

2023-11

# Filling the data gaps: Transferring models from data-rich to data-poor deep-sea areas to support spatial management

Bridges, Amelia

<https://pearl.plymouth.ac.uk/handle/10026.1/21052>

---

10.1016/j.jenvman.2023.118325

Journal of Environmental Management

Elsevier BV

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*



## Research article

# Filling the data gaps: Transferring models from data-rich to data-poor deep-sea areas to support spatial management

Amelia E.H. Bridges<sup>a,b,c,\*</sup>, David K.A. Barnes<sup>b</sup>, James B. Bell<sup>c</sup>, Rebecca E. Ross<sup>d</sup>, Lizette Voges<sup>e</sup>, Kerry L. Howell<sup>a</sup>

<sup>a</sup> School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK

<sup>b</sup> British Antarctic Survey, NERC, Cambridge, UK

<sup>c</sup> Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK

<sup>d</sup> Benthic Communities Research Group, Institute of Marine Research (IMR), Bergen, Norway

<sup>e</sup> South East Atlantic Fisheries Organisation, Swakopmund, Namibia



## ARTICLE INFO

Handling Editor: Jason Michael Evans

## Keywords:

Habitat suitability modelling  
Novel approaches  
Cold-water coral reef  
Marine spatial planning  
Model transfer  
Area beyond national jurisdiction

## ABSTRACT

Spatial management of the deep sea is challenging due to limited available data on the distribution of species and habitats to support decision making. In the well-studied North Atlantic, predictive models of species distribution and habitat suitability have been used to fill data gaps and support sustainable management. In the South Atlantic and other poorly studied regions, this is not possible due to a massive lack of data. In this study, we investigated whether models constructed in data-rich areas can be used to inform data-poor regions (with otherwise similar environmental conditions). We used a novel model transfer approach to identify to what extent a habitat suitability model for *Desmophyllum pertusum* reef, built in a data-rich basin (North Atlantic), could be transferred usefully to a data-poor basin (South Atlantic). The transferred model was built using the Maximum Entropy algorithm and constructed with 227 presence and 3064 pseudo-absence points, and 200 m resolution environmental grids. Performance in the transferred region was validated using an independent dataset of *D. pertusum* presences and absences, with assessments made using both threshold-dependent and -independent metrics. We found that a model for *D. pertusum* reef fitted to North Atlantic data transferred reasonably well to the South Atlantic basin, with an area under the curve of 0.70. Suitable habitat for *D. pertusum* reef was predicted on 20 of the assessed 27 features including seamounts. Nationally managed Marine Protected Areas provide significant protection for *D. pertusum* reef habitat in the region, affording full protection from bottom trawling to 14 of the 20 suitable features. In areas beyond national jurisdiction (ABNJ), we found four seamounts that provided suitable habitat for *D. pertusum* reef to be at least partially protected from bottom trawling, whilst two did not fall within fisheries closures. There are factors to consider when developing models for transfer including data resolution and predictor type. Nevertheless, the promising results of this application demonstrate that model transfer approaches stand to provide significant contributions to spatial planning processes through provision of new, best available data. This is particularly true for ABNJ and areas that have previously undergone little scientific exploration such as the global south.

## 1. Introduction

As the global human population increases, so does the demand for a variety of natural resources, including some from the deep ocean (Ramirez-Llodra et al., 2011; Halpern et al., 2015; Van Dover et al., 2017; Kroodsma et al., 2018). Increased anthropogenic pressure on the deep sea, in the form of mining, fishing, and climate change, means that effective, integrated management, including marine spatial planning

and the use of area-based management tools (ABMTs), is becoming ever more critical (Mengerink et al., 2014; Wright et al., 2019). Marine protected areas (MPAs) are one of several ABMTs that could be employed. Historically, most MPAs have been designated individually on an ad-hoc basis to meet a range of national-level conservation targets (UNEP-WCMC, 2008). However, high connectivity between marine ecosystems means that the concept of 'ecological coherence' within networks of MPAs is now considered in numerous pieces of legislation

\* Corresponding author. School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK.  
E-mail address: [amelia.bridges@plymouth.ac.uk](mailto:amelia.bridges@plymouth.ac.uk) (A.E.H. Bridges).

<https://doi.org/10.1016/j.jenvman.2023.118325>

Received 21 February 2023; Received in revised form 2 June 2023; Accepted 3 June 2023

Available online 28 June 2023

0301-4797/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

(e.g. United Nations, 2002; Convention on Biological Diversity, 2004CBD, 2004). An important aspect of ensuring the ecological coherence of any MPA network is to ensure decisions are evidence-based with regards to the location of areas identified for protection, the species/habitats named as protected features, and which/how activities are restricted to meaningfully protect these areas. Having access to accurate ecological/biological maps is therefore integral to any spatial management process, something which becomes progressively more difficult with increasing area and remoteness, and therefore broad-scale management has frequently been based on assumptions underpinned by little or no relevant data. Since there is a widespread impetus for basin-scale spatial management networks, the largely data-limited nature of the deep sea stands to pose a major challenge to evidence-based decision making.

Habitat suitability modelling (HSM) has the potential to be an important tool when it comes to building maps of the spatial distribution of species and habitats across ocean basins. There are many different HSM techniques (García-Callejas and Araújo, 2016), but all are founded on the same basic principle: using knowledge of where species/habitats are known to occur to predict where else they might occur based on environmental envelope similarities. HSM has been used successfully to predict the distributions of a variety of deep-sea taxa including scleractinian corals across multiple basins (Davies et al., 2008; Davies and Guinotte, 2011; Yesson et al., 2012; Ross and Howell, 2013; Ashford et al., 2014; Howell et al., 2016; Rowden et al., 2017). Increasing the amount of data used to characterise the relationship between the environment and ecological occurrences results in better performing models (Wisiz et al., 2008), and thus in data-rich areas like the northeast Atlantic, the concept of mapping and modelling the distribution of vulnerable habitats has been explored. This is particularly true for so termed Vulnerable Marine Ecosystems (VMEs; see Gos et al., 2023), designated by the UN General Assembly (UNGA) under Resolution 61/105. Outputs of these predictive models have been used to assess MPA networks and efficacy of conservation policy (Ross and Howell, 2013; Ross et al., 2015; Howell et al., 2016; Howell et al., 2022).

Globally, around 93% of the seafloor lies below 200 m depth, and therefore represents a logistically challenging and cost-intensive environment to study. Collation of large basin-scale datasets is more achievable for ocean basins that have been the focus of scientific research for decades, but for less studied basins where very few biological data have been collected, this remains nearly impossible (Menegotto and Rangel, 2018; Howell et al., 2021). The strong bias in sampling effort towards the northern hemisphere means that for many southern hemisphere deep-sea habitats and species, fundamental knowledge of their distribution is lacking. Consequently, there are very few accurate biological maps that can facilitate evidence-based marine spatial planning in under-explored regions.

One such region is the South Atlantic where, despite representing 11.1% of the global ocean area (Eakins and Sharman, 2010), multiple studies have highlighted it as particularly data-poor (Howell et al., 2020; Bridges et al., 2023; McQuaid et al., 2023). Consequently, it is not currently possible to build reliable HSMs using data from the South Atlantic, for the South Atlantic. However, it is possible to transfer established HSMs into different regions (Torres et al., 2015). Model transfer occurs when the model is used to predict in a different area/region from which the model is calibrated, an example of which would be across ocean basins. This technique therefore has the potential to become a particularly valuable tool, as it provides an opportunity to mediate historic geographic biases. Specifically, it allows models to be transferred from 'data-rich' areas where data is comparably plentiful (e.g. the North Atlantic), to 'data-poor' areas where historically there has been little scientific survey effort (e.g. the South Atlantic). Good performance across this data gradient could facilitate evidence-based marine management in areas that historically have not been the scientific focus.

In this study we ask if models built in relatively data-rich regions can

perform well when applied to otherwise appropriate but data-poor regions. Specifically, we transfer the model described in Howell et al. (2022) from the northeast Atlantic to the South Atlantic, evaluate transfer performance using an independent dataset, and demonstrate how the predictions and resulting modelled map can be used to inform area-based management in the basin.

## 2. Methods

### 2.1. The northeast Atlantic model (Howell et al., 2022)

*Desmophyllum pertusum* (Linnaeus, 1758) reef, formerly *Lophelia pertusa*, is a VME that Regional Fisheries Management Organisations (RFMOs) have a responsibility to protect from significant adverse impacts arising from fishing activity. Howell et al. (2022) comprises a two-pronged approach whereby authors (1) independently validated a published model for *D. pertusum* reef, and (2) constructed a new model, incorporating additional large datasets collated from multiple research cruises, with a spatial extent covering the NE Atlantic to the west of the United Kingdom and Ireland. Howell et al. (2022) used maximum entropy modelling (MaxEnt, Phillips et al., 2006) to build the final models as, in addition to being a proven popular choice among ecologists (Elith et al., 2011; Merow et al., 2013), MaxEnt performs well when compared to other HSM techniques (Piechaud et al., 2015; Kaky et al., 2020). Duque-Lazo et al. (2016) also found that MaxEnt transferred best compared to other modelling techniques, making the Howell et al. (2022) model suitable for use in this study. Key parameters for this model are listed in Table 1 and full details are available in the supplementary material. This is henceforth referred to as 'the data-rich model'.

### 2.2. South Atlantic bathymetry and derivatives data

To create a comparable environmental dataset on which to transfer the data-rich model, high-resolution 200 m bathymetry from the South Atlantic basin was collated from multiple sources (Table 2) to obtain the largest geographical extent possible. As per Howell et al. (2022), the Benthic Terrain Modeller plug-in (Walbridge et al., 2018) in ArcGIS v10.7 was used to derive fine-scale bathymetric position index (FBPI) and rugosity layers using the same flexible calculation options (Table 1). Using the same approach as Howell et al. (2022) and Bridges et al.

**Table 1**

Key parameters and details on the Howell et al. (2022) *Desmophyllum pertusum* reef model that was transferred from the northeast Atlantic to the South Atlantic in this study. A full breakdown of the model and evaluation process is detailed in the supplementary material.

Model parameter	Model details
Resolution	200 m/~0.002°
Algorithm	Maximum Entropy (MaxEnt; Phillips et al., 2006)
Regularisation parameter	1
Response curve features allowed	Linear, quadratic and product
Available predictor variables (all at 200 m resolution)	Depth (max. 1500 m), rugosity (neighbourhood = 3), curvature, plan curvature, profile curvature, slope, broad-scale bathymetric position index (BBPI, inner and outer radii = 5 and 50), fine-scale bathymetric position index (FBPI, inner and outer radii = 1 and 5), temperature and salinity
Variable pre-selection method	Covariance checks, iterative removal of variables using MaxEnt jackknife procedure to promote model parsimony
Final variables used (explanatory percentage contribution)	Temperature (70.5%), rugosity (23.3%) and FBPI (6.2%)
No. of <i>D. pertusum</i> reef presence points	227
No. of <i>D. pertusum</i> reef (pseudo-) absence points	3064

**Table 2**  
Sources of high-resolution 200 m multibeam bathymetry in the South Atlantic.

Data provider	Description	Citation
Global Multi-Resolution Topography (GMRT)	All available bathymetry in the database covering the region 0 °N, 30 °E, 70 °W, 60 °S.	(Ryan et al., 2009)
UK Government Blue Belt Programme	Data collected during the 2018 and 2019 cruises aboard the <i>RRS James Clark Ross</i> (JR17004) and <i>RRS Discovery</i> (DY100) within the Exclusive Economic Zones (EEZs) of Tristan da Cunha and Saint Helena.	(Morley et al., 2018; Whomersley et al., 2019)
British Antarctic Survey	Data collected during the 2013 cruise aboard the <i>RRS James Clark Ross</i> (JR287) within the EEZ of Tristan da Cunha	Barnes et al. (2013)
British Antarctic Survey/ National Geographic	Data collected from the 2015 and 2017 cruises aboard the <i>RRS James Clark Ross</i> (JR864 and JR16NG) within the EEZ of Ascension Island	(Barnes et al., 2019)
Alfred Wegener Institute	Data collected from the 2012 cruise (MSM20/2) aboard the <i>R/V Maria S. Merian</i> from Namibia to Brazil	(Jegen et al., 2015; Geissler et al., 2020)
Southeast Atlantic Fisheries Organisations (SEAFO)/ Food and Agriculture Organisation (FAO) EAF-Nansen Programme	Data collected during the 2015 and 2019 surveys in the SEAFO Convention Area aboard the <i>R/V Dr Fridtjof Nansen</i> .	(Bergstad et al., 2019; FAO, 2019)

(2021, 2022), generalised additive models (GAMs) built using the *mgcv* package (Wood, 2011) in R (R Core Team, 2019) were used to create a continuous bottom temperature layer using data from CTD (conductivity, temperature and depth) sensors deployed during the UK Overseas Territories (UKOTs) cruises (Table 2) and data archived by the British Oceanographic Data Centre (BODC; full details available in the supplementary material). The South Atlantic was deemed an appropriate basin for transfer due to the similarity in predictor variable ranges between the two regions (full details available in the supplementary material).

### 2.3. South Atlantic biological data

*D. pertusum* reef habitat is found in many of the world's oceans and is therefore a good candidate for model transfer between basins. Reef presence locations were extracted from an image dataset described in Bridges et al. (2021), with additional data from cruise DY159 aboard the *RRS Discovery* in late 2022 (Whomersley et al., 2023). These data were collected from the EEZs of Saint Helena, Ascension, and Tristan da Cunha – a UK Overseas Territory in the South Atlantic spanning 7 °S to 40 °S and comprising three oceanic islands/archipelagos. Presence and absence points were formatted to 1 point per 200 m cell based on the high-resolution bathymetry, resulting in 13 presences and 110 absences used to independently validate the transferred predictions.

### 2.4. Model transfer and independent validation

The data-rich model was used to predict habitat suitability for *D. pertusum* reef across the newly created South Atlantic environmental dataset using the MaxEnt Java graphical user interface (GUI), applying the same model parameterisation (e.g. regularisation parameter, permitted response features) as Howell et al. (2022). Predictions were masked by the MaxEnt 'novel climate' output to remove areas where environmental values fell outside the data range on which the model

was trained. Prediction values were extracted for each of the South Atlantic presence and absence points, and independent validation of the transferred predictions was performed using the PresenceAbsence package (Freeman and Moisen, 2008) in R. Area under the Receiver Operating Characteristic (ROC) curve, also known as the AUC, was calculated as a threshold-independent metric. Threshold-dependent performance was assessed using both the threshold of 0.44 selected in Howell et al. (2022), and three new thresholds that were calculated based on the independent data using the `optimal.threshold()` function. The `presence.absence.accuracy()` function was used to obtain validation metrics for each thresholding method. Metrics used were sensitivity and specificity, percent correctly classified (PCC), and the true skill statistic (TSS). These refer to the model's ability to correctly predict whether known points are presences (sensitivity) or absences (specificity); while PCC is a similar metric but one that does not discriminate between presences and absences. TSS, calculated using sensitivity and specificity, was used in place of Cohen's kappa as it allows for the correction of the overall accuracy of the model predictions using the accuracy expected to occur by chance – it is particularly suited to presence-only/presence-pseudo-absence modelling like MaxEnt (Allouche et al., 2006).

## 3. Results

### 3.1. North Atlantic model performance

The data-rich model from Howell et al. (2022) received an AUC value of 0.9, deemed excellent (0.9+), and generated good (0.8–0.9) results when assessed using the selected threshold of 0.44 (Table 3).

### 3.2. Transferred model performance

When presented with the independent dataset from the South Atlantic, the model built and reported in Howell et al. (2022) performs reasonably well (Table 4). When assessed using the previously selected threshold of 0.44, the AUC drops from 0.90 (excellent) to 0.70 (fair). Using the `optimal.threshold()` function, three new thresholds were calculated using the South Atlantic data points. The same thresholding methods as in the original model were chosen; sensitivity-specificity equality (Sens = Spec), sensitivity-specificity sum maximisation (MaxSens + Spec) and minimum distance to the top left corner in the receiver operating characteristic curve plot (MinROCdist), also in Table 4. Although Sens = Spec was selected as the favourable thresholding method for the data-rich model in its original domain, the metrics when using this thresholding method in the transfer region report poorly. MaxSens + Spec and MinROCdist both use a higher threshold of 0.41 (compared to 0.39 for Sens = Spec), and report higher scores for both PCC and specificity (ability to correctly predict absences), thus this threshold is used in further evaluation and discussion of the transferred model.

### 3.3. Modelled distribution of areas suitable for *D. pertusum* reef habitat in the South Atlantic

Very little environmental data was available for the southwest Atlantic, and of the small coverage acquired, none was for geomorphological features appropriate for *D. pertusum* to form reef structures. We therefore present predictions in the context of the southeast Atlantic only. Predictions were made across 27 features (seamounts, islands and banks) in the southeast Atlantic (Fig. 1). Of the 5584.48 km<sup>2</sup> of seabed for which environmental data were suitable to predict on, 5384.92 km<sup>2</sup> received predictions above the threshold of 0.41 (approximately 9.7% of the area), and thus are classed as suitable habitat for *D. pertusum* reef.

Of the 27 features for which there was sufficient environmental data on which to transfer the model, 20 received at least one cell with a prediction above the threshold (Table 5). Fourteen of the 27 features are

**Table 3**

Threshold-dependent evaluation indices for the data-rich *Desmophyllum pertusum* reef habitat suitability model from Howell et al. (2022). Data are presented for the training, test, and full models.

Thresholding approach	Average Training Models			Average Test Models			Full Model			Threshold
	PCC (SD)	Sens. (SD)	Spec. (SD)	PCC (SD)	Sens. (SD)	Spec. (SD)	PCC (SD)	Sens. (SD)	Spec. (SD)	
Sens = Spec	0.83 (0.01)	0.82 (0.03)	0.83 (0.01)	0.83 (0.01)	0.83 (0.05)	0.83 (0.01)	0.83 (0.01)	0.82 (0.03)	0.83 (0.01)	0.44

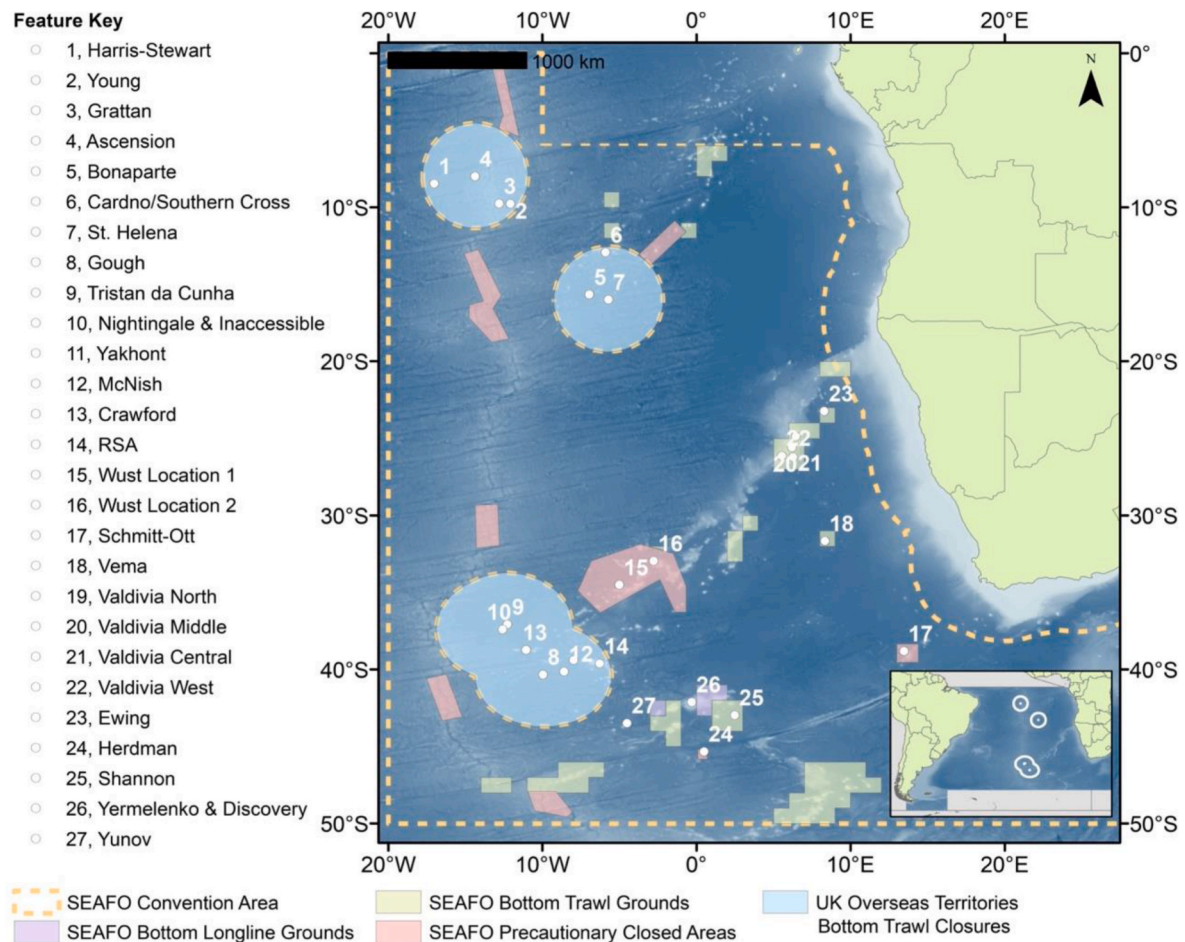
PCC = percent correctly classified; Sens. = sensitivity; Spec. = specificity.

**Table 4**

Model transfer independent validation metrics calculated using the PresenceAbsence package in R.

	Thresholding method	PCC (SD)	Sens. (SD)	Spec. (SD)	TSS (Sens + Spec -1)	AUC (SD)	Threshold
Threshold independent evaluation	-	-	-	-	-	0.70	-
Threshold-dependent evaluation		0.72	0.62	0.73	0.34	0.70	0.44 (from Howell et al., 2022)
Re-threshold	Sens = Spec	0.69 (0.04)	0.69 (0.13)	0.69 (0.04)	0.38	0.70 (0.09)	0.39
	MaxSens + Spec and MinROC dist	0.72 (0.04)	0.69 (0.13)	0.72 (0.04)	0.41	0.70 (0.09)	0.41

PCC = percent correctly classified; Sens. = sensitivity; Spec. = specificity.



**Fig. 1.** All features with suitable environmental data that allowed for the transfer of the *D. pertusum* reef model. The dashed line depicts the South East Atlantic Fisheries Organisation (SEAFO) Convention Area. Designated fishing grounds and closures are also shown. Map drawn in WGS84.

within nationally managed MPAs that legislate against bottom trawling (within the EEZs of Saint Helena, Ascension Island and Tristan da Cunha). Of the 13 features in ABNJ, the South East Atlantic Fisheries Organisation (SEAFO) have designated precautionary full VME closures on five, and a sixth feature falls partially within their existing VME

Closed Area on Valdivia Central. The 7 remaining features in ABNJ are undesignated (i.e. they are not identified as fishing grounds nor closed areas) or remain open to bottom trawling. .

The mean depth of suitable habitat for *D. pertusum* reef was 655 m and generally occurred on feature flanks, creating a ring-like pattern,

**Table 5**

Prediction area for each feature/complex with the percentage of which were above the selected threshold of 0.41. STSE = Subtropical southeast. TSE = Temperate southeast. Asc = Ascension Island. SH = St Helena. TdC = Tristan da Cunha. 'Open' fishing zones are still subject to their respective SEAFO conservation measures.

Number in Fig. 1.	Feature/Complex	Broad Location	Prediction Area (km <sup>2</sup> ; 2 d. p.)	% of predictions >0.41 (2 d. p.)	Bottom fishing status
1	Harris-Stewart	Asc EEZ	58.88	51.29	Closed
2	Young	Asc EEZ	71.64	30.49	Closed
3	Grattan	Asc EEZ	115.04	25.03	Closed
4	Ascension	Asc EEZ	312.24	17.15	Closed
5	Bonaparte	SH EEZ	78.64	23.60	Closed
6	Cardno/Southern Cross	SH EEZ	177.68	22.06	Closed
7	Saint Helena	SH EEZ	249.68	19.91	Closed
8	Gough	TdC EEZ	75.32	27.08	Closed
9	Tristan da Cunha	TdC EEZ	75.92	22.76	Closed
10	Nightingale and Inaccessible	TdC EEZ	334.92	19.04	Closed
11	Yakhont	TdC EEZ	323.24	18.08	Closed
12	McNish	TdC EEZ	90.08	14.65	Closed
13	Crawford	TdC EEZ	444.2	9.00	Closed
14	RSA	TdC EEZ	425.48	8.47	Closed
15	Wust Seamount 1	STSE	187.68	0.19	Closed
16	Wust Seamount 2	STSE	447.56	9.42	Closed
17	Schmitt-Ott	TSE	66.52	0.00	Closed
18	Vema	STSE	2.2	38.18	Closed
19	Valdivia North	STSE	14.08	0.00	Open
20	Valdivia Middle	STSE	19.44	3.09	Open
21	Valdivia Central	STSE	93.52	2.78	Mostly open, partial VME closure
22	Valdivia West	STSE	18.64	4.41	Open
23	Ewing	Tropical southeast Atlantic	19	0.00	Open
24	Herdman	TSE	4.36	0.00	Closed
25	Shannon	TSE	195.08	0.00	Open
26	Yermelenko and Discovery	TSE	1641.08	0.00	Open and/or not designated
27	Yunov	TSE	42.36	0.00	Not designated

often tracing the summit-slope break (presence histograms for each variable are available in the supplementary material). Predictions for Wust (seamount 2) and Valdivia Central are shown (Fig. 2); these features were selected to provide examples of predictive patterns.

#### 4. Discussion

Large scale model transferability can be challenging (see e.g. Bamford et al., 2009; Roach et al., 2017) but the current work showed that a model transfer approach, in our case using a habitat suitability model for North Atlantic *D. pertusum* reef, can give significant and robust power to aid spatial planning across important, but data-poor ocean basins. When the transferred model was evaluated using an independent dataset from the South Atlantic, the model performed reasonably well, with the AUC decreasing from what is deemed excellent to fair. The decrease in performance is reflected equally across all major metrics (PCC, specificity and sensitivity).

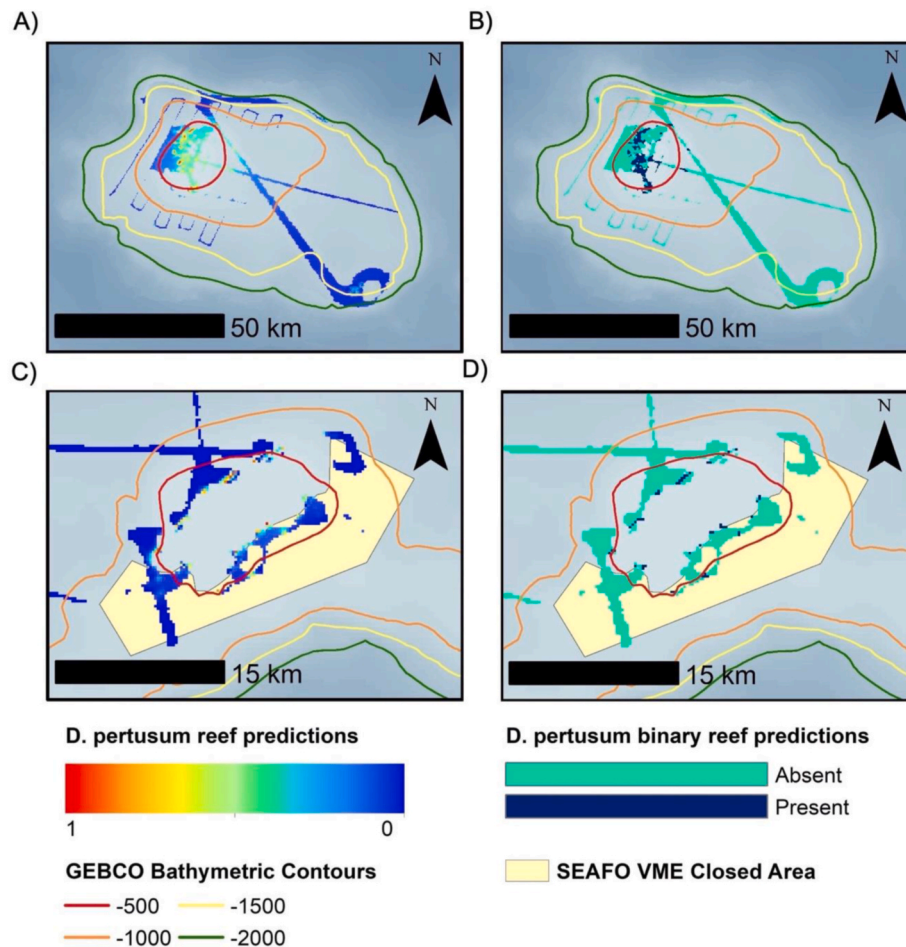
##### 4.1. Is model transfer an option for data poor regions of the deep sea?

There are several factors that may have contributed towards the successful transfer of this model, not least because of the unique environments it deals with. At a global scale, the deep sea is typically a more uniform environment than the terrestrial biome, with much greater similarity in environmental conditions between ocean basins than between, for example, terrestrial continents. Previous studies have reported poor and/or variable model transferability across large regions, but these have largely targeted terrestrial habitats/species (Bamford et al., 2009; Torres et al., 2015; Roach et al., 2017). The environmental similarity and long-term stability in deep ocean conditions between basins may mean that deep-sea habitats and species are particularly suited to model transfer (*sensu* Yates et al., 2018). This said, there are stark differences in the water mass structure between ocean basins which means predictor choice is key in designing a well-performing,

transferrable model. Whilst depth is often the variable with the highest predictive power (e.g. the *Pheronema carpenteri* model from Howell et al., 2022), a reliance upon depth, without acknowledgement of its key correlates, in models designed for transfer across ocean basins may inhibit success; this is because high dissimilarity (e.g. water mass structure) between the reference and target systems will increase prediction error (Yates et al., 2018). Therefore, when building models for the purpose of transfer, it is important to consider the generality of the predictors and where possible, select the most appropriate without compromising model performance.

In addition to its improved generality compared to depth, the selection of temperature as a predictor may also contribute to successful model transfer because it's a *direct* predictor. Direct and indirect gradients are initially described in Austin (1980, 1985) and Austin and Smith (1990). Direct predictors are variables that are required for physiological maintenance but are not consumed (e.g. temperature, pH). Indirect predictors are those that are not directly linked to physiological performance but are thought to be linked via other processes (e.g. bathymetrically derived variables such as rugosity and curvature). Several studies and reviews focusing on both marine and terrestrial fauna have found that SDMs based on direct predictors are more transferable than those that use indirect predictors (Graf et al., 2006; Randin et al., 2006; Strauss and Biedermann, 2007; Gray et al., 2009; Sundblad et al., 2009). Whilst there are three predictor variables used in Howell et al. (2022), temperature is significantly more important than bathymetrically-derived (indirect) predictors. The strong reliance of the model on the only direct predictor may contribute to the success of the transfer.

When considering models of deep-sea habitat and/or species distribution for transfer, it is important to understand the pertinence of parsimony (i.e. model simplicity). Less complex models with fewer predictors and smooth response curves could, in theory, facilitate greater transferability (Yates et al., 2018). In the current study, the selection of only three predictor variables and the smooth response curves



**Fig. 2.** Both continuous and threshold-dependent (0.41) predictions for Wust seamount 2 (A, B) and Valdivia Central (C, D). Approximate locations of these features can be found on Fig. 1.

of the model likely contribute to its successful transfer. Therefore, although complex models do have their uses (e.g. in very dynamic, data-rich systems), model parsimony is a key consideration for effectively transferring models from data-rich to data-poor regions.

Yates et al. (2018) consider whether model transferability is trait- or taxon-specific, and this is another factor that would be helpful to consider prior to building models with the intent of transfer. *D. pertusum* is a sessile coral with a relatively well-defined niche thanks to many focused deep-sea studies (Rogers, 1999; Roberts et al., 2006; Dodds et al., 2007; Howell et al., 2011). Such niche knowledge has likely contributed to the successful transfer in our study. On the contrary, building transferrable models for taxa with high behavioural and/or adaptive plasticity is more challenging as the assumption that underpins distribution modelling, that the relationship between taxa and the environment is constant despite geographic location, is less rational (Yates et al., 2018). Therefore, to build reliable models for transfer from data-rich to data-poor deep-sea regions, it is perhaps safer to focus on sessile taxa with well-defined niches that often provide habitat for other species.

Manzoor et al. (2018) investigated the role of resolution (also known as grain-size) on the transferability of plant models and found that although fine-scale (50 m) models predicted best in the region in which they were calibrated, intermediate-scale (300 m) models transferred better than both fine- and broad-scale (1 km) models. Similarly, Olivier and Wotherspoon (2008) address the issue of scale in transferability of HSMs. They investigated nest selection by snow petrels in Antarctica, and found that when transferred, models at the habitat-scale were more successful than those at the nest-scale, attributing this to high variability

at smaller scales. The transferred model in this study has a resolution of 200 m, similar to the medium-scale resolution in Manzoor et al. (2018). Finer-scale models can be prone to over-fitting (Olivier and Wotherspoon, 2008), where predictions are too specific to the dataset on which the model was trained and thus the model is unable to predict in new areas. Conversely, the coarser a model, the greater the extent to which it will over-estimate distribution (Marshall, 2011), and depending on the size of the ecosystems/features that are targeted, may not be useful from a management perspective. Therefore, when building models for transfer in the deep sea, intermediate resolutions will likely perform better. This is of course only if the variability of the predictors is relevant to that resolution. Nevertheless, the biggest hurdle in creating transferrable models at oceanographic basin scales is the lack of intermediate resolution environmental data, evidenced in this study by the lack of predictions for the southwest Atlantic. This is despite the known presence of geomorphological structures suitable for reef-building scleractinians to inhabit (e.g. the Rio Grande Rise). Although collecting this type of data is considered 'easier' than physical samples, in 2022 less than 25% of the seafloor had been directly mapped using multibeam sonar data (Seabed 2030 Project, 2023).

When assessed against threshold-dependent metrics, the performance of our transferred model (Table 4) drops in all three by approximately 0.12, equivalent to 12%, from the performance of the Howell et al. (2022) model (Table 3). In the current study, there were only 13 presences available to validate the model, acutely highlighting just how little data is available for some large areas, such as the South Atlantic. Resultantly, it is difficult to ascertain to what extent the reduction in model performance can be attributed to the methodology (i.e. model

transfer), versus the drop being an artefact of the limited validation data. This said, the excellent validation performance of the model in the North Atlantic is important to consider with regards to the model's predictive power. Eight of the 13 validation presence points received predictions above the 0.41 threshold calculated to determine *D. pertusum* reef presence, but five points received lower predictions, ranging from 0.01 to 0.41, and there are several possible reasons for this. Firstly, it is extremely unlikely that a model should predict every point correctly; even in its calibration domain, the data-rich model does not achieve 100% accuracy and therefore it would be unrealistic to expect a transferred model to. For example, *D. pertusum* reef clumps can grow on soft sediment (Howell et al., 2009). The data-rich model does not predict these formations well in the North Atlantic, and therefore the poor predictive performance for this particular type of reef formation will carry over. The second reason relates to the scale at which models are built. Two of the incorrectly predicted true presence points were located on seamount summit centres, whilst a further two were located just above the seamount summit-shelf break. In all four cases, points were in areas where the 200 m multibeam bathymetry showed flat seabed with low topographic complexity. Vertical walls and overhangs are known to provide important habitat for reef-building cold-water corals including *D. pertusum* (Huvette et al., 2011; Davies et al., 2017), but features such as pinnacles that provide vertical habitat can have a small footprint. In these cases, it is plausible that multibeam bathymetry gridded at 200 m resolution is too coarse to resolve these features, and instead artificially smooths the seabed within cells where these features are present. This would explain the presence of *D. pertusum* reef, but the low prediction likelihood values for these cells. Whilst this result does raise the questions of whether key predictors are missing, the good performance of the Howell et al. (2022) model in the North Atlantic suggests this is unlikely.

In summary, model transfer is an option for data poor regions of the deep sea. However, if building a model with the intention of transferring it, care should be taken, and decision be considered carefully, to maximise transferability based on the information above.

#### 4.2. How is *D. pertusum* reef distributed across the study area?

The transferred model in our study provides best available data on the likely occurrence of *D. pertusum* reef habitat in the southeast Atlantic. Suitable habitat is predicted to occur on 20 of 27 modelled features, suggesting *D. pertusum* reef is widespread. All features where more than 5% of the modelled surface was suitable for *D. pertusum* reef have legislation in place that prohibits bottom trawling, although these closures were not necessarily designated based on the presence of *D. pertusum* reef.

Features within the EEZs of Ascension Island, Saint Helena and Tristan da Cunha provide large areas, highly suitable for *D. pertusum* reef as represented by their high percentages of presence predictions per feature (Table 5). The governments of Ascension and Saint Helena and Tristan da Cunha have all approved large MPAs/Marine Protection Zones that prohibit bottom-trawling and therefore protect VMEs including cold-water coral reefs. Whilst full habitat mapping of the South Atlantic is required in order to quantify the basin-scale importance of these MPAs, it is likely they play an important role in conserving *D. pertusum* reef given the high number of features they cover and the high percentages of each feature that receive presence predictions.

The model predicts presence of *D. pertusum* reef across seven acoustically mapped seamounts in ABNJ (Table 5) but finds no likely presence on six features. These findings are important in the context of fisheries management of the region. The South East Atlantic Fisheries Organisation (SEAFO) is the RFMO for ABNJ east of 20 °W in the South Atlantic (Fig. 2). RFMOs are required to regulate bottom fisheries in ABNJ and adopt the precautionary principle to avoid significant adverse impacts to VMEs. In reality, this is managed by bottom fishery closures, and through enforcing more reactive measures such as the move-on protocol which requires fishing vessels to move away at least 2

nautical miles if they come into contact with VME indicator taxa when fishing. Up to this point, VME data for the region has largely been collected through the FAO EAF-Nansen programme (Bergstad et al., 2019), or ad-hoc reporting from vessels whose encounters have triggered the move-on protocol. This approach has resulted in several spatial closures to bottom trawl fishing. Four of the seven features with above-threshold predictions for *D. pertusum* reef are already either entirely closed or have a portion closed to bottom trawling (Table 5).

Valdivia Bank is a seamount complex in the subtropical southeast Atlantic and has previously been bottom-trawled for orange roughy and/or alfonsino (FAO, 2011). In 2016 a small area of Valdivia Central, one of the seamounts in the complex, was closed to all fishing except for pots and set longlines (CM 30/15, 2015) to protect VMEs. The closure roughly tracks the 550 m bathymetric contour around the southern flank of the feature, and whilst it does encompass some areas with high prediction values, the northern flank of Valdivia Central appears to provide more (both spatially and environmentally) suitable area for *D. pertusum* reef (Fig. 2. 3C-D). This VME closure, although not providing maximum coverage for *D. pertusum* reef, will likely incorporate other VMEs such as *Solenosmilia variabilis* reef, or deep-sea sponge aggregations, and therefore predictive outputs for other taxa like those created in this study will be valuable to fisheries managers during reviews of existing and future VME closed areas. The modelled outputs presented here identify all four features within the wider Valdivia Bank complex as likely harbouring *D. pertusum* reef. They also represented the only features within ABNJ that have a high predicted likelihood of *D. pertusum* reef habitat, whilst still being open to bottom trawling. Therefore, in the case of Valdivia Bank, our data suggest that additional closures could further prevent significant adverse impacts to *D. pertusum* reef in the subtropical southeast Atlantic.

Six features in ABNJ show no likely presence of *D. pertusum* reef in the modelled outputs, and this is based on their environmental profiles. Despite their varying latitudes, Herdman, Ewing and Schmitt-Ott all receive no presence prediction for *D. pertusum* reef, likely because they all have deep (>800 m) summit depths, although both Herman and Schmitt-Ott fall within VME precautionary closures. On the contrary, from the small amount of high-resolution bathymetry available, Shannon, Yunov, Yermelenko and Discovery all appear to have shallower summits (<500 m). However, they are all located below the South Subtropical Front at approximately 39 °S, and are therefore permanently surrounded by cooler subantarctic water (Deacon, 1937; Smythe-Wright et al., 1998) below 6 °C, outside the known thermal niche cold of *D. pertusum* reef (Rogers, 1999). Nevertheless, lower temperatures do not rule out the presence of other VMEs including *S. variabilis* reef that is also found in the South Atlantic (Bridges et al., 2021). Shannon, Yermelenko and Discovery all harbour open fishing grounds, whilst Yunov remains undesignated to either closure or fishing. Whilst the lack of *D. pertusum* reef suitable habitat on these features suggests that any fishing taking place may not adversely impact this VME, further exploration should be undertaken to ascertain whether other VMEs are present on these features and if so, act accordingly to protect these from significant adverse impacts.

## 5. Conclusion

This study is the first example of a deep sea HSM being transferred from a data-rich to a data-poor ocean basin. Knowledge gaps in species and habitat distribution in the deep ocean will become more apparent with increasing human use, and without accurate maps of where habitats occur or are likely to occur, it will be difficult to implement an ecologically coherent, evidence-based High Seas MPA network to help achieve global sustainability targets. This encroaching need to consider areas for protection, means that successful transfer of basin-scale HSMs stands to provide significant contributions to the spatial planning process, particularly in ABNJ and areas that have previously undergone little scientific exploration.



The results of this initial application are promising, however more research is urgently needed to understand when model transfer is likely to work and when not; it is only after this that the full potential of this method will be realised. We have demonstrated how model transfer stands to offer best available data for understudied regions which could significantly benefit environmental managers. For example, promoting the precautionary principle through avoidance of areas with high likelihoods of VME presence from transferred models, rather than relying on physical encounters to trigger other protocols.

Whilst ensuring access to robust independent validation data is important, further collection of intermediate resolution (i.e. 200–300 m) environmental data, particularly in the understudied global south and ABNJ, is critical to maximising the efficacy of model transfer. Thus, initiatives such as the Nippon Seabed 2030 Project, 2023 Project that advocate for 100% of the ocean floor to be mapped by 2030 could help significantly advance our understanding of model transfer techniques, ultimately facilitating more evidence-based decision making in spatial management processes.

#### Credit author statement

Amelia Bridges: Conceptualization, Methodology, Formal Analysis, Original Draft; Kerry Howell: Conceptualization, Review & Editing, Supervision; David Barnes: Resources, Review & Editing, Supervision; James Bell: Resources, Review & Editing, Supervision; Rebecca Ross: Review & Editing, Supervision; Lizette Voges: Resources, Review & Editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Code can be shared on request, but authors do not have permission to share the bathymetry data from SEAFO.

#### 6.1 Acknowledgements

We would like to thank the scientists and crew of all research cruises that have contributed to the collection of the data used in this study. The FAO EAF-Nansen programme was instrumental in providing multibeam bathymetry for the SEAFO Convention Area. Multibeam bathymetry, temperature and biological validation data from within the UKOTs was collected through work led by the British Antarctic Survey, Cefas and National Geographic; we would like to thank the governments of Ascension Island, Saint Helena and Tristan da Cunha for permission to use data from the UKOTs in this study and their general support of the work. Research cruises were funded by the UK Natural Environment Research Council, and the Foreign and Commonwealth Office 'Blue Belt' Programme. We would like to also thank the Global Multi-Resolution Topography Data Synthesis for their support in downloading additional multibeam data for ABNJ in the South Atlantic. The temperature data for all casts outside the UKOTs came from the British Oceanographic Data Centre funded by the Natural Environment Research Council.

This paper/report uses data collected through the scientific surveys with the R/V Dr Fridtjof Nansen as part of the collaboration between the FAO EAF-Nansen Programme and SEAFO. The programme supports the implementation of the ecosystem approach to fisheries management in the partner countries. The EAF-Nansen Programme is executed by the Food and Agriculture Organisation of the United Nations (FAO), in close collaboration with the Norwegian Institute of Marine Research (IMR) and funded by the Norwegian Agency for Development Cooperation

(Norad).

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2023.118325>.

#### References

- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43 (6) <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.
- Ashford, O.S., Davies, A.J., Jones, D.O.B., 2014. Deep-sea benthic megafaunal habitat suitability modelling: a global-scale maximum entropy model for xenophophores. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 94 <https://doi.org/10.1016/j.dsr.2014.07.012>.
- Austin, M.P., 1980. Searching for a model for use in vegetation analysis. *Veg* 42 (1–3). <https://doi.org/10.1007/BF00048865>.
- Austin, M.P., 1985. Continuum concept, ordination methods, and niche theory. *Annu Rev Ecol Evol* 16 (1). <https://doi.org/10.1146/annurev.es.16.110185.000351>.
- Austin, M.P., Smith, T.M., 1990. A new model for the continuum concept. In: Grabherr, G. (Ed.), *Progress in Theoretical Vegetation Science*. Springer Publishing, Dordrecht, pp. 35–47.
- Bamford, A.J., Monadjem, A., Anderson, M.D., Anthony, A., Borello, W.D., Bridgeford, M., Bridgeford, P., Hancock, P., Howells, B., Wakelin, J., Hardy, I.C.W., 2009. Trade-offs between specificity and regional generality in habitat association models: a case study of two species of African vulture. *J. Appl. Ecol.* 46 (4) <https://doi.org/10.1111/j.1365-2664.2009.01669.x>.
- Barnes, D.K.A., Convey, P., Dömel, J., Edmonston, J., Enderlein, P., Goodall-Copestake, W., Hancox, E., Hogg, O.T., Klepacki, J., Moreau, C., Scott, S., Stowasser, G., 2013. Cruise Report RRS James Clark Ross JR287. South Atlantic wilderness; assessment of Tristan da Cunha's seabed biodiversity. British Antarctic Survey, Cambridge, UK.
- Barnes, D.K.A., Sands, C.J., Richardson, A., Smith, N., 2019. Extremes in benthic ecosystem services; blue carbon natural capital shallower than 1000 m in isolated, small, and young ascension island's EEZ. *Front. Mar. Sci.* 6 <https://doi.org/10.3389/fmars.2019.00663>.
- Bergstad, O.A., Høines, Å.S., Sarraide, R., Campanis, G., Gil, M., Ramil, F., Maletzky, E., Mostarda, E., Singh, L., António, M.A., 2019. Bathymetry, substrate and fishing areas of Southeast Atlantic high-seas seamounts. *Afr. J. Mar. Sci.* 41 (1) <https://doi.org/10.2989/1814232X.2019.1569160>.
- Bridges, A.E.H., Barnes, D.K., Bell, J.B., Ross, R.E., Howell, K.L., 2021. Benthic assemblage composition of South Atlantic seamounts. *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.660648>.
- Bridges, A.E.H., Barnes, D.K., Bell, J.B., Ross, R.E., Howell, K.L., 2022. Depth and latitudinal gradients of diversity in seamount benthic communities. *J. Biogeogr.* 49 (5) <https://doi.org/10.1111/jbi.1435>.
- Bridges, A.E.H., Howell, K.L., Amaro, T., Atkinson, L., Barnes, D.K.A., Bax, N., Bell, J.B., Bernardino, A.F., Beuck, L., Braga-Henriques, A., Brandt, A., Bravo, M.E., Brix, S., Butt, S., Carranza, A., Doti, B.L., Elegebe, I.O., Esquete, P., Freiwald, A., Gaudron, S.M., Guilhon, M., Hebbeln, D., Horton, T., Kainge, P., Kaiser, S., Lauretta, D., Limongi, P., McQuaid, K.A., Milligan, R.J., Miloslavich, P., Narayanaswamy, B.E., Orejas, C., Paulus, S., Pearman, T.R.R., Perez, J.A., Ross, R.E., Saedi, H., Shimabukuro, M., Sink, K., Stevenson, A., Taylor, M., Titschack, J., Vieira, R.P., Vinha, B., Wienberg, C., 2023. Review of the central and South Atlantic shelf and deep-sea benthos: science, policy and management. *Oceanogr. Mar. Biol. Annu. Rev.* <https://doi.org/10.1201/9781032426969-4>.
- CM 30/15, 2015. Conservation Measure on Bottom Fishing Activities and Vulnerable Marine Ecosystems in the SEAFO Convention Area. Conservation Measure on Bottom Fishing Activities and Vulnerable Marine Ecosystems in the SEAFO Convention Area. SEAFO. No. 30/15).
- Convention on Biological Diversity, 2004. Programme of Work on Protected Areas. CBD Programmes of Work), Montreal.
- Davies, A.J., Wisshak, M., Orr, J.C., Roberts, J.M., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 55 (8) <https://doi.org/10.1016/j.dsr.2008.04.010>.
- Davies, A.J., Guinotte, J.M., 2011. Global habitat suitability for framework-forming cold-water corals. *PLoS One* 6 (4). <https://doi.org/10.1371/journal.pone.0018483>.
- Davies, J.S., Guillaumont, B., Tempera, F., Vertino, A., Beuck, L., Ólafsdóttir, S.H., Smith, C.J., Fosså, J.H., van den Beld, I.M.J., Savini, A., Rengstorf, A., Bayle, C., Bourillet, J.F., Arnaud-Haond, S., Grehan, A., 2017. A new classification scheme of European cold-water coral habitats: implications for ecosystem-based management of the deep sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 145 <https://doi.org/10.1016/j.dsr2.2017.04.014>.
- Deacon, G., 1937. *The Hydrology of the Southern Ocean*. Cambridge University Press, Cambridge.
- Dodds, L.A., Roberts, J.M., Taylor, A.C., Marubini, F., 2007. Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *J. Exp. Mar. Biol. Ecol.* 349 (2) <https://doi.org/10.1016/j.jembe.2007.05.013>.
- Van Dover, C.L., Ardron, J.A., Escobar, E., Gianni, M., Gjerde, K.M., Jaekel, A., Jones, D.O.B., Levin, L.A., Niner, H.J., Pendleton, L., Smith, C.R., Thiele, T., Turner, P.J.,

- Watling, L., Weaver, P.P.E., 2017. Biodiversity loss from deep-sea mining. *Nat. Geosci.* 10 (7) <https://doi.org/10.1038/ngeo2983>.
- Duque-Lazo, J., van Gils, H., Groen, T.A., Navarro-Cerrillo, R.M., 2016. Transferability of species distribution models: the case of *Phytophthora cinnamomi* in Southwest Spain and Southwest Australia. *Ecol. Model.* 320 <https://doi.org/10.1016/j.ecolmodel.2015.09.019>.
- Eakins, B.W., Sharman, G.F., 2010. Volumes of the World's Oceans from ETOPO1. NOAA National Geophysical Data Center, Boulder, Colorado. Available at: [https://www.ngdc.noaa.gov/mgg/global/etopo1\\_ocean\\_volumes.html](https://www.ngdc.noaa.gov/mgg/global/etopo1_ocean_volumes.html).
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17 (1) <https://doi.org/10.1111/j.1472-4642.2010.00725.x>.
- FAO, 2011. *Worldwide Review of Bottom Fisheries in the High Seas* (Rome).
- FAO, 2019. *Investigation of Vulnerable Marine Ecosystems (VMEs), Fisheries Resources and Biodiversity in the Convention Area of the South East Atlantic Fisheries Organisation (SEAFO), 24 January-24 February 2019*. NORAD-FAO Project No: GCP/GLO/690/NOR Cruise Report. Rome.
- Freeman, E.A., Moisen, G., 2008. PresenceAbsence: an R package for presence-absence model analysis. *J. Stat. Software* 23 (11), 1–31.
- García-Callejas, D., Araújo, M.B., 2016. The effects of model and data complexity on predictions from species distributions models. *Ecol. Model.* 326 <https://doi.org/10.1016/j.ecolmodel.2015.06.002>.
- Geissler, W.H., Wintersteller, P., Maia, M., Strack, A., Kammann, J., Eagles, G., Jegen, M., Schloemer, A., Jokat, W., 2020. Seafloor evidence for pre-shield volcanism above the Tristan da Cunha mantle plume. *Nat. Commun.* 11 (1) <https://doi.org/10.1038/s41467-020-18361-4>.
- Gos, C., Jansen, J., Untiedt, C., Pearman, T.R.R., Downey, R., Barnes, D.K.A., Bowden, D.A., Welsford, D.C., Hill, N.A., 2023. Identifying vulnerable marine ecosystems: an image-based vulnerability index for the southern ocean seafloor. *ICES J. Mar. Sci.* 80 (4) <https://doi.org/10.1093/icesjms/fsad021>.
- Graf, R.F., Bollmann, K., Sachot, S., Suter, W., Bugmann, H., 2006. On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. *Ecography* 29 (3) <https://doi.org/10.1111/j.2006.0906-7590.04328.x>.
- Gray, T.N.E., Borey, R., Hout, S.K., Chamnan, H., Collar Nigel, J., Dolman, P.M., 2009. Generality of models that predict the distribution of species: conservation activity and reduction of model transferability for a threatened bustard. *Conserv. Biol.* 23 (2) <https://doi.org/10.1111/j.1523-1739.2008.01112.x>.
- Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6 (1) <https://doi.org/10.1038/ncomms8615>.
- Howell, K.L., Davies, J.S., Jacobs, C., Narayanaswamy, B.E., 2009. *Broad-scale Survey of the Habitats of Rockall Bank and Mapping of Annex I "Reef" Habitat: JNCC Report 422*. Joint Nature Conservation Committee, Peterborough, UK.
- Howell, K.L., Holt, R., Endrino, I.P., Stewart, H., 2011. When the species is also a habitat: comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. *Biol. Conserv.* 144 (11) <https://doi.org/10.1016/j.biocon.2011.07.025>.
- Howell, K.L., Piechaud, N., Downie, A.L., Kenny, A., 2016. The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 115 <https://doi.org/10.1016/j.dsr.2016.07.005>.
- Howell, K.L., Hilário, A., Allcock, L.A., Bailey, D.M., Baker, M., Clark, M.R., Colaço, A., Copley, J., Cordes, E.E., Danovaro, R., Dissanayake, A., Escobar, E., Esquete, P., Gallagher, A.J., Gates, A.R., Gaudron, S.M., German, C.R., Gjerde, K.M., Higgs, N.D., Le Bris, N., Levin, L.A., Manea, E., McClain, C., Menot, L., Mestre, N.C., Metaxas, A., Milligan, R.J., Muthumbi, A.W.N., Narayanaswamy, B.E., Ramalho, S.P., Ramirez-Llodra, E., Robson, L.M., Rogers, A.D., Sellanes, J., Sigwart, J.D., Sink, K., Snelgrove, P.V.R., Stefanoudis, P.V., Sumida, P.Y., Taylor, M.L., Thurber, A.R., Vieira, R.P., Watanabe, H.K., Woodall, L.C., Xavier, J.R., 2020. A blueprint for an inclusive, global deep-sea ocean decade field program. *Front. Mar. Sci.* 7 <https://doi.org/10.3389/fmars.2020.584861>.
- Howell, K.L., Hilário, A., Allcock, L.A., Bailey, D.M., Baker, M., Clark, M.R., Colaço, A., Copley, J., Cordes, E.E., Danovaro, R., Dissanayake, A., Escobar, E., Esquete, P., Gallagher, A.J., Gates, A.R., Gaudron, S.M., German, C.R., Gjerde, K.M., Higgs, N.D., Le Bris, N., Levin, L.A., Manea, E., McClain, C., Menot, L., Mestre, N.C., Metaxas, A., Milligan, R.J., Muthumbi, A.W.N., Narayanaswamy, B.E., Ramalho, S.P., Ramirez-Llodra, E., Robson, L.M., Rogers, A.D., Sellanes, J., Sigwart, J.D., Sink, K., Snelgrove, P.V.R., Stefanoudis, P.V., Sumida, P.Y., Taylor, M.L., Thurber, A.R., Vieira, R.P., Watanabe, H.K., Woodall, L.C., Xavier, J.R., 2021. A decade to study deep-sea life. *Nat. Ecol. Evol.* 5 (3) <https://doi.org/10.1038/s41559-020-01352-5>.
- Howell, K.L., Bridges, A.E., Graves, K.P., Allcock, L., la Bianca, G., Ventura-Costa, C., Donaldson, S., Downie, A.L., Furey, T., McGrath, F., Ross, R., 2022. Performance of deep-sea habitat suitability models assessed using independent data, and implications for use in area-based management. *Mar. Ecol. Prog. Ser.* 695 <https://doi.org/10.3354/meps14098>.
- Huvenne, V.A.I., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach, V., Le Bas, T.P., Wolff, G.A., 2011. A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS One* 6 (12) <https://doi.org/10.1371/journal.pone.0028755>.
- Jegen, M., Geissler, W., Maia, M., Baba, K., Kirk, H., 2015. TRISTAN: Electromagnetic, gravimetric and seismic measurements to investigate the Tristan da Cunha hot spot and its role in the opening of the South-Atlantic - Cruise No. MSM20/2 - January 17 - February 15, 2012 - Walvis Bay (Namibia) - Recife (Brazil). DFG-Senatskommission für Ozeanographie, Bremen, Germany. [https://doi.org/10.2312/cr\\_msm20\\_2](https://doi.org/10.2312/cr_msm20_2).
- Kaky, E., Nolan, V., Alatawi, A., Gilbert, F., 2020. A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. *Ecol. Inf.* 60 <https://doi.org/10.1016/j.ecoinf.2020.101150>.
- Kroodtsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B., 2018. Tracking the global footprint of fisheries. *Science* 359 (6378) <https://doi.org/10.1126/science.aao5646>.
- Manzoor, S.A., Griffiths, G., Lukac, M., 2018. Species distribution model transferability and model grain size-finer may not always be better. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-25437-1>.
- Marshall, C.E., 2011. *Species Distribution Modelling to Support Marine Conservation Planning*. PhD Thesis. University of Plymouth, Plymouth.
- McQuaid, K.A., Bridges, A.E.H., Howell, K.L., Gandra, T.B.R., de Souza, V., Currie, J.C., Hogg, O.T., Pearman, T.R.R., Bell, J.B., Atkinson, L.J., Baum, D., Bonetti, J., Carranza, A., Defeo, O., Furey, T., Gasalla, M.A., Golding, N., Hampton, S.L., Horta, S., Jones, D.O.B., Lombard, A.T., Manca, E., Marin, Y., Martin, S., Mortensen, P., Passadore, C., Piechaud, N., Sink, K.J., Yool, A., 2023. Broad-scale benthic habitat classification of the South Atlantic. *Prog. Oceanogr.* 214 <https://doi.org/10.1016/j.pocean.2023.103016>.
- Menegotto, A., Rangel, T.F., 2018. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nat. Commun.* 9 (1) <https://doi.org/10.1038/s41467-018-07217-7>.
- Mengerink, K.J., Van Dover, C.L., Ardron, J., Baker, M., Escobar-Briones, E., Gjerde, K., Koslow, J.A., Ramirez-Llodra, E., Lara-Lopez, A., Squires, D., Sutton, T., Sweetman, A.K., Levin, L.A., 2014. A call for deep-ocean stewardship. *Science* <https://doi.org/10.1126/science.1251458>.
- Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36 (10) <https://doi.org/10.1111/j.1600-0587.2013.07872.x>.
- Morley, S.A., Collins, M.A., Barnes, D.K.A., Sands, C., Bell, J.B., Walmsley, S., Goodall-Copestake, W.P., Howard, F.J.F., Stamford, T.A.M., Laptikhovskiy, V., Martin, S.M., Schofield, R.A., Shreeve, R.S., Cotton, A.R., Evans, D.R., Piechaud, N., Brewin, P.E., Bridgen, K., Apeland, B.H., Clark, W.D.J., Davies, C., Polfrey, S.D., Quirk, S.J., Lens, P.C.D., 2018. JR17-004 Cruise Report. Helping Tristan da Cunha and St Helena manage their marine environments. British Antarctic Survey, Cambridge.
- Olivier, F., Wotherspoon, S.J., 2008. Nest selection by snow petrels *Pagodroma nivea* in East Antarctica. Validating predictive habitat selection models at the continental scale. *Ecol. Model.* 210 (4) <https://doi.org/10.1016/j.ecolmodel.2007.08.006>.
- Phillips, S.B., Aneja, V.P., Kang, D., Arya, S.P., 2006. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *Int. J. Global Environ. Issues* 6 (2–3) <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Piechaud, N., Downie, A., Stewart, H.A., Howell, K.L., 2015. The impact of modelling method selection on predicted extent and distribution of deep-sea benthic assemblages. *Earth Environ. Sci. Trans. R.* 105 (4) <https://doi.org/10.1017/S1755691015000122>.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. [www.R-project.org/](http://www.R-project.org/).
- Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., van Dover, C.L., 2011. Man and the last great wilderness: human impact on the deep sea. *PLoS One* 6 (8) <https://doi.org/10.1371/journal.pone.0022588>.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33 (10) <https://doi.org/10.1111/j.1365-2699.2006.01466.x>.
- Roach, N.S., Hunter, E.A., Nibbelink, N.P., Barrett, K., 2017. Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States. *Ecosphere* 8 (3) <https://doi.org/10.1002/ecs2.1715>.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312 (5773) <https://doi.org/10.1126/science.1119861>.
- Rogers, A.D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *Int. Rev. Hydrobiol.* 84 (4) <https://doi.org/10.1002/iroh.199900032>.
- Ross, R.E., Howell, K.L., 2013. Use of predictive habitat modelling to assess the distribution and extent of the current protection of "listed" deep-sea habitats. *Divers. Distrib.* 19 (4) <https://doi.org/10.1111/ddi.12010>.
- Ross, L.K., Ross, R.E., Stewart, H.A., Howell, K.L., 2015. The influence of data resolution on predicted distribution and estimates of extent of current protection of three 'listed' deep-sea habitats. *PLoS One* 10 (10) <https://doi.org/10.1371/journal.pone.0140061>.
- Rowden, A.A., Anderson, O.F., Georgian, S.E., Bowden, D.A., Clark, M.R., Pallentin, A., Miller, A., 2017. High-resolution habitat suitability models for the conservation and management of vulnerable marine ecosystems on the louisville seamount chain, south pacific ocean. *Front. Mar. Sci.* 4 <https://doi.org/10.3389/fmars.2017.00335>.
- Ryan, W.B.F., Carbotte, S.M., Coplan, J., O'Hara, S., Melkonian, A., Arko, R., Weissel, R. A., Ferrini, V., Goodwillie, A., Nitsche, F., Bonczkowski, J., Zemsky, R., 2009. *Global Multi-Resolution Topography (GMRT) synthesis data set*. *Geochem Geophys* 10.
- Smythe-Wright, D., Chapman, P., Duncombe Rae, C., Shannon, L.V., Boswell, S.M., 1998. Characteristics of the South Atlantic subtropical frontal zone between 15°W and 5°E. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 45 (1) [https://doi.org/10.1016/S0967-0637\(97\)00068-X](https://doi.org/10.1016/S0967-0637(97)00068-X).
- Strauss, B., Biedermann, R., 2007. Evaluating temporal and spatial generality: how valid are species-habitat relationship models? *Ecol. Model.* 204 (1–2) <https://doi.org/10.1016/j.ecolmodel.2006.12.027>.

- Sundblad, G., Härmä, M., Lappalainen, A., Urho, L., Bergström, U., 2009. Transferability of predictive fish distribution models in two coastal systems. *Estuar. Coast Shelf Sci.* 83 (1) <https://doi.org/10.1016/j.ecss.2009.03.025>.
- Torres, L.G., Sutton, P.J.H., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G., Phillips, R.A., 2015. Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PLoS One* 10 (3). <https://doi.org/10.1371/journal.pone.0120014>.
- UNEP-WCMC, 2008. *National and Regional Networks of Marine Protected Areas: a Review of Progress* (Cambridge, UK).
- United Nations, 2002. *Johannesburg, South Africa. Report of the World Summit on Sustainable Development, vol. 26. August-4 September 2002. Johannesburg, South Africa.*
- Walbridge, S., Slocum, N., Pobuda, M., Wright, D.J., 2018. Unified geomorphological analysis Workflows with benthic Terrain modeler. *Geosci. J.* 8 (3) <https://doi.org/10.3390/geosciences8030094>.
- Whomersley, P., Morley, S., Bell, J., Collins, M., Pettafor, A., Campanella, F., May, K., Stowasser, G., Barnes, D., Flint, G., Appland, B., Ward-Neale, J., Lloyd, K., 2019. RRS Discovery 100 survey report: Marine Biodiversity of Tristan da Cunha and St Helena. Centre for Environment, Fisheries and Aquaculture Science, Lowestoft.
- Whomersley, P., Bell, J., Augustus, K., Barnett, S., Baum, D., Brash, R., Campanella, F., Capel, T., Clingham, E., Comben, D., Cotmore, A., Defriez, E., Eagling, L., Fletcher, C., Fletcher, M., Flint, G., Fremand, A., Geary, N., Henderson, P., Henry, L., Hogg, O., Jones, K., Joshua, C., Kiff, G., La Bianca, G., MacLaine, J., McGarry, E., Meadows, M., Murray, S., Naulaerts, J., Nelson, P., O'Loughlin, R., Shearer, L., Simpson, T., Stowasser, G., Watkins, S., Wells, J., West, L., 2023. *Blue Belt Expedition: Ascension and St Helena Marine Protected Areas: RRS Discovery 159 Cruise Report.* Centre for Environment, Fisheries and Aquaculture Science, Lowestoft.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008. NCEAS predicting species distributions working group. *Divers. Distrib.* 14 (5) <https://doi.org/10.1111/j.1472-4642.2008.00482.x>. Effects of sample size on the performance of species distribution models.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Series B Stat. Methodol.* 73 (1) <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.
- Wright, G., Gjerde, K.M., Johnson, D.E., Finkelstein, A., Ferreira, M.A., Dunn, D.C., Chaves, M.R., Grehan, A., 2019. Marine spatial planning in areas beyond national jurisdiction. *Mar. Pol.* 132 <https://doi.org/10.1016/j.marpol.2018.12.003>.
- Yates, K.L., Bouchet, P.J., Caley, J.M., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H., Bamford, A.J., Ban, S., Barbosa, M.A., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N., Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S., Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C., Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Oppel, S., Ortuño Crespo, G., Townsend Peterson, A., Rapacciolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D., Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger, S., Whittingham, M.J., Zharikov, Y., Zurell, D., Sequeira, A.M.M., 2018. Outstanding challenges in the transferability of ecological models. *Trends Ecol. Evol.* 33 (10) <https://doi.org/10.1016/j.tree.2018.08.001>.
- Yesson, C., Taylor, M.L., Tittensor, D.P., Davies, A.J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J.M., Rogers, A.D., 2012. Global habitat suitability of cold-water octocorals. *J. Biogeogr.* 39 (7) <https://doi.org/10.1111/j.1365-2699.2011.02681.x>.
- Seabed 2030 Project, 2023. Mapping progress. <https://seabed2030.org/mapping-progress> (accessed 16 February 2023).