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**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**

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**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 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). The 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 methods for managing and protecting the world’s oceans have also changed with the adoption of marine protected areas, sustainable fishing policies, improved and reduced land-based pollution and runoff. Many of these policy decisions are targeted to specific regions or fisheries. For example, changes to fisheries management has led to Australian Orange Roughy stocks to recover 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 and this is having ecosystem level impacts (Boyd et al., 2016; Constable et al., 2014; Johnson et al., 2011; Wassmann et al., 2011). The changing oceans are resulting in changes to species distributions and leading to biological invasions, and range extensions or contractions (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 pivotal role in oceanic primary production, exports nutrients and oxygen the world’s ocean and supports valuable biodiversity (Auger et al., 2021; Constable et al., 2014; Le Quéré et al., 2007; Van de Putte et al., 2021). However, the physical attributes the Southern Ocean, such as water temperature, CO2 sequestration, and ocean currents are changing (Constable et al., 2014; Van de Putte et al., 2021). The Conservation of Antarctic Marine Living Resources (CCAMLR), a leading management body for this region, 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). This is particularly driven by the sub-order Notothenioids, where 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 Antarctica and the Southern Ocean Island such as Heard and McDonald Islands. Both historical and predicted changes in Southern Ocean fish assemblages are mostly unknown. It is expected that the southward shifting ocean frontal systems is likely to have the largest influence on species distributions. However, interpretations of changes in distribution and abundance of fish communities need to be careful when incorporating the confounding effects of fishing and fisheries management.

The key to understanding these environmental processes and ecological change is to have suitable long-term data sets. Oceanographic data has been collected over large spatial scales for decades (e.g. NOAA ref). However, long term (>10 years) biological monitoring or ecological datasets (i.e. species’ occurrence and abundance data), while integral 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). This includes working with whole species assemblage data across large spatial scales using joint species distribution models (Norberg et al., 2019; Ovaskainen et al., 2017; Tikhonov, Duan, et al., 2020). These modelling approaches allow ecologist to explore correlations across environmental gradients and produce full-coverage ecological maps for each species as well as community attributes such as species richness. Ecologist are also interested in using the same model for making 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 large dominant geographic feature. It is a productivity hotspot, supporting a diversity of marine life as well as supporting a lucrative demersal fishery, primarily for Patagonian toothfish (Duhamel & Welsford, 2011; Hill et al., 2017). 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. This includes providing the information needed by fisheries agencies, such as the Australian Fisheries Management Authority, to ensure these lucrative fisheries are management using 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. Australia has an exclusive economic zone that encompasses Heard and McDonald Islands. The uniqueness and ecological importance of this region were globally recognised with Heard Island and McDonald Island being World Heritage Listed in 1997 and the formation of a no-take marine reserve in 2002. Species of key economic importance have been well studied for stock assessment and fisheries management. There is a significant knowledge gap of how the fish assemblage as a whole is structured across the Plateau and if and how it has changed through time (Hill et al., 2017). Within the Australian EEZ, Patagonian toothfish and mackerel icefish are the two targeted 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. Understanding how changes in management and fishery decisions and increased compliance have led to changes at a species assemblage level is important for ecosystem-based management.

In the study we aimed to establish if the benthic fish community of the HIMI region of the Kerguelen Plateau has changed through time. We then relate any changes in prevalence and abundance of benthic fishes to environmental change, marine reserve zoning or changes to management or fishery practices. To achieve this, we use a joint species distribution modelling (JSDM) approach. We were able establish how much of the variation in each species prevalence and abundance is due to environmental filtering and random process, and how these vary across spatial and temporal scales. This joint species modelling approach provides assemblage level information on the impacts of climate change and fishing and will provide information to facilitate the ecosystem-based management requirements of CCAMLR. The results from this study have the potential to be applied to other regions of the Southern Ocean and help better understand the implications of climate change, fisheries management, and conservation management at a much larger scale.

# 2 | METHODS

## 2.1 | Study site

This study was completed within the Australian EEZ of the Kerguelen Plateau (Figure 1). As the name suggests, it is a large is a large plateau the rises from depths >3000 m, has steep banks, with numerous seamounts, and breaks the surface with three large islands and numerous rocky outcrops. The data used in this study originates from around Heard Island and McDonald Island (HIMI) that are located on the northern half the Kerguelen Plateau (Figure 1). 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 71,000 km2 of ocean. The HIMI region is also of economic interest as it supports valuable fisheries that are managed by Australia and consistent with the CCAMLR ecosystem-based management approach (Constable, 2011). Commercial fisheries primarily target Patagonion Toothfish, *Dissostichus*

*eleginoides*, by long-line fisheries and Mackeral Icefish, *Champsoscephalus gunnari*, by trawl fisheries. Other species, such as Marbled Rockcod, *Notothenia rossii* and Grey Rockcod *Lepidonotothen squamifrons* were historically targeted by trawling (Duhamel & Williams, 2011). The region also supports many long-lived, large, and endemic species that are also caught as by-catch species by these fisheries.



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 20016 as black. The Heard Island and McDonald Island Marine Reserve boundaries are marked by the red polygons. Inset: Location of the study map in relation to the world.

## 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 begun. The survey design consists of the HIMI plateau being divided into 10 strata that are defined by regions of similar morphology and commercial fishing effort. Sampling sites are then randomly located within each of these strata. The survey design and methodology has remained mostly the same since 1997, with a few minor adjustments. The consistency in methodology enables comparisons of fish abundance and biomass through time.

The RSTS uses an otter beam trawl net with a 500 mm mesh codend 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.

While every attempt is made to sample the same area, i.e. trawl tow duration, there is some variability in the distance of the trawls (min = 1.3 km, max = 6.4 km, mean = 2.9 km, SD = 0.3 km). Given the differences in towed distances, for the purposes of modelling, the count estimates are divided by the towed distance to provide CPUE (number of fish per kilometre).

Species that occurred in 10 or fewer trawl samples were removed as these species were considered very rare and too difficult to model. Also, incidental catches of pelagic species were removed.

## 2.3 | Spatial and environmental variables

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

All environmental variables were tested for correlations using Pearsons correlation to ensure the coefficients between variable was <|0.7| to avoid collinearity.

Table 1. Descriptions for each of the covariates used in the HMSC model, including the range and justification for inclusion.

|  |  |  |  |
| --- | --- | --- | --- |
| **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 1/4° 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 1/4° 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 1/4° 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 – 2006 | The years we had RSTS with reliable taxonomic resolution and coverage of the above environmental variables | RSTS metadata. |

## 2.4 | Statical 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 asking how a species response to environmental covariates depend on species-species and species traits relationships (Abrego et al., 2017). HMSC also utilizes spatially structured latent variables proposed by Ovaskainen et al. (2017) and later expanded to big spatial data by Tikhonov et al. (2020) (i.e. 10,000s points). This approach allows us to investigate how each individual species responds to the environmental covariates, while taking into account species co-occurrences through space.

The RSTS data comprises of the abundance of 38 fish, shark, and ray species from between 111 and 195 trawl sites sampled per year from 2003 to 2016. We excluded those species that had less than 10 occurrences in these data, resulting in 35 species ( ). The 2,186 individual trawls were treated as a sampling units (. As the response variable (the matrix of HMSC; see Ovaskainen et al. 2017 ELE), we used the CPUE data for each of the 35 species. 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 abundance COP model). We applied probit regression in the presence-absence model, and linear regression for log? transformed count data in abundance COP model. The count data were transformed by declaring zeros as missing data, log-transforming, and then scaling the data to zero mean and unit variance within each species.

We included as fixed effects (the matrix **X** of HMSC; see Ovaskainen et al. 2017 ELE; where is the number of covariates) 15 variables that we believed would 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, in our study 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 strata as a random factor. To control for temporal correlation we used the numbers of days since the start of the study as a random factor. (i.e. 1 January 2003 = 1).

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 Monto Carlo (MCMC) chains. The chains were thinned by 100 to yield 500 posterior samples per chain and so generating 2000 posterior samples in total. We checked MCMC convergence by ensuring the mean and standard deviation of the potential scale reduction factors (Gelman & Rubin, 1992) were close to 1 for the majority of the model parameters.

We examined the explanatory and predictive powers of the probit model through species specific AUC (Pearce & Ferrier, 2000) and Tjur’s R2 (Tjur, 2009) values. The explanatory and predictive powers of the abundance COP model were measured by R2. To compute explanatory power, we made model predictions based on models fitted to all data. 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. if and how species communities have changed over the study period, we examined species responses to the explanatory variables of the study period, counting what proportion of species 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, 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 generate maps by taking the mean probability of occurring across the first three years of study and then the last three years of the study. This was to account for minor inter-annual variability. We then subtract the values for the two rasters to establish where change had occurred. Using these predictions, we could also estimate species richness and 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 data (CPUE) 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*, *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 HMSC 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), The 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, bathymetry related variables explained on average 33% of the variance across species, satellite derived data 15%, climate related variables 14%, year 9%, seafloor modelled oceanographic variables 4%, and marine reserve zoning 0.5% (Figure 2b).

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%, satellite derived data 24%, 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 significant positive increase in prevalence across the study period from 2003 to 2016 (Figure 2a). No significant declines in species prevalence were detected during across the study period. The abundance conditional of presence model had 25 % of species showing a significant increase in abundance (Figure 2b). No species were predicted to decline in abundance between 2003 and 2016. Bathymetry, depth and slope, were important at explaining the prevalence of species for 71% and 20% of species respectively showing significant effect sizes (Figure 3a). A 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 be 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 of presence with 34% of species having a negative or positive response (Figure 3b). Slope was significant for 11% of species (Figure 2b).

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 significant positive or negative response to IOD or SAM (Figure 3a). For abundance conditional presence the effect wasn’t as strong with six species significantly (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 significant 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 seafloor modelled variables had a notably smaller significant 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 fishery managed species *Lepidonotothen mizops* and *L. squamifrons* (Figure 3a). For the abundance conditional of presence model *Gobionotohen acuta* and *Zanchlorhynchus spinifer* were the only species to show a significant 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. B) The variation partitioning of the fixed and random effect within the presence absence HMSC. C) The R2 values for each species from the abundance COP HMSC. D) The variation partitioning of the fixed and random effect within the abundance COP HMSC. The species names 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 did not gain strong statistical support are shown in white. The species are ordered alphabetically.

## 3.2 | Changes in species distribution

The prevalence of 80% of benthic fishes increased through the duration of this study (Figure 3). Spatial predictions converted to rasters demonstrate where these changes in probability of occurrence is happening (Figure 5). 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 5). The change in occurrence for *B. eatonii* was far more widespread the *B. murrayi* and *B. irrasa* (Figure 5). An increase *Macrourus* sp. Tended to be to the northern half of the study regions and in deeper high relief regions (Figure 5). Other species maybe include grey rockcod, icefish?

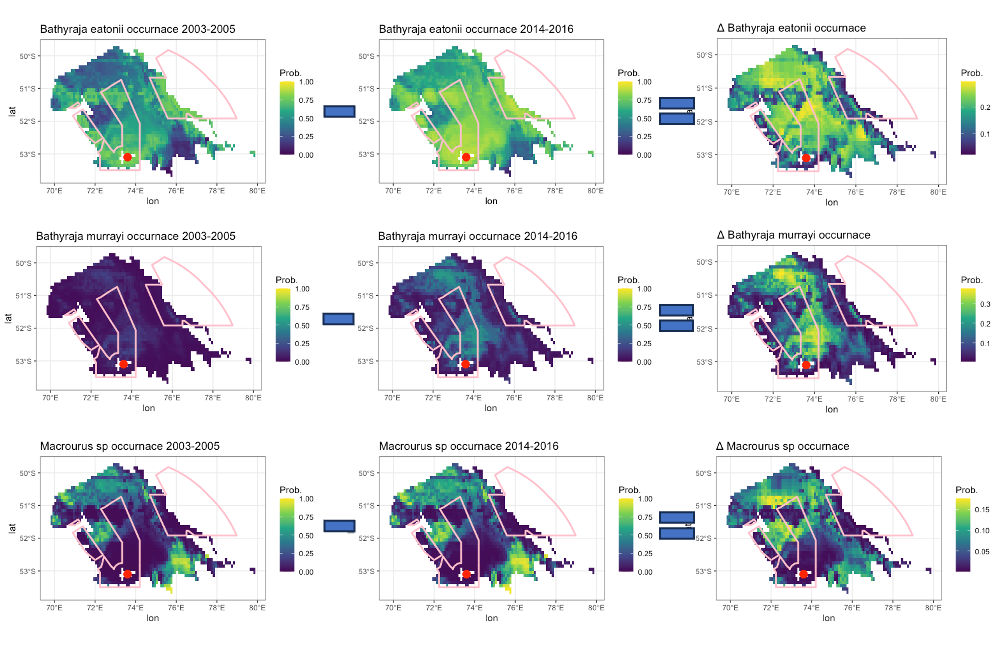


Figure 5. Change in distribution of X species of interest, taking the mean probability of occurrence from the first three years (2003-2005) and the last three years (2014-2016) and calculating the delta change in probability of occurrence.

## 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 6). Species richness also decreased with depth from a mean of 8 species per a trawl in 200 m depth to 5 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 over 3 degrees of sea surface temperature (Figure 6).

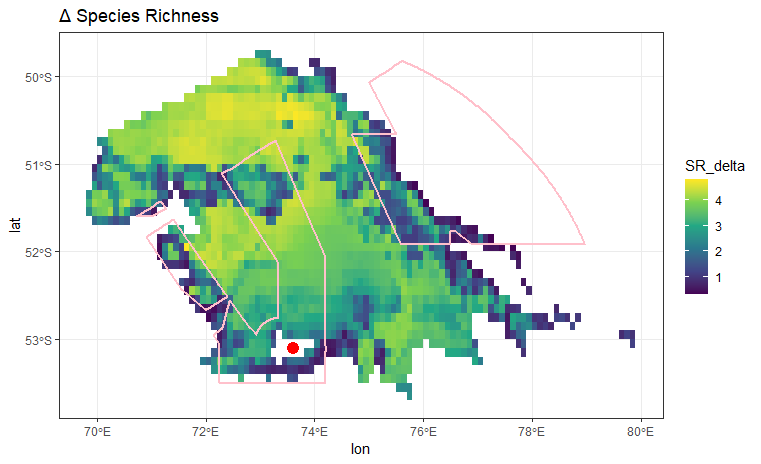
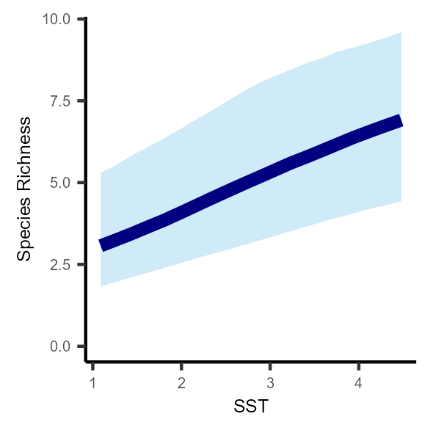
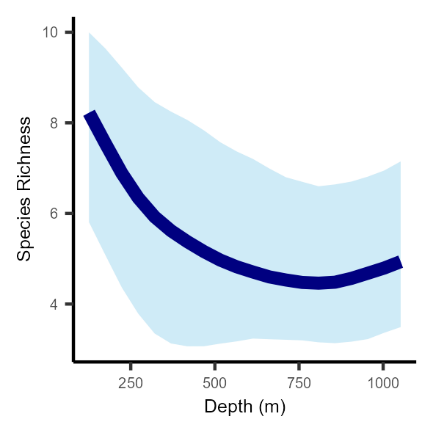
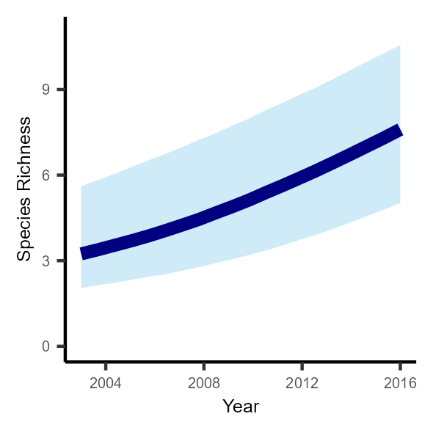


Figure 6. Model predictions of species richness through time (Year), across depth, and across sea surface temperature (SST). The delta species richness represents the differences in species richness between the first three year (2003-2005) and the last three year (2014-2016). The pink polygons represent the HIMI Marine Reserve boundaries and the red dot is the location of Heard Island.

# 4 | Discussion

The Kerguelen Plateau 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, compliance has removed illegal fishing, and fishery-led changes in operating to minimise by-catch have occurred. This multitude of factors combined is likely to have a cumulative influence on the benthic fish community. In this study we have demonstrated how the benthic fish community of the Heard and McDonald Island region of the Kerguelen Plateau has changed since 2003. While the species assemblage structure can be defined by physical geography i.e. depth and location, some change could be attributed to climate and oceanography. The use of a joint species distribution modelling approach as allowed us to provide novel insights into in individual species and the fish assemblage as whole through species richness. Most notably the prevalence of most species increased throughout the study period. This is mostly likely a combination of the probability of catching a certain species across their historical distribution has increased or an expanded distribution. Noting that pre-fishing species community data is lacking and we are unable to make true historical comparisons. This has also resulted in an increase in species richness across the study area with the largest changes on top of the plateau.

Most of the species recorded during the trawl surveys have a relatively unknown global and localised distribution, let alone an understanding of their ecology and biology. This makes it difficult to make inferences about changes in distribution. 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 was the fishery by-catch managed species, species that are potentially sensitive to fishery pressures, that showed increases in both prevlenace and abundance. This suggests that the removal of illegal fishing, fisheries management, and 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). 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 small changes in environmental conditions, for example higher SST, have increased productivity to the benefit if benthic fishes. It is suggested that warming waters in high latitude areas is resulting in increase in primary productivity due to reduce water column mixing (Doney, 2006). Chlorophyll-a from satellite data was included in the model and 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 on 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 these region but they tend to group fish into broad pelagic or benthic groups (Subramaniam et al., 2020). As demonstrated in this study benthic fishes often have 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 productivty. 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).

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 that is already occurring at depth (Gille, 2002; Haumann et al., 2020). There is also evidence pulse extreme events such as marine heatwaves impacting are also 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 is this region is resulting in warmer and more productive waters. Though this hypothesis near impossible 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 dependant. The prevalence of some species was highest when SAM was natural, while other species showed a positive response, i.e. highest 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 change driven fluctuations in 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 believe 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 random stratified trawl survey, a fisheries independent survey. Without long-term data collected using the same comparable methodology it would 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 the inhabit soft sediments and low relief reefs. Other methods, such as remote underwater video, are needed to capture baseline data for benthic fish that inhabit the more complex reefs systems that are known to occur in this region.

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 managed 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 climate change driven environmental 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 joint species distribution modelling approach is also beneficial for understanding the distribution of benthic fish across the HIMI marine reserve.

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