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Seamounts as refugia from ocean acidification for cold-water stony corals

Derek P. Tittensor[1,2], Amy R. Baco[3], Jason M. Hall-Spencer[4], James C. Orr[5] & Alex D. Rogers[2]

1 Department of Biology, Dalhousie University, Halifax, Canada
2 Institute of Zoology, Zoological Society of London, Regent's Park, London, UK
3 Department of Oceanography, Florida State University, Tallahassee, FL, USA
4 Marine Biology and Ecology Research Centre, Marine Institute, University of Plymouth, UK
5 LSCE/IPSL, Laboratoire des Sciences du Climat et de l'Environnement, CEA-CNRS-UVSQ, Gif-sur-Yvette, France

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Correspondence
Derek P. Tittensor, Department of Biology, Dalhousie University, Halifax, Canada.
E-mail: derekt@mathstat.dal.ca

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Abstract

Cold-water stony corals create habitat for a diverse range of deep-water species but are thought to be threatened by ocean acidification due to oceanic uptake of anthropogenic CO_2. Knowledge of the severity of this threat is hampered by our limited understanding of the distribution and habitat requirements of these corals. Here we estimate the global acidification threat to these organisms using a global database of cold-water stony coral records and a species distribution modelling approach. We parameterised the models using present-day environmental data, and then replaced these data with future projections of ocean chemistry from the year 2099. We found suitable coral habitat to be very heterogeneously distributed, being concentrated in the northern North Atlantic and around New Zealand. Projected changes in ocean chemistry induced a pronounced reduction in habitat suitability in the North Atlantic, and a low-to-moderate impact elsewhere under both the IPCC IS92a and S650 scenarios. Seamount summits are impacted by these changes, but consistently provide more suitable habitat than the surrounding seafloor, with around 98% of seamount summits having higher suitability in both future scenarios; this is because they lie in shallower waters with a higher aragonite saturation state. These results suggest that anthropogenic-induced changes in ocean chemistry are likely to severely impact cold-water stony coral habitat in the deep-sea of the North Atlantic, and that impacts will be less severe elsewhere. We predict that coral communities on the summits and upper slopes of seamounts will be less susceptible to ocean acidification during this century than those on the surrounding seafloor, and thus that seamounts may serve as temporary refugia.

Introduction

Patterns of species diversity and distribution at bathyal and abyssal depths are poorly understood. This has become problematic as human activities with the potential to damage and deplete benthic communities, such as fishing, hydrocarbon production and mineral extraction, have expanded into the deep ocean (Davies *et al.* 2007). To enhance our understanding of deep-sea biogeography and address knowledge gaps, models can be used to predict which areas of the deep-sea are likely to be suitable habitat for particular taxa, and what physical factors may affect their distribution (*e.g.* cold-water corals, Davies *et al.* 2008; Tittensor *et al.* 2009).

It is well established that bottom trawling is causing severe damage to deep-water habitats worldwide (Roberts *et al.* 2009; Clark *et al.* 2010; Clark & Tittensor 2010) but ocean acidification has also recently emerged as a threat (Feely *et al.* 2004, 2008; Orr *et al.* 2005; Guinotte *et al.* 2006). Uptake of anthropogenic CO_2 from the atmosphere has led to an average global decrease of about 0.1 pH units and is projected to reduce the global pH of the oceans by a further 0.3–0.44 units this century under the IPCC IS92a scenario, with wide-ranging impacts on the ecology of the oceans (Doney *et al.* 2009). As CO_2 levels increase and pH decreases, carbonate ion concentrations decline (Orr *et al.* 2005; Cao & Caldeira 2008). The decreased availability of carbonate ions can reduce the ability of calcifying marine species to form shells and skeletons (Findlay *et al.* 2009; Moy *et al.* 2009). This effect has been demonstrated in the naturally acidified marine environments of volcanic CO_2 vents where calcareous taxa are severely reduced or absent from low pH sites (Hall-Spencer *et al.* 2008), and acidified water causes carbonate skeletons to dissolve (Tunnicliffe *et al.* 2009; Rodolfo-Metalpa *et al.* 2010). Seawater with high CO_2 levels also has a number of physiological effects on marine organisms affecting growth, reproduction and larval survival (Ishimatsu *et al.* 2004; Kikkawa *et al.* 2004; Ellis *et al.* 2009; Havenhand *et al.* 2009).

Cold-water scleractinians are stony corals that can form extensive deep-water reefs, and the complex habitat provided may result in high levels of faunal diversity (Roberts *et al.* 2009). All stony corals have an exoskeleton made from the metastable form of $CaCO_3$ known as aragonite. Studies have suggested that stony deep-sea corals will be affected by ocean acidification as it will cause a shallowing of the depth of aragonite saturation horizon (ASH), the interface between over- and under-saturation of aragonite (Orr *et al.* 2005). Guinotte *et al.* (2006) estimated that ~95% of their cold-water stony coral records (n = 410) were from water that was saturated with respect to aragonite, but that by the end of the century 70% of these locations will be under-saturated (Guinotte *et al.* 2006). Aragonite saturation states have already begun to decline on shallow-water tropical coral reefs, with decreased coral growth on the Great Barrier Reef attributed to acidification or a combination of climate change impacts (De'ath *et al.* 2009).

Here we used a large database of stony coral records (>5000) to model coral niche requirements and to estimate the severity and spatial heterogeneity of the effects of changing ocean chemistry on habitat suitability. We built upon previous work hypothesising a relationship between cold-water stony coral distributions and the aragonite saturation horizon (Guinotte *et al.* 2006) by using an explicit species distribution modelling approach incorporating multiple potential drivers. We focused in particular on whether seamount summits are more or less vulnerable than the surrounding seafloor to such changes. We modelled the effects of ocean acidification on cold-water stony coral habitat by calculating present-day habitat suitability, and then extrapolating to future projections of ocean chemistry (Orr *et al.* 2005). Anthropogenic-induced changes in earth's climate system are likely to affect ocean temperature (*e.g.* Delworth *et al.* 2002), salinity (*e.g.* Clark *et al.* 2002), oxygen (Keeling *et al.* 2010), and food supply through the effects of these patterns on primary production (*e.g.* Polovina *et al.* 2008) as well as ocean chemistry. It is a challenging prospect to accurately predict such potentially abrupt events; we limit this study to the effects of ocean chemistry, while recognising that there may be additive or interactive effects between multiple changing environmental parameters.

Methods

Coral database

Our stony coral database was derived from records compiled by Rogers *et al.* (2007), Hall-Spencer *et al.* (2007) and a database of *Lophelia pertusa* records compiled by the United Nations Environment Programme – World Conservation Monitoring Centre (UNEP-WCMC). Fossil records and records without geo-referenced coordinates or depth data were removed, leaving 5852 records. Coral records below 5500 m (n = 4) were excluded because many environmental layers were missing information in the grid cells where these corals were located. Records of corals shallower than 50 m (n = 57) were also removed as our focus is on deep-water corals. Figure 1 shows the locations of the remaining coral records. These records were then gridded to an Equal-Area Scalable Earth (EASE) grid (http://nsidc.org/data/ease; Armstrong & Brodzik 1995; grid as per Tittensor *et al.* 2009) to prevent latitudinal bias in the habitat model. Data were then partitioned into 250-m vertical depth boxes (to match environmental data), and duplicate records removed. In the end, 905 grid cells contained coral presence records, with a latitudinal range from 65° N to 63° S.

Environmental layers

Environmental layers thought to be important for the distribution of cold-water stony corals at a global scale (Davies *et al.* 2008; Tittensor *et al.* 2009) were combined from published sources (Table 1). Data were globally gridded on the same EASE grid as used for the corals; the finest grain available for the majority of the data was 1° by 1°, and using this particular EASE grid ensured that there was at least one data point per grid cell. Vertically, we gridded data into 250-m boxes from 0 to 5500 m. Physical data and primary productivity model output

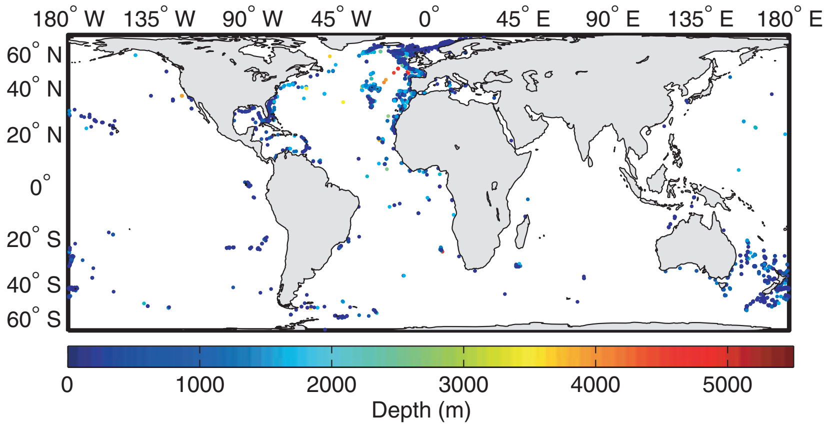

Fig. 1. Locations of cold-water stony coral coral records (see text for source details). Fossil records and those <50 m or >5500 m in depth excluded. Colour indicates depth in metres.

Table 1. Sources of environmental data used to predict cold-water stony coral habitat suitability.

layer	present (P)/ future (F)	units	source[a]	reference(s)
alkalinity (total)	P	μmol·kg^{-1}	GLODAP	(Key *et al.* 2004)
$\Delta[CO_3^{2-}]_A$ (aragonite saturation state)	P	μmol·kg^{-1}	derived from GLODAP data	(Orr *et al.* 2005)
depth	P	m	WOA	(Locarnini *et al.* 2006)
dissolved oxygen	P	ml·l^{-1}	WOA	(Garcia *et al.* 2006a)
export primary productivity	P	mg·C·m^{-2}·year^{-1}	VGPM	(Behrenfeld & Falkowski 1997)
nitrate	P	μmol·l^{-1}	WOA	(Garcia *et al.* 2006b)
percent oxygen saturation	P	%	WOA	(Garcia *et al.* 2006a)
primary productivity (overlying water)	P	mg·C·m^{-2}·year^{-1}	VGPM	(Behrenfeld & Falkowski 1997)
salinity	P	pss[b]	WOA	(Antonov *et al.* 2006)
total CO_2 (dissolved inorganic carbon)	P	μmol·kg^{-1}	GLODAP	(Key *et al.* 2004)
temperature	P	°C	WOA	(Locarnini *et al.* 2006)
regional current velocity	P	cm·s^{-1}	SODA	(Carton *et al.* 2000)
$\Delta[CO_3^{2-}]_A$ (aragonite saturation state in 2099 under IS92a and S650)	F	μmol·kg^{-1}	derived from GLODAP data & model projections	(Orr *et al.* 2005)

[a] GLODAP , Global Ocean Data Analysis Project; SODA, simple ocean data assimilation 1.4.2; VGPM, vertically generalized production model; WOA, World Ocean Atlas 2005.
[b] pss, practical salinity scale.

were all long-term annual means. Where possible, data were selected from the 1990s for maximum congruence with the Global Ocean Data Analysis Project (GLODAP) environmental data. Environmental layers needed to be in two-dimensional form for input into our models, which we achieved by concatenating depths horizontally and using dummy variables for latitude and longitude.

The World Ocean Atlas 2005 data (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html) used in our model were composite annual objectively analysed means. GLODAP gridded data (Key *et al.* 2004) were mostly derived from 1990′s WOCE (World Ocean Circulation Experiment) cruises. VGPM (Vertically Generalized Production Model) outputs (Behrenfeld & Falkowski 1997) were depth-integrated surface values of productivity corrected for cloudiness, derived from CZCS (Coastal Zone Color Scanner) pigment data collected between 1977 and 1982. SODA (Simple Ocean Data Assimilation) modelled current velocities (Carton *et al.* 2000) were the grand mean of the annual means for the period 1990–99, using the 1.4.2 version of the model.

The thermodynamic stability of aragonite in seawater is indicated by the aragonite saturation state Ω_A, which is the product of the seawater calcium and carbonate ion concentrations divided by the solubility product for aragonite: $\Omega_A = ([Ca^{2+}][CO_3^{2-}])/([Ca^{2+}]_{satA}[CO_3^{2-}]_{satA})$. The 'satA' subscript indicates the concentration in seawater in equilibrium with pure aragonite at a given temperature, salinity and pressure. Here we use the 1994 saturation state expressed as $\Delta[CO_3^{2-}]_A = [CO_3^{2-}] - [CO_3^{2-}]_{satA}$ computed by Orr *et al.* (2005) to parameterise the model, where positive values indicate supersaturation, and negative values under-saturation.

Orr *et al.* (2005) also provide projections up to the year 2099, by (i) using modern ocean chemistry observational data as a reference, (ii) adding to that baseline reference the dissolved inorganic carbon (DIC) perturbations (between the reference year 1994 and the future year, *e.g.* 2099) from simulations in 10 ocean carbon-cycle models forced with future atmospheric CO_2 from the IPCC IS92a and S650 scenarios, and (iii) recomputing saturation states and pH. This approach eliminates part of the bias; it replaces a model's simulated modern field with observational data to eliminate the 'modern' bias, but it does not eliminate the 'future' bias associated with modelled transient after 1994. To further reduce bias, we used the median from the range of 10 model projections for each scenario, because the median outperformed any individual model in the simulations of Orr *et al.* (2005). In terms of atmospheric CO_2 levels, these older IPCC scenarios bracket most of the IPCC SRES scenarios. Atmospheric CO_2 levels from IS92a are similar to those from SRES A2, and CO_2 levels from S650 are similar to those from SRES B1 (Fig. 2). Hence, projected saturation states are also similar between these same pairs of scenarios.

Habitat suitability model

There are a range of modelling methods available for predicting habitat suitability and species distributions (Guisan & Thuiller 2005). Habitat suitability models follow different paradigms, but commonly attempt to relate field observations of species to environmental predictors (Guisan & Zimmermann 2000). Most of these models are designed for situations in which both presence and

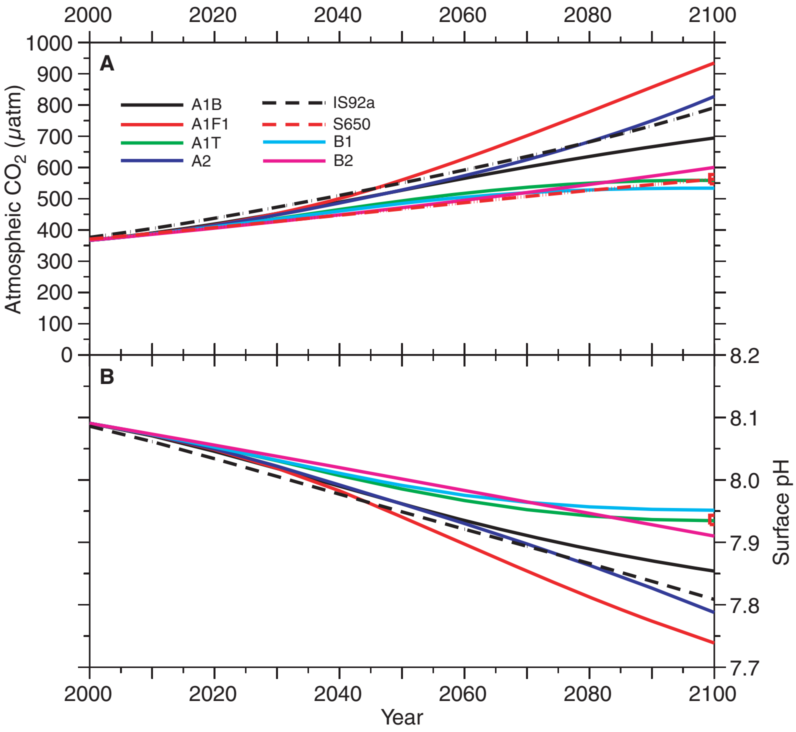

Fig. 2. IPCC scenarios for atmospheric CO_2 (A), and resulting changes in simulated results from the PIUB-Bern ocean model for global-average surface-ocean pH (B). The IS92a and A2 scenarios are similar, as are the S650 and B1 scenarios. The red symbol indicates the projected result for S650 scenario in 2099. S650 pH only calculated for the year 2099. Redrawn from Meehl *et al.* (2007).

absence data are available. When only presences are available, such as for cold-water stony corals, it is necessary to use models specifically designed for such data (Segurado & Araújo 2004).

We used the maximum entropy method (Maxent) to model habitat suitability. Maxent is a machine-learning method that approximates an unknown probability distribution by maximising entropy (Shannon 1948) subject to constraints representing incomplete information; it was first applied as a species distribution modelling approach by Phillips *et al.* (2006). Maxent was one of two presence-only models tested on the seamount subset of the present coral database (Tittensor *et al.* 2009), and it was found to consistently provide the best classification of presence records. We extend the previous version of this model by incorporating a more comprehensive coral database with samples from many deep-ocean habitats, and by extending the model vertically down to a depth of 5500 m, more than twice the depth of the original model. This is possible due to the increased numbers of records at depths >2500 m in our full database. We were particularly interested in whether habitat suitability was different for corals on and off seamounts, and how seamount and non-seamount habitat changed under future ocean chemistry scenarios.

Many coral records in the database come from seamounts, ridges or other elevated features that are too fine-scale to be detected on a 1° resolution global bathymetry, the scale at which most of the environmental data are available. To properly categorise these coral records in an appropriate vertical stratification scheme relative to the coarse data that were available, we calculated habitat suitability and coral presence for every 250-m environmental depth layer, and then mapped results to World Ocean Atlas bathymetry. Using this method more accurately locates coral records in the vertical axis, because many records come from features well over 1000 m higher than the bathymetric seafloor (*i.e.* the mismatch between coral presences and coarse-resolution environmental data can be substantial). It also allowed us to model changes in habitat suitability for predicted seamount summit locations that have been identified from a bathymetric analysis (Kitchingman & Lai 2004), by mapping from the appropriate depth layer. Thus we can depict changes for the summit locations of >14,000 predicted seamounts.

We used a cross-validation procedure to evaluate the performance of our models, by creating 10 random partitions of occurrence localities, and splitting the data in each partition between calibration (70%) and evaluation (30%) datasets. We used the AUC (area-under-the-curve) statistic to evaluate the fit of our model (Fielding & Bell 1997) to the evaluation data; the value of an AUC index typically varies between 0 (performance worse than random) and 1 (perfect discrimination), with 0.5 being indistinguishable from random. In a presence-only model, however, the maximum achievable AUC is $1 - a/2$, where a is the fraction of grid cells that the species' distribution covers (Wiley *et al.* 2003; Phillips *et al.* 2006). This is typically an unknown quantity, so it is not possible to determine an optimal AUC value; it is, however, possible to determine whether the AUC is statistically distinguishable from a random model (AUC value of 0.5) by a Wilcoxon rank-sum test statistic, and to compare the prediction strength of models using a non-parametric test based on the theory of generalized *U*-statistics (DeLong *et al.* 1988).

We tested the effect of correlated predictor variables on the predictive power of the model through non-parametric tests comparing the full model to a model with all variables correlated at >0.5 removed. All 10 cross-validation runs had lower AUC values in the second instance, three of which were significantly lower at $P < 0.05$ and another four of which were significant at $P < 0.1$. We thus concluded that leaving the correlated variables in the model resulted in better predictive ability, but refrained from drawing any inference on the relative contributions of individual environmental variables (which may be sensitive to collinear inputs). We note that results were qualitatively similar but stronger when correlated variables were removed, as more influence is exerted by the remaining ocean chemistry parameters.

We used MAXENT software version 3.31 (Phillips *et al.* 2006) to fit the Maxent model, using default model parameters (a convergence threshold of 10^{-5}, a maximum iteration value of 1000, and automatic regularisation with a value of 10^{-4}); these parameters have been shown to consistently provide a good fit to data (Phillips & Dudík 2008). A jack-knifing procedure was used to examine the importance of each variable, by comparing the model with that variable absent; to that with it present. Standard methods for analysing the effects of spatial autocorrelation cannot be used with presence-only models, and there is not currently a method suitable for such data (Dormann *et al.* 2007). However, for reasons covered in detail in Tittensor *et al.* (2009), namely the grain of the study, and the longevity of these corals, we anticipate that such effects would not be substantial.

Habitat suitability maps (Figs 3 and 4) were constructed by calculating a raw probability value $P(x)$ for each grid cell x, such that the total of all cell probabilities sum to one. This value was then scaled logistically using the equation $c\,P(x)/(1 + c\,P(x))$, where c is the exponential of the entropy of the raw distribution, resulting in a relative habitat suitability value ranging from zero to one, where larger values indicate higher relative habitat

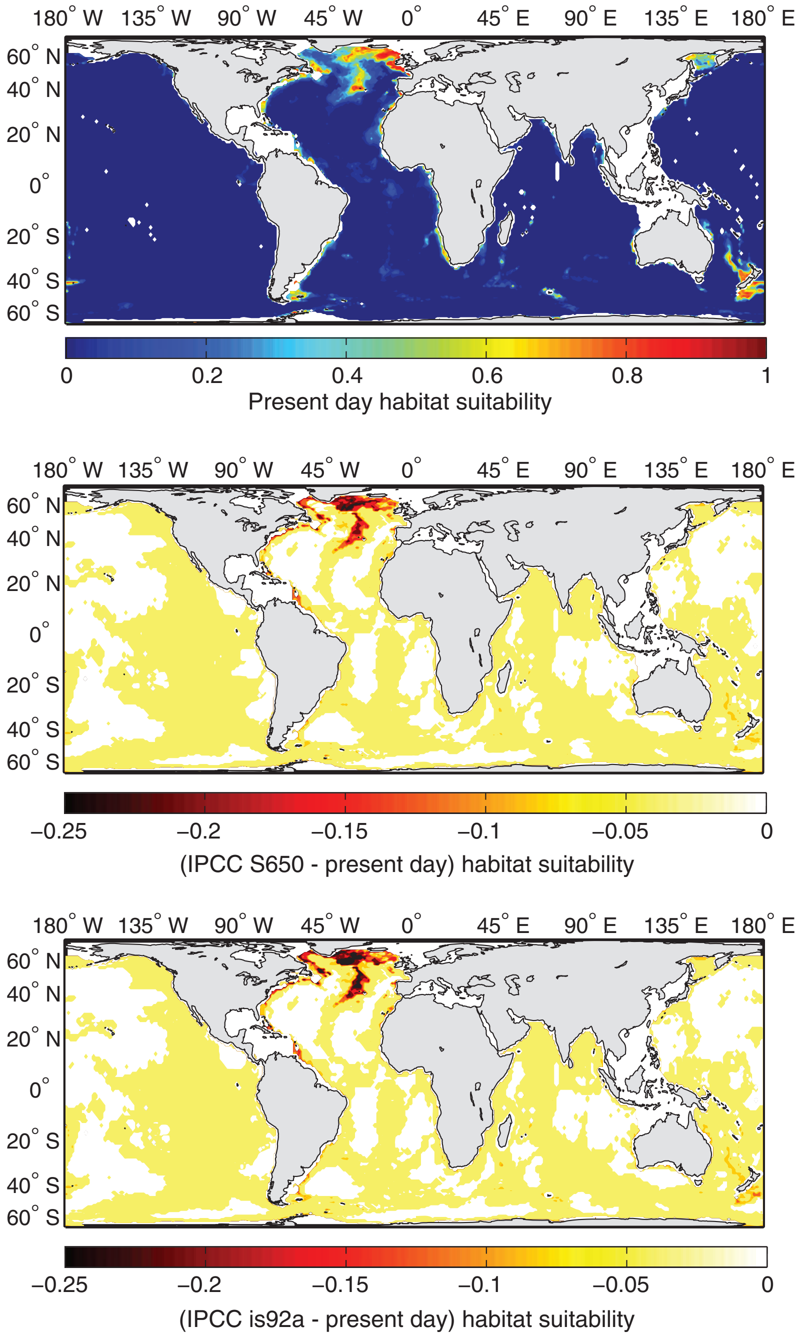

Fig. 3. Predicted seafloor habitat suitability for cold-water stony corals. Top: present day; higher values represent more suitable habitat. White areas indicate locations where one or more environmental layers were missing data. Middle: S650 IPCC emissions scenario (2099) minus present day. Bottom: IS92a IPCC scenario (2099) minus present day. For the difference panels (middle and bottom), lower values indicate a greater decrease in suitability for the future projection.

suitability. Habitat suitability values can be interpreted as a probability of presence given a similar level of sampling effort as needed to acquire the occurrence data used in the model (Phillips & Dudík 2008). Whereas we constructed the model on the EASE grid to prevent changing the spatial influence of parameters by latitude, once the model was parameterised we projected habitat suitability maps onto a 1° grid to achieve a finer resolution, and to ascertain more accurately the difference between seamount summits and the surrounding benthos. Where 1°

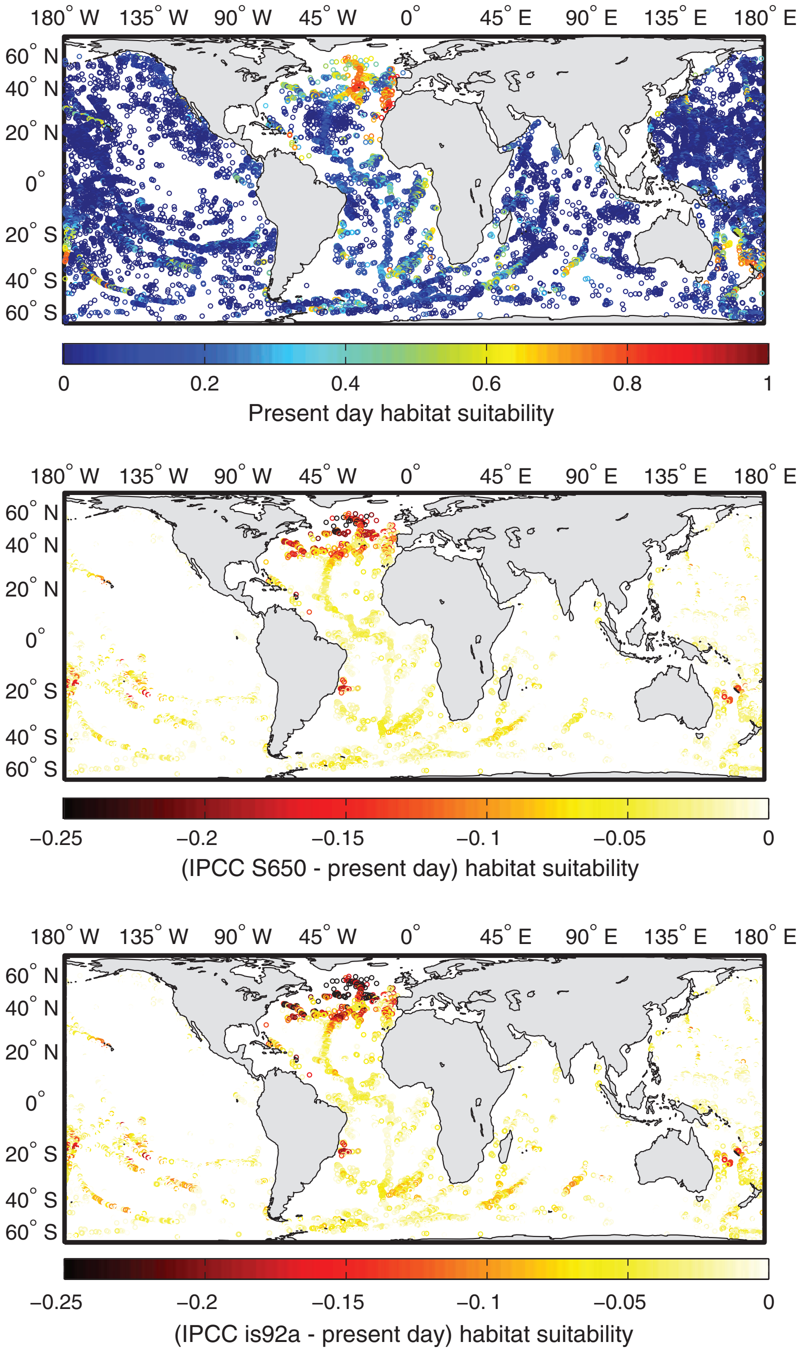

Fig. 4. Predicted habitat suitability for cold-water stony corals on likely large seamount summits (Kitchingman & Lai 2004). Top: present day; higher values represent more suitable habitat. White areas indicate locations where one or more environmental layers were missing data. Middle: S650 IPCC emissions scenario (2099) minus present day. Bottom: IS92a IPCC scenario (2099) minus present day. For the difference panels (middle and bottom), lower values indicate a greater decrease in suitability for the future projection.

environmental layers were missing some (but not all) variables at depth, for the purposes of predicting suitability we used co-kriging to interpolate values, using a separately calculated isotropic semivariogram for each depth level and layer. Seafloor depths of >5500 m were assigned a habitat suitability of zero for comparison to seamounts in the same location; the mean habitat suitability for benthos of 5000–5500 m was <0.001, so using this value instead produces virtually indistinguishable results. As we did not require binary predictions, we did not set an arbitrary threshold for species presence. Cross-validation procedures and statistical comparisons were carried out in MATLAB v. 7.2 (http://www.mathworks.com).

Results

All 10 cross-validation partitions classified presence records significantly better than at random, with all AUC values >0.9 (Table 2). From the jack-knifing procedure (results not shown), the aragonite saturation state, temperature and primary productivity were identified as the most important factors associated with the distribution of stony corals, though due to strong correlation between many environmental factors (*e.g.* aragonite saturation state, total CO_2 and temperature all correlated at $r > 0.75$ at coral presence locations) the relative importance of the various factors should be interpreted with caution. Thus, as previously explained, we refrain from further evaluating the relative importance of such highly correlated variables.

Habitat suitability maps of the present-day seafloor are shown in the upper panel of Fig. 3. Three distinct seafloor regions appear to have high relative suitability for these corals: the North Atlantic, the area around New Zealand, and the shallow water along the continental shelves and slopes. These distributions are consistent with current knowledge about cold-water stony coral distribution (Davies *et al.* 2008; Roberts *et al.* 2009; Tittensor *et al.* 2009), although because of missing environmental data we were not able to make predictions for the Caribbean, the Norwegian coast or the Philippines, where stony corals have been observed in deep water (*e.g.* Freiwald *et al.* 2002; Lutz & Ginsberg 2007). Habitat suitability for likely seamount summits (Kitchingman & Lai 2004) appears high in the North Atlantic, in areas around New Zealand and Hawaii, and in a scattering of shallow summits throughout the rest of the oceans, particularly the South Atlantic and South Indian (Fig. 4, top).

Table 2. AUC values for all cross-validation model runs. Models were calibrated using 70% of occurrence points (randomly selected), and AUC values calculated from the remaining 30% of occurrence points. All model runs fit significantly better than random ($P < 0.0001$).

partition	Maxent AUC
1	0.943
2	0.950
3	0.940
4	0.943
5	0.939
6	0.939
7	0.941
8	0.954
9	0.948
10	0.947
mean	0.944
standard deviation	0.005

Habitat suitability maps for projected global changes under the S650 and IS92a scenarios on the seafloor environment (Fig. 3, middle and bottom panels) reveal that the effects of changes in ocean chemistry are most visible in the North Atlantic. In this region, habitat suitability declines substantially for many seafloor locations at latitudes greater than around 30° north. Changes to continental shelf regions elsewhere and the area around New Zealand are apparent, but are of low to moderate impact in comparison with the large decreases in the northern North Atlantic. Both IPCC scenarios show similar spatial patterns of change in habitat suitability, although the IS92a scenario projects a somewhat larger decrease in habitat suitability. The effects on seamount summits are also pronounced in this region (Fig. 4, middle and bottom panels), and in the area around New Zealand and Eastern Australia, and regions of the South Atlantic and South Indian oceans at around 40° S. Similarly, both scenarios show qualitatively similar patterns of declining suitability.

To quantify the extent of integrated spatial changes, we calculated differences between present day and future scenarios (Table 3) and plotted cumulative percentages of cells by habitat suitability value (Fig. 5). This further revealed the geographic heterogeneity of projected changes. Globally, the mean habitat suitability decline for seafloor cells is small, but again statistically significant (Table 3) for both scenarios, and the cumulative percentage of seafloor cells with habitat suitability between ~ 0.1 and ~ 0.9 (where higher values indicate more suitable habitat) is very slightly reduced (Fig. 5A). However, the majority of global seafloor cells have habitat suitability <0.1 in both present and future predictions due to their depth, thus swamping the signal of any change. For the North Atlantic at between 30° and 60° N, however, the cumulative proportion of cells with habitat suitability of between ~ 0.1 and ~ 0.8 is more substantially reduced, suggesting a severe localised reduction in suitable habitat (Fig. 5B). This is supported by the fact that the mean habitat suitability decrease is an order of magnitude larger (Table 3). The S650 scenario is intermediate in habitat decline relative to the IS92a scenario.

At the global scale, a greater proportion of seamount summits provide more suitable habitat than seafloor grid cells, so the decline under projected changes in ocean chemistry is more apparent (Fig. 5C). The mean change in habitat suitability for seamount summits is relatively small but significant (Table 3). In the North Atlantic at

Table 3. Effect of ocean acidification scenarios on seamount and surrounding seafloor habitat suitability for cold-water stony corals. All future scenario changes are significantly different at P < 0.0001 from the present day model, as are all differences between seamount summits and surrounding seafloor (paired *t*-tests). Habitat suitability of the surrounding seafloor is calculated from the grid cell containing the seamount.

	percentage of seamount summits with higher habitat suitability than surrounding seafloor	mean habitat suitability for seamount summits. Mean change *versus* present day in brackets[a]	mean habitat suitability for seafloor. Mean change *versus* present day in brackets[a]	mean difference in habitat suitability between seamount summits and surrounding seafloor[b]
Global				
present	98.69	0.11 [–]	0.02 [–]	0.086
S650	98.52	0.092 [−0.016]	0.018 [−0.0033]	0.074
IS92a	98.28	0.088 [−0.019]	0.017 [−0.0036]	0.071
North Atlantic > 30° N				
present	95.65	0.54 [–]	0.26 [–]	0.28
S650	96.30	0.43 [−0.11]	0.20 [−0.058]	0.23
IS92a	91.74	0.40 [−0.14]	0.19 [−0.068]	0.21

[a] (Future scenario – present day) habitat suitability.

[b] (Seamount – surrounding seafloor) habitat suitability.

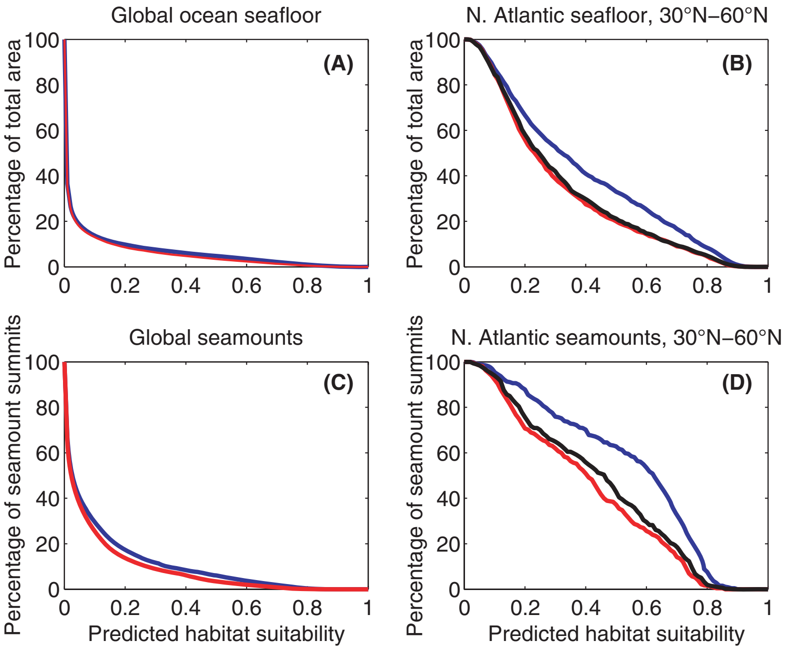

Fig. 5. Global and regional changes in cold-water stony coral habitat suitability.Included are curves for present day (blue), and projections for 2099 under the two scenarios, IS92a (red) and S650 (black). Lines represent percentage of area with a given or higher predicted habitat suitability. (A) Global ocean seafloor. (B) North Atlantic seafloor between 30 and 60° N. (C) Global ocean seamount summits. (D) North Atlantic seamount summits between 30° and 60° N. For clarity, S650 results are not shown in the left-column panels because they are very similar to the IS92a red line.

>30° N the mean declines are again greater than for the seafloor in the same region (Table 3).

A further comparison between seamounts and the seafloor is shown in Fig. 6. Seamount summits retain significantly higher mean habitat suitability for all three models than the surrounding seafloor in the grid cell containing the seamount (Table 3, Fig. 6). Similarly, although the difference in habitat suitability for seamount summits and the seafloor for the Atlantic between 30 and 60° N visibly declines in the lower panel of Fig. 6, even with this

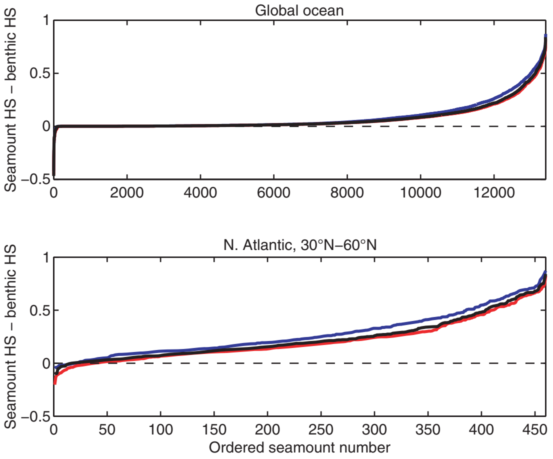

Fig. 6. Difference between seamount summit habitat suitability (HS) and HS of surrounding seafloor from the grid cell containing the seamount. Positive values indicate seamount summit HS is larger than surrounding seafloor HS. Seamounts are ordered from lowest to highest difference. Lines are shown for the present day (blue) and the projections in 2099 for the IS92a (red) and S650 (black) scenarios. Top: Global ocean seamount summits. Bottom: North Atlantic seamount summits between 30° and 60° N.

impact the mean difference in suitability remains >0.2 (Table 3).

Discussion

Distribution of present and future coral habitat

We have presented the results of a global habitat suitability model for cold-water stony corals on seamounts and on the seafloor using the projected changes from anthropogenic perturbations of the oceanic carbonate system. In the present day, the most suitable seafloor habitat for Scleractinia is predicted to be located in two areas in the northern North Atlantic and around New Zealand, with further areas of high suitability in the shallower water overlying continental shelves. This agrees well with previous studies on the distributions and habitat requirements of members of this Order (Hall-Spencer *et al.* 2007; Davies *et al.* 2008; Tittensor *et al.* 2009). Seamount summit habitat suitability is also high in these regions, but high seamount habitat suitability was also found in other scattered locations where summits are in shallower water that is more suitable than the surrounding seafloor. Indeed, seamounts could be viewed as 'shallow water' in areas of the ocean that are otherwise deep-sea, and due to this relative shallowness they provide habitat that in the vast majority of cases is predicted to be more suitable for stony corals than the surrounding seafloor.

Projected changes in ocean carbonate chemistry under the IS92a scenario for 2099 resulted in a decrease in habitat suitability for non-seamount seafloor stony corals that was most apparent in the northern half of the North Atlantic (~30°–60° N), and a low-to-moderate decrease in habitat suitability elsewhere. The decrease in habitat suitability for seamount summits was greater, but they still retained on average significantly higher habitat suitability than the surrounding seafloor. The S650 scenario showed similar, but moderately less pronounced, impacts. Experimental and empirical evidence suggests that a decrease in the aragonite saturation state may affect the distribution of cold-water corals (Orr *et al.* 2005; Guinotte *et al.* 2006; Maier *et al.* 2009); our habitat modelling study finds consistent results, while providing detail about the potential spatial heterogeneity of this effect. High habitat suitability in the North Atlantic is likely because of the deeper aragonite saturation horizon and thus higher aragonite saturation states relative to comparable depths in other parts of the global ocean. Similarly, waters overlying seamount summits typically have higher habitat suitability than those overlying the adjacent deeper seafloor, again due to the decline in the aragonite saturation state with depth.

Seamounts as refugia

Although there is a substantial decrease in habitat suitability for most seamount summits in the northern North Atlantic under the IPCC projections, they still have habitat suitability that is on average over twice as high as the surrounding seafloor (absolute differences 0.23 S650; 0.21 IS92a, Table 3). Thus the summits and upper flanks of large seamounts in the Northeast Atlantic and elsewhere may act as temporary refugia as the shallower waters are not (or are less) corrosive to aragonite. The influence of such refugia on coral species will depend on their vertical and horizontal distribution. Depth is known to have a strong influence on the occurrence of deep-sea Scleractinia, with the greatest diversity occurring at depths of 100–1000 m (Rogers *et al.* 2007). In addition, the coral fauna of, for example, the Northeast Atlantic, is not uniformly distributed across the continental slope, seamounts and oceanic islands (Hall-Spencer *et al.* 2007). Some coral species, such as *Paracyathus arcuatus* are only known on seamounts (or are rare elsewhere) or are confined to oceanic settings such as seamounts or the flanks of oceanic islands (Hall-Spencer *et al.* 2007). Other species appear to be restricted to the continental slope, such as *Caryophyllia seguenzae* (Hall-Spencer *et al.* 2007). Thus, although seamounts are unlikely to act as safe havens for all deep-sea

Scleractinia in the Northeast Atlantic, they may serve that function for some species.

By analogy, model projected shoaling of the ASH during the Anthropocene suggests the possibility that during past ocean changes of increased acidification, seamounts may have also provided refugia (Veron 2008), and thus acted as reservoirs of diversity for the surrounding benthos. Since the evolution of carbonate-secreting Scleractinia following the post-Permian extinction reef gap (Stanley 2003), there have been several episodes of high atmospheric CO_2. These include major events in the Triassic and the Late Cretaceous or Early–Middle Eocene, the latter associated with periods of rapid acidification (Zachos *et al.* 2005; Veron 2008). These events were all associated with significant extinctions of corals and other marine fauna and subsequent low diversity of Scleractinia (Stanley 2003; Veron 2008). It is possible that seamounts and the flanks of oceanic islands may have acted as refugia during these times of environmental crisis for azooxanthellate deep-sea corals, and might have acted as sources of calcifying organisms for recolonisation of the deep sea following climatic perturbations of ocean chemistry. Thus, seamounts may have acted not only as spatial stepping stones in the biogeography of corals (Rogers 1994), but also as temporal stepping stones, allowing deep-water corals to survive during periods of ocean acidification in the past.

Model performance and caveats

An AUC value of >0.9 represents very good model discrimination between presence points and random background points (Pearce & Ferrier 2000). This suggests that the model performs consistently well in determining appropriate habitat, assuming that the input coral data span the true environmental range for this Order, which seems reasonable given the large number of records gathered in the coral database. A key limitation of our model, however, is the coarse resolution. Using higher resolution data for either parameterising or projecting the model, or both, could be an important future step as such data become available, and would enable more localised predictions of habitat suitability.

When species distribution models are used to project to future scenarios, the results must be interpreted with caution. It can be problematic when models make predictions outside of the environmental range of the underlying data; in such cases Maxent 'clamps' distributions to the maximum and minimum of the original range as appropriate. Thus, ranges of environmental variables in future scenarios are restricted to the same ranges as model calibration data. Our model shows virtually no evidence of 'clamping'. In a previous study, the performance of Maxent under scenarios of past and future climates has been shown to overlap well with mechanistic models (Hijmans & Graham 2006). In addition, the model does not account for potential adaptation of corals to lower aragonite saturation states. Species may have the capacity to adjust physiologically to lower levels of aragonite, although it is likely that this is limited given their long lifetimes and the lack of corals in areas of the deep sea where the ASH is shallow (*e.g.* the North Pacific; Rogers *et al.* 2007). However, we note that recent experiments indicate that calcification may occur even at an aragonite saturation state below 1.0 (Maier *et al.* 2009), albeit at a substantially reduced rate. Evolutionary changes at the genomic level are unlikely to provide additional capacity for corals to adjust to low aragonite saturation states because of the rapidity of the current anthropogenic changes to ocean chemistry, which appear unparalleled during at least the last 40 million years (Zachos *et al.* 2005).

Management implications, caveats, and future model development

The results, both present day and future, could have management implications for cold-water stony corals and their associated biodiversity, though we caution that the model assumptions and caveats need to be carefully considered. The two largest patches of suitable present-day habitat within our model are located in two global 'hotspots' around New Zealand and in the northern North Atlantic. The patch around New Zealand is almost entirely within that country's exclusive economic zone (EEZ), whereas that in the northern North Atlantic is over 50% in EEZs, with the remainder in the high seas. Most of the suitable habitat elsewhere in the global ocean is within coastal EEZs. Thus it would appear that much can be done by individual countries to protect cold-water stony coral habitat from the effects of present-day impacts such as trawling, particularly those in the two key regions (*e.g.* Hall-Spencer *et al.* 2002; Clark & Rowden 2009). This is especially the case as the model of future habitat suitability under further ocean acidification suggests that populations of deep-sea corals may become more fragmented (Fig. 3, central North Atlantic), especially in the Northeast Atlantic, one effect of which may be decreased resilience of populations to direct human impacts through impairment of larval recruitment. We also speculate that protection of suitable future cold-water coral habitat may be most effective through the protection of the continental slope, seamounts and other elevated features rather than surrounding deep-sea areas, due to the impending shallowing of the ASH. However, we add five cautionary notes to this interpretation.

1. Other factors may affect future habitat suitability, including unmeasured parameters and biotic interactions. We also only project changes in the aragonite saturation state, and corresponding changes in other ocean chemistry parameters could have an additional effect. However, we note that due to their high 'natural' concentrations both DIC and alkalinity exhibit relatively small changes (<10% in surface waters, lower in subsurface waters) in projected scenarios (Orr *et al.* 2005). Changes in the emission scenario (*e.g.* a reduction in the input of CO_2 into the atmosphere) would also affect predictions. It is notable that currently CO_2 emissions are accelerating at a rate of 3% per year above the worst-case projected by IPCC SRES scenarios (Raupach *et al.* 2007).

2. It is possible for predicted highly suitable habitat to contain no stony corals because of biological interactions or other mechanisms that have prevented this taxon from becoming established.

3. There are uncertainties associated with the response of calcifying organisms to changes in ocean chemistry (Jury *et al.* 2010), and responses may be diverse and species-specific.

4. The scaling issues inherent in such a large-scale analysis mean that local variation is not captured by the model (Tittensor *et al.* 2009), and hence fine resolution detail will be obscured. Higher spatial resolution models will be a key step towards capturing local-scale processes that also exert an influence on cold-water coral distributions.

5. Our models do not include all known locations of these corals, including areas such as the Caribbean, Philippines and the Norwegian coast (Roberts *et al.* 2009), because of missing environmental data in these regions. These may potentially be important regions for stony cold-water corals, and we caution against ignoring them simply because they were not able to be modelled.

In light of these caveats, our predictions should not be interpreted without appropriate consideration of the limitations and assumptions involved in species distribution modelling (*e.g.* Pearson & Dawson 2003; Guisan & Thuiller 2005), calcification processes, and future scenarios. We suggest, however, that our results provide a useful measure of the potentially damaging effects of changes in ocean carbonate chemistry on the distribution of, and habitat suitability for, cold-water stony corals.

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