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Straddling the line: high potential impact on vulnerable marine ecosystems by bottom-set longline fishing in unregulated areas beyond national jurisdiction

Paul E. Brewin (1,2*, Thomas J. Farrugia³, Chris Jenkins⁴, and Paul Brickle^{1,2,5}

¹South Atlantic Environmental Research Institute, Stanley Cottage, Stanley FIQQ 1ZZ, Falkland Islands

²Shallow Marine Surveys Group, 2 Philomel Pl, Stanley FIQQ 1ZZ, Falkland Islands

³Falkland Islands Government Fisheries Department, Stanley FIQQ 1ZZ, Falkland Islands

⁴INSTAAR, University of Colorado Boulder, 4001 Discovery Dv, Boulder, CO 80309, USA

⁵School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland

*Corresponding author: tel: +500 27374; e-mail: pbrewin@saeri.ac.fk.

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Impacts of Patagonian toothfish bottom-set longline fishing on vulnerable marine ecosystems (VMEs) are examined in a licenced fishery and adjacent areas beyond national jurisdiction (ABNJ) lacking fishery management. VME taxa distributions were predicted using MaxEnt and compared to fishing footprints of ABNJ and licenced fleets. The ABNJ fishery footprint was almost twice as large as in licenced waters. Whilst the footprint of low fishing effort $(0.0-3.4 \text{ h km}^{-2})$ was similar between areas, footprints of medium $(3.4-10.2 \text{ h km}^{-2})$ and high $(10.2-45.3 \text{ h km}^{-2})$ fishing effort were 4 and 13 times greater, respectively, in ABNJ. Percent overlap of licenced fishing distribution of VME indicator taxa groups was low (6.45–9.82%) compared to the considerably higher (32.62–61.99%) percentage fishing overlap on VME indicator distribution in ABNJ. Our results show that, despite the main area of VME indicator taxa being found within jurisdictional waters, there are important VME habitats on the adjacent high-seas that are potentially highly impacted by unregulated fishing. This raises concerns regarding the potential for ABNJ fisheries to undermine domestic VME management where VMEs straddle managed areas and areas that are inconsistently managed or unmanaged. Management of VMEs would benefit from strengthening regional high-seas fishing governance and monitoring procedures.

Keywords: ABNJ, benthic impacts, deep-sea, Dissostichus eleginoides, fisheries, MaxEnt, VME

Introduction

Global pressure on marine resources is increasing (Halpern *et al.*, 2015) with fishing contributing significantly to overall impact. Among commercial fisheries, such pressure affects distribution and abundance of not only target and by-catch species but also those species and habitats that directly or indirectly support fisheries (Borja *et al.*, 2016). Commercial fishing activities that employ seabed (bottom-contact) fishing methods have been linked

to a variety of negative impacts on deep-sea benthic ecosystems (Clark *et al.*, 2016 for review), where acute damage to seabed ecosystems can cause long-lasting degraded biodiversity, habitat quality, and altered function (Hiddink *et al.*, 2017). Indeed, in regions of improved fisheries management, there has been likely concomitant broad environmental benefit (Amoroso *et al.*, 2018).

Advances in deep-water fishing technology have led to increased fishing activity beyond continental shelves (Roberts,

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2002; Wright et al., 2019). Of critical concern are the impacts of deep-water seabed fisheries on vulnerable marine ecosystems (VMEs) (FAO, 2008), where vulnerability is related to susceptibility to alteration and rate of recovery from short-term or chronic disturbance and assessed in relation to specific threats and mitigations (FAO, 2008). VMEs encompass species and habitats that may be coincident with relatively high levels of productivity and biodiversity, may contribute to important ecosystem processes, or, more likely, all three of these features (Rogers et al., 2007). Key VME indicator species include hard and soft corals, sea fans, sea pens, anemones, and sponges that often form complex threedimensional structures providing habitat for other organisms (e.g. Roberts et al., 2006; Rogers et al., 2007) and may, in turn, support a wider assemblage of invertebrates and fish (Henry and Roberts, 2007). Due to their fragile structures, variable recruitment, and likely slow growth characteristics in deep-water ecosystems (Clark et al., 2016), these species may be particularly vulnerable to impacts of fishing gear. Moreover, considering that VMEs are often distributed across regionally discontinuous features such as seamounts and ridges, impacts of fishing may negatively affect both local recovery and regional population stability through reduced metacommunity processes (sensu Leibold et al., 2004; Thrush et al., 2013). In this sense, understanding the resilience and recoverability of benthic ecosystems and mitigating for impacts on rare and/or sensitive species and habitats is needed by policymakers and managers of marine resources for good policy and management development (EC, 2008; Borja et al., 2016).

The United Nations General Assembly (UNGA) Resolution 61/105:80 recommends the precautionary protection and management of VMEs among deep-sea fisheries with the aim of conserving regional biodiversity as well as protecting the ecosystem that supports fish stocks (UNGA, 2007; FAO, 2008). However, assessing impacts of such fisheries on VMEs is operationally challenging in the deep-sea. Progress is further hindered because some deep-water fisheries operate outside jurisdictional waters in so-called areas beyond national jurisdictions (ABNJ) (Clark et al., 2006). Although high-seas Regional Fisheries Management Organisations or Arrangements (RFMO/A) are encouraged to identify, monitor, and regulate impacts of fishing on VMEs, uptake of such recommendations varies between RMFO/As and effectiveness of VME management tools have been questioned in some cases (e.g. Watling and Auster, 2017). Harmonization between RFMO/A areas can occur, for example under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), Resolution 10/XII states that, in areas adjacent to the Convention Area, Member States should operate "responsibly and with due respect for the conservation measures it had adopted under the Convention"; however, this applies only to areas where there is an RFMO/A in the adjacent waters to which fishing operations can be harmonized. Of concern are the large areas of the high-seas that are not managed by any RFMO/A with respect to bottom fishing (FAO, 2016); management of those areas is left to the discretion of the Flag State.

We focus on one gap in the understanding of impacts of fishing on VMEs, that is for the Patagonian toothfish (*Dissostichus eleginoides*) fishery operating in the Falkland Islands and the adjacent high-seas (Figure 1). The Falkland Islands' toothfish fishery is a licenced, Marine Stewardship Council certified fishery (www. msc.org) operating year-round in the Falkland Islands Interim Conservation Zone and Falkland Islands Outer Conservation Zone (herein collectively referred to as the FCZ), fishing between

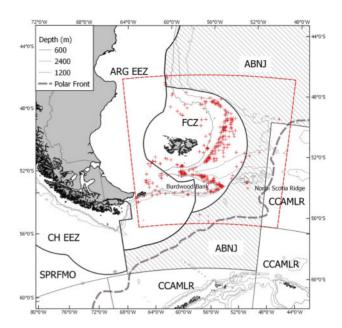


Figure 1. Managed fishing areas of the Patagonian Shelf indicating the Falkland Islands Conservation Zones (FCZ), Argentina EEZ (ARG EEZ), Chile EEZ (CH EEZ), South Pacific Regional Fisheries Management Organisation (SPRFMO), and the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). ABNJ (shaded) are areas not managed. Depth and the Antarctic Polar Front are indicated. Also shown are the MaxEnt model domain (red dashed line) and taxa sample occurrences (red crosses) input into the model.

600 and 1800 m depth (Figure 1). Like other Antarctic and sub-Antarctic toothfish fisheries, vessels use bottom-set baited hook and line systems anchored to the seabed aimed at targeting the general seabed habitat of toothfish (Collins et al., 2010). Such systems can vary considerably in their anchoring and hook deployment configuration; in the FCZ, the "trotline" longline system is used consisting of clusters of hooks hanging from a single mainline suspended above the seabed and includes the use of cetacean exclusion nets ("umbrellas" or "cachalotera") (Brown et al., 2010). Immediately adjacent to the FCZ on the high-seas around the north, north-east, and east of the FCZ along the North Scotia Ridge, unlicensed longline vessels also target Patagonian toothfish. Due to the lack of any RFMO/A, data on gear type and total catch and effort data are not readily available. This makes regionwide assessments of fishing impacts challenging for managers in the Falkland Islands and near-by controlled fisheries of Chile and Argentina, as well as the RFMO/As, the South Pacific Regional Fisheries Management Organisation (SPRFMO) and CCAMLR (Figure 1).

VME indicator taxa are often by-caught in deep-sea demersal longline fisheries (e.g. Muñoz *et al.*, 2011 and citations therein; present study). Deep-sea demersal longline fishing may have low impacts on VMEs compared to other bottom impact fishing (such as bottom trawl fishing) due to fishing gear being more or less stationary on the seabed and having a long but narrow physical footprint area (Pham *et al.*, 2014; Welsford *et al.*, 2014). However, conservation concerns remain. By-catch of VME indicator taxa varies between species groups (e.g. branched corals, solitary corals, sea pens, sponges) reflecting, in part, an effect of catchability rather than actual impact (Parker and Bowden, 2010; Muñoz *et al.*, 2011;

Welsford *et al.*, 2014), in addition to natural species' abundance and distribution variability. The cumulative impacts of repeated longline fishing on VMEs are equally not well resolved (but see Sharp *et al.*, 2009; Pham *et al.*, 2014; Welsford *et al.*, 2014).

We examine the regional footprint and fishing effort of deep-sea bottom-set longline fishing on VMEs in the region of the Patagonian Shelf, South West Atlantic. Our aims are to: (i) describe VME indicator taxa distribution throughout the region of Patagonian toothfish longline fishing using a presence-only species predictive distribution model and (ii) assess the comparative potential impact of fishing effort on VME indicator taxa within a domestic licenced fishery and an unmanaged fishery in the adjacent ABNJ. To achieve this, we compare predicted VME taxa distribution maps to vessel e-log book recorded effort within jurisdictional waters and, in the adjacent ABNJ, S-AIS (Satellite—Automatic Identification System) data gathered by Global Fishing Watch (GFW) (Kroodsma *et al.*, 2018). The implications of fishing exposures across contiguous VME habitats are discussed with recommendations made for improved VME conservation in the region.

Material and methods

Ecological setting

The Falkland Islands is situated in a highly productive region of the Patagonian Shelf Large Marine Ecosystem (Marrari et al., 2017). The southern flank of the shelf connects Tierra del Fuego in the west and the Burdwood Bank south of the Falkland Islands, and the North Scotia Ridge (Figure 1) continuing eastward eventually reaching the island of South Georgia. The eastward flowing Antarctic Circumpolar Current (ACC) water branches northward at the Burdwood Bank forming the Falklands Current, whilst the main ACC flows east along the North Scotia Ridge (Arhan et al., 2002). There are few descriptions of VME species assemblages in the region. The notable exception is work conducted west of the Burdwood Bank in the Argentinean EEZ where the Namuncurá Marine Protected Area was established in 2004 (Scheiter et al., 2016), albeit considerably shallower (200 m depth) than the region examined in the present study.

Modelling approach

The species presence-only distribution model MaxEnt (Phillips et al., 2006) was used to predict habitat suitability for VME indicator taxa (CCAMLR VME Taxa Classification Guide 2009 (https://www.ccamlr.org/en/system/files/VME-guide.pdf), where model predictions are assumed to represent the combined factors contributing to suitable habitat for VME indicator taxa. MaxEnt is a machine-learning style species distribution model (SDM) suited to applications where true absences are not available (Merow et al., 2013). MaxEnt has been used to better understand VME indicator taxa distribution in deep-sea habitats globally (e.g., Tittensor et al., 2009; Ross and Howell, 2012; Anderson et al., 2016b). The model domain (47-57°S, 50-65°W) encompasses toothfish bottom-set longline fishing on the Patagonian Shelf/slope and inclusive of ABNJ fished areas to the northern continental shelf edge, south to deep water beyond the Burdwood Bank, and east along the North Scotia Ridge (Figure 1). Depths shallower than 300 m and deeper than 2000 m are not included in the model, eliminating additional potentially confounding environmental factors in the near-shore or near-abyssal depths (Anderson et al., 2016b).

Default MaxEnt model parameters were used, which have been shown to achieve good performance (Phillips and Dudík, 2008). A "background" dataset (c.f. pseudo-absences) was constructed by first creating a "bias file" to account for observation sample bias (Kramer-Schadt et al., 2013), consisting of the twodimensional kernel density estimate of 10 000 occurrence points under a Gaussian assumption. Background points were then sampled, weighted by the kernel density raster (Guillaumot et al., 2018). A regularization parameter (the "betamultiplier") of 3 was chosen to reduce overfitting of the model (Ross and Howell, 2012) after the post hoc analysis of response curves (Supplementary material S2). Model performance was evaluated using the area under the receiver operating characteristic curve (AUC) calculated from K-fold (K=4) cross-validation. AUC scores of 0.5 indicate a model with no discriminatory power, and a value of 1 indicates a model that correctly identifies all presence records. Presence-only data for each VME indicator taxon were randomly partitioned to create 75% training and 25% test data sets. MaxEnt provides estimates of percent contributions of each environmental variable in predicting the distribution of taxa groups through a heuristic method of obtaining the ratio of the sum of changes in variation accounted for by each variable added, and the total variation accounted for by the full model (Halvorsen, 2013).

Taxa data

Taxa presence data were extracted from locally held and online sources: (i) The Falkland Islands Government Fisheries Department Scientific Observer database of benthic invertebrate species occurrences, identified to the lowest practical taxonomic level, were used for the period January 2012 (when records began) to December 2016 (N=286 lines hauled that contained VME indicator taxa); (ii) The Ocean Biogeographic Information System (OBIS http://www.iobis.org/ last accessed 6 October 2017) was used to select all records of VME indicator taxa from the study region (1557 occurrence records); (iii) A total of 2945 georeferenced benthic still images from hydrocarbon exploration throughout the FCZ (Falkland Islands Government Department of Mineral Resources, unpublished data) were examined and the presence of VME indicator taxa was recorded, ensuring that no duplicate counts from overlapping images were made; (iv) A total of 29 video recordings during two research cruises conducted in 2017 and 2018 on the commercial toothfish longline vessel CFL Hunter (Farrugia and Keningale, 2018; Farrugia et al., 2018) where, using normal fishing gear deployments, a digital camera (Git2 Pro camera, GitUp Ltd., Shenzhen, China) in an underwater housing with a light (Group Benthic, Jensen Beach, FL, USA) was attached to droplines with the aim of observing the behaviour of longline gear on the seabed. Camera observations were used to gain initial insights into longline dynamics on the seabed and other scenarios of deployment and hauling that may impact the seabed (e.g. Welsford et al., 2014).

Because VME indicator taxa are not well described in this region, species occurrences were aggregated into higher taxonomic groupings according to the CCAMLR VME Taxa Classification Guide 2009 (https://www.ccamlr.org/en/system/files/VME-guide. pdf). Parker and Bowden (2010) summarize the assessments underpinning VME taxa groupings.

Table 1. Predictor variables tested in MaxEnt model.

Environmental variable	Units	Native resolution ($^{\circ}$)	Temporal resolution	Source	Reference
Seabed terrain					
Bathymetry ^a	Μ	0.0083	_	https://www.gebco.net/	GEBCO_2014 (v20150318)
Slope ^a	Degrees	0.0083	_	Derived from bathymetry	Hogg <i>et al</i> . (2016)
Bathymetric Position	-	0.0083	_	Derived from bathymetry	Anderson et al. (2016a)
Index (BPI)—broad ^a					
BPI—fine ^a	-	0.0083	_	Derived from bathymetry	Anderson <i>et al</i> . (2016a)
TRI ^a	-	0.0083	_	Derived from bathymetry	Wilson <i>et al.</i> (2007)
Roughness	-	0.0083	_	Derived from bathymetry	Wilson <i>et al</i> . (2007)
Aspect—northness ^a	-	0.0083	_	Derived from bathymetry	Hogg et al. (2016)
Aspect—eastness ^a	-	0.0083	_	Derived from bathymetry	Hogg et al. (2016)
Curvature—general ^a	-	0.0083	_	Derived from bathymetry	Wilson <i>et al.</i> (2007)
Curvature—planar ^a	-	0.0083	_	Derived from bathymetry	Wilson <i>et al</i> . (2007)
Curvature—profile ^a	-	0.0083	_	Derived from bathymetry	Wilson <i>et al.</i> (2007)
Seabed sediment					
Gravel	%	0.05	_	dbSEABED	Jenkins (2019)
Mud	%	0.05	_	dbSEABED	Jenkins (2019)
Sand	%	0.05	_	dbSEABED	Jenkins (2019)
Rock	%	0.05	_	dbSEABED	Jenkins (2019)
Carbonates ^a	%	0.05	_	dbSEABED	Jenkins (2019)
Sand: gravel ^a	-	0.05	_	dbSEABED	Jenkins (2019)
Sand: mud ^a	-	0.05	_	dbSEABED	Jenkins (2019)
Productivity					
SS Chl_a Mean/C.V.ª	${ m mg}~{ m m}^{-3}$	0.04	Monthly	MODIS-A L3 SMI 2002-17	https://oceancolor.
					gsfc.nasa.gov
Physical water properties					
SST mean/C.V.	°C	0.04	Monthly	http://sose.ucsd.edu/	Mazloff et al. (2010)
Seabed Temp mean/C.V. ^a	°C	0.04	Monthly	http://sose.ucsd.edu/	Mazloff et al. (2010)
Seabed salinity mean/C.V. ^a	PSU	0.04	Monthly	http://sose.ucsd.edu/	Mazloff et al. (2010)
Seabed density mean/C.V. ^a	$kg m^{-3}$	0.04	Monthly	http://sose.ucsd.edu/	Mazloff et al. (2010)
Seabed current	$m s^{-1}$	0.04	Monthly	http://sose.ucsd.edu/	Mazloff et al. (2010)
speed mean/C.V. ^a					
Chemical water properties					
Aragonite saturation state ^b	μ mol kg $^{-1}$	1.0	_	GLODAPv2.2016b	Lauvset et al. (2016))
Dissolved oxygen	μ mol kg ⁻¹	1.0	_	GLODAPv2.2016b	Lauvset <i>et al</i> . (2016)
Dissolved inorganic carbon	μ mol kg ⁻¹	1.0	_	GLODAPv2.2016b	Lauvset <i>et al</i> . (2016)
Calcite saturation state	μ mol kg ⁻¹	1.0	-	GLODAPv2.2016b	Lauvset <i>et al</i> . (2016)
Nitrate	μ mol kg ⁻¹	1.0	-	GLODAPv2.2016b	Lauvset et al. (2016)
Silicate	μ mol kg ⁻ '	1.0	-	GLODAPv2.2016b	Lauvset et al. (2016)
Phosphate	μ mol kg ⁻¹	1.0	-	GLODAPv2.2016b	Lauvset et al. (2016)
Total alkalinity ^a	μ mol kg ⁻¹	1.0	_	GLODAPv2.2016b	Lauvset et al. (2016)

Full descriptions and full citations are found in Supplementary material S2.

^aFactors retained after the examination of correlation matrices.

^bAragonite saturation (Omega A) was used only for AXT and CSS only.

Predictor data

The mean and variability (Huston, 1999; Leichter and Witman, 2009) of a suite of 38 environmental variables was selected (determined through literature reviews) for their potential to be useful predictors of VME indicator taxa distributions (Table 1). Details of predictor variables are found in Supplementary material S1. All variables were gridded as rasters and resampled to 0.0083° resolution (i.e. variable with finest resolution). All environmental variables were screened for correlation within groups (seabed terrain, seabed sediments, physical water properties, chemical water properties), improving model parsimony and reducing overfitting. Scatterplot matrices were produced, and variables were removed at 0.75 correlation (Pearson) cut-off where the variable that was least correlated with other variables was retained (Anderson *et al.*, 2016b). After screening, 25 variables were

retained for the final base model (Table 1). Although aragonite saturation state and depth were highly correlated, aragonite saturation state was retained in models for hard corals (Stylasteridae and Scleractinia) due to its importance in their structure.

To determine the percentage overlap of fishing footprint on predicted habitat, we reduced probability maps to maps of binary distributions (e.g., Ross and Howell, 2012) using a threshold probability value calculated using the "average predicted probability/suitability approach" (Liu *et al.*, 2005), which is the average predicted probability/suitability across raster cells in the model output. Separate thresholds were used for each taxa group. This threshold method allows for wider predicted spatial distribution of species, which in this case is desirable given that species distributions are modelled for taxonomic groups rather than individual species. This threshold combined with the regularization parameter (see above) provides for a conservative prediction of habitat and better represents the broader niche envelope of a grouped taxa compared to a narrower niche envelope of individual species.

Fishing effort of licenced and high-seas fisheries

Line-by-line commercial longline position data were gathered from the Falkland Islands Government Fisheries Department electronic logbook database for fishing occurring between January 2012 and December 2016 (N = 2496). Latitude and longitude for the line "setting-start" and "setting-end" positions were used to map each longline set. This assumes that the longline is set in a straight line, whereas eacusevessel speed, position, and bottom topography vary during line setting the line is likely to take a less uniform pattern along the seabed. . We use GFW data (http://globalfishingwatch.org, last accessed February 2017) to examine fishing effort within the FCZ and on the high-seas adjacent to the FCZ for the period January 2012 to December 2016. GFW gathers global S-AIS data and processes it using convolutional neural networks to identify fishing vessels and fishing activity (Kroodsma et al., 2018). GFW has a 95% accuracy in predicting vessel type (six classes of fishing vessel and six classes of nonfishing vessel), and of fishing vessels, it predicts fishing activity with >90% accuracy (Kroodsma et al., 2018). The product used in the present study was gridded (1 km² resolution) daily hours of fishing. GFW data were filtered for toothfish bottom longline vessels by first, selection of either "drifting_longlines" or "fixed_gear" records. Records were then further filtered by the Flag States known to fish for toothfish in the region; retained vessel flags are Chile (CHL), Falkland Islands (FLK), South Korea (KOR), and Ukraine (UKR). This second step ensures selection of toothfish bottom-set longline vessels and not pelagic longline fishing vessels from other Flag States targeting other species. Given the accuracy of GFW algorithms, our own detailed scrutiny of identified vessels, and our knowledge of the regional fishing fleet, we are confident that GFW data used here accurately represent the toothfish fishing fleet in the FCZ and ABNJ. The final GFW data set consisted of 133 297 records for the ABNJ and 21 334 records for the FCZ.

Before ABNJ GFW fishing effort could be compared directly to the FCZ licenced fishery effort, we first determined if GFW data were an accurate proxy of recorded FCZ longline fishing effort. All fishing effort data (GFW and licenced) within the FCZ were aggregated into a $10 \,\text{km} \times 10 \,\text{km}$ resolution grid such that GFW fishing hours (fishing hours 100 km⁻²) and licenced fishery line-by-line data (lines 100 km⁻²) could be compared directly. This grid resolution was large enough to aggregate the two data sets simultaneously in the same grid square removing artefacts of misalignment of spatial resolution of the two data sets, whilst at the same time providing sufficiently fine spatial resolution for detailed representativeness. Within the FCZ, the relationship between cumulative line-by-line fishing effort and fishing hours was described by the second order polynomial expression $y = 0.275x^2 - 9.605 \times 10^{-5}x +$ 0.69 (residual s.e. =5.07; adjusted $R^2 = 0.85$; $F_{2,720} = 1964$; p < 2.2e - 16), indicating that GFW data are a good proxy for FCZ longline fishing effort in our region of interest. Consequently, we define fishing footprint to be the fishing spatial extent as defined by GFW grid squares where longline fishing activity has been estimated in both the licenced and ABNJ fisheries at the native spatial scale of GFW data (1 km² scale resolution), and fishing effort

represented as the effort (total h km⁻²) across years per grid square. The level of effort was partitioned into "low", "medium", and "high" effort based on Jenks Natural Breaks classification of the frequency distribution of cumulative hours per grid square. The resulting categories in terms of fishing effort are "low" = 0.0 - 3.4 h km⁻², "medium" = 3.4 - 10.2 h km⁻², and "high" = 10.2 - 45.3 h km⁻². Note that the absolute values of effort are proportionate to the grid size chosen.

All data processing, MaxEnt modelling, and spatial data manipulation were done in R (v3.5.1) using a range of standard base packages and specialized packages ("ncdf4", "robis", "oce", "dismo", "sdm", "BAMMtools", "MASS"). All spatial data were projected in coordinated system UTM21S for the calculation of areas (km²). Map visualizations were constructed in QGIS (v3.4.2).

Results

Indicator taxon occurrence

A total of 1570 presence records of indicator taxa were examined across 18 VME taxa groups, which were distributed widely across the fishing area of the FCZ but with limited distribution in the ABNJ (Figure 1). In terms of percentage across all occurrence records, Cnidarian groups were most common in the dataset, particularly the Scleractinia (23.06%), Gorgonacea (15.41%), Alcyonacea (7.90%), and Stylasteridae (7.39%) (Table 2). Among other groups, the Euryalida (9.75%) and Demospongiae (8.60%) were also relatively well represented in the dataset. VME indicator taxa groups with broad spatial coverage and high numbers of records were selected for MaxEnt analysis: Alcyonacea, Scleractinia, Gorgonacea, Stylasteridae, and Demospongiae. Pennatulacea were also chosen, given this group is indicative of habitats possibly not represented in the other groups (Greathead *et al.*, 2014).

Benthic camera imagery collected within the FCZ in toothfish fishing grounds indicates a wide variety of habitats with varying dominance of different groups (Figure 2). Notable from images is patchiness of VME indicator taxa groups, particularly encrusting species found on rock or cobble patches in broadly soft-sediment areas. Longline-mounted cameras capture some evidence of disturbance by "trotline" longline gear to the seabed (Figure 2), where narrow furrows (~20 cm in width) were seen in sediments caused by dragging of drop-line weights during hauling. Drop-line weights may also strike patches of VME indicator taxa attached to hard substrates in areas of soft sediments.

MaxEnt model prediction

Predicted taxa distributions show that some groups are widely distributed across the model domain (e.g., Scleractinia, Demospongiae) (Figure 3). In contrast, the predicted distribution of Pennatulacea is constrained to the western region of the northern flank of the Burdwood Bank. Alcyonacea predicted habitat is primarily within the FCZ, particularly around the northern edge of the FCZ and surrounding the Burdwood Bank. However, it was poorly represented along the North Scotia Ridge in the ABNJ. Stylasteridae habitat was well represented along the Burdwood Bank (FCZ) and North Scotia Ridge (ABNJ) but had less probability of occurrence to the north within or in adjacent ABNJ. AUC scores indicate that all models performed well (Figure 3), ranging between 0.793 (Scleractinia) and 0.938 (Pennatulacea). Threshold values ranged between 0.333 (Demospongiae) and 0.047 (Pennatulacea).

VME taxa	VME group (CCAMLR)	Common name	Total occurrences	Proportion of observations (%) 23.1		
Scleractinia	CSS	Stony corals	362			
Gorgonacea	GGW	Sea fans, Sea whips	242	15.4		
Alcyonacea	AJZ	Soft corals	124	7.9		
Pennatulacea	NTW	Sea pens	87	5.5		
Anthoathecatae	AZN	Hydroids	47	3.0		
Stylasteridae	AXT	Hydrocorals	116	7.4		
Actiniaria	ATX	Sea anemones	52	3.3		
Antipatharia	AQZ	Black corals	3	0.2		
Zoantharia	ZOT	Zoanthids	1	0.1		
Echinodermata						
Euryalida	OEQ	Basket stars	153	9.7		
Cidaroida	CVD	Pencil urchins	41	2.6		
Stalked crinoid	CWD	Stalked sea lilies	6	0.4		
Porifera						
Demospongiae	DMO	Sponges	135	8.6		
Hexactinellida	HXY	Glass sponges	34	2.2		
Chordata	SSX	Sea squirts	57	3.6		
Brachiopoda	BRQ	Lamp shells	25	1.6		
Bryozoan	BZN	Lace corals	75	4.8		
Ánnelida	SZS	Polychaets	10	0.6		

Table 2. VME group occurrences on the Patagonian Shelf from all datasets.

Groups in bold are used for modelling in MaxEnt.

An examination of percent contribution of each environmental variable in predicting the distribution of taxa groups (Table 3) shows that seabed depth had strong predictive power for Gorgonacea and Pennatulacea habitats and a narrow range of depth preference (Table 3, Supplementary material S2). The factors slope, TRI (terrain ruggedness index), and aspect-north were somewhat important in predicting taxa habitat. Sediment variables showed some predictive power, particularly carbonates for Stylasteridae and sand:gravel ratio for Demospongiae. Mean monthly surface productivity (chl_a) and variability were relatively important predictors of all groups. There were mixed levels of importance of mean and C.V. of water physical properties (temperature, salinity, density), although seabed salinity cv showed a strong inverse relationship with habitat suitability for Pennatulacea (Table 3, Supplementary material S2). Mean seabed current speed and variability predictors were important for all groups except Pennatulacea. Of the chemical properties of water tested, aragonite saturation state was relatively important when used in the models for Scleractinia, Gorgonacea, and Stylasteridae (noting that this variable was not included in models for other groups). Finally, alkalinity was a strong predictor for all groups, in some cases a stronger predictor than depth. Although beyond the scope of this study, a detailed examination of response curves can be done (Supplementary material S2) which will contribute to better describing the environmental envelope of VME indicator taxa groups in the Patagonian Shelf.

Comparison of fished area and VME predicted habitat

The total area of fishing footprint spanning both FCZ and ABNJ is $36\ 924\ \text{km}^2$ (Figure 4 and Table 4). The total footprint of fished ground in the ABNJ is almost twice as large as the FCZ (23 928 and 12 997 km²). Within each area, the areas of low effort were relatively similar between the ABNJ and FCZ (15 404 and 11 195 km², respectively); however areas of medium and high effort were four times greater and 13 times greater respectively in the ABNJ compared to the FCZ fishing area (Table 4).

The predicted habitat for each VME indicator taxa group within the FCZ is an order of magnitude larger than the predicted habitat in the ABNJ (Table 5). Areas of predicted habitat for the FCZ ranged from 113 850 km² (Pennatulacea) to 179 299 km² (Scleractinia) compared to the ABNJ where predicted VME habitat areas ranged from 12 110 km² (Pennatulacea) to 36 560 km² (Demospongiae) (Table 5). The total fishing footprint area within predicted habitats was relatively similar for both fisheries for Alcyonacea, Scleractinia, Gorgonacea, and Stylasteridae, whilst the fished areas of Pennatulacea in the FCZ (9102 km²) were higher than in the ABNJ (3950 km²), and the fished area for Demospongiae was higher in the ABNJ (17 859 km²) compared to the FCZ (10 266 km²). Because the predicted VME habitats are large in the FCZ compared to ABNJ but the fishing footprint is similar, this means that the percentage fishing footprint of predicted area of VME indicator taxa was concordantly an order of magnitude lower in the FCZ-ranging between 6.45% (Demospongiae) and 9.82% (Stylasteridae)-compared to the ABNJ-32.62% (Pennatulacea) to 61.99% (Stylasteridae).

The fishing effort occurring within predicted VME habitat was examined by comparing the total predicted habitat area for each VME indicator taxa group to the areas of relatively "low", "medium", or "high" effort of fishing (Table 5). There is a proportion of fishing effort that does not overlap with any predicted VME habitats, and this is not included in this analysis. The area of low fishing effort within each predicted VME habitat was similar between areas; in the FCZ, the area ranged from 7918 km² (Pennatulacea) to 10 657 km² (Gorgonacea), and in the ABNJ between 2260 km² (Pennatulacea) and 10 881 km² (Demospongiae). In contrast, the area of medium and high fishing effort in predicted VME habitats in the FCZ was less than half of the areas of medium and high fishing effort in the ABNJ (Table 5), meaning that in terms of percentage area the fishing effort in predicted VME habitat areas was also considerably smaller proportionally in the FCZ compared to the ABNJ.

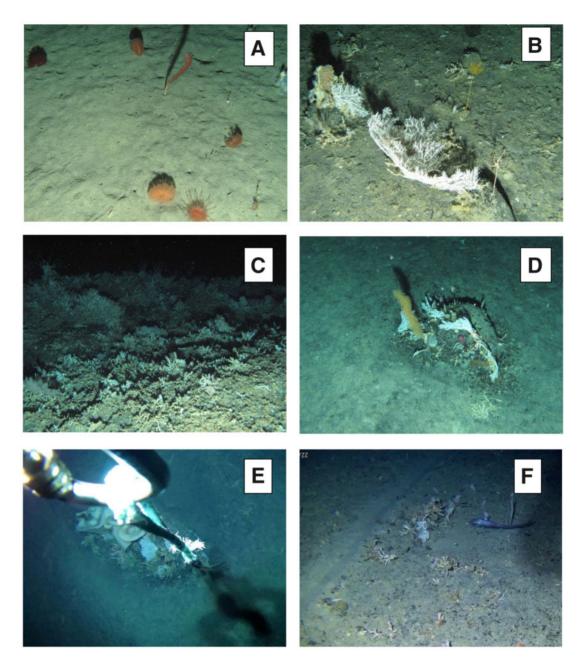


Figure 2. VME indicator taxa examples showing the range of species and patchiness. (a) Soft sediment dominated by sea pens; (b) various coral species and a stalked crinoid; (c) coral reef-like habitat; (d) VME indicator taxa on rock patches; (e) down-line with weight adjacent to rock patch with large sponge; and (f) Soft-gravel sediment showing furrow caused by the dragging of drop weight. Track is \sim 20 cm wide.

Discussion

The predicted habitat distribution of deep-sea VME indicator taxa in the Patagonian Shelf, Southwest Atlantic, spans contiguous habitat straddling the jurisdictional waters of the Falkland Islands and adjacent areas on the high-seas. Associated with these VME habitats are bottom-set longline Patagonian toothfish fisheries where fishing effort within the FCZ is managed whilst on the high-seas, fishing effort is unreported and unregulated by any RFMO/A. The lack of high-seas management in this region has allowed for unrestricted longline fishing effort impacting between 32 and 62% of predicted high-seas VME habitat depending on the taxa (Table 5), compared to between 6 and 9% within the Falklands zone. These data support the growing concern over the lack of suitable management of VMEs in ABNJ areas (e.g. Rowden *et al.*, 2019; Wright *et al.*, 2019). Moreover, this study highlights the case where such pressure on VME habitats is exhibited in areas directly adjacent to managed fisheries, in this case, the Falkland Islands to the west, and CCAMLR to the east, raising concern over the efficacy of fishery and VME management, and the risk of being undermined by adjacent unmanaged but potentially heavily impacted areas. Although such cross-boundary harmonization of fisheries management is considered best-practice

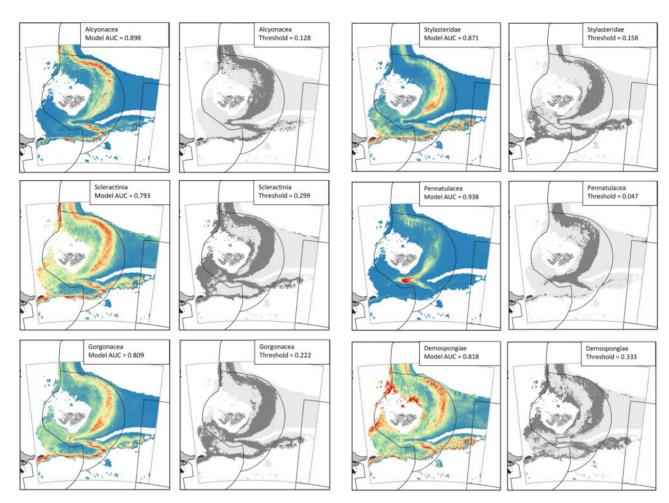


Figure 3. Mapped MaxEnt full model (left) and binary (right) predicted distribution shown, including AUC scores and threshold values. Full model probabilities range between 0 (blue) and 1 (red). Threshold values are either 0 (light grey) or 1 (dark grey). Solid lines are related borders (see Figure 1). Dashed line denotes the model domain.

for targeted fish stocks, little attention has been given to this with respect to VMEs (but see CCAMLR Resolution 10/XII for member State harmonization between the Convention areas and adjacent RMFO/A).

Critical to our analysis is the establishment of a realistic estimate for fishing effort on the ABNJ. Recent work in the Falklands toothfish fishery (Farrugia and Keningale, 2018), as well as in other managed toothfish fisheries (Sharp, 2010; Welsford et al., 2014), has suggested that impact of longline fishing on the seabed may be spatially limited to 10-100 s of metres in the immediate vicinity of the longline. Such detailed analysis is possible in managed fisheries where there is reporting of gear type, effort, lineby-line positional data, scientific observer reports and coordinated research investigations. However, fleets operating in unregulated waters do not have the same statistical or scientific reporting obligations; this makes the use of model/proxy data such as GFW necessary. Although these data have the advantage of being globally available, it is limited in two significant ways. First, although S-AIS is required for all vessels of 300 gross tonnes or larger (which would include bottom-set toothfish longline vessels) as part of the International Maritime Organization (IMO) Safety of Life At Sea Treaty (SOLAS Treaty, Chapter V, www.imo. org), enforcement of this requirement is highly variable among organizations or Flag States (Dunn *et al.*, 2018). This is particularly true in ABNJs, meaning that GFW data may be somewhat conservative in its estimates of fishing effort. Other errors may include signal loss due to signal traffic, or gaps in the record due to satellite over-pass times. In terms of GFW data itself, although error rates for GFW predictions are low (Kroodsma *et al.*, 2018), data used for specific fisheries should be closely examined for real-world accuracy and anomalous predictions. In the present study, systematic misclassifications were found related to the detection of either benthic or pelagic longlines, and longline vessels and jigging vessels. In the Patagonian Shelf region, these are easily accounted for by examining vessel Flag, as well as region being fished (i.e. the combined constraints of bathymetric distribution of targeted toothfish and territorial boundaries).

Second, our method assumes that fishing gear used on the highs-seas is similarly configured and deployed to vessels in the FCZ. A like-for-like metric of fishing effort was established in this study for licenced fishing within the FCZ. However, the assumption that all vessels in the ABNJ are using trotline systems, set at similar line lengths, deployed by vessels of similar capacity, and with similar judgements for choice of fishing area as vessels in the FCZ may be at best, only partly correct. Indeed, "Spanish line" and "auto-line" longline systems are commonly used elsewhere

Table 3. Relative contributions (%) of the environmental variable	es to predicted habitat suitability of each VME group.
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Variable	Alcyonacea	Scleractinia	Gorgonacea	Stylasteridae	Demospongiae	Pennatulacea	
Bathymetry	22	34	46.8	26	14.9	43.8	
Slope	4.4	4.6	6.3	1.3	0.5	0.2	
BPI—broad	1.7	0.4	3	3.5	4.3	0.1	
BPI—fine	-	-	_	-	-	-	
TRI	8.5	1.2	0.4	2.5	0.8	-	
Aspect—northness	7.7	2.9	1.3	0.8	5.4	0.4	
Aspect—eastness	1	0.7	1.1	1.9	4.5	0.3	
Curvature—general	-	-	_	0.5	0.1	-	
Curvature—planar	0.4	-	_	1	-	-	
Curvature—profile	-	-	_	-	-	-	
Carbonates	0.2	3.3	3.1	11.5	2.4	3.1	
Sand: gravel	1.2	0.1	0.5	1.5	11.4	0.2	
Sand: mud	0.7	1.1	1.5	2.9	1.8	1	
SS Chl_a mean	2.5	4	3.1	1.8	8.5	0.1	
SS Chl_a C.V.	1.3	4.8	1.7	5	2.4	0.7	
Seabed Temp mean	0.4	1	1.6	1.1	3.4	0.3	
Seabed Temp C.V.	0.7	0.6	0.7	0.3	0.2	0.3	
Seabed salinity mean	2.6	1.5	0.7	0.2	1.2	0.6	
Seabed salinity C.V.	6.6	4.9	5.6	1.1	4.6	27.4	
Seabed density mean	-	-	-	-	-	-	
Seabed density C.V.	0.2	0.3	8.3	7.1	0.3	0.1	
Seabed current speed mean	4.3	3.7	1.7	2.7	7.3	0.1	
Seabed current speed C.V.	2.8	3.5	2.2	3.3	5.4	0.1	
Aragonite	-	3	2.8	7.8	-	-	
Alkalinity	30.7	24.4	7.4	13.5	20.7	21.4	

(Collins et al., 2010). Trotline and Spanish line systems are similar in that they may have limited contact with the seabed with only drop-line weights meeting the seabed (although this is unlikely), whilst auto-line systems may completely lie on the seabed, and there are other variations of these gear configurations presently used in the fishery. This suggests that our estimates of exposure to the high-seas seabed are likely to be more uncertain and conservative. This, in addition to the conservative estimate of impact due to the unknown factor of S-AIS data being activated or not in the ABNJ, our overall estimate of potential impact is likely to be highly conservative. A more detailed examination of the relative impact of different longline gear types would be useful for better understanding the impacts of longline fishing on VMEs particularly in areas where mixed gear types are used (e.g. CCAMLR waters) as is most likely the case in the ABNJ adjacent to the FCZ.

Predicted habitat suitability maps suggest that most taxa groups are distributed widely through much of the FCZ (Figure 3) and demonstrate continuity of such habitat into ABNJ. Equally, locations of individual samples (Figure 1) can be found across a range of habitat suitability probabilities. Predicted distributions of VME indicator taxa varied in their distribution, ranging from very widely distributed (e.g. Demospongiae) to relatively narrow distributions (e.g. Pennatulacea). Noting that in the present study taxa examined have been grouped (i.e. not examined at the species level), predicted distribution may be reflective of the aggregated niche envelope of the group. For example, the Demospongiae can occupy relatively diverse habitats (e.g. soft and hard substrates) and have varied morphologies (e.g. erect or encrusting), which may have an impact on predicted distributions (e.g. Rooper et al., 2017). In contrast, the Pennatulacea (sea pens) showed a narrow predicted distribution with highest habitat suitability probability somewhat restricted the North-western flank of the Burdwood Bank. Sea pens are the only Octocorallia adapted for life on soft muddy or sandy sediments (Greathead *et al.*, 2014), suggesting a narrow niche envelope and consequently, aggregating these species into a taxa group may have less impact on habitat prediction. In the case of sea pens, results here suggest that further investigation into sea pen biology and ecology in the Falklands is warranted given the recognized importance of sea pens as indicators of vulnerable habitat (OSPAR, 2010) as well as potentially providing a significant ecological role in supporting biodiversity and fisheries (Greathead *et al.*, 2014). In general, a detailed examination of, for example response curves (Supplementary material S2) and improved species identification, would better elucidate the physical/biological drivers and better define the fundamental niche envelope for each group/species (e.g., Davies and Guinotte, 2011).

Whilst model performance was found to be relatively good (as assessed by the AUC model fit score), predicted habitat could be further constrained (and model fit improved) through improved taxonomic resolution of species identification as well as extending sampling throughout the model domain; AUC scores can be lower when presence data do not span the full spatial extent of the region of interest (Fourcade et al., 2014), and this may be the case in the present study. In addition, resolution of predictor variables can have an impact on predicted habitat distribution. For example, Ross and Howell (2012) suggested that the coarse resolution of GEBCO (www.gebco.net) bathymetry used in their study was likely to have produced an overestimation of habitat distribution in the NE Atlantic deep-sea VMEs. Similarly, in the present study, limited benthic video evidence revealed significant patchiness of hard substrates (Figure 2) that may not be well resolved in seabed sediment and terrain metrics; such patchiness would likely impact the true VME taxa distribution and density in the case of encrusting taxa such as the Gorgonacea or

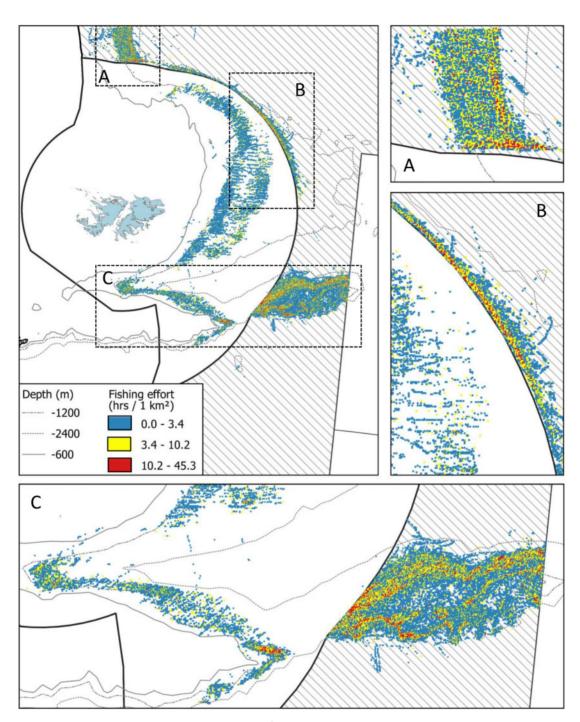


Figure 4. Fishing effort within the FCZ and in ABNJ areas (hrs/km²) using GFW effort data (2012–2016). Also, shown are the 600- and 2400- m depth contours, the FCZ and CCAMLR borders, and ABNJ (shaded) for reference.

Table 4. Footprint area (km^2) of toothfish fishing effort categorised as low, medium, and high intensity effort for each fishing zone.

Effort category	FCZ	ABNJ	Total
Total footprint	12 997	23 928	36 925
Low effort	11 195	15 404	26 599
Med effort	1 665	6 737	8 401
High effort	137	1 788	1 925

Stylasteridae. Higher-resolution empirical data in all predictor variables would facilitate better sensitivity testing of threshold values when producing binary prediction maps for management decision-making (Merow *et al.*, 2013). Anderson *et al.* (2016a) highlight further that limitations on data precision of predictor variables, missing predictor variables, lack of true absence data, and spatial bias (as noted above) will limit model quality and that interpretation of model results should be made with an *a priori*

Table 5. Total predicted habitat area for taxa groups compared to total fishery footprint, and areas of low, medium, and high fishing effort in terms of area (km²) and percentage of predicted habitat area.

VME group	Predicted habitat area (km²)	Fishery footprint within predicted habitat (km²)	Footprint as % of predicted habitat	Low effort fishing area (km²)	Low effort fishing as % of predicted habitat	Medium effort fishing area (km²)	Medium effort fishing as % of predicted habitat	High effort fishing area (km²)	High effort fishing as % of predicted habitat
Footprint in the FC	Z								
Alcyonacea	140 814	11 212	7.96	9 687	6.88	1 404	1.00	121	0.09
Scleractinia	179 299	12 001	6.69	10 335	5.76	1 540	0.86	126	0.07
Gorgonacea	155 834	12 374	7.94	10 657	6.84	1 591	1.02	127	0.08
Stylasteridae	115 328	11 329	9.82	9 838	8.53	1 372	1.19	119	0.10
Pennatulacea	113 850	9 102	7.99	7 918	6.96	1 097	0.96	87	0.08
Demospongiae	159 248	10 266	6.45	8 852	5.56	1 296	0.81	118	0.07
Footprint in the Al	BNJ								
Alcyonacea	18 080	7 882	43.59	4 853	26.84	2 400	13.27	629	3.48
Scleractinia	26 599	12 676	47.66	7 452	28.02	4 118	15.48	1 106	4.16
Gorgonacea	24 450	13 667	55.90	7 889	32.26	4 520	18.49	1 258	5.14
Stylasteridae	23 496	14 565	61.99	8 602	36.61	4 688	19.95	1 276	5.43
Pennatulacea	12 110	3 950	32.62	2 260	18.66	1 348	11.13	342	2.82
Demospongiae	36 560	17 859	48.85	10 881	29.76	5 492	15.02	1 486	4.06

understanding of appropriate spatial scales. At least some of these may be limiting interpretation in the present study. However, given that VME indicator taxa were examined in terms of their grouping rather that at the species level, overall predictions of VME taxa distribution are likely to be highly conservative with respect to estimating niche envelope, albeit accepting some underperformance that may have arisen due to biases introduced when assuming wide-niche space (Guillaumot *et al.*, 2018). Finally, as with all SDMs, various model assumptions can offer their own intrinsic biases to model output; future modelling efforts in the South Atlantic should consider ensemble approaches (Robert *et al.*, 2016; Rowden *et al.*, 2019).

The discontinuity of management of VMEs across the region found here may have consequences for the resilience and/or recovery of local VME taxa populations (Thrush et al., 2013), particularly as it relates to impacts on local recruitment rates as well as import/export of recruits throughout the region. VME taxa metacommunities are maintained by the way of intra- and interspecies ecological processes of competition and predation, as well as local and regional physical processes of oceanographic currents, forcings, and water structures that modulate larval dispersal connectivity (e.g. Kenchington et al., 2019). For example, meanfield flow south of the Patagonian Shelf is characterized by eastward flow along the Burdwood Bank and North Scotia Ridge, with a northward branch crossing the North Scotia Ridge onto to the eastern Patagonian Shelf (Figure 1) forming the Falklands Current (Arhan et al., 2002). Broadly speaking, this would suggest that VME taxa populations in the west may act as sources of recruits supporting resilience/recovery of more eastern and northern populations of species with dispersive larvae. VME taxa assemblages in the ABNJ may be supported by those found in the FCZ and further west but could have reduced resilience/recovery potential to the east of the ABNJ (e.g., in CCAMLR waters). There is relatively poor knowledge of the reproductive and larval biology, and dispersal potential of deep-sea VME species (Watling et al., 2011; Hilário et al., 2015) critical to understanding scales of species' dispersal (Kinlan *et al.*, 2005). In the absence of knowledge of true local recruitment processes or regional dispersal dynamics of VME taxa, and assuming that deep-sea VME assemblages have limited recovery potential (Clark *et al.*, 2016), precautionary management strategies based on predicted habitat distributions will mitigate potential impacts of longline fishing and promote post-impact recovery of VMEs in managed and ABNJ fisheries. Future modelling of VME taxa distribution could be enhanced by integrating such ecological processes in the prediction algorithm where possible (Staniczenko *et al.*, 2017).

Conclusion

We show that predicted habitats of VME indicator taxa "straddle" across management regimes, similar to straddling fish stocks. However, whereas in the case of straddling fish stocks where stock management is ideally harmonized between management areas, our understanding of the effects of discontinuous management of VMEs across such spatial extents is much less clear. There is an urgent need for the better understanding of VME indicator taxa distributions and the impacts of fishing when VME habitats cross contrasting management and conservation regimes; in the absence of such knowledge, then interim precautionary management measures should be introduced. Whilst recent work has highlighted improvement in fisheries management in some areas (Worm et al., 2009; Halpern et al., 2015; Amoroso et al., 2018), unregulated ABNJ fishing may undermine such initiatives. New ABNJ conservation initiatives such as the high-seas treaty targeting Biodiversity Beyond National Jurisdictions (BBNJ) (UNGA, 2015) may require such harmonisation for VMEs. Knowledge gaps could be reduced significantly through the establishment of an RFMO/A-styled multilateral agreement in ABNJ where none currently exist. A regional, cohesive view of VME distribution and fishing impact can then be gained through regulated scientific and industry reporting of effort, and regulated use of electronic vessel monitoring (e.g. S-AIS) that can then be used by managers and policymakers (Ardron *et al.*, 2014; Wright *et al.*, 2019) to aid the development of area-based management tools (ABMT) in contiguous managed and ABNJ fishery areas.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Author's contribution

PEB, TJF, and PB conceived the original concepts of this study; PEB designed the methodology; PEB and TJF collected the data; PEB analysed the data; CJ developed the sediment modelling and data analysis; PEB led the writing of the manuscript. All authors contributed critically to original text and drafts and gave the final approval for publication.

Data archiving

All Falkland Islands Government data used in this article are available through the South Atlantic Environmental Research Institute (SAERI) IMG-GIS Data Centre. Data request forms and data management policies can be found through the website https://www.south-atlantic-research.org/research/data-science. All other data are publicly available and web-distributed through cited institutions.

References

- Amoroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., Eigaard, O. R., *et al.* 2018.
 Bottom trawl fishing footprints on the world's continental shelves.
 Proceedings of the National Academy of Sciences of the United States of America, 115: E10275–E10282.
- Anderson, O. F., Guinotte, J. M., Rowden, A. A., Clark, M. R., Mormede, S., Davies, A. J., and Bowden, D. A. 2016a. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: implications for the use of broad-scale models in fisheries management. Ocean & Coastal Management, 120: 110–126.
- Anderson, O. F., Guinotte, J. M., Rowden, A. A., Tracey, D. M., Mackay, K. A., and Clark, M. R. 2016b. Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. Deep-Sea Research I, 115: 265–292.
- Ardron, J. A., Clark, M. R., Penney, A. J., Hourigan, T. F., Rowden, A. A., Dunstan, P. K., Watling, L., *et al.* 2014. A systematic approach towards the identification and protection of vulnerable marine ecosystems. Marine Policy, 49: 146–154.
- Arhan, M., Naveira Garabato, A. C., Heywood, K. J., and Stevens, D. P. 2002. The Antarctic Circumpolar Current between the Falkland Islands and South Georgia. Journal of Physical Oceanography, 32: 1914–1931.
- Borja, A., Elliott, M., Snelgrove, P. V. R., Austen, M. C., Berg, T., Cochrane, S., Carstensen, J., et al. 2016. Bridging the gap between

policy and science in assessing the health status of marine ecosystems. Frontiers in Marine Science, 3: 175.

- Brown, J., Brickle, P., Hearne, S., and French, G. 2010. An experimental investigation of the 'umbrella' and Spanish' system of longline fishing for the Patagonian toothfish (*Dissostichus eleginoides*) in the Falkland Islands: implications for stock assessment and seabird by-catch. Fisheries Research, 106: 404–412.
- Clark, M. R., Althaus, F., Schlacher, T. A., Williams, A., Bowden, D. A., and Rowden, A. A. 2016. The impacts of deep-sea fisheries on benthic communities: a review. ICES Journal of Marine Science, 73: i51–i69.
- Clark, M. R., Tittensor, D., Rogers, A. D., Brewin, P., Schlacher, T., Rowden, A., and Stocks, K. 2006. Seamounts, Deep-Sea Corals and Fisheries: Vulnerability of Deep-Sea Corals to Fishing on Seamounts beyond Areas of National Jurisdiction. UNEP-WCMC, Cambridge, UK.
- Collins, M. A., Brickle, P., Brown, J., and Belchier, M. 2010. The Patagonian toothfish: biology, ecology and fishery. Advances in Marine Biology, 58: 227–300.
- Davies, A. J., and Guinotte, J. M. 2011. Global habitat suitability for framework-forming cold-water corals. PLoS One, 6: e18483.
- Dunn, D. C., Jablonicky, C., Crespo, G. O., McCauley, D. J., Kroodsma, D. A., Boerder, K., Gjerde, K. M., *et al.* 2018. Empowering high seas governance with satellite vessel tracking data. Fish and Fisheries, 19: 729–739.
- EC. 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union, 164: 19–40. http://data.europa.eu/eli/dir/2008/56/oj (last accessed 26 June 2020).
- FAO. 2008. International Guidelines for the Management of Deep-Sea Fisheries in the High-Seas. Food and Agriculture Organization of the United Nations. Adopted in Rome, Italy on 29 August 2008.
- FAO. 2016. Vulnerable Marine Ecosystems: Processes and Practices in the High Seas. Ed. by A. Thompson, J. Sanders, M. Tandstad, F. Carocci and J. Fuller. FAO Fisheries and Aquaculture Technical Paper 595. Rome, Italy.
- Farrugia, T. J., Goyot, L., and Kuepfer, A. 2018. Scientific Report, Fisheries Cruise ZDLK3-11-2018. Fisheries Department, Directorate of Natural Resources, Falkland Islands Government, Stanley, Falkland Islands.
- Farrugia, T. J., and Keningale, B. 2018. Scientific Report, Fisheries Cruise ZDLK3-02-2018. Fisheries Department, Directorate of Natural Resources, Falkland Islands Government, Stanley, Falkland Islands.
- Fourcade, Y., Engler, J. O., Rödder, D., and Secondi, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS One, 9: e97122.
- Guillaumot, C., Martin, A., Eléaume, M., and Saucède, T. 2018. Methods for improving species distribution models in data-poor areas: example of sub-Antarctic benthic species on the Kerguelen Plateau. Marine Ecology Progress Series, 594: 149–164.
- Greathead, C., González-Irusta, J. M., Clarke, J., Boulcott, P., Blackadder, L., Weetman, A., and Wright, P. J. 2014. Environmental requirements for three sea pen species: relevance to distribution and conservation. ICES Journal of Marine Science, 72: 576–586.
- Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S., *et al.* 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6: 7615.
- Halvorsen, R. 2013. A maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. Sommerfeltia, 36: 1–132.

- Henry, L.-A., and Roberts, J. M. 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight. NE Atlantic. Deep-Sea Res I, 54: 654–672.
- Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp, A. D., *et al.* 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proceedings of the National Academy of Sciences of the United of America, 114: 8301–8306. doi/10.1073/pnas. 1618858114.
- Hilário, A., Metaxas, A., Gaudron, S. M., Howell, K. L., Mercier, A., Mestre, N. C., Ross, R. E., *et al.* 2015. Estimating dispersal distances in the deep sea: challenges and application to marine reserves. Frontiers in Marine Science, 2: 1–14.
- Hogg, O. T., Huvenne, V., Griffiths, H. J., Dorschel, B., and Linse, K. 2016. Landscape mapping at sub-Antarctic South Georgia provides a protocol for underpinning large-scale marine protected areas. Scientific Reports, 6, doi 10.1038/srep33163
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos, 86: 393–401.
- Jenkins, C.J. 2019. dbSEABED: Information Integration System for Marine Substrates. http://instaar.colorado.edu/~jenkinsc/dbseabed (last accessed 29 June 2020).
- Kenchington, E., Wang, Z., Lirette, C., Murillo, F. J., Guijarro, J., Yashayaev, I., and Maldonado, M. 2019. Connectivity modelling of areas closed to protect vulnerable marine ecosystems in the northwest Atlantic. Deep Sea Research Part I, 143: 85–103.
- Kinlan, B. P., Gaines, S. D., and Lester, S. E. 2005. Propagule dispersal and the scales of marine community process. Diversity and Distributions, 11: 139–148.
- Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., *et al.* 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions, 19: 1366–1379.
- Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., Wilson, A., *et al.* 2018. Tracking the global footprint of fisheries. Science, 359: 904–908.
- Lauvset, S. K., Key, R. M., Olsen, A., van Heuven, S., Velo, A., Lin, X., Schirnick, C., .. 2016. A new global interior ocean mapped climatology: the $1^{\circ} \times 1^{\circ}$ GLODAP version 2. Earth System Science Data, 8: 325–340.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., *et al.* 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7: 601–613.
- Leichter, J. J., and Witman, J. D. 2009. Chapter 8. Basin-scale oceanographic influences on marine macroecolgical patterns. *In* Marine Macrecology, pp. 205–226. Ed. by J. D. Witman and K. Roy. University of Chicago Press, London. 442 pp.
- Liu, C., Berry, P. M., Dawson, T. P., and Pearson, R. G. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography, 28: 385–393.
- Marrari, M., Piola, A. R., and Valla, D. 2017. Variability and 20-year trends in satellite-derived surface chlorophyll concentrations in large marine ecosystems around south and western Central America. Frontiers in Marine Science, 4: 372.
- Mazloff, M. R., Heimbach, P., and Wunsch, C. 2010. An Eddy-Permitting Southern Ocean State Estimate. Journal of Physical Oceanography, 40: 880–899.
- Merow, C., Smith, M. J., and Silander, J. A. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography, 36: 1058–1069.
- Muñoz, P. D., Murillo, F. J., Sayago-Gil, M., Serrano, A., Laporta, M., Otero, I., and Gómez, C. 2011. Effects of deep-sea bottom

longlining on the Hatton Bank fish communities and benthic ecosystem, north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom, 91: 939–952.

- OSPAR. 2010. Background Document for Sea Pen and Burrowing Megafauna Communities. Biological Diversity and Ecosystems Series 481/2010. OSPAR Commission. https://qsr2010.ospar.org/ media/assessments/Species/P00481_Seapen_and_burrowing_ megafauna.pdf.
- Parker, S. J., and Bowden, D. A. 2010. Identifying taxonomic groups vulnerable to bottom longline fishing gear in the Ross Sea region. CCAMLR Science, 17: 105–127.
- Pham, C. K., Diogo, H., Menezes, G., Porteiro, F., Braga-Henriques, A., Vandeperre, F., and Morato, T. 2014. Deep-water longline fishing has reduced impact on Vulnerable Marine Ecosystems. Scientific Reports, 4: 4837.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. 2006. Maximum entropy modelling of species geographic distributions. Ecolological Modelling, 190: 231–259.
- Phillips, S. J., and Dudík, M. 2008. Modeling of species distribution with Maxent: new extensions and a comprehensive evaluation. Ecography, 31: 161–175.
- Robert, K., Jones, D. O. B., Roberts, J. M., and Huvenne, V. A. I. 2016. Improving predictive mapping of deep-water habitats: considering multiple model outputs and ensemble techniques. Deep Sea Research Part I, 113: 80–89.
- Roberts, C. M. 2002. Deep impact: the rising toll of fishing in the deep sea. Trends in Ecology & Evolution, 17: 242–245.
- Roberts, J. M., Wheeler, A. J., and Freiwald, A. 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science, 312: 543–547.
- Rogers, A. D., Baco, A., Griffiths, H., and Hall-Spencer, J. M. 2007. Corals on seamounts. *In* Seamounts: Ecology, Fisheries and Conservation, pp. 141–169. Ed. by T. J. Pitcher, T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan and R. S. Santos. Blackwell Publishing, Oxford.
- Rooper, C. N., Etnoyer, P. J., Stierhoff, K. L., and Olson, J. V. 2017. Effects of fishing gear on deep-sea corals and sponges in U.S. waters. *In* State of Deep-Sea Coral and Sponge Ecosystems of the United States. Ed. by T. F. Hourigan, P. J. Etnoyer and S. D. Cairns. NOAA Technical Memorandum NMFS-OHC-4, Silver Spring, MD.
- Ross, R. E., and Howell, K. L. 2012. Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. Diversity and Distributions, 19: 433–413.
- Rowden, A. A., Stephenson, F., Clark, M. R., Anderson, O. F., Guinotte, J. M., Baird, S. J., Roux, M.-J., *et al.* 2019. Examining the utility of a decision-support tool to develop spatial management options for the protection of vulnerable marine ecosystems on the high seas around New Zealand. Ocean and Coastal Management, 170: 1–6.
- Schejter, L., Rimondino, C., Chiesa, I., Díaz de Astarloa, J. M., Doti, B., Elías, R., Escolar, M., *et al.* 2016. Namuncurá Marine Protected Area: an oceanic hot spot of benthic biodiversity at Burdwood Bank, Argentina. Polar Biology, 39: 2373–2386.
- Sharp, B. R. 2010. Revised Impact Assessment Framework to Estimate the Cumulative Footprint and Impact on VME Taxa of New Zealand Bottom Longline Fisheries in the Ross Sea Region. WG-SAM-10/20. CCAMLR. 22 p. https://www.ccamlr.org/en/wgsam-10/20.
- Sharp, B. R., Parker, S. J., and Smith, N. 2009. An impact assessment framework for bottom fishing methods in the CAMLR Convention area. CCAMLR Science, 16: 195–210.
- Staniczenko, P. P. A., Sivasubramaniam, P., Suttle, K. B., and Pearson, R. G. 2017. Linking macroecology and community

ecology: refining predictions of species distributions using biotic interaction networks. Ecology Letters, 20: 693–707. doi: 10.1111/ele.12770.

- Thrush, S. F., Hewitt, J. E., Lohrer, A. M., and Chiaroni, L. D. 2013. When small changes matter: the role of cross-scale interactions between habitat and ecological connectivity in recovery. Ecological Applications, 23: 226–238.
- Tittensor, D. P., Baco, A. R., Brewin, P. E., Clark, M. R., Consalvey, M., Hall-Spencer, J., Rowden, A. A., *et al.* 2009. Predicting global habitat suitability for stony corals on seamounts. Journal of Biogeography, 36: 1111–1128.
- UNGA. 2007. Resolution 61/105 Sustainable fisheries, Including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 Relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, and Related Instruments. UNGA A/RES/61/105. 21 pp.
- UNGA. 2015. Resolution 69/292 Development of an International Legally Binding Instrument under the United Nations Convention on the Law of the Sea on the Conservation and Sustainable Use of Marine Biological Diversity of Areas beyond National Jurisdiction. UNGA A/RES/69/292. 3 pp.

- Watling, L., and Auster, P. J. 2017. Seamounts on the high seas should be managed as vulnerable marine ecosystems. Frontiers in Marine Science, 4: 14.
- Watling, L., France, S. C., Pante, E., and Simpson, A. 2011. Biology of deep-water octocorals. Advances in Marine Biology, 60: 42–122.
- Welsford, D. C., Ewing, G. P., Constable, A. J., Hibberd, T., and Kilpatrick, R. 2014. An Assessment of the Vulnerability of Benthic Habitats to Impact by Demersal Gears. FRDC project 2006/042. The Department of the Environment, Australian Antarctic Division and the Fisheries Research and Development Corporation. 266 pp.
- Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., and Grehan, A., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy, 30: 3–35.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding global fisheries. Science, 325: 578–585.
- Wright, G., Gjerde, K. M., Johnson, D. E., Finkelstein, A., Ferreira, M. A., Dunn, D. C., Chaves, M. R., *et al.* 2019. Marine spatial planning in areas beyond national jurisdiction. Marine Policy, in press, doi.org/10.1016/j.marpol.2018.12.003.

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