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# Species distribution models describe spatial variability in mesopelagic fish abundance in the Southern Ocean

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**Introduction:** Mesopelagic fishes play a central role in the transfer of energy through open-ocean food webs, particularly in the Southern Ocean where they are both important predators of zooplankton and a key prey group for many higher predators. However, they are notoriously difficult to sample, which has limited our understanding of the bio-physical predictors of their abundance and spatiotemporal variability. Species distribution models can be used to help understand species' ecological requirements by relating records of their presence or abundance to environmental data.

**Methods:** Here, we used data from *Myctobase* – a new circumpolar database of mesopelagic fishes – to model patterns in abundance of eight key myctophid species (family Myctophidae) and the genus *Bathylagus* in the Southern Ocean south of 45°S. We developed species-specific boosted regression tree models to obtain circumpolar predictions of abundance. Average daytime and night-time summer predictions for the period 1997 to 2011 at 0 to 200m depths were generated for each species.

**Results:** Depth and solar position were important predictors and species were stratified in their depth distribution. For all species, except for *G. nicholsi*, there was an interaction between depth of capture and solar position, reflecting diel vertical migration. Other important variables included sea surface temperature, dissolved oxygen at 200 m, chlorophyll *a*, and sea surface height, indicating an association with water mass properties. Circumpolar patterns of abundance varied between species with some displaying affinities for oceanic regions at Antarctic latitudes (e.g., *E. antarctica* and *Bathylagus* spp.) or sub-Antarctic latitudes (e.g., *K. anderssoni* and *P. tenisoni*); and affinities for shelf regions (e.g., *P. bolini* and *G. nicholsi*).

**Discussion:** Our findings suggest that the abundance of mesopelagic fish is influenced by diel vertical migration and meso- and sub-mesoscale oceanographic features, with the Polar Front being a major delimiting feature. Our study showed contrasting patterns in community composition with higher species diversity north of the Polar Front that might be indicative of latitudinal variability in food web structure. Our spatial analysis is an important step toward resolving what determines important habitat for mesopelagic fishes, providing foundational information for understanding shifting food web dynamics into the future.

#### KEYWORDS

ecosystem modelling, micronekton, Myctophidae, diel vertical migration (DVM), food web, open-ocean, Polar Front, trawl net

## 1 Introduction

Mesopelagic fish (predominantly inhabiting the mesopelagic zone, 200 – 1000 m) are a central part of open-ocean food webs and play an important role in both top-down and bottom-up ecosystem structuring processes (Griffiths et al., 2013; Caccavo et al., 2021). Myctophids (family Myctophidae) are the most diverse and abundant group of mesopelagic fishes globally, including in the Southern Ocean, where they comprise more than 60 species (Duhamel et al., 2014) and an estimated biomass between 212 and 396 million tonnes (Lubimova et al., 1987), although this is likely to be an underestimate due to previously unaccounted for net avoidance (Kaartvedt et al., 2012). In some regions of the Southern Ocean, particularly the Indian and West Pacific sectors, myctophids are the dominant prey resource sustaining top-predator biomass (McCormack et al., 2019; Saunders et al., 2019; McCormack et al., 2021). In turn, myctophids are important zooplanktivores, consuming copepods, amphipods and euphausiids, including Antarctic krill *Euphausia superba* (Saunders et al., 2018; Clarke et al., 2020; Riaz et al., 2020). Myctophids are key to linking this secondary productivity to higher predators *i.e.* flying seabirds, penguins, seals and Patagonian toothfish (e.g., Olsson and North, 1997; Gaskett et al., 2001; Cherel et al., 2002; Lea et al., 2002; Collins et al., 2007; Stowasser et al., 2012; O'Toole et al., 2014). Many species undertake diel vertical migration (DVM), where they reside at depths during the day and migrate to shallower waters at night (Brierley, 2014; Duhamel et al., 2014). DVM is a behavioral adaptation with important implications for prey availability to higher predators and enhances carbon sequestration by active transport of organic carbon from the surface to the deep ocean (Brierley, 2014; Irigoien et al., 2014; Anderson et al., 2018; Saba et al., 2021).

The critical importance of myctophids in Southern Ocean pelagic ecosystems is increasingly well-recognized, however,

major gaps remain in our knowledge of their biodiversity, abundance and the processes that shape their distribution (Kaartvedt et al., 2012; Anderson et al., 2018; Caccavo et al., 2021). Their open-ocean habitats are logistically difficult to access and costly to sample given the remoteness of such environments (Rogers, 2015). Mesopelagic fishes are difficult to sample adequately at the ocean basin scale with pelagic nets (Kloser et al., 2009); catch efficiency is known to vary between net types (Pakhomov and Yamamura, 2010) and is poorly constrained for any given net (Davison et al., 2015). In contrast, acoustic methods can rapidly sample vast spatial extents (Benoit-Bird and Lawson, 2016; Dornan et al., 2022), however they are unable to capture changes in community composition (Dornan et al., 2019). Consequently, net sampling remains an important tool for examining patterns in biodiversity, abundance, and community composition (McClatchie et al., 2000; St John et al., 2016).

Species distribution models are a commonly used method in the study of biogeography, ecology, evolution, and conservation biology (Guisan and Zimmermann, 2000; Peterson, 2006; Elith et al., 2008). The overarching objective of species distribution models is to determine species' ecological requirements by relating records of their presence or abundance to environmental predictors and to provide predictions of species' geographic distribution (Guisan and Zimmermann, 2000; Peterson, 2006). Such models can provide many important insights to ecological and biogeographical dynamics of communities and broad scale projected species' distribution under different climate change scenarios (Kissling et al., 2018; Freer et al., 2019; Jetz et al., 2019).

Circumpolar descriptions of mesopelagic fish distribution are most often based on occurrence (presence-absence or presence-only) data (Hulley and Duhamel, 2011; Koubbi et al., 2011b; Duhamel et al., 2014; Freer et al., 2019). Occurrence data are easier to collect compared to abundance data, particularly in

logistically difficult to sample environments and are readily available in online data repositories (Kissling et al., 2018; Jetz et al., 2019). These occurrence-based studies have demonstrated the importance of meso- and sub-mesoscale oceanographic features on community composition where frontal zones are the major delimiting factors to species distributions (Hulley and Duhamel, 2011; Koubbi et al., 2011b; Duhamel et al., 2014; Freer et al., 2019). While a high probability of occurrence provides a broadscale picture of distribution it does not necessarily equate to a high density of individuals or indicate core habitat (Renwick et al., 2012; Johnston et al., 2015). Abundance trends of populations are additionally important to examine when assessing the status of species (O'Grady et al., 2004; Shoo et al., 2005; Clements et al., 2017), in particular for understanding prey fields for higher predators (Green et al., 2020), and the relative importance of different trophic pathways in food webs (Trebilco et al., 2020). A baseline understanding of the patterns in myctophid abundance would also underpin knowledge of how the mesopelagic fish population may change into the future and the implications of such changes to broader food web dynamics (Constable et al., 2014; Rogers, 2015; St John et al., 2016; Hidalgo and Browman, 2019).

Here, we make the important advance of investigating the drivers of circumpolar abundance of key mesopelagic fish species, taking advantage of *Myctobase* – a new data collation project that integrates and standardizes existing abundance, biomass, biodiversity, and methodological data on Southern Ocean mesopelagic fishes (Woods et al., 2021; Woods et al., 2022). We used data from *Myctobase* to develop species-specific models of the abundance of eight myctophid species and the genus *Bathylagus*. We used a set of environmental variables to develop species distribution models and subsequently used these models to obtain a circumpolar prediction of abundance for each species. The specific objectives of this study are to: 1) establish a robust framework for analyzing complex net data from *Myctobase*, accounting for differences in gear type and spatial and temporal coverage of surveys; 2) describe the environmental, vertical, and geographic patterns of Southern Ocean mesopelagic fish abundance at a circumpolar scale; and 3) compare model outputs with those from previous models based on occurrence data.

## 2 Materials and methods

### 2.1 Myctobase: Data collection

Survey data for mesopelagic fish species from midwater trawls in the Southern Ocean were collated in a purpose-built database, *Myctobase*. A detailed description of the database, including the data collection and processing steps can be found in Woods et al. (2022). The database currently holds 17,491 records of occurrence from 4780 net hauls conducted across 72 different Southern Ocean research cruises between 1991 and

2019 by eight national research programs (Figure 1). The database includes detailed metadata for each sample (e.g. latitude, longitude, depth, date-time of trawl, net type and volume filtered), as well as taxonomic information, estimated species abundance and length-weight measurements.

Samples were collected from pelagic trawls using opening-closing net systems with a range of net types including Rectangular Midwater Trawl (RMT) and International Young Gadoid Pelagic Trawl (IYGPT) nets, an Isaacs-Kidd Midwater Trawl (IKMT) net and a Matsuda-Oozeki-Hu Trawl (MOHT) net. Detailed information for each net type can be found in Woods et al. (2022). Opening-closing net systems enabled the sampling of discrete depth intervals.

### 2.2 Species abundance records

This study focused on the eight most abundant myctophid species within *Myctobase* (*Electrona antarctica*, *E. carlsbergi*, *Gymnoscopelus braueri*, *G. fraseri*, *G. nicholsi*, *Krefflichthys*

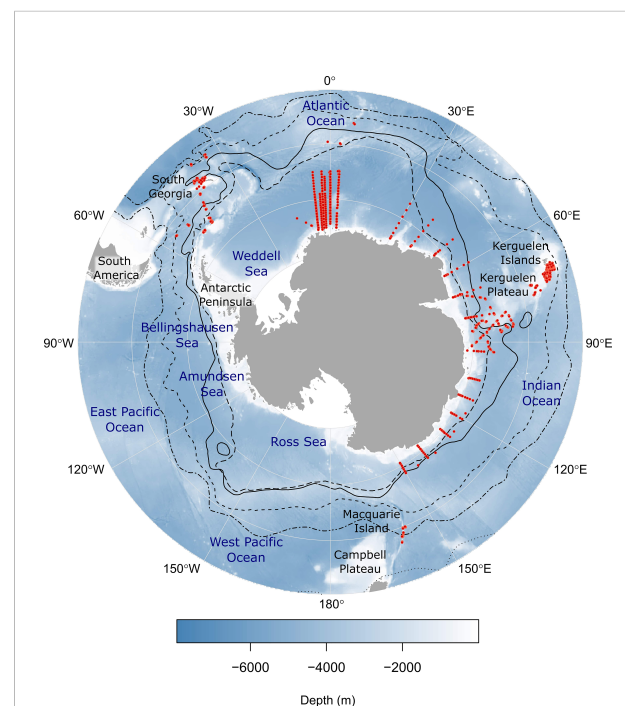


FIGURE 1

The sampling locations of 1905 mesopelagic trawl nets (red points) from which abundance records of mesopelagic fish species were used for this study. Black lines indicate mean frontal positions (Orsi et al., 1995). Starting from the outer line, frontal features are as follows: Subtropical Front (dotted line); sub-Antarctic Front (dash-dot line); Polar Front (dashed line); southern Antarctic Circumpolar Current Front (solid line); southern boundary of the ACC (long-dashed line). Numbered labels around the outside of the map indicate the longitude. Each latitude line represents 10° of latitude where 75°S is at the Antarctic continent and 45°S is at the external line.

*anderssoni*, *Protomyctophum bolini* and *P. tenisoni*) and species of the genus *Bathylagus* (family Bathylagidae). Records for *Bathylagus* spp. were rarely identified to species level within the database and were grouped and analyzed at the genus level. Abundance records underwent a process of data cleaning and error checking as described in Woods et al. (2022). Target trawls (trawls undertaken on acoustically detected aggregations of fish) were excluded and only data from the most common net types were included (IYGPT with MIDOC, IYGPT, RMT 25 and RMT 8). Abundance was calculated as the number of individuals per filtered volume of water (individuals 1000 m<sup>-3</sup>) for each net haul.

## 2.3 Environmental data

We developed species-specific boosted regression tree models to obtain circumpolar predictions of relative abundance. Eleven environmental covariates were used to model the abundance of each species, guided by previous research demonstrating their importance in determining suitable habitat for mesopelagic fish species (Loots et al., 2007; Koubbi et al., 2011b; Flynn and Marshall, 2013; Duhamel et al., 2014; Proud et al., 2017; Freer et al., 2020; Dornan et al., 2022). We predominantly used variables from the top 200 m of the water column. Subsurface (deeper than 200 m) environmental variables have been suggested to be more informative than

surface variables (Koubbi et al., 2011b); however, obtaining the appropriate data to achieve this is not always possible as at-depth environmental parameters are often unavailable or unrecorded. Freer et al. (2020) constructed depth-resolved occurrence models for several myctophid species using environmental predictor variables at different depth intervals, but due to the paucity and uncertainty in depth data used for the 3D models they found that this resulted in smaller sample sizes compared to 2D models increasing the uncertainty around predictions. They also showed high overlap between the two types of models in their final outputs, demonstrating that a balance must be struck between the quantity of data versus the quality of observations and that 2D and 3D models are often comparable (Freer et al., 2020). Given these findings, we consider the use of predominantly surface environmental variables in this study to provide a reasonable proxy for preferred conditions of mesopelagic fish species.

Environmental predictors were compiled in the statistical software R, version 4.0.4 (R Core Team, 2021) using the *raadtools* package (Sumner, 2018, Table 1) and the package *maptools* for solar position (Bivand et al., 2021). Monthly means were used for dynamic environmental variables across the temporal range of the data (January 1991 – February 2016). However, where monthly data were not available, monthly climatologies or annual means were used (e.g. mixed layer depth). All variables were resampled to a 0.1° x 0.1° grid using

TABLE 1 Environmental covariates used to model the abundance of a selection of mesopelagic fish species in the Southern Ocean.

Abbreviation (unit)	Description	Spatial resolution	Temporal resolution	Source	Biological relevance
BATH (m)	Measured and estimated seafloor bathymetry from satellite altimetry and ship depth soundings.	1 minute	static	Smith and Sandwell (1997) V15.1	Indicator of shelf, slope or pelagic environments (Duhamel et al., 2014).
CHLA (mg/m <sup>3</sup> )	Chlorophyll-a concentration calculated from satellite-based remote sensing	9 km monthly	mean	NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Sea-viewing Wide Field-of-view Sensor. (SeaWiFS) Chlorophyll Data; 2018 Reprocessing. NASA OB.DAAC, Greenbelt, MD, USA. doi: data/10.5067/ORBVIEW-2/SEAWIFS/L3M/CHL/2018. NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) AquaChlorophyll Data; 2018 Reprocessing. NASA OB.DAAC, Greenbelt, MD, USA. doi: data/10.5067/AQUA/MODIS/L3M/CHL/2018.	Proxy for phytoplankton production. May indicate upwelling of nutrient-rich water stimulating phytoplankton growth (Sokolov and Rintoul, 2007b).
DO200 (ml/L)	Objectively interpolated mean field for dissolved oxygen at 200 m depths	1°	monthly climatology	World Ocean Database 2013 (Boyer et al., 2013)	Proxy for different water masses (Pardo et al., 2012) and dissolved oxygen concentrations have been shown to influence migration depths (Bianchi

(Continued)

TABLE 1 Continued

Abbreviation (unit)	Description	Spatial resolution	Temporal resolution	Source	Biological relevance
					et al., 2013; Klevjer et al., 2016).
MLD (m)	Compilation of Argo float data and ship-based observations for mixed layer depth.	1°	monthly climatology	Retrieved from <i>raadtools</i> (Sumner, 2018)	MLD is the depth of change from homogenized mixed water of the surface to dense stratified water of the deep ocean. It provides an indicator of water mass properties (Bost et al., 2009; Sallée et al., 2021), and influences light availability, nutrient supply (Sallée et al., 2021), and gas exchange between the atmosphere and ocean (Verdy et al., 2007).
POC (g C/m <sup>2</sup> /day)	Particulate organic carbon flux calculated from the seasonal variation index of net primary production monthly layers	0.1°	annual mean	<a href="http://sites.science.oregonstate.edu/ocean.productivity/custom.php">http://sites.science.oregonstate.edu/ocean.productivity/custom.php</a>	Proxy for primary productivity. May indicate prey availability (Proud et al., 2017).
SSHa (m)	Altimeter satellite gridded sea surface height anomalies computed with respect to a twenty-year mean	0.25°	monthly mean	Generated and produced by Copernicus Marine and Environment Monitoring Service <a href="https://resources.marine.copernicus.eu/?option=com_csw&amp;view=details&amp;product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047">https://resources.marine.copernicus.eu/?option=com_csw&amp;view=details&amp;product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047</a>	Variability in sea surface height. Proxy for shifting frontal systems (Sokolov and Rintoul, 2007a). Regions of high activity may indicate upwelling of nutrients (Moore and Abbott, 2000).
SSHg (rad)	sea surface height spatial gradient	0.25°	monthly mean	Generated and produced by Copernicus Marine and Environment Monitoring Service <a href="https://resources.marine.copernicus.eu/?option=com_csw&amp;view=details&amp;product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047">https://resources.marine.copernicus.eu/?option=com_csw&amp;view=details&amp;product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047</a>	Proxy for frontal systems (Sokolov and Rintoul, 2007a; Bost et al., 2009). Regions of high activity may indicate upwelling of nutrients (Moore and Abbott, 2000)
SST (°C)	sea surface temperature	1°	monthly mean	NOAA Optimum Interpolation Sea Surface Temperature (OISST) v2.1 (Huang et al., 2021).	Proxy for different water masses (Bost et al., 2009). Marine taxa also have distinct thermal tolerance ranges that constrain their distributions (Poloczanska et al., 2013; Freer et al., 2019).
SSTa (°C)	Sea surface temperature anomaly calculated by subtracting the long-term monthly mean from the monthly values in SST (°C) layer.	1°	monthly mean	NOAA Optimum Interpolation Sea Surface Temperature (OISST) v2.1 (Huang et al., 2021).	Variability in sea surface temperature. Proxy for ocean circulation variability (Vivier et al., 2010).
VEL250 (mm/s)	Upward sea water velocity at 250 m depth from CSIRO Mk3.5 model.	0.1°	derived data	(Gordon et al., 2010)	Proxy for mesoscale eddy activity, which can indicate upwelling of nutrients suggesting areas of increased primary productivity (Bost et al., 2009). May also influence

(Continued)

TABLE 1 Continued

Abbreviation (unit)	Description	Spatial resolution	Temporal resolution	Source	Biological relevance
					the diel vertical migration of taxa (Cisewski et al., 2021) or advection of organisms (Bost et al., 2009).
NET	Net type used for trawling: IYGPT with MIDOC, IYGPT, RMT 25, RMT 8	per net haul	per net haul	(Woods et al., 2021)	Can influence abundance estimates through differences in catch efficiency (Pakhomov and Yamamura, 2010) (Kaartvedt et al., 2012) (Irigoien et al., 2014).
CODEND (m)	cod-end mesh size	per net haul	per net haul	(Woods et al., 2021)	Can influence abundance estimates through differences in catch efficiency (Pakhomov and Yamamura, 2010) (Kaartvedt et al., 2012) (Irigoien et al., 2014).
DEPTHmax (m)	maximum depth the net fished.	per net haul	per net haul	(Woods et al., 2021)	Indicates the vertical distribution of species.
DEPTHmin (m)	minimum depth the net fished.	per net haul	per net haul	(Woods et al., 2021)	Indicates the vertical distribution of species.
SOLp (°)	Calculated using maptools based on algorithms provided by the National Oceanic & Atmospheric Administration (NOAA)	per net haul	per net haul	Meeus (1991) accessed via maptools.	Proxy for diel vertical migration; behavior of residing at depths during the day and migrating to shallower waters at night (Brierley, 2014; Duhamel et al., 2014).

bi-linear interpolation (Figure S1). This bi-linear interpolation was a necessary step to fill gaps in covariate coverage. While unavoidable, we do acknowledge that this may introduce some bias/error (see discussion for further consideration of the implications of limited data coverage).

We selected physical oceanographic variables such as sea surface temperature, mixed layer depth, sea surface height and vertical velocity to act as proxies for different water masses, mesoscale eddies, and oceanic fronts that can indicate regions of increased primary productivity or influence the transport of taxa through advective processes (Bost et al., 2009, Table 1). We also selected two variables that relate to productivity, chlorophyll-*a* and particulate organic carbon that can indicate regions of high prey availability (Sokolov and Rintoul, 2007b; Proud et al., 2017).

Catch efficiency varies between net types, which may lead to differences in estimates of abundance (Pakhomov and Yamamura, 2010; Kaartvedt et al., 2012; Irigoien et al., 2014). To account for differences in the catch efficiency between sampling gear, net type and cod-end mesh size were included as categorical predictors for abundance. Further, the minimum and maximum depth of each net haul was included to account for depth preferences and varying DVM behaviors.

Spatial autocorrelation (SAC) is a common characteristic of ecological data. This occurs when observations close to one another have more similar values compared to observations further apart (Cruse et al., 2012). Given our data were collected along transects we anticipated the presence of spatial autocorrelation. To account for this, we included an additional term as a predictor in the model (auto-covariate) to specify the relationship between observations at a location and the observations at a neighbouring location. We followed the three-step process outlined in Cruse et al. (2012) to fit the models with an auto-covariate term. First, we fitted our full model, without an auto-covariate term, and extracted the residuals from the model for each grid cell. Using these residuals we calculated the auto-covariate with a mean focal operation for a first order neighborhood. The final step was to fit the full model again including the auto-covariate as an explanatory term within the model (Cruse et al., 2012).

## 2.4 Boosted Regression Tree model fitting and evaluation

The boosted regression tree (BRT) modelling technique was used to model and predict the abundance of mesopelagic fish

species in the Southern Ocean. BRT is an ensemble method that combines the strengths of many simple models to build a prediction model (Hastie et al., 2001). BRT uses two algorithms to achieve this, simple regression trees and a machine learning technique known as boosting. Simple regression trees partition the response data into subgroups by recursive binary splits as determined by the predictor variables. One of the advantages of regression trees is that they can accommodate missing values within predictor variables by using surrogates (Hastie et al., 2001; Leathwick et al., 2006; Elith et al., 2008). For example, when the best variable to determine the split is missing, the split will be performed on the next best variable. Regression trees structure the data hierarchically, meaning that a response to one input variable will depend on values at higher levels of the tree (Hastie et al., 2001; Elith et al., 2008). An advantage of this is interactions between predictors are automatically modelled. However, less favorably, this can lead to high variability in the final outputs. Any small change in the data can result in a very different series of splits and errors within the data will be propagated to lower levels of the tree (Hastie et al., 2001). However, the second algorithm used in BRT, boosting, reduces the variance introduced by tree-based methods and enhances predictive performance of regression trees (Hastie et al., 2001).

Boosting is a stagewise process in which regression trees are repeatedly fit to the training data and added to the model. At each step of the process, a new tree is added that best reduces the loss function, which is a measure of the loss in predictive performance due to a suboptimal model (Hastie et al., 2001; Elith et al., 2008). The first regression tree best reduces the loss function and at each new iteration the emphasis is placed on the more difficult observations to predict by fitting to the residuals of the previous collection of trees (Elith et al., 2008). The resulting output is an additive regression model in which each tree is an individual term (Elith et al., 2008). The BRT modelling approach has been shown to outperform more traditional approaches, such as generalized additive models that aim to fit a single best model (Elith et al., 2006; Escobar-Flores et al., 2018; Guillaumot et al., 2018).

In this study, a BRT model was fitted for each species in the statistical software R, version 4.0.4 (R Core Team, 2021) using the *gbm* package (Ridgeway, 2006) and additional custom functions from Elith et al. (2008). Abundance models were fitted using a Gaussian distribution. Prior to model fitting, abundance data were log transformed to account for the skewed nature of the data. Data were subsequently reverse log-transformed using Duan's Smearing Estimator (Duan, 1983) for interpretation of model outputs.

Boosted regression trees have three key parameters that must be fine-tuned to prevent over-fitting the models. The learning rate (*lr*) specifies the amount each new tree will contribute to the growing model; tree complexity (*tc*), also known as the interaction depth, specifies the number of nodes in a tree that

determines the potential for fitting interactions; and the bag fraction (*bf*) controls the amount of stochasticity within the model by specifying the proportion of data to be randomly selected at each iteration (Elith et al., 2008). The parameters combine to specify the number of trees (*nt*) needed to achieve the lowest predictive deviance (Elith et al., 2008). To determine optimal parameters for final BRT models, we systematically altered: *lr* = 0.1, 0.5, 0.01 or 0.05; *tc* = 1 to 5; and *bf* = 0.5, 0.7 or 0.8, as recommended in Elith et al. (2008). The resulting candidate models were evaluated using the mean correlation coefficient between observed and predicted values and by comparing the deviance explained of the models resulting from 10-fold cross validation (Leathwick et al., 2006; Elith et al., 2008). The deviance explained is a measure of goodness-of-fit between the predicted and measured values (Elith et al., 2008). This was calculated following Leathwick et al. (2006), where deviance explained (%) = total deviance – CV residual deviance/total deviance × 100. We applied the random 10-fold cross-validation procedure recommended by Elith et al. (2008) where the data were randomly partitioned into testing and training sets. Here, the data were split into ten distinct subsets where the bag fraction determined the size of the subsets. In turn, each subset was used as test data and the remainder as training data (see Table S1 for the final model parameters). Finally, the relative importance of an environmental variable in the final model was based on the number of times it was selected for splitting in individual decision trees, weighted by the squared improvement to the model from each split and averaged across all trees (Friedman and Meulman, 2003; Elith et al., 2008).

Final fitted models (Table S1) were used to obtain circumpolar predictions of the abundance of individual species (areas south of 45°S). Predictions were made for the period of 1997 – 2011 for the summer months of November to February (the period in which most trawl data came from) and averaged to generate an overall summer prediction at 0 – 200 m depths for each species. The epipelagic depth layer (0 – 200 m) was selected for circumpolar predictions to match the common foraging depth of mesopelagic fish predators (Bost et al., 2009; McMahon et al., 2019; Proud et al., 2021). Net type and cod-end mesh were held constant for predictions (RMT 25 with a cod-end mesh of 5 mm) and separate predictions were made for both the daytime (SOLp = 30°) and night-time (SOLp = -30°) periods.

Uncertainty in model predictions were estimated using a bootstrap approach following the procedure outlined in Hindell et al. (2020). Each model was refitted 50 times to a bootstrap sample of the data, and the interquartile range was calculated for each cell from the 50 iterations. To demonstrate the size of the IQR in relation to the mean prediction for each cell, we divided the IQR by the prediction to determine a coefficient of variation. Optimized model parameters were used for each of the 50 iterations and half the data were sampled with replacement to fit the model each time.

### 3 Results

A total of 5446 records of abundance were analyzed for 8 different myctophid species and the genus *Bathylagus* from 1905 net trawls (Figure 1; Table S1). Approximately 67% of records were from the Indian sector and 29% were from the Atlantic sector of the Southern Ocean. The remaining 4% of records originated from the West Pacific sector of the Southern Ocean from the Macquarie Island region (Figure 1).

#### 3.1 Model performance and prediction uncertainty

The mean cross-validated correlation coefficients from 10-fold cross validation ranged from a minimum of 0.49 for *G. fraseri* to a maximum of 0.69 for *K. anderssoni* explaining 23% and 47% of the deviance, respectively (Figure 2; Table S1). Differences in model performance across species did not appear to be related to differences in sample size ( $F_{1,7} = 0.320$ ,  $r^2 = 0.09$ ,  $p = 0.59$ ; Figure S2). For example, *E. antarctica* had the largest sample size ( $n = 1069$ ) and a deviance explained of 39%, while *E. carlsbergi* had the smallest sample size ( $n = 337$ ) and the BRT model performed similarly (deviance explained 39%) to that of *E. antarctica* (Figure S2). Additionally, including a spatial autocorrelation term (SAC) as a predictor in the model did not improve performance (Table S1). As such, we did not include the SAC term in our final predictions.

To assess the robustness of individual BRT models, we analyzed prediction uncertainties using a coefficient of variation. Uncertainties in model predictions were highest for sample data poor regions, for which the predictions were necessarily extrapolations based on geographically distant data from other regions. Furthermore, areas in which abundance predictions were low were more variable compared to areas in which abundance predictions were high (Figure S3). There tended to be less variability for night-time predictions versus daytime. The highest level of uncertainty was seen for *E. carlsbergi* south of the Polar Front (PF) in the Atlantic Ocean where the IQR was 9 times the mean for some grid cells. Abundance models of *Bathylagus* spp. had the lowest levels of uncertainty compared to all other myctophid species with a maximum IQR approximately equal to the mean. The region of highest certainty for *Bathylagus* spp. was the Atlantic Sector south of the PF in areas associated with the highest abundance predictions (Figure S3).

#### 3.2 Environmental predictors

The predictor variables differed in their relative importance (% contribution to the final model) across species (Figure S4).

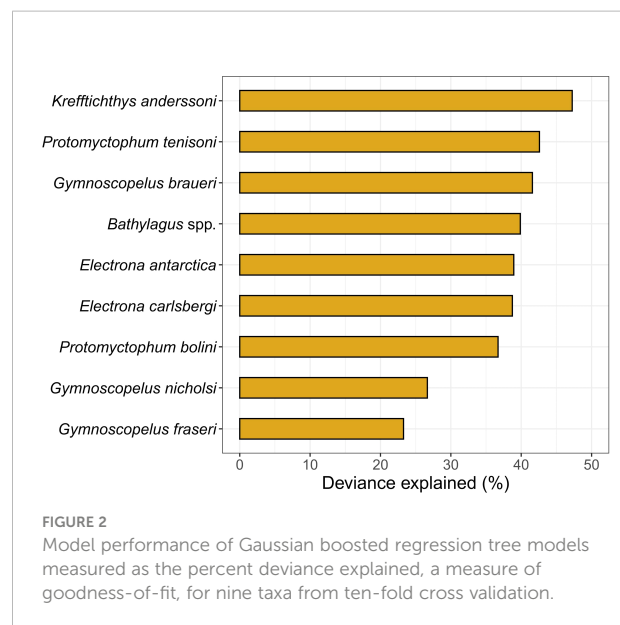


FIGURE 2

Model performance of Gaussian boosted regression tree models measured as the percent deviance explained, a measure of goodness-of-fit, for nine taxa from ten-fold cross validation.

Dissolved oxygen at 200 m ( $DO_{200}$ ) showed the highest relative contribution score as the most important predictor of abundance for *K. anderssoni* (48.8%).  $DO_{200}$  also ranked in the top four covariates for two other species, *P. bolini* (28.4%) and *E. antarctica* (10.2%). Solar position (SOLp) and the maximum depth of the trawl (DEPTHmax) were consistently within the top four most important variables for predicting the abundance of species (six out of nine species models for SOLp and eight out of nine species models for DEPTHmax). The average contribution of SOLp and DEPTHmax across the nine species models was 10.5% and 13.6%, respectively. Chlorophyll-*a* concentration (CHLA) also commonly ranked in the top four most important covariates featuring in five out of the nine species models with an average contribution of 8.4% across the nine species models. Vertical velocity at 250 m (VEL250) was important only to *G. nicholsi* ranking in the top four most important covariates with a relative importance of 19.4%. Similarly, particulate organic carbon (POC) was important only to *G. braueri* (12.1%).

The four most influential predictors for the abundance of each species are shown in Figure 3. Species responses to  $DO_{200}$  (for *K. anderssoni*, *P. bolini* and *E. antarctica*) were similar with the highest abundance predictions across a narrow range of 6–7 ml/L (Figure 3) suggesting an affinity for certain water masses. Abundance of *E. antarctica* and *P. bolini* increased with increasing CHLA; however, the overall response was more complex for *P. tenisoni*, *E. carlsbergi* and *G. fraseri*. Further, abundance estimates for *G. braueri* declined with increasing POC, which contrasts with what we might expect as POC is a proxy for productivity, which would indicate areas of high prey abundance (Proud et al., 2017). Sea surface temperature (SST) was important for *P. bolini*, *G. braueri* and *Bathylagus* spp. Physical oceanographic variables such as VEL250, sea surface



height gradient (SSHg) and sea surface height anomaly (SSHa) were important for *E. carlsbergi*, *P. tenisoni*, *G. nicholsi*, *G. fraseri* and *Bathylagus* spp. suggesting affinities for certain frontal features and mesoscale eddies.

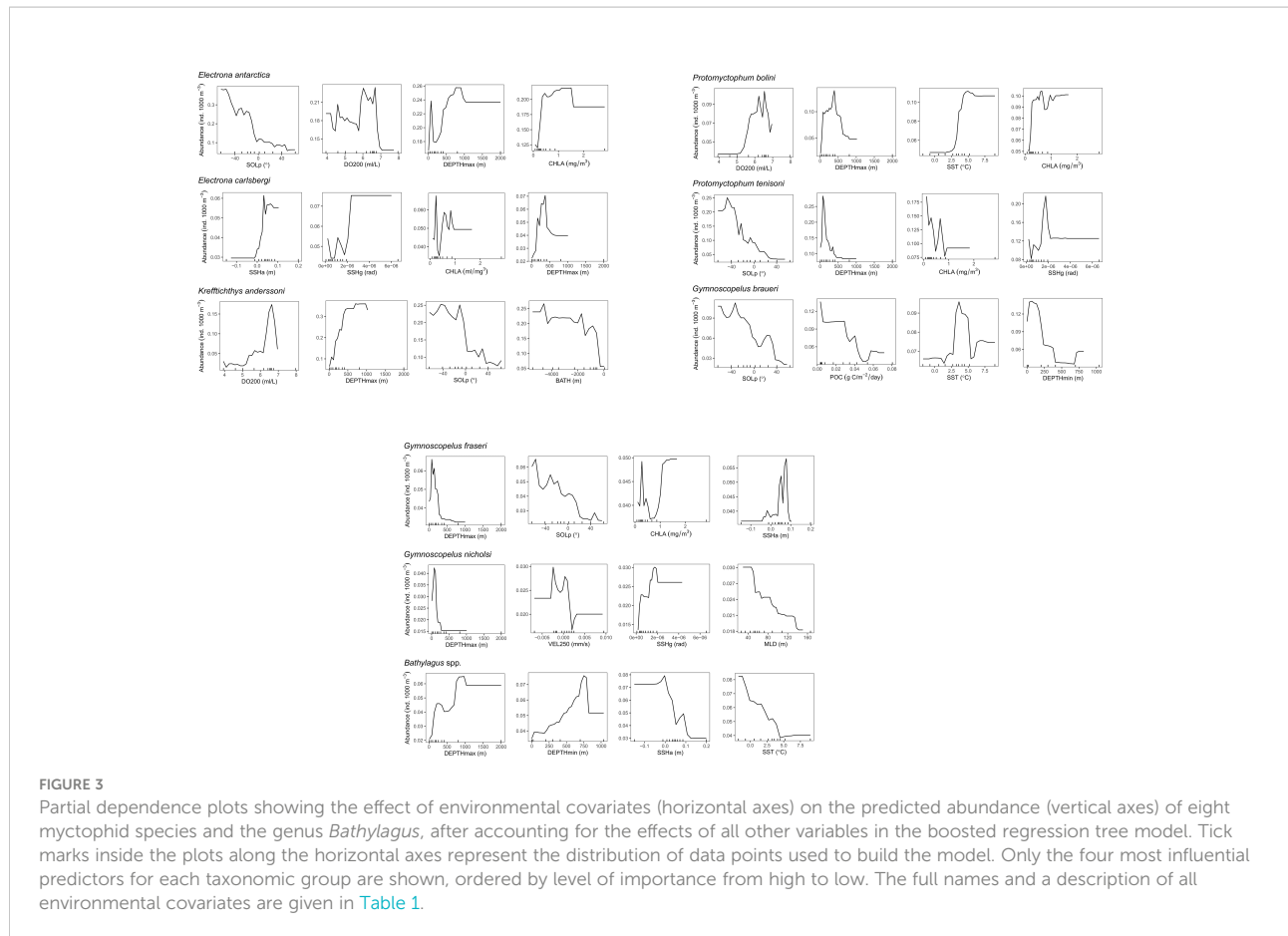
Abundance predictions varied between net type (NET) and codend mesh size (CODEND) with the highest predictions for the RMT 25 with a codend mesh of 5 mm (see example Figure S5). However, different gear types produced the same patterns in relative abundance between predictions (Figure S5). Net type and codend mesh size did not fall within the top four most important covariates for any species-specific models and consistently showed the lowest relative contribution scores with an average of 1.0% and 1.9%, respectively.

### 3.2.1 Predictions in vertical space

The vertical distribution of all species, except for *G. nicholsi*, depended on SOLp (Figures 3–5); and depth preferences varied across species (Figures 3, 4). Clear day-night differences in abundance predictions were observed with higher abundances at night-time (SOLp < 0°) compared to daylight hours (SOLp > 0°). Although abundance predictions seemed to decrease later in the day (larger solar angle) for *P. bolini* compared to other species and abundance was relatively consistent across day and night for

*G. nicholsi* (Figure 4). It must be noted that all species occurred in the top 200 m of the water column at night-time as depicted by the DEPTHmin covariate (Figure 5; Figure S6-S14). However, discussion of proceeding results is in relation to the DEPTHmax variable that reflects the maximum depth of capture for a species.

In the epipelagic zone (0 – 200 m) *E. antarctica*, *P. tenisoni*, *G. braueri* and *G. fraseri* were abundant at night (Figures 3, 4). Abundance predictions declined with depth and increasing SOLp. *Electrona carlsbergi* was sparse in the epipelagic (Figure 4). Predictions showed this species to be most abundant in the upper mesopelagic (200 – 400 m) at night where abundance gradually declined with increasing depth and SOLp. *Kreftlichthys anderssoni* was less constrained by depth and predictions showed a consistent level of abundance across both the upper and lower mesopelagic (200 – 1000 m). However, this was constrained to the night-time hours as abundance predictions decreased from sunrise. *Bathylagus* spp. were most abundant at SOLp < 0° (i.e. night time) in the lower mesopelagic (600 to 1000 m). Abundance was predicted to reduce only marginally at depths deeper than 1000 m and during the daylight hours, showing minimal day-night differences. *Bathylagus* spp. were also relatively sparse at depths shallower than 600 m. *Protomyctophum bolini* showed highest abundances



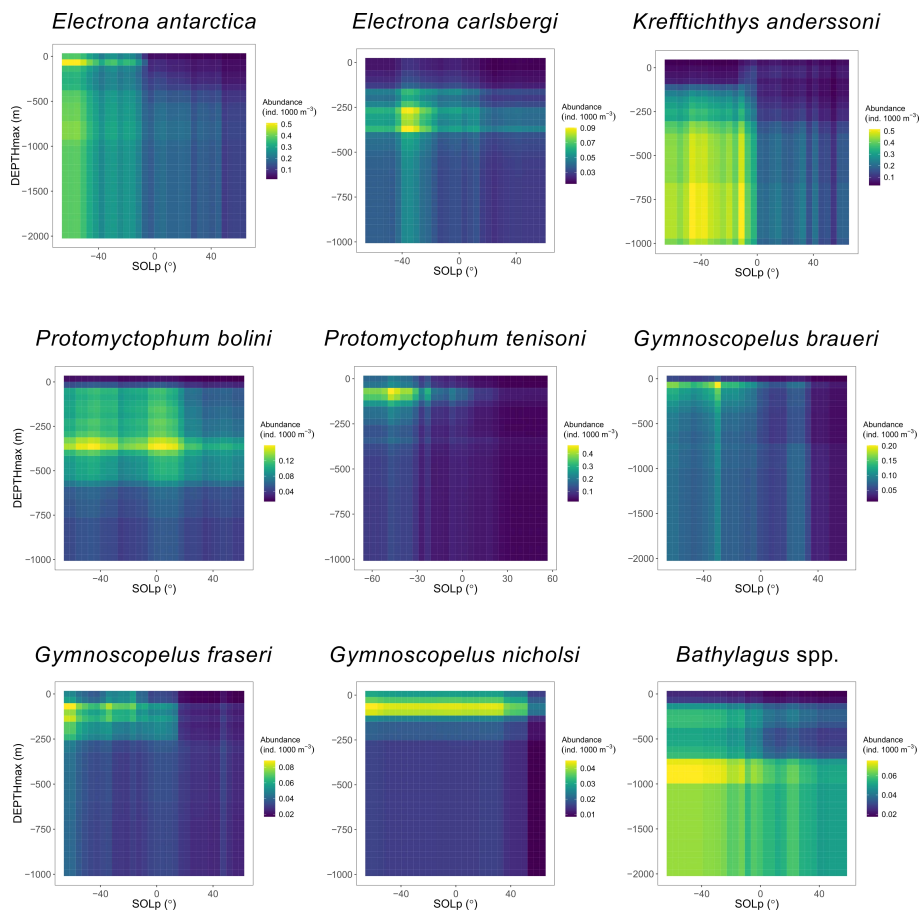


FIGURE 4

Predicted abundance of eight species of myctophid and the genus *Bathylagus* in relation to maximum depth (DEPTHmax) of the trawl, given the variation in solar position (SOLp; negative values indicate night-time, positive values indicate daytime) as predicted by species-specific boosted regression tree models. Color depicts abundance.

for the upper mesopelagic with their distribution extending into both the epipelagic and the lower mesopelagic. *Gymnoscopelus nicholsi* was most abundant in the epipelagic zone.

### 3.3 Spatial predictions

Abundance predictions for species groups revealed broadly circumpolar distribution patterns and clear day-night differences in the epipelagic zone (Figure 5). Predicted abundance in the epipelagic was lower during the day (Figure 5A) compared to the night (Figure 5B) for all species except for *G. nicholsi*.

Two taxonomic groups, *E. antarctica* and *Bathylagus* spp. showed distinct Antarctic distributions with the top decile of their predicted total abundance located south of the PF. *Electrona carlsbergi* showed a patchy spatial distribution with the highest densities close to the PF. Dense aggregations were predicted in areas of high productivity, for example frontal zones

of the Scotia Sea, north of South Georgia, and the southern Patagonian slope spanning to the Falkland Islands. Highest abundance predictions were mainly associated with oceanic regions, except for the Argentinian slope region.

*Krefftichthys anderssoni* and *P. tenisoni* were distributed as circumpolar bands from the PF to north of the sub-Antarctic Front (SAF). The most densely distributed 10% of the total abundance for both species was centered on the SAF. The predicted distribution of both species extended as far north as 45°S off the eastern side of South America. *Protomyctophum tenisoni* appeared to be less common in the eastern sector of the Southern Ocean (from 0° to 90°E), while high abundance estimates were shown for *K. anderssoni* north of the Kerguelen Islands congruent with the SAF. *Protomyctophum bolini* abundance was sparsely distributed south of the PF, but it was densely distributed north of the SAF. The top decile of their predicted total abundance appeared to be constrained to three different regions: the southern Argentinian slope to the Falkland

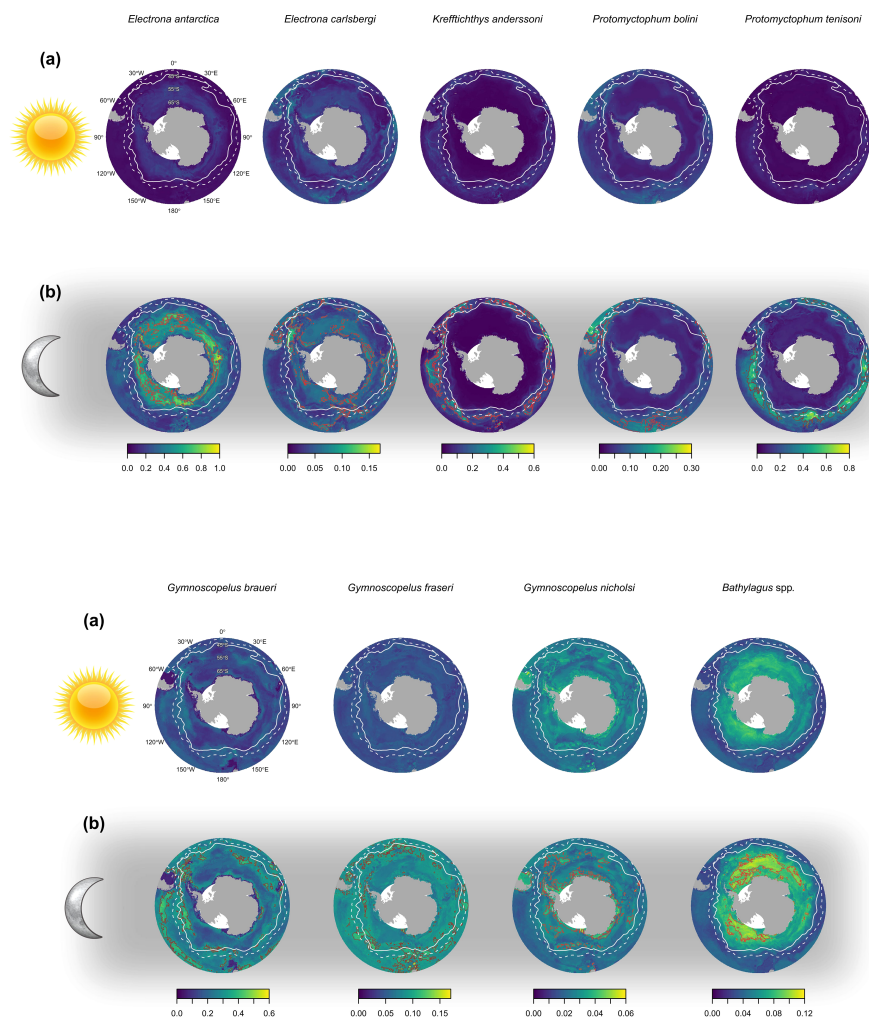


FIGURE 5

The predicted abundance (ind. 1000 m<sup>-3</sup>) of eight species of myctophid and the genus *Bathylagus* at (a) day and (b) night in the top 200 meters of the water column. The brown outline depicts the 90th percentile (top decile) that represents the most densely distributed 10% of the total abundance for the study area. The white solid line shows the position of the polar front (PF), and the white dashed line shows the position of the sub-Antarctic front (SAF). Predictions are for an RMT 25 with a codend mesh of 5 mm.

Islands and north of South Georgia, within the frontal zones to the north of the Kerguelen Islands, and in the region of the Campbell plateau south of New Zealand.

*Gymnoscopelus braueri* and *G. fraseri* showed a spatially broad and patchy circumpolar distribution from the Antarctic continent to 45°S. However, abundance predictions suggested an oceanic distribution for *G. braueri* with the highest densities associated with the sub-Antarctic, Polar Frontal and Antarctic zones. In contrast, high abundance areas for *G. fraseri* appeared to be associated with the slope waters around Falkland Islands, South Georgia, the Kerguelen Islands and south of New Zealand as well as the oceanic regions of frontal zones. *Gymnoscopelus nicholsi* showed a similarly patchy circumpolar distribution, however, distribution patterns were broadly Antarctic with

highest densities predominantly south of the PF. The highest abundances were associated with the Antarctic continental shelf, Argentinian slope waters and the Kerguelen Islands, as well as the oceanic regions of the Antarctic zone.

Species were categorized into three broad groupings based on abundance predictions (Figure 6). We used the categories proposed by McGinnis (1982): “Antarctic”, “Broadly Antarctic”, and “sub-Antarctic”. Most of our study species were categorized as “Broadly Antarctic” (*E. carlsbergi*, *K. anderssoni*, *P. tenisoni*, *G. nicholsi* and *G. braueri*), while *E. antarctica* and *Bathylagus* spp. were classified as “Antarctic” and only one species was considered sub-Antarctic (*P. bolini*). We did not categorize *G. fraseri* as clear patterns in their distribution were difficult to distinguish.

## 4 Discussion

This study provides the first circumpolar predictions of the abundance of eight myctophid species and the genus *Bathylagus*. We used data from *Myctobase*, a database of survey data of mesopelagic fishes, which integrates and standardizes disparate biodiversity data. Boosted regression trees allowed us to examine the environmental, vertical, and geographic patterns of abundance. The novel findings from this study demonstrate the power of a collaborative database and modelling framework approach for dealing with data from heterogenous sources adding information value to existing data. This approach can be used to examine patterns in the circumpolar distribution of myctophid abundance building upon existing modelling efforts that have previously used presence-absence or presence only data. By examining patterns in abundance, we were able to highlight important geographic areas of mesopelagic fish occurrence.

### 4.1 Environmental predictors

The relative importance of selected environmental variables suggests some of the factors that influence the patterns of abundance of our study species. Depth and solar position were consistently important and interacting predictors of abundance. This result is not unexpected given that many mesopelagic fish species undertake diel vertical migration (Duhamel et al., 2000; Collins et al., 2008; Van de Putte et al., 2010; Collins et al., 2012; Saunders et al., 2015; Lourenco et al., 2017). The predominant driving factors of diel vertical migration include the physiological requirement to feed on high concentrations of zooplankton in the epipelagic and to avoid visual predators by migrating to depths during the day (Catul et al., 2011). However, the depth distributions of our study species may be confounded

by the daytime net avoidance behaviors of mesopelagic fishes (Collins et al., 2008; Fielding et al., 2012), which might explain the higher abundances at night compared to day (e.g. Figure 4). Studies conducting daytime trawls on acoustically detected fish in the epipelagic have failed to catch aggregations whilst nighttime trawls consistently yield higher catch rates, suggesting that fish are avoiding the trawl net (Collins et al., 2008; Collins et al., 2012). In this study, the depth distribution and day-night differences in abundance were likely the result of both diel vertical migration and net avoidance.

Maximum migration depth has been linked to dissolved oxygen levels, with the depth of migration shallower in regions with low oxygen levels at the subsurface (Bianchi et al., 2013; Klevjer et al., 2016). A suggested hypothesis for the link between migration depth and dissolved oxygen is that individuals need only travel as far as the oxygen minimum zone to use this region as a refuge from visual predators who generally have higher oxygen demands (Song et al., 2022). We suggest that the high relative importance of DO<sub>200</sub> for predicting abundance of *E. antarctica*, *P. bolini* and *K. anderssoni* might be a consequence of these species utilizing oxygen minimum zones as a predator avoidance strategy. Alternatively, studies on *Benthosema glaciale* in the Boreal to Arctic northeast Atlantic show that the latitudinal variation in seasonal light regime may also be an important control of mesopelagic fish depth distribution patterns (Langbehn et al., 2019; Langbehn et al., 2022), highlighting the need for further investigations into the environmental drivers of myctophid vertical migration behavior in the Southern Ocean.

Chlorophyll-*a* (CHLA) concentration is a proxy for phytoplankton biomass indicating regions of nutrient rich water (Sokolov and Rintoul, 2007b) and potentially profitable foraging areas (Bost et al., 2009; Block et al., 2011). We found that CHLA concentration was important for some species,

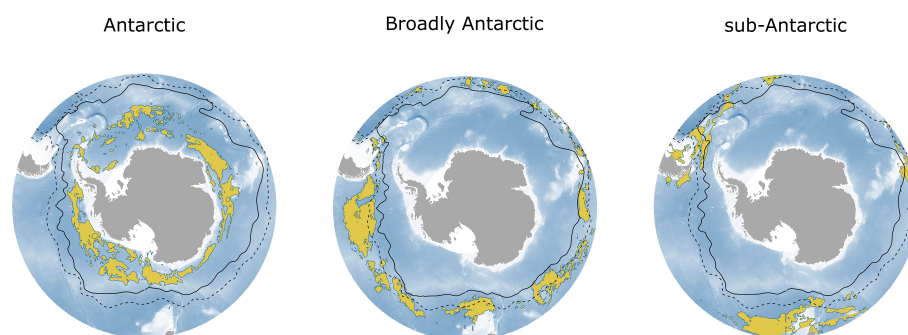


FIGURE 6

The total combined night-time abundance by the broad groupings: 'Antarctic', 'Broadly Antarctic' and 'sub-Antarctic'. Abundance is shown in yellow as the 90th percentile (top decile) of the predicted abundance across the Southern Ocean. The 'Antarctic' grouping includes *Bathylagus* spp. and *E. antarctica*; 'Broadly Antarctic' includes *E. carlsbergi*, *K. anderssoni*, *P. tenisoni*, *G. nicholsi* and *G. braueri*; and 'sub-Antarctic' includes *P. bolini* only. The black solid line shows the position of the polar front (PF), and the black dashed line shows the position of the sub-Antarctic front (SAF).

however the response curves between abundance and CHLA were complex. There might be a temporal or spatial lag between increased CHLA concentration and increasing fish abundance due to the temporal separation of primary and secondary production (Loots et al., 2007; Lehodey et al., 2010). Previous studies have shown similarly mixed results with negative relationships found for *E. antarctica* abundance and CHLA concentration at Kerguelen Islands (Loots et al., 2007), and the absence of a relationship between mesopelagic fish biomass and CHLA in the northeast Pacific Ocean (Saijo et al., 2017). Our results and those from previous studies suggest a decoupling in time and space between CHLA concentration and mesopelagic fish abundance.

Prey availability is likely to be a strong determinant of mesopelagic fish distribution. Direct measurements of prey availability across large spatial extents are difficult to obtain, so researchers typically rely on remotely sensed or modelled products that are linked to prey availability. We used particulate organic carbon (POC) as a proxy for prey availability, which was calculated from the seasonal variation index of net primary production monthly layers (Table 1). Ecological theory states that primary production constrains biomass at higher trophic levels (Jennings et al., 2008). Additionally, mesopelagic fish biomass has been linked to primary production (Irigoin et al., 2014; Proud et al., 2017). However, in this study POC was important for only one species, *G. braueri*. Ultimately, pelagic food webs are fuelled by the primary production produced in the epipelagic zones of the world's ocean (Choy et al., 2017). Here, the biomass generated in the form of zooplankton and filter feeding gelatinous organisms is consumed by a range of taxa including mesopelagic fishes (Choy et al., 2017; Drazen and Sutton, 2017). Production is transported vertically by migratory species or sinking particles, partitioning energy across large depth gradients (Choy et al., 2015). Further, movement of organisms among habitats such as higher predators or expatriate populations can introduce new production and pathways for energy transfer enhancing local production (Polis et al., 1997; Trebilco et al., 2016). Clearly, pelagic food web dynamics are complex, and the lack of clear relationships in this study might be due to the mesopelagic fish assemblage being subsidized by production outside of what is captured by POC measurements.

In ectotherms, metabolism is temperature dependent, which affects physiological functions such as growth and reproduction of marine organisms (Gillooly et al., 2001; Clarke, 2009). Mesopelagic fish species have a range of thermal tolerances with some having a narrower range than others (Freer et al., 2019). In this study, we suggest that SST was a proxy for this tolerance range as all species in this study either migrate to surface waters at night or inhabit near-surface waters as larvae or juveniles (Lancraft et al., 1989; Duhamel et al., 2000; Pusch et al., 2004; Collins et al., 2012). In this study *G. braueri* showed a narrower optimal temperature range compared to that of *P.*

*bolini*, which agrees with predicted future distributions of myctophids (Freer et al., 2019). Freer et al. (2019) showed that *G. braueri* was predicted to lose suitable habitat under different climate change scenarios given its narrow thermal tolerance, while conversely, *P. bolini* was predicted to fair better as it had a wider thermal range.

Other important predictors included  $VEL_{250}$ , SSHg and SSHa, which indicate ocean fronts and eddies. Regions of high water velocity increases the availability of nutrients fuelling marine food webs (Moore and Abbott, 2000). The increase in nutrients promotes increased productivity and zooplankton biomass (Bost et al., 2009) and areas of upwelling and downwelling help to aggregate prey. Myctophid fish concentrate along the periphery of anti-cyclonic eddies where other prey species aggregate (Pakhomov and Froneman, 2000). Additionally, abundance at Antarctic latitudes is driven by oceanic processes, such as high intensity eddies, which facilitate expatriation of mesopelagic fish (Langbehn et al., 2022), for example this has been shown to occur in the Scotia Sea (Saunders et al., 2017; Murphy et al., 2021).

Variability in abundance predictions between net type and codend mesh size aligns with previous research, which demonstrates differences in catch efficiency between net types (Pakhomov and Yamamura, 2010; Kaartvedt et al., 2012). However, we note the minimal influence of net type and codend mesh size on the explanatory power of the final models, which suggests that other environmental variables were more important in predicting abundance.

#### 4.1.1 Vertical distribution

Patterns in the vertical distribution of mesopelagic fish exhibited clear diurnal differences in abundance for all species except for *G. nicholsi*. The night-time vertical habitat trends broadly followed that of previous research (Duhamel et al., 2000; Collins et al., 2008; Hulley and Duhamel, 2011; Saunders et al., 2015; Lourenco et al., 2017; Moteki et al., 2017). The epipelagic zone (0 – 200 m) was important night-time habitat for *E. antarctica*, *P. tenisoni*, *G. braueri* and *G. fraseri*, which follows their reported distribution in the Kerguelen region (Duhamel et al., 2000; Hulley and Duhamel, 2011), the Scotia Sea (Collins et al., 2008; Saunders et al., 2015), and off Wilkes Land, East Antarctica (Moteki et al., 2017). Deeper in the water column, *E. carlsbergi*, *K. anderssoni* and *P. bolini* showed highest night-time abundances within the upper mesopelagic zone (200 – 400 m) consistent with observations from the Kerguelen region (Duhamel et al., 2000) and the Scotia Sea (Collins et al., 2008; Lourenco et al., 2017). High night-time abundance for *K. anderssoni* extended beyond the upper mesopelagic to depths of 1000 m. Previous research has shown an increase in size of individuals with depth suggesting ontogenetic descent (Lourenco et al., 2017), which may reflect the presence of adults within the data we analyzed here. Typically, *Bathylagus* spp. are deep-sea species dominating the lower mesopelagic zone

and are thought to undertake DVM (Lancraft et al., 1989; Koubbi et al., 2011a; Collins et al., 2012), which was reflected in this study. The observed reduced abundance for species during the day provided evidence of DVM consistent with previous reports (Duhamel et al., 2000; Collins et al., 2008; Van de Putte et al., 2010; Collins et al., 2012; Saunders et al., 2015; Lourenco et al., 2017), this is difficult to disentangle from net avoidance behaviors as we described earlier.

We found minimal day-night differences in abundance for *G. nicholsi*. Previously, *G. nicholsi* have been sampled across all three depth zones (epipelagic, upper, and lower mesopelagic) with the highest abundance observed in the top 200 m at night with evidence of DVM (Duhamel et al., 2000; Pusch et al., 2004; Collins et al., 2008; Saunders et al., 2015). In our study the depth range of *G. nicholsi* appeared to be limited to the epipelagic zone with no evidence of DVM.

Overall, our findings provide evidence for non-synchronous DVM patterns for some species. The presence of individuals over broad depth ranges at night-time, for example *E. antarctica* and *K. anderssoni*, could suggest foray-type behaviors among myctophids. Studies in the Scotia Sea have similarly demonstrated the presence of myctophid species at depth during the night (Collins et al., 2008; Saunders et al., 2014). Discrepancies between our findings and those of other studies may be linked to the spatially and temporally dynamic nature of the DVM habits of fish. DVM can vary with season (Saunders et al., 2015; Langbehn et al., 2019; Langbehn et al., 2022) and latitude (Proud et al., 2017; Langbehn et al., 2019; Langbehn et al., 2022), for example, during the summer months at high latitudes the longer daylight hours confine mesopelagic fish to greater depths to avoid predators, leading to a decline in vertical migration amplitude (Langbehn et al., 2019; Langbehn et al., 2022). Further, DVM behaviors can vary depending on the life stage of some species (Collins et al., 2008; Moteki et al., 2009; Lourenco et al., 2017). Survey data of mesopelagic fishes are sparse and highly heterogeneous in space and time (Lehodey et al., 2010). The abundance data we had access to for these species may be inadequate to truly represent the nuanced nature of their DVM behaviors. For example, observations may not be representative of the life stages that exhibit DVM, possibly a consequence of the selectivity differences of trawl nets (Pakhomov and Yamamura, 2010; Kaartvedt et al., 2012). Accurately capturing the subtleties of DVM behavior would require repeated sampling to depict temporal dynamics and expanding the spatial extent and vertical resolution of sampling for broader geographical coverage.

## 4.2 Geographic distribution

We draw comparisons with habitat modelling studies that have used a range of modelling algorithms and data types at both regional and circumpolar scales (Loots et al., 2007; Hulley and

Duhamel, 2011; Koubbi et al., 2011b; Flynn and Williams, 2012; Duhamel et al., 2014; Freer et al., 2019; Freer et al., 2020). In most instances our estimated regions of high abundances aligned with previous circumpolar habitat modelling studies (Duhamel et al., 2014; Freer et al., 2019). These studies used ensemble approaches with presence-only data, or presence-absence data, which provides a species' probability of presence mapped to a geographic area giving an indication of suitable habitat. The relationship between a species presence and its abundance varies spatially, temporally and by species (Karlson et al., 2011; Johnston et al., 2015). Thus, a high probability of occurrence in a location might not always equate to a high abundance and may not effectively capture the core habitat of a species (Renwick et al., 2012; Johnston et al., 2015). The differences between our model predictions and those from the studies described may be explained by the different types of output information and differences in the spatial extent of datasets resulting from variability in modelling approaches.

Species distributions of mesopelagic fish have been categorized into the three broad groupings proposed by McGinnis (1982): "Antarctic", "Broadly Antarctic", and "sub-Antarctic" (Duhamel et al., 2014; Freer et al., 2020). In this study, *E. antarctica* showed an "Antarctic" distribution in agreement with circumpolar occurrence models (Duhamel et al., 2014; Freer et al., 2019; Freer et al., 2020) and abundance models at the Kerguelen Plateau (Loots et al., 2007). *Bathylagus* spp. were similarly "Antarctic" in their distribution. In the Southern Ocean, there are five known species, two of which match this distributional range, *Bathylagus antarcticus* (Gon and Heemstra, 1990; Moteki et al., 2009; Collins et al., 2012) and *Bathylagus niger* (Gon and Heemstra, 1990; Kobylanski, 2006). Put together with our vertical distribution findings for *Bathylagus* spp. this may indicate that most of the individuals here were that of *B. antarcticus* and *B. niger*.

*Krefflichthys anderssoni*, and *P. tenisoni* were "Broadly Antarctic" in their distribution, again in agreement with occurrence models (Duhamel et al., 2014; Freer et al., 2020); and models of biomass at Macquarie Island (Flynn and Williams, 2012). *Protomyctophum bolini* showed a more northerly distribution compared to previous habitat models suggesting a "sub-Antarctic" distribution pattern. Models based on occurrence data have described their distribution as "broadly Antarctic", ranging from the SACCF to the SAF (Duhamel et al., 2014; Freer et al., 2020). However, in this study, the core abundance for this species was located north of the SAF in three localized and highly productive regions (Moore and Abbott, 2000). Our findings agree with previous research showing core reproductive populations for *P. bolini* along with other myctophid species are centered at sub-Antarctic latitude (Saunders et al., 2017).

*Gymnoscopelus nicholsi* has been described as "broadly Antarctic" with an affinity for shelf and slope areas (Duhamel et al., 2014; Freer et al., 2020). Adults are benthopelagic and are

typically distributed close to the seabed over the Argentinian slope, the Crozet slope, South Georgia slope and the Kerguelen Plateau (Linkowski, 1985). Larvae and juveniles are generally located in pelagic waters shallower in the water column (Linkowski, 1985). This may explain our abundance predictions across a diverse range of habitat types.

Predictions for *E. carlsbergi* show patterns of high abundance extending from the SAF to the continent suggesting a “broadly Antarctic” distribution. Freer et al. (2020) found high habitat suitability north of the PF at depths of 500 – 1000 m and high habitat suitability south of the PF at shallower depths (0 – 200 m) with 3D species distribution models. This pattern of deeper residency at lower latitude was first hypothesized by (Hulley, 1981). This corroborates our findings of regions of high abundance south of the PF in the epipelagic zone.

High abundance regions for *G. braueri* were predominately located near the PF. Previous habitat modelling studies have predicted suitable habitat in restricted regions south of the PF (Freer et al., 2020). High abundances have also been recorded at the South Orkneys and South Shetland Islands (Pusch et al., 2004; Saunders et al., 2015); and in the Polar Frontal Zone of the Scotia Sea (Saunders et al., 2015). However, this species has been documented north of the PF at Ridge Gap, Macquarie Island (Flynn and Williams, 2012). Our results match with the “broadly Antarctic” distribution suggested in Duhamel et al. (2014), rather than “Antarctic” as indicated by Freer et al. (2020).

Abundance predictions for *G. fraseri* were dispersed across the study area from 45°S to the Antarctic continent. Clear patterns in their distribution were difficult to distinguish from our predictions. *Gymnoscopelus fraseri* have previously been recorded between the SACCF and the PF (Collins et al., 2012; Saunders et al., 2015). Suitable habitat has also been predicted as far north as the SAF (Duhamel et al., 2014). The discrepancy between our study and observed distributions may be explained by the relatively poor performance of this model.

### 4.3 Developing ecological perspectives

Patterns in myctophid abundance are influenced by meso- and sub-mesoscale oceanographic features where the Polar Front acts as a major delimiting feature for community composition. The Polar Front is one of the most important oceanic fronts in delineating ecological communities in the Southern Ocean (Grant et al., 2006; Longhurst, 2007; Koubbi et al., 2011b; De Broyer et al., 2014). Southern Ocean marine ecosystems are heavily influenced by frontal systems that separate regions with distinct physical and chemical properties (Grant et al., 2006; Longhurst, 2007). The varying physical and chemical properties are important determinants of regional food web structure and function (Murphy et al., 2012). In our study

the Polar Front marked a clear transition from a diverse mesopelagic fish community in the sub-Antarctic zone to a less diverse community south of the Polar Front in the Antarctic zone. Previous studies have demonstrated latitudinal variability in food web structure as indicated by the presence of longer food chains in the north (Stowasser et al., 2012; Ward et al., 2012; Saporiti et al., 2015; Woods et al., 2020). The increase in food chain length from south to north is accompanied by an increase in species richness (Koubbi et al., 2011b; Ward et al., 2012; Saporiti et al., 2015). Food chain theory dictates that food chain length increases with increasing ecosystem size and species richness (Cohen and Newman, 1991; Post et al., 2000; Post, 2002). In our study the contrasting patterns in community composition with higher species diversity north of the Polar Front may be indicative of latitudinal variability in food web structure.

Southern Ocean ecosystems are additionally characterized by a high degree of ecological connectivity between regions due to cross-frontal processes such as surface currents and eddy activity (Hunt et al., 2016; Murphy et al., 2021). Many myctophid species, such as *E. carlsbergi*, *P. bolini*, *P. tenisoni*, *G. braueri*, *G. fraseri* and *G. nicholsi*, found south of the Polar Front do not recruit locally and are thought to be of sub-Antarctic origin (Saunders et al., 2017). Spawning and recruitment is suggested to occur in waters north of the Polar Front and high-intensity eddies facilitate the movement of adults into Antarctic waters (Saunders et al., 2017). The mesopelagic fish biomass north of the Polar Front is likely to be of crucial importance to sustaining mesopelagic fish biomass at Antarctic latitudes (Murphy et al., 2013; Saunders et al., 2017). This means that expatriate populations may play a key role in the maintenance of ecosystem stability and sustaining higher-level predator biomass at Antarctic latitudes. Habitat modelling studies do not currently consider the extent that expatriation plays in determining habitat range. Future ecological studies are needed to resolve important areas for reproduction, migration pathways and connectivity processes.

### 4.4 Conclusion

We used data from *Myctobase* to model patterns in abundance of key mesopelagic fish taxa in the Southern Ocean. Data originated from multiple research cruises, each employing a specific sampling strategy. We accounted for the complexity and uncertainty in the data by explicitly modelling aspects of the survey methodology, providing an example of data usage from *Myctobase*. We demonstrate the value of net data to resolve patterns in relative abundance of species, providing a complementary approach to acoustic methods. Detailed knowledge of the environmental and latitudinal preferences of mesopelagic fishes is imperative to understand how the

community may respond to future environmental change in the Southern Ocean. Our findings suggest that abundance could be influenced by meso- and sub-mesoscale oceanographic features where the Polar Front is a major delimiting feature for the distribution of species. Although finer resolution data are needed to test this hypothesis further. Specific environmental and latitudinal preferences will likely influence the vulnerability of certain species to shifting environmental conditions. For example, *G. braueri* showed a narrow optimal temperature range suggesting this species is likely to be vulnerable to ocean warming in the future, which corroborates findings by Freer et al. (2019). Further, a shift in frontal features may disrupt the influx of expatriate fish to Antarctic latitudes, leading to localized population depletion and a decrease in prey availability for predators. Our study highlights remaining uncertainties such as mesopelagic fish habitat in the Pacific sector. We found regions of high abundance for some species in the Ross, Bellingshausen, and Amundsen Seas despite this being a data poor region. Subsequently, this area would benefit from increased sampling effort. Our spatial analysis is an important step toward resolving important habitat of mesopelagic fishes, which underpins knowledge of shifting food web dynamics into the future. Future modelling efforts should investigate the use of more direct indicators of prey availability by including data layers such as those from the spatial ecosystem and population dynamics model or SEAPODYM (Lehodey et al., 2008). Continued contributions to *Myctobase* will allow improvement of the models we created here and establishment of a solid foundation upon which to understand future population change.

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## Data availability statement

Publicly available datasets were analysed in this study. This data can be found on Zenodo: <https://zenodo.org/record/6809070>, GBIF: <https://doi.org/10.15468/u25dy5>, OBIS <https://obis.org/dataset/d8b738c8-6eda-4735-8136-53630eedab6a> and the SCAR Antarctic biodiversity Portal <https://ipt.biodiversity.aq/resource?r=myctobase&v=1.0>. The R code used in this paper can be found on GitHub: <https://github.com/BreeWoods/Myctobase-SDMs>.

## Author contributions

BW led the project. BW, AVP, RT, and AW were responsible for the conceptualization and design of the project. All authors contributed to the data analysis. All authors contributed to the writing and editing of this manuscript and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.981434/full#supplementary-material>



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