.86	92.1	314	342	−47.9	−47.9	−19
Stylaster spp.	0.78	0.77	0.81	64.6	549	423	−38.7	−41.9	+100

Note: Percent overlap is the percentage of cells in future primary habitat that were represented also in present primary habitat. Habitat gain/loss is the percentage increase or decrease in area where habitat suitability is predicted to be above the minimum habitat suitability of present primary habitat. Highlighted cells indicate a more negative response to climate change, or a predicted shallower or more southern future distribution.

and dispersed into locations beyond present primary habitat, such as northern parts of the West Norfolk, Kermadec, and Colville ridges. Therefore, these isolated and fragmented future areas of primary suitable habitat distant from present primary habitat of these deep-water corals may be beyond the reach of new migrants for establishing populations with a rapidly changing climate. For the remaining taxa modelled, there is predicted to be more of a mixture of new, isolated, primary habitat along with areas with strong overlaps with present primary habitat.

4.2 | Implications of change for future conservation management

Overlap between currently protected areas in New Zealand waters (Benthic Protection Areas [BPAs], seamount closures, and large marine reserves) and present primary habitat is limited, and predicted to decrease, for most taxa (Table 5). A key location in the north of the region is the BPA surrounding the Kermadec Islands. This BPA is by far the largest in the region and affords a relatively high level of protection to primary suitable habitat for *Corallium*, *S. variabilis*, and *M. oculata* as well as providing virtually the only protection of such habitat for *E. rostrata*, *Bathypathes* and *Stylaster*. However, the area of primary habitat within this BPA is predicted to decrease for each of these taxa excluding *S. variabilis*, so that it will offer less refuge overall by the end of the century (Figure 9). And for the remaining taxa, this BPA offers little or no protection—either now or in the future. Of the other protected areas, the nine outside of the Chatham Rise and southern plateaus show almost no overlap with present or future distributions of primary habitat for any of the deep-water coral taxa included in this study (see Appendix S1). The BPA on the central Chatham Rise is well placed for both present and future primary habitat of *G. dumosa* on that feature but does not overlap with the primary habitat of any other taxon. The three large BPAs on the southern plateaus provide some protection for two of the scleractinian species (*S. variabilis* and *M. oculata*) as well as for *Paragorgia*, *Primnoa*, and *Errina*, but tend to overlap less with future primary habitat than with present primary habitat. These BPAs also show some overlap with predicted present primary habitat for *Keratoisis* & *Lepidisis*, but models predict this primary habitat will be lost by the end of the century. Little overlap with present primary habitat is shown for these BPAs for the remaining taxa, although small patches of future primary habitat appear for *Bathypathes* in the southwest BPA. Overall, the results of our analysis raise the concern that current spatial protection measures in New Zealand waters do not include a sufficient amount of future primary suitable habitat for deep-water corals to enable them to assist in the conservation of these protected taxa by the end of the 21st century.

4.3 | Sources of uncertainty

It is worth noting that there are several sources of uncertainty associated with the predictions from our models which should be noted as caveats to our findings. One stems from the coarse native resolution of the NZESM; ocean biogeochemistry predictions from this ESM are currently only available at 1° resolution (~90 km at the latitudes around New Zealand) while ocean physical variables (e.g., ocean currents, temperature) are on finer 0.2° (~17 km) grid. Although we are able to upscale to a 1 km resolution for 3-D

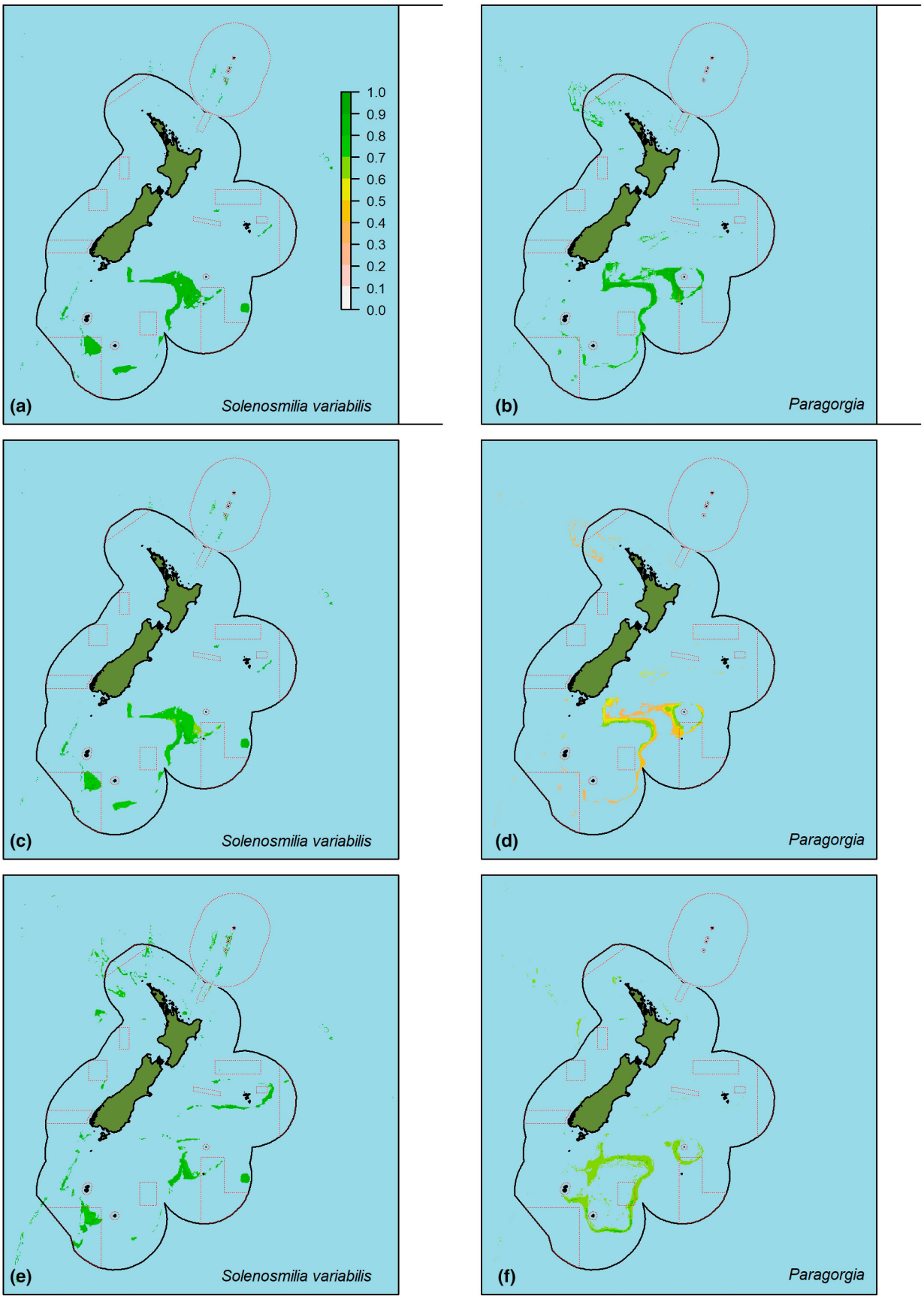

FIGURE 7 Predicted habitat suitability in areas of primary habitat (habitat suitability above the 95th percentile of cell values within the modelled area) for *Solenosmilia variabilis* (left; a, c, e) and *Paragorgia* spp. (right; b, d, f). Top, present habitat suitability within present primary habitat; middle, future habitat suitability (under a strong greenhouse concentration trajectory; SSP3-7.0) within present primary habitat; bottom, future habitat suitability within future primary habitat.

variables, this is artificial and deep-water corals will respond to some environmental variables at finer scales than currently available with these methods. The 1 km resolution used here is appropriate given that the sampling data comes mostly from research and commercial trawls, but more reliable models may be produced in the future based on camera survey data coupled with fine-scale multibeam echosounder bathymetry-based variables (as in, e.g., Rengstorf et al., 2014; Rowden et al., 2017), as more such data is collected over broader spatial scales. We also use long-term averages to represent dynamic variables (1995–2014 and 2080–2099 for present and future conditions, respectively) so that any temporary climate events affecting coral survival are not considered. Although mass mortality events from marine heat waves are mostly reported from shallow waters (e.g., Piazzi et al., 2021), marine heat waves can also affect the deep-sea (Elzahaby & Schaeffer, 2019), with potential for increased mortality for deep-sea corals and associated taxa if sufficiently severe.

Uncertainty from unevenness in sampling effort manifests in two main ways, spatial bias (where sampling effort is more focussed on areas that are more accessible, of higher biological interest, or of importance to fishing, etc.), and spatial autocorrelation (the tendency for sites that are physically closer to have similar properties). These uncertainties are partially accounted for here by the use of target-group background data, so that spatial bias in the presence data is matched by that in the absence data, and in the calculation of cross-validated performance metrics where spatial block size is based on spatial autocorrelation. Note, however, that this cross-validation approach may underestimate model fit (see, e.g., Wadoux et al., 2021) leading to a level of conservatism in the calculation of AUC values. In addition, uncertainty arises where predictions are made within areas of low environmental coverage, and here we have explicitly modelled and mapped the spatial distribution of this coverage to enable an assessment of this uncertainty to be made for each taxon modelled, and this can be used alongside predicted habitat suitability when considering these data in spatial management initiatives.

In this study we have focussed on future predictions for a strong (SSP3-7.0) increase emissions scenario, although predictions were broadly similar for a moderate (SSP2-4.5) increase future (see Appendix S1). Other scenarios could be tested (outputs from the NZESM can also be produced for SSP12-6), but SSP3-7.0 was felt to be as likely as any other scenario and allowed a level of contrast without the pessimism of a worst-case scenario (SSP5-8.5) where no mitigations are considered and the emissions trajectory is increasingly steep.

TABLE 5 Percentage of estimated present and future area of primary habitat for deep-water coral taxa (under a strong greenhouse gas concentration trajectory; SSP3-7.0) provided by the existing network of marine protected areas of seafloor in the New Zealand region

	Percentage of primary habitat within marine protected areas	
Taxon	**Present**	**Future**
Enallopsammia rostrata	13	3
Solenosmilia variabilis	19	26
Goniocorella dumosa	9	7
Madrepora oculata	23	16
Paragorgia spp.	6	8
Primnoa spp.	17	12
Corallium spp.	39	24
Keratoisis & *Lepidisis* spp.	8	5
Bathypathes spp.	8	7
Leiopathes spp.	0	1
Errina spp.	9	10
Stylaster spp.	10	8

4.4 | Future research directions

This study indicates that a review of the placement of the current network of spatial protection measures in New Zealand waters is

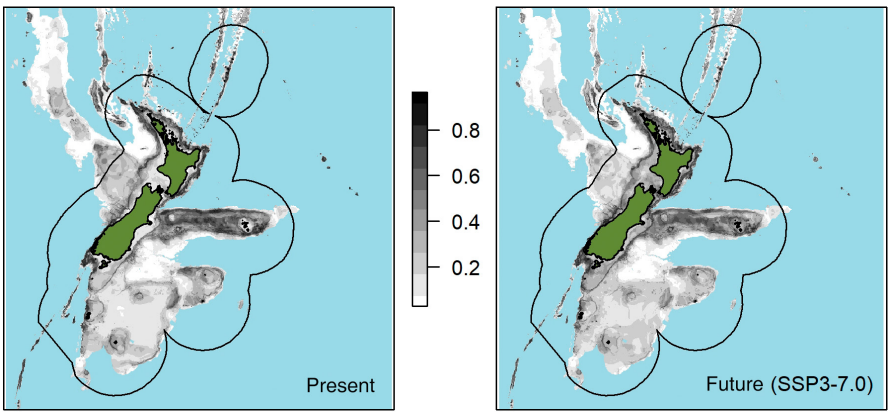

FIGURE 8 Environmental coverage (0–1) within the study area generated by building a BRT model using sample data from all coral taxa combined and an equal number of absence points sampled at random from across the study region, fitted to NZESM model data for present conditions (left) and predicted conditions for SSP3-7.0 (right). Low values of environmental coverage (paler) indicate parts of the environmental space that contained few samples—Meaning greater caution should be placed in the HSI predictions.

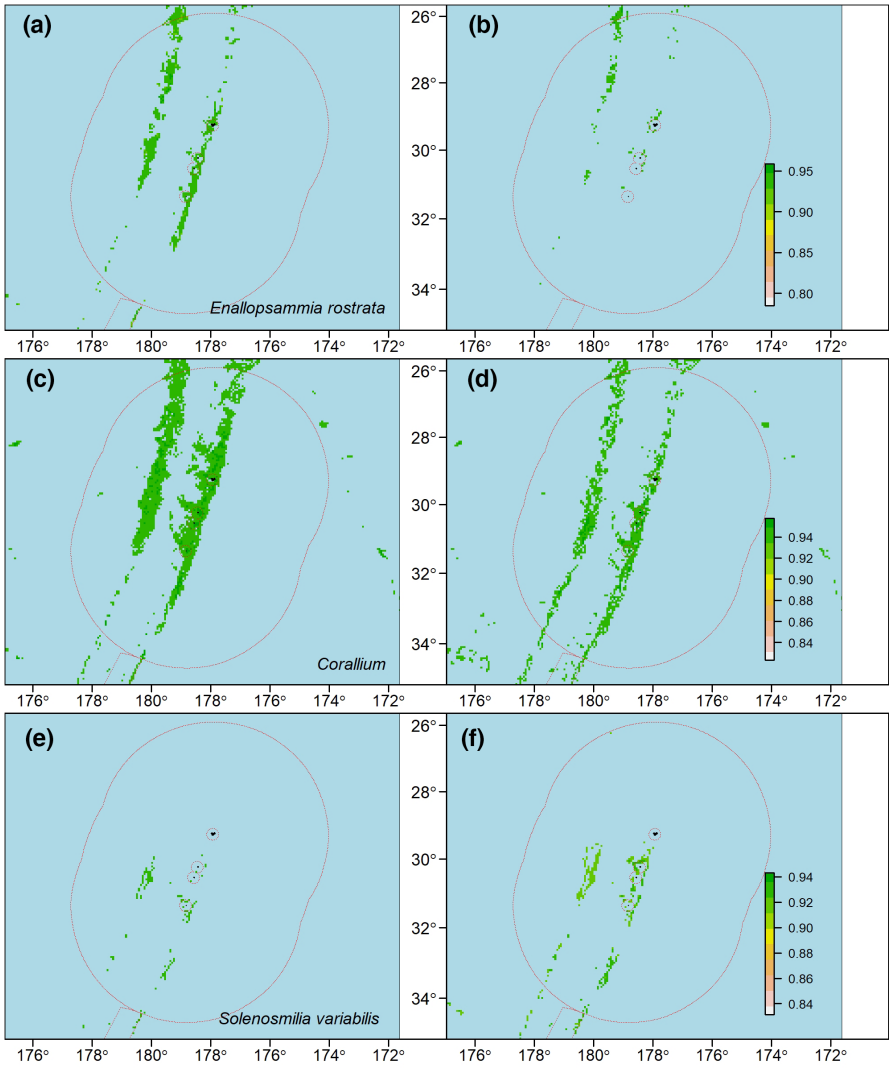

FIGURE 9 Predicted habitat suitability in areas of primary habitat (habitat suitability above the 95th percentile of cell values within the modelled area) in the Kermadec benthic protection area. Top, *Enallopsammia rostrata* (a, b); middle, *Corallium* (c, d); bottom, *Solenosmilia variabilis* (e, f). Left, present primary habitat (a, c, e); right, future primary habitat suitability (b, d, f) (under strong greenhouse gas concentration trajectory; SSP3-7.0). [See Appendix S1 for a complete set of plots—All taxa].

necessary to ensure a meaningful level of protection for deep-water corals in the face of future climate change effects for the ocean environment. For such a review to be useful to environmental managers it should also take into account spatial information on other factors that may help to balance the need for protection against future value from resource use of the region, such as the potential future location and level of fishing activities and known seabed mineral resources that may be exploited in the future. Furthermore, this review should consider the current status of the coral habitat following decades of damage by bottom trawling, which could also affect the suitability of future habitat for deep-water coral taxa. With substantial predicted shifts in areas of primary suitable habitat it would also be useful to account for connectivity pathways (Kenchington et al., 2019; Wang et al., 2021), especially as these corals are reliant on larval dispersal for colonising new areas (Andrello et al., 2015; Baco et al., 2016; Hilário et al., 2015). Such a review can be undertaken using spatial planning software, for example, Zonation (Moilanen, 2007) and Marxan (Ball & Possingham, 2000), which enables consideration of multiple factors alongside the predicted spatial distribution of habitat suitability for the protected corals produced in this study. We aim to complete some of the contributory analysis steps in a follow-up study.

ACKNOWLEDGMENTS

We are grateful to the New Zealand Department of Conservation and their Conservation Services Programme (Project: POP202801) for funding this research, and to the New Zealand Ministry of Business, Innovation and Employment Sustainable Seas National Science Challenge project 3.2 "Communicating Risk and Uncertainty to Aid Decision Making" (Contract No: C01X1901) for partial funding to support the writing of this manuscript. The authors also thank Di Tracey, Sadie Mills, and Diana MacPherson (NIWA), for their compilation of species presence records, and Fisheries New Zealand for the partial funding of this compilation under various contracts. We especially thank two anonymous experts for their excellent reviews. Open access publishing facilitated by National Institute of Water and Atmospheric Research, as part of the Wiley - National Institute of Water and Atmospheric Research agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors are not aware of any financial or non-financial interests that may directly undermine, or be perceived to undermine the objectivity, integrity and value of this publication.

DATA AVAILABILITY STATEMENT

The data that support the habitat suitability models produced in this study, as well as all model outputs, are openly available Dryad at 10.5061/dryad.41ns1rnht. All analyses were conducted using publicly available routines from the Comprehensive R Archive Network (https://cran.r-project.org/), specifically the R packages gbm.simplify, randomForest, and Dismo.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Anderson, O. F., Stephenson, F., Behrens, E., & Rowden, A. A. (2022). Predicting the effects of climate change on deep-water coral distribution around New Zealand—Will there be suitable refuges for protection at the end of the 21st century? *Global Change Biology*, *28*, 6556–6576. https://doi.org/10.1111/gcb.16389