**Global Change Biology (8000 word limit, main body text)**

**Research Article**

**Changes in fish community structure in the Southern Ocean can be related to climate change and fisheries management**

**Fish community change in the Southern Ocean**

Joel Williams1 | Nicole Hill1 | Scott Foster2 | Skip Woolley3 | Philippe Ziegler4 | Cara Masere4 | Kerrie Swadling1 | Kaitlin Naughton5 | Otso Ovaskainen6,7 | Craig Johnson1

1Institute for Marine and Antarctic Science, University of Tasmania, Hobart, Tasmania, Australia

2Data61, CSIRO, Hobart, Tasmania, Australia

3 Environment, CSIRO, Hobart, Tasmania, Australia

4Australian Antarctic Division, Kingston, Tasmania, Australia

5British Antarctic Survey, Cambridge, United Kingdom

6Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (Survontie 9C), FI-40014 Jyväskylä, Finland

7Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Helsinki 00014, Finland

**Correspondence**

Joel Williams, Institute for Marine and Antarctic Science, University of Tasmania, 20 Castray Esplanade, Battery Point, Tasmania, Australia.

Email: joel.williams@utas.edu.au

**Funding information**

Australian Antarctic Science Program (Project No. 4501).

**Abstract**

Heard Island and McDonald Island are located within the northern half of the Kerguelen Plateau in the Southern Ocean. The Kerguelen Plateau is a biodiversity hotspot with many endemic fish species and the region has economic importance as it supports large fisheries. This region is also a climate change hotspot; water temperatures and oceans currents are changing and shifting. Most existing information on fish species and their distribution in this region is derived from annual random trawl surveys, fishery observations, and indirectly from research on fish predators. In this study we use trawl survey data and contemporary joint species distribution models to understand how the fish assemblages have changed through time and space. Using a hierarchical model of species community approach, we demonstrate that several species, including mackerel icefish, have had substantial changes in distribution and abundance through time and these changes could be related to environmental factors such as SST anomaly and southern annular mode. We found evidence of several species’ distributions responding to temperature variability and these species are potentially exposed to the ongoing impacts of climate change. This added information can be used by managers and policy makers to ensure sustainable fisheries and the protection of biodiversity into the future.

KEYWORDS

Joint species distribution, fish assemblage, marine park, trawl survey, climate change, fisheries management, ocean

# 1 | INTRODUCTION

The world’s oceans and their ecosystems are changing due to accumulating anthropogenic pressures such as climate change, extractive activities (fishing, mining etc), and pollution (litter, land runoff, etc.) (Coll et al., 2008; Cooley et al., 2022; Hoegh-Guldberg & Bruno, 2010; Jennings & Kaiser, 1998; Pauly et al., 2005). Over exploitation of a single species or degradation of a habitat can have dire consequence at the ecosystem level (Coll et al., 2008; Jackson et al., 2001; Pauly et al., 1998; Worm et al., 2006). The responses and strategies for managing and safeguarading the world’s oceans include adoption of marine protected areas, more sustainable fishing policies and practices, and reducing land-based pollution and runoff.(Brodie et al., 2012; Edgar et al., 2014; Eigaard et al., 2014; J. E. Johnson & Welch, 2009). Many of these policy decisions are targeted at specific regions or fisheries. For example, changes in fisheries management have led to recovery of Australian Orange Roughy stocks and the fishery becoming sustainable (Doonan et al., 2015; Kloser et al., 2015), and marine protected areas in New Zealand and Australia have demonstrated increases in fish abundance and biodiversity (Allard et al., 2022; Edgar et al., 2014, 2017; Knott et al., 2021).

Climate change adds another layer of complexity and uncertainty. Global ocean water temperatures are warming or cooling, pH is altering, CO2 sequestration is changing, ocean currents are shifting direction and intensity, and the timing and quantity of sea ice melt is changing, all of which is resulting in ecosystem level impacts (Boyd et al., 2016; Constable et al., 2014; C. R. Johnson et al., 2011; Wassmann et al., 2011). The changing oceans are resulting in substantial shifts in species’ distributions and relative abundances, often manifest as range extensions or contractions (C. R. Johnson et al., 2011; Schickele et al., 2021). Understanding how these pressures and climate influence a species or whole communities is important to aid adaptive management, monitoring programs, and identify areas that require protection or greater management to avoid further loss (Arafeh-Dalmau et al., 2021; Emblemsvåg et al., 2022).

The Southern Ocean represents approximately 10% of the world’s oceans and it plays a significant role in global primary production, the export of nutrients and oxygen to the world’s oceans, and supports valuable biodiversity (Auger et al., 2021; Constable et al., 2014; Le Quéré et al., 2007; Van de Putte et al., 2021). However, analysis of various properties of the Southern Ocean, such as water temperature, CO2 sequestration, and ocean currents reveal that there are large scale changes taking place (Constable et al., 2014; Van de Putte et al., 2021). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) have acknowledged the need to better incorporate the effects of climate change into decisions on resource, biodiversity, and ecosystem management in the Southern Ocean (Cresswell et al., 2021).

The biodiversity of the Southern Ocean is unique and characterised by a high level of endemism in fish species (Constable et al., 2014), notably the suborder Notothenioids of which 86% of species are endemic to this region (Eastman & McCune, 2000). This group of fishes is also the most abundant on the shelf regions of the Antarctic continent as well as both Antarctic and Subantarctic Islands such as Heard Island and McDonald Islands (HIMI). Temporal changes in Southern Ocean benthic fish composition, distribution, and abundance are mostly unknown (Subramaniam, Melbourne-Thomas, et al., 2020). It is expected that southward shifting ocean frontal systems are likely to have the largest influence on species distributions. However, interpretations of changes in distribution and abundance of fish communities need to be cautious given the confounding effects of fishing and fisheries management as well as environmental change.

A valuable approach to understanding these environmental processes and ecological change is to explore trends and patterns within robust long-term data sets. Oceanographic data has been collected over large spatial scales for decades (e.g. NOAA). However, long term (>10 years) biological monitoring or ecological datasets (i.e. species’ occurrence and abundance data), while critical for detecting ecological changes, are relatively rare. In the era of big data, increased computing capacity and innovative approaches to ecological modelling, researcher’s abilities to ask more complex questions and to model at larger spatial and temporal scales had become increasingly possible (Franklin et al., 2017; Tikhonov, Duan, et al., 2020). Furthermore, quantitative methods have developed from single species approaches to methodologies which consider whole species assemblage data across large spatial scales using approaches such as joint species distribution models (Norberg et al., 2019; Ovaskainen et al., 2017; Tikhonov, Duan, et al., 2020). These modelling approaches allow ecologists to explore correlations across environmental gradients and produce full-coverage ecological maps for each species as well as community attributes such as species richness. These kinds of statistical techniques also enable future predictions under different scenarios (Evans, 2012).

The Kerguelen Plateau, located halfway between South Africa and Australia in the Indian Ocean sector of the Southern Ocean, is a dominant geographic feature (Duhamel & Welsford, 2011). The Plateau is a productivity hotspot, supporting a diversity of marine life as well as a lucrative demersal fishery, primarily for Patagonian toothfish (*Dissostichus eleginoides*) (Duhamel & Welsford, 2011; Hill et al., 2017). Both the location and geography of the Kerguelen Plateau means it is highly exposed to the effects of climate change through warming waters and changing ocean currents and polar fronts. Knowledge and information on how climate change is influencing the ecosystem is important for the management and conservation of biodiversity and for managers to meet the obligations of the CCAMLR convention. It is also necessary for fisheries’ agencies, such as the Australian Fisheries Management Authority (AFMA), to ensure adherence to ecosystem-based management practices.

The management of this region is split with France managing the northern half of the Plateau and Australian managing the central portion of the Plateau. [talk more formally about the AU and FR EEZs?] Australia has an exclusive economic zone that encompasses Heard Island and McDonald Island (HIMI). The uniqueness and ecological importance of HIMI has global recognition through a World Heritage listing in 1997 and the formation of a no-take marine reserve in 2002 which was subsequently expanded in 2014. Scientific research on fish species in the HIMI EEZ have been strongly linked to species of commercial importance as well as those with fisheries’ bycatch limits. However, there are notable gaps in understanding of the composition and structure of fish assemblages along with knowledge about how these communities may have changed through time (Hill et al., 2017). Within the Australian EEZ, Patagonian toothfish and mackerel icefish are the two targeted fisheries species of the Kerguelen Plateau. The fishery started as trawl fishery in the 1990s but a change to long-line fishing started in 2003 to maximise catches of Patagonian toothfish while minimising bycatch (Welsford et al., 2011). There is still some trawling effort to target mackerel icefish. Historically this region was also exposed to significant illegal fishing. This has led to increase is surveillance of the area since the 1990s.

In the study we aimed to assess whether the benthic fish community of the HIMI region of the Kerguelen Plateau has changed through time. We relate the observed changes in presence/absence and abundance of benthic fishes to environmental change, marine reserve zoning, and changes in fishery management practice. To achieve this, we apply joint species distribution modelling (JSDM). We establish how much of the variation in each species presence/absence and abundance is due to environmental filtering and random process, and how these factors vary across spatial and temporal scales. These models were then used to spatially predict the prevalence and distribution of each species and species richness for each year of the study. These predictions were then compared through time to investigate where and when any change in prevalence and distribution occurred across the study site. The results from this study provide a useful case study and point of comparison for other regions of the Southern Ocean, which will facilitate better understanding of the likely effects of climate change, fisheries management, and conservation management at a much larger scale.

# 2 | METHODS

## 2.1 | Study site

The study area was within the Australian external territory of HIMI on the Kerguelen Plateau in the Subantarctic region of the Indian Ocean (Figure 1). The Plateau rises from depths >3000 m, has steep banks, comprises numerous seamounts, and breaks the surface with three large islands and numerous rocky outcrops. This region is managed and protected by the World Heritage Listed Heard Island and McDonald Island Marine Reserve (Figure 1). This included two areas that are listed as IUCN category 1A marine reserves. HIMI Marine Reserve was established in 2002 and the reserve boundaries were extended in 2014 to encompass a total of 71,000 km2 of ocean. The HIMI region supports valuable fisheries managed by Australia and consistent with the conservation measures of CCAMLR (Constable, 2011). Commercial fisheries primarily target Patagonian Toothfish, *Dissostichus eleginoides*, by long-line fisheries and Mackerel Icefish, *Champsoscephalus gunnari*, by trawl fisheries. Other species, such as Marbled Rockcod, *Notothenia rossii* and Grey Rockcod *Lepidonotothen squamifrons* were historically targeted by trawling and illegal fishing activities (Duhamel & Williams, 2011). The region also supports many long-lived, large, and endemic species that are caught as by-catch.



Figure 1. A bathymetry map of the location of each research trawls from the random stratified trawl survey located on the Kerguelen Plateau. The grey-scaled dots represent the year the sample was collected and is scaled 2003 as white through to 2016 as black. The Heard Island and McDonald Island Marine Reserve boundaries are marked by the red polygons. Inset: Location of the study location on the world map.

## 2.2 | Benthic fish data

Benthic fish data used in the study comes from a long-term, annual scientific survey used for monitoring changes in Patagonian Toothfish, mackerel icefish and other bycatch managed species referred to as the random stratified trawl survey (RSTS). The RSTS provides count data for benthic fish in the HIMI region of the Kerguelen Plateau. The RSTS has been conducted each year since 1997, when the fishery began. The survey design divides the HIMI plateau (waters generally less than 1000 m) into 10 strata defined by regions of similar morphology and commercial fishing effort. Sampling sites are randomly located within each of these strata with a consistent number of stations per stratum every year. The survey design and methodology has remained mostly the same since 1997, with a few minor adjustments.

The RSTS uses an otter beam trawl net with a 500 mm mesh cod end liner, and is towed at a speed of 3 knots (1.5 m/s) for a duration of 30 minutes. Trawling occurs from a fishing vessel and scientific observers record catches using the same observer methods as the fishery. Priority is given to record data on toothfish, icefish, and rays and skates but count and biomass data is available for all other species. [Observer instructions?] Tow duration was relatively consistent however variability in environmental conditions provided some differences in trawl distance (min = 1.3 km, max = 6.4 km, mean = 2.9 km, SD = 0.3 km). Given these differences, for the purposes of modelling, the count estimates are divided by the towed distance to provide catch per unit effort (CPUE) (number of fish per swept area).

## 2.3 | Environmental variables

We selected 15 spatial and environmental variables that could potentially help explain any change in benthic fish prevalence, abundance, and community structure (Table 1). This included data derived from the trawls, combined satellite and multibeam bathymetry data, satellite sea surface temperature, climate indices, and outputs from oceanographic models.

All environmental variables were tested for correlations using Pearsons correlation to ensure pairwise coefficients were <|0.7| to avoid collinearity.

Table 1. Descriptions of covariates used in the hierarchical modelling of species communities (HMSC).

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable name** | **Range** | **Description** | **Source** |
| Depth | 150-1340 m | Depth (m) at location of the research trawl. | RSTS metadata |
| Slope | 0.00 – 0.75 | Slope calculated from the bathymetry data (100m resolution) using the terrain() function in the R raster package | GeoScience Australia |
| Southern annular mode (SAM) | -2.61 – 3.02 |  | <https://psl.noaa.gov/data/20thC_Rean/timeseries/monthly/SAM/> |
| Indian Ocean dipole (IOD) | -0.49 – 0.56 |  | <https://psl.noaa/gov/data/timeseries/DMI> |
| Mean monthly sea surface temp. | 1.0 – 4.5 | The monthly mean optimal interpolation SST. Provided by NOAA at ¼° resolution. The SST data incorporates different platforms, satellites, ships, buoys and argo floats and calculated into regular grids. | NOAA |
| Mean monthly sea surface temp. anomaly | -0.57 – 1.00 | The monthly mean optimal interpolation SST anomaly. Provided by NOAA at ¼° resolution. The SST anomaly is the difference from the 30 year mean and the data incorporates different platforms, satellites, ships, buoys and argo floats and calculated into regular grids. | NOAA |
| Mean monthly sea surface height | -0.78 - -054 | The monthly mean optimal interpolation sea surface height (SSH). Provided by NOAA at ¼° resolution. | NOAA |
| Mean monthly Chlorophyl A | 0.02 – 1.82 |  |  |
| Seafloor water temp. | 0.79 – 2.07 | FESOM | FESOM (Naughten et al., 2018) |
| Seafloor current speed | 0 – 0.06 | FESOM | FESOM (Naughten et al., 2018) |
| Marine reserve status | Fished / No-take | The zoning status for the HIMI Marine Reserve established in 2002. | Australian Antarctic Division. |
| Year | 2003 – 2016 | Fitted as a continuous variable to investigate general trends through time. | RSTS metadata. |

## 2.4 | Statistical analyses

We analysed the RSTS data using Hierarchical Modelling of Species Communities (HMSC) (Ovaskainen et al., 2017; Ovaskainen & Abrego, 2020). HMSC is a joint species distribution model (Warton et al., 2015) that includes a hierarchical layer to assess the extent to which a species response to environmental covariates depends on species-species and species’ traits relationships (Abrego et al., 2017). HMSC also utilizes spatially structured latent variables as proposed by Ovaskainen et al. (2017) and later expanded to big spatial data by Tikhonov et al. (2020) (i.e. >10,000s points). The approach enables investigation of how each individual species responds to the environmental covariates, while also considering species co-occurrences through space.

The RSTS data includes records for 38 fish, shark, and ray species sampled from between 111 and 195 trawl sites annually from 2003 to 2016. We excluded those species that had less than 10 occurrences in the data set, resulting in 35 species ( ). The 2,186 individual trawls were treated as sampling units (. The response variable) was CPUE for each of the 35 species (the matrix of HMSC; see Ovaskainen et al. 2017. Due to the zero-inflated nature of the data, we applied a hurdle model, i.e. one model for presence/absence and another one for abundance conditional on presence (henceforth referred to as the ‘abundance COP’ model). We applied probit regression in the presence-absence model, and linear regression for log transformed count data in the abundance COP model. The count data were transformed by declaring zeros as missing data, log-transforming the remaining data, and then standardising data within each species (*μ* = 0, *σ* = 1).

We included as fixed effects (the matrix **X** of HMSC; see Ovaskainen et al. 2017; where is the number of covariates) 15 variables that could potentially explain the presence and abundance of the benthic fish assemblage through time (Table 1). We used a sample (trawl) level random factor to account for spatially-structured species’ correlations. Due to the large number of samples (>1,000), and the computational overhead in calculating spatially structured correlation using the default spatial HMSC, we implemented a nearest neighbour Gaussian process as per Tikhonov et al (2020). Furthermore, due to the study design and the use of sampling strata, we also included stratum as a random factor. To control for potential temporal correlations we used the numbers of days since the start of the study as a random factor (i.e. 1 January 2003 = 1) for which we assumed exponentially decaying correlation structured with respect to time lag.

We fitted the HMSC model using the R-package Hmsc v3.0-12 (Tikhonov, Opedal, et al., 2020) assuming the default prior distributions (see Chapter 8 of Ovaskainen and Abrego 2020). We sampled the posterior distribution with four Markov chain Monte Carlo (MCMC) chains. The transient was set to omit the first 25,000 samples. The four chains were thinned by 100 to yield 500 posterior samples per chain, generating 2000 posterior samples in total. We checked MCMC convergence by ensuring the mean and standard deviation of the potential scale reduction factors were close to unity for the majority of the model parameters (Gelman & Rubin, 1992).

We examined the explanatory and predictive powers of the probit model through species specific AUC (Pearce & Ferrier, 2000) and Tjur’s R2 values (Tjur, 2009). The explanatory and predictive powers of the abundance COP model were measured by R2. To compute explanatory power, we used the full data-set to fit models. To compute predictive power, we performed 2-fold cross validation, in which the sampling units were assigned randomly to two folds, and prediction for each fold were based on model fitted to data on the remaining fold.

To quantify the drivers of community structure, we partitioned the explained variation among the fixed and random effects included in the model. To address our main study question, i.e. whether and how species communities have changed over the study period, we examined species responses to the explanatory variables, counting the proportion of species that showed a positive or negative response with at least 95% posterior probability.

The presence-absence model was used to make predictions to produce species distribution maps. A predictive grid was generated at 20x20 km resolution across the study area from 200 m to 1,000 m depth, aligning with the depth limits of the RSTS survey. The probability of occurrence as estimated for every grid cell, for every species, for every year. Using these predictions, we generated species distribution rasters. To investigate where the changes in distribution were occurring with the study site, we generated maps by taking the mean probability of occurring across the first and last three years of the study. This was to account for minor inter-annual variability. We then subtracted the values for the two rasters to establish where change had occurred. Using these predictions, we could also estimate species richness at the same spatial and temporal scales. Repeating the mapping process for individual species, we estimated where the greatest change in species richness was occurring.

# 3 | RESULTS

Catch per unit effort (CPUE) data from a total of 2,186 trawls from 2003 to 2016 were used in the HMSC. These data included CPUE data for 35 species, after accounting for the removal of very rare species (observed in < 10 trawls). The 35 species included 29 ray-finned fish and six Chondrichthyes. The species assemblage was dominated by three commercially targeted fishery species, *C. gunnari*, *D. eleginoides*, and *Channichthys rhinoceratus*, that represented >70% of the total CPUE across all years. *D. eleginoides* was the most ubiquitous species being present in 91% of trawls, follow by *C. rhinoceratus* that was present in 56% of trawls.

The MCMC convergence of the presence-absence model was satisfactory; the potential scale reduction factors for the -parameters (that measure the responses of the species to environmental covariates; Ovaskainen et al. 2017 ELE) were on average 1.03 (maximum 1.55) for the presence-absence model and for the abundance COP a mean value of 1.00 (maximum 1.01).

## 3.1 | Species responses

The presence-absence model showed a variable fit to the data, the Tjur R2 values ranged from 0.06 to 0.78 among species, with the mean being 0.33 (SD 0.22) (Figure 2a). AUC values ranged from 0.75 to 0.99 among species, with the mean being 0.94 (SD 0.06). On average, the fixed components of the presence/absence model explained 77% of the explained variance for each species (Figure 2b). Specifically, depth and slope explained on average 33% of the variance across species, satellite derived environmental data 15%, climate related variables 14%, year 9%, seafloor modelled oceanographic variables 4%, and marine reserve zoning 0.5% (Figure 2b). [It might be good to add a little more about the five species with highest Tjur R2 values (i.e., Add the top 5 species – mackerel icefish, unicorn icefish, Macrourus sp., *Gobionotothen acuta*, and *Muraenolepis microps*]

The abundance COP model showed reasonable fit to the data, the R2 values ranges from 0.17 to 0.98 among species, the mean being 0.48 (SD 0.23, Figure 2c). On average the fixed components of the abundance COP model explained 79% of the explained variance for each species (Figure 2d). Specifically, bathymetry related variables explained on average 26% of the variance across species, satellite derived data 24%, climate related variables 15%, seafloor modelled oceanographic variables 8%, year 6%, and marine reserve zoning 1% (Figure 2d).

Accounting for only responses that were positive or negative with at least 95% posterior probability, in the presence-absence model 80% of species showed a positive increase in prevalence across the study period from 2003 to 2016 (Figure 3a). No statistically supported declines in species prevalence were detected. The abundance COP model had 25% of species showing a statistically supported increase in abundance (Figure 3b). No species were predicted to decline in abundance between 2003 and 2016. Bathymetry, depth and slope, were all important at explaining the prevalence of species for 71% and 20% of species respectively showing substantial effect sizes (Figure 3a). Higher prevalence in deeper water was observed for 49% of species. Higher prevalence in shallow waters was observed for 23% of species. Most depth responses also had a significant quadratic second degree term (curved or bell shape gradient), highlighting that many species have well defined depth ranges. For example, *C. gunnari* was only observed in depth <500 m and conversely *Macrourus* sp. was only be seen in depths >500 m (Figure S1). Depth was also most important at describing abundance conditional on presence with 34% of species having a negative or positive response (Figure 3b). Seafloor slope was significant for 11% of species (Figure 3b).

The climate variables, IOD and SAM had variable response on the prevalence of benthic fish species (Figure 3). Almost half of the species included in the presence-absence model had a statistically supported positive or negative response to IOD or SAM (Figure 3a). For abundance conditional on presence the effect wasn’t as strong with only six species (three positive, three negative) responding to IOD and six species positively responding to SAM (Figure 3b). One third of the species had a positive relationship with SST for presence-absence (Figure 3a). However, there were no statistically supported responses in the abundance COP model (Figure 3b). SST anomaly had a mixed response for the presence-absence model with three species having a significant positive relationship and eight species having a negative relationship (Figure 3a). SSH, Chlorophyl A, and the modelled seafloor variables had a notably smaller number of (?) statistically supported responses for the presence-absence model (Figure 3b). However, these variables were more significant for the abundance COP model. Their responses were highly variable and species specific.

Six benthic fish species were more prevalent inside the no-take marine reserves, including the fishery managed species *Lepidonotothen mizops* and *L. squamifrons* (Figure 3a). For the abundance conditional on presence model, *Gobionotohen acuta* and *Zanchlorhynchus spinifer* were the only species to show a statistically supported response and were more abundant inside the no-take marine reserve (Figure 3b).

Chart, timeline

Description automatically generated

Figure 2. A) The Tjur R2 values for each species from the presence-absence HMSC model. B) The variation partitioning of the fixed and random effects within the presence-absence HMSC model. C) The R2 values for each species from the abundance COP HMSC. D) The variation partitioning of the fixed and random effects within the abundance COP HMSC. The species names and species groups are listed in alphabetical order.

Chart, scatter chart

Description automatically generated

**Figure 3.**  The responses of the species to environmental covariates. Panel A showed the results for the presence-absence model and panel B for the abundance COP model. In both panels, responses that are positive with at least 95 % posterior probability are shown in red, response that are negative with at least 95 % posterior probability are shown in blue, and responses that were not statistically **supported** are shown in white. The species and species groups are ordered alphabetically.

## 3.2 | Changes in species distribution

The prevalence of 80% of benthic fishes increased across the duration of this study (Figure 3). Spatial predictions converted to rasters demonstrate where these changes in probability of occurrence are located (Figure 4). All three skate species show similar changes in occurrence with 20-30% increases in prevalence across the top of the plateau in low relief areas (Figure 4). The change in occurrence for *B. eatonii* was far more widespread than *B. murrayi* and *B. irrasa* (Figure 4). An increase in *Macrourus* sp. tended to be to the northern half of the study regions and in deeper high relief regions (Figure 4). Other species maybe include grey rockcod, icefish?

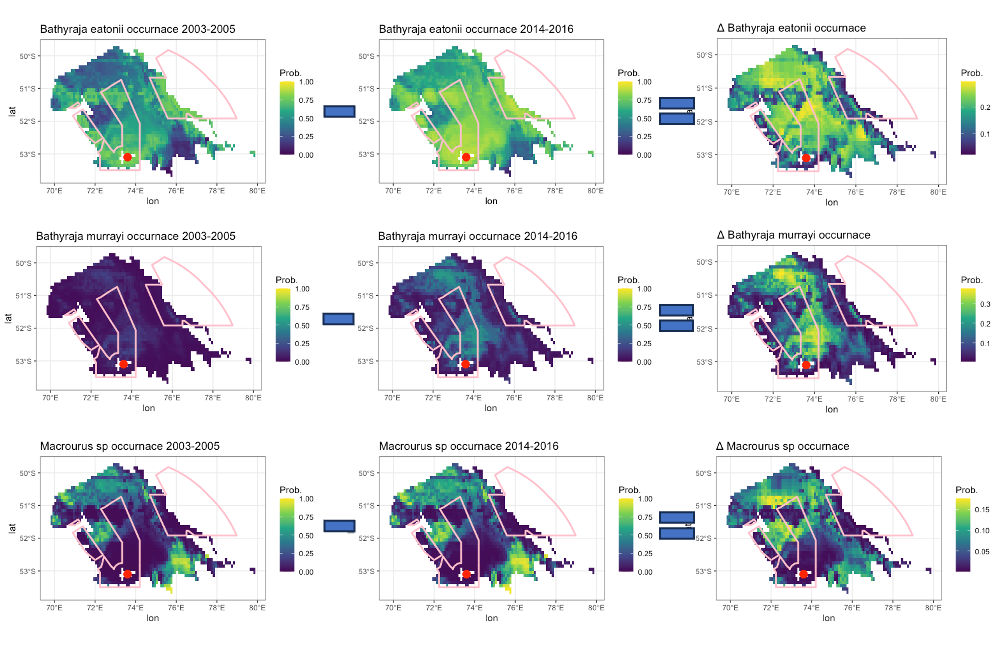


Figure 4. Change in distribution of X species of interest, taking the mean probability of occurrence from the first three years (2003-2005) and the last three years (2014-2016) and calculating the delta change in probability of occurrence.

## 3.2 | Species richness

At the assemblage level, the HMSC model predicted that species richness increased through time, with a mean species richness of three species per trawl in 2003 increasing to seven species per trawl in 2016 (Figure 5). Species richness also decreased with depth from a mean of eight species per trawl in 200 m depth to five species per trawl in 1,000 m depth (Figure 6). There was a positive correlation with species richness and SST, with species richness more than doubling with an increase of 3°C in sea surface temperature (Figure 5).

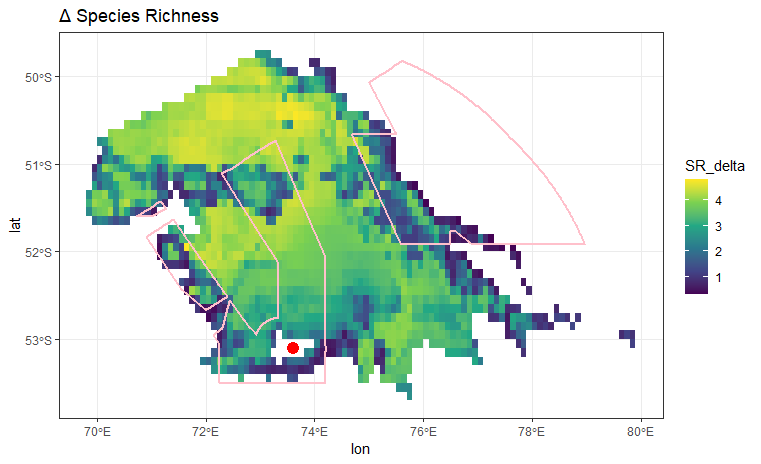
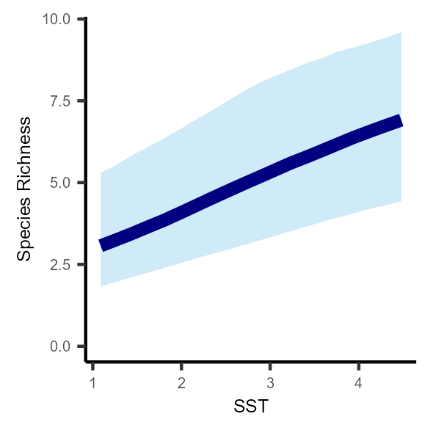
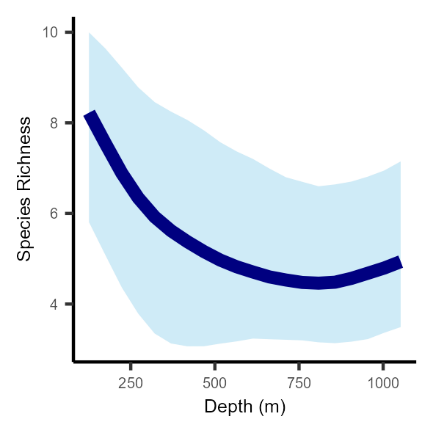
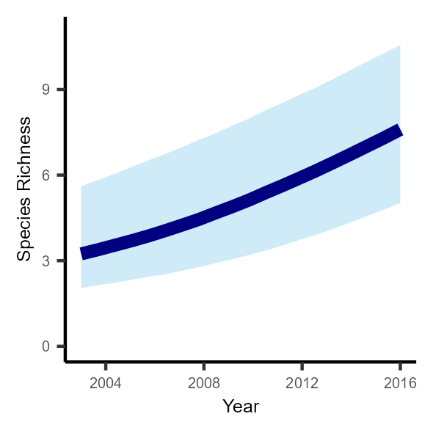


Figure 5. Model predictions of species richness through time (Year), across depth, and across sea surface temperature (SST). The delta species richness represents the differences in species richness between the first three year (2003-2005) and the last three year (2014-2016). The pink polygons represent the HIMI Marine Reserve boundaries and the red dot is the location of Heard Island.

# 4 | Discussion

Marine Reserve update?

The Kerguelen Plateau ocean climate has changed and will continue to change into the future (Cavanagh et al., 2021; Pinkerton et al., 2021; Su et al., 2021). Furthermore, over the last few decades, management practices have improved, there has been a reduction in IUU fishing, and fishery-led changes to minimise by-catch have occurred. This multitude of factors is likely to have a combined influence on the benthic fish community. In this study we have demonstrated how the benthic fish community in waters less than 100 m have changed between 2003 and 2016. While the species assemblage structure can be defined to a large extent by physical geography, i.e. depth and location, some change in the fish community can be attributed to shifts in climate and oceanography. The use of a joint species distribution modelling approach provides novel insights into individual species as well as the fish assemblage as a whole through species richness. Our findings suggest that distribution of most species has increased throughout the study period. However, further interrogation of whether this trend might be driven by an increase in the likelihood of higher and more diverse catches, , changes in species co-occurrences, a true expansion of geographical distribution, alterations or decreases in fishing pressures, or additional factors is warranted.

Most of the species recorded during the trawl surveys have a relatively unknown global and localised distribution, and a detailed understanding of their ecology and biology is lacking. It is therefore tenuous to tie inferences about changes in distribution to species’ traits and life history. The two targeted fishery species, Patagonian toothfish and mackerel icefish, which are well studied, were ubiquitous in distribution across the study area and throughout the study period. It is the fishery by-catch species, i.e. non-targeted species that are potentially sensitive to fishery pressures, that showed increases in both prevalence and abundance. This suggests that any or all of the decline in illegal fishing, improved fisheries management, and shifts in fishing methods have all had a positive influence on these species.

In 2003, the commercial Patagonian Toothfish fishery operating in this area started moving away from benthic trawling to long-line fishery. This also included a move to targeting fish in deeper water (>1,000 m). However, it should be noted that some trawling targeting the mackerel icefish still occurs in the shallower region. This change in gear type and locations of fishing was driven by the fishery itself to maximise efficiency and minimise bycatch. It is undoubtable that seabed trawling has an impact on benthic habitats and recovery times from trawl impacts can be varied from years to decades (Pitcher et al., 2015, 2022). It is plausible that the reduction of trawl fishing effort has allowed for the recovery of habitats to the benefit of benthic fishes.

It is also possible that changes in environmental conditions, for example higher SST, have increased productivity to the benefit of benthic fishes. It has been suggested that warming waters in high latitude areas is resulting in increase in primary productivity due to reduced water column mixing (Doney, 2006). Chlorophyll-a concentration (from satellite data) showed mixed results for prevalence and little explanation for abundance (Doney, 2006).

To improve the understanding of benthic fishes on the Kerguelen Plateau additional information and monitoring is required. To date knowledge of benthic habitats has been limited to shallow coastal regions surrounding the islands. It is well known that highly complex habitats support biodiversity and increased biomass of benthic fishes. A large focus of research in this region is based on mammals and shorebirds which often feed on benthic fishes. However, there is little information linking productivity with the distribution of zooplankton and mesopelagic fish. The are several ecosystem models for the region but they tend to group fish into broad pelagic or benthic groups (Subramaniam, Corney, et al., 2020). As demonstrated in this study benthic fishes often have geographic and environmental niches that aren’t captured in these broad ecosystem models. Most of the benthic species recorded during this study feed on mesopelagic fish species. Mesopelagic species often aggregate around areas of primary and secondary productivity. Bioregionalisation work is this region has found the HIMI region of the Plateau was a region of high productivity supporting a distinct group of zooplankton (Godet et al., 2020). Climate change is likely to be influencing primary productivity that is likely to flow through the food chain and influence benthic fishes (Constable et al., 2014; Godet et al., 2020; Su et al., 2021).

[There may be room for another paragraph re taxonomy … both current understanding and future changes and how this may impact our understanding of biodiversity. This would also be another way to bolster the findings related to species richness].

The Kerguelen Plateau is located immediately above the polar front and spanning the transition from polar to sub-tropical zones. It is the largest topographic feature and barrier to the eastward moving Antarctic Circumpolar Current (ACC; (van Wijk et al., 2010). This is one of the reasons why this region has unique and important biodiversity values. It also means the region is particularly susceptible to climate change driven changes to ocean currents and climate. Climate change is already influencing Southern Ocean and there is evidence that long-term gradual warming is already occurring at depth (Gille, 2002; Haumann et al., 2020). There is also evidence that extreme pulse events such as marine heatwaves are impacting this region (Su et al., 2021). Not a lot is known about how marine heatwaves will impact benthic communities in remote areas of the Southern Ocean. This study found that many benthic fish species have defined thermal niches. Continued warming or marine heatwaves are likely to thermally stress these species or force fish to move to deeper cooler waters or move poleward. One of our hypotheses for the increased prevalence and abundance of many species is that warming in this region is resulting in warmer and more productive waters, although this notion is not possible to test with the current data. This study also found the Southern Annular Mode (SAM) to be a significant climate variable that explains the prevalence and abundance of benthic species. The response to SAM was mixed and species dependent. The prevalence of some species was highest when SAM was natural, while other species showed greatest prevalence during positive SAM periods. Positive SAM events have been attributed to high climate variability and marine heatwaves (Fogt & Marshall, 2020; Le Quéré et al., 2007; Su et al., 2021). SAM is believed to be the leading mode of climate variability in this region yet the direct links between SAM and the ecosystem function and dynamics are still relatively unknown (Fogt & Marshall, 2020).

The Patagonian toothfish and mackerel icefish fisheries are highly managed fisheries. Quotas for fishing within the Australian EEZ or HIMI region are set and reviewed annually by AFMA and CCAMLR. This includes quotas for bycatch species and other restrictions such as move on rules. The adaptive ecosystem-based management approach applied by AFMA and CCAMLR can incorporate natural and climate-driven fluctuations in the distribution and stock structure of fishery managed species. The HIMI region is also spatially managed through no-take marine reserves. The HIMI marine reserve is significant in size and covers are area of the Plateau, including the high diversity of the high relief banks. Marine reserves are a viable and effective adaptation strategy to improve the outlook of climate change (Roberts et al., 2017). However, in a region that is highly exposed to the impact of climate change and with little ecological and biological knowledge of the biota, fishery-independent monitoring programs are highly important. At the regional scale, climate change is difficult to manage, however it is believed that adaptive ecosystem-based management approaches to fisheries management and marine protected areas can help mitigate the impacts of climate change on biodiversity of the Kerguelen Plateau.

This study demonstrates the immense benefit and value of the annual RSTS as a fisheries independent survey. Without long-term data collected using the same comparable methodology it would not be possible to detect these changes accurately and confidently. The random stratified component ensures adequate special coverage and avoids sampling biases that increase or decrease effect sizes. It should be noted that trawl surveys do target lower complexity habitat to minimise risk of entanglement of nets. Therefore, the RSTS is likely to have a bias towards species that inhabit soft sediments and low relief reefs. Other methods, such as long-line surveys, remote underwater video, eDNA are needed to capture baseline data for benthic fish that inhabit the more complex reefs systems that are known to occur in this region. Additional research such as taxonomic and biological (age at length, diet etc) studies should be linked with these surveys. There is also benefit to expand surveys to deeper waters to capture all life stages and allow for greater spatial coverage.

In conclusion, this study has demonstrated that benthic fish community has changed over a 13-year period. The prevalence, abundance, and specie richness have all increased across the HIMI region of the Kerguelen Plateau. This includes for many of the fisheries by-catch species such as the skates and macrourids. While it is difficult to disentangle what has driven this change in distribution and abundance, we conclude that it is likely a combination of factors including improved fisheries management and fishing practices, removal of illegal fishing, and environmental change as a result of climate change. For most species this is the first investigation into their distribution through space and time in the HIMI region, providing novel insights into these benthic fish species. The HIMI fisheries management is built on the ecosystem-based management principles of CCAMLR. To date most of the benthic fish knowledge in the HIMI region has been based on the two fishery species. This study provides valuable data and knowledge the on the benthic fish community that can help with the assessment of fisheries management practices such as allowable catches and ‘move-on’ rules. Furthermore, the approach using joint species distribution modelling has proved to be highly beneficial for understanding the distribution of benthic fish across the HIMI marine reserve.

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