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Spatial structuring in early life stage fish diversity in the Scotia Sea region of the Southern Ocean

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Abstract

The fish community of the Scotia Sea is diverse and plays key roles in Antarctic food webs and biogeochemical cycling. However, knowledge of the spatial and community structure of their early life stages is limited, particularly in the region surrounding the South Orkney Islands. Here we examine the structure of the early life stage fish community in the epipelagic using data from a basin-scale survey conducted in early 2019, which sampled the top 200 m of the water column. 347 early life stage fish from 19 genera were caught in 58 hauls. A third of all specimens belonged to the genus *Notolepis* and the nine most common genera comprised over 90% of specimens. Cluster analysis revealed five distinct groupings, the most common were a group dominated by pelagic and shelf slope genera (*Notolepis*, *Muraenolepis* and *Electrona*) found mainly in oceanic waters (depth ≥ 1000 m), and a group dominated by species with demersal or benthopelagic adults (*Chionodraco*, *Chaenocephalus* and *Nototheniops*) found mainly in shelf waters. Bottom depth was the main environmental determinant of community structure, separating the diverse on-shelf assemblage at the South Orkneys from the less species-rich community of widespread oceanic taxa. Our results indicate the highest diversities of early life stages of endemic fish occur on the shelf and near-shelf areas. Dedicated monitoring is recommended to understand the seasonal differences in larval community assemblages and the implications of early life stages fish bycatch within the krill fishery.

Keywords Scotia Sea · Larval fish · Community structure · Distribution · South Orkney

Introduction

The Southern Ocean is home to a diverse fish community, comprising of at least 374 species of which 88% are endemic (Eastman 2005; Duhamel et al. 2014). One of the most productive areas in the Southern Ocean is the Scotia Sea region (a term which we use to refer to the Scotia Sea basin and the neighbouring seas to the north and west of the Antarctic Peninsula—Fig. 1). This region supports large populations of higher predators and commercial fisheries for Antarctic krill (*Euphausia superba*), mackerel icefish (*Champsocephalus gunnari*) and two species of toothfish (*Dissostichus* spp.) (Murphy et al. 2007). Within the Scotia

Sea, the community of adult finfishes (hereafter fishes) can broadly be categorised as pelagic or benthic-shelf associated based on their habitat preference, with further subdivisions based on their depth of occupation (Duhamel et al. 2014; Caccavo et al. 2021).

In the pelagic realm, mesopelagic lanternfishes (Myctophidae) dominate the Scotia Sea community in both species richness and biomass (Collins et al. 2012). Myctophidae are known to play important roles in biogeochemical cycling through vertical migration (Belcher et al. 2019) and are prey for iconic predators including Antarctic fur seals (*Arctocephalus gazella*) and King penguins (*Aptenodytes patagonicus*) (Duhamel 1998; Lea et al. 2002). In addition, Bathylagidae, Paralepididae and Gonostomatidae are commonly encountered in the open ocean regions of Scotia Sea (Duhamel et al. 2014; Dornan et al. 2019). Antarctic silverfish (*Pleuragramma antarctica*, Nototheniidae) dominate the pelagic fish community close to the continent, where they are a vital component in the food web of the cryopelagic ecosystem (La Mesa and Eastman 2012; Duhamel et al.

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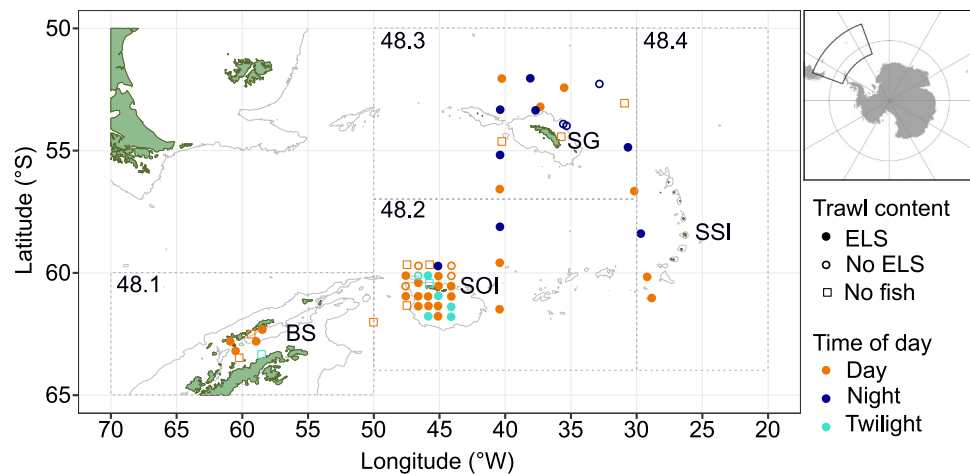2 Institute of Marine Research, Nordnes, P.O. Box 1870, 5817 Bergen, Norway

Fig. 1 Macroplankton trawl sampling locations, filled circles indicate samples containing early life stage (ELS) fish, empty circles indicate samples containing adult fish but no ELS, and empty squares indicate no fish in catch. Colours indicate daylight conditions at start of trawl, 'day', 'night' or 'nautical twilight' (where the sun was 0–12° below the horizon), as calculated using r package 'maptools' (Bivand and Lewin-Koh 2018). Land mass is filled green, 1000 m bathymetry grey, CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) sub areas 48.1–48.4 dashed boxes. *BS* Bransfield Strait, *SOI* South Orkney Islands, *SG* South Georgia, *SSI* South Sandwich Islands. Inset map shows plot area in relation to Antarctica

2014; Caccavo et al. 2018). The demersal biomass on island and continental shelves is dominated by Nototheniidae and icefishes (Channichthyidae) (Duhamel et al. 2014). These families respectively include the commercially fished toothfishes and mackerel icefish. The Nototheniidae also includes the marbled rock cod (*Notothenia rossii*), which was heavily fished in the 1970s (Kock et al. 2004) and is now showing signs of a slow recovery (Hollyman et al. 2021).

Whilst there are no truly epipelagic fish species present in the Scotia Sea, many have epipelagic larval and juvenile phases (Loeb et al. 1993). According to the review by Loeb et al. (1993), the distribution of larval Antarctic fish is best described in the Scotia Sea region, although studies tend to be spatially restricted, with most data being collected in the 1970s and 1980s. In addition, data on the larval fish fauna around the South Orkneys are very limited (Kock and Jones 2005). The few studies that have considered the ecology or distribution of early life stages since Loeb et al. (1993) include an exploration of temporal trends in larval fish abundance in Cumberland Bay, South Georgia (Belchier and Lawson 2013), a study of the distribution of the larval notothenioid assemblage of the West Antarctic Peninsula (La Mesa et al. 2016), a model of larval transport and retention of *C. gunnari* and *N. rossii* (Young et al. 2015), and the circumpolar genetic connectivity of *P. antarctica* (Caccavo et al. 2018). Addressing knowledge gaps on the distribution of early life stage fish is essential to monitor change in the ecosystem.

There are concerns about the potential impact of human activities on the biodiversity of the Southern Ocean (Rintoul et al. 2018). Foremost amongst these are the effects of

anthropogenic climate change and fishing (Brooks et al. 2018; Meredith et al. 2019; Rogers et al. 2020). The Scotia Sea region has had one of the fastest rates of warming on the planet, with ocean warming particularly concentrated in the surface layers (Meredith & King 2005; Whitehouse et al. 2008). Whilst there has been a pause in warming in the early twenty-first century, modelling indicates that this is consistant with natural variability and further warming is predicted (Turner et al. 2016). The Scotia Sea is also the focus of the Antarctic krill fishery (Nicol and Foster 2016). Managed by Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the fishery was originally widespread, but since the 1990s has operated only in the Scotia Sea region (Kawaguchi and Nicol 2020). Krill is harvested using pelagic trawls in the upper water column, with fishing quotas allocated between sub areas to distribute catch (Fig. 1). However, fishing pressure has become more spatially concentred within the region over time (Kawaguchi and Nicol 2020; Watters and Hinke 2022). Larval and juvenile fish are regularly found in krill bycatch (La Mesa and Ashford 2008), and whilst bycatch rates are lower than for other trawl fisheries globally (Krafft et al. 2022) knowledge of vulnerable periods and areas are important to manage the spatial distribution of the fishery, particularly as it develops and environmental conditions change (Meyer et al. 2020; Cavanagh et al. 2021; Trathan et al. 2022). There is also a risk of indirect (competitive) impacts of the fishery as many adult fish species also feed on Antarctic krill (Kock et al. 2012; Saunders et al. 2015).

Here we report the distribution and diversity of the epipelagic early life stages of the fish community in the Scotia

Sea region based on a basin-scale, near-synoptic net survey conducted in austral summer 2019. In the current paper, we use the term early life stages to refer to larval and a subset of juvenile fish sampled using a macroplankton trawl in the upper 200 m of the water column (see Methods "Trawl sampling"). The survey included intensive sampling on the South Orkneys shelf as well as transects in open-ocean areas for which data are otherwise scarce. We use cluster analysis to characterise the assemblages of co-occurring species observed in the survey and we assess the relationship between the composition of these assemblages and candidate environmental variables. We then discuss our results in the context of adult distribution and community connectivity.

Methods

Trawl sampling

As part of a large-scale survey to assess krill abundance and develop knowledge on the marine environment (Krafft et al. 2021), fish and ichthyoplankton sampling was undertaken on the RV *Kronprins Haakon* between 17/01/2019 and 14/02/2019. Samples were collected using a fine-meshed Macroplankton trawl, at 58 predetermined sampling locations across the Scotia Sea region (Fig. 1). Scanmar depth and speed/symmetry sensors were mounted on the trawl headline to monitor and record trawl performance during towing. A hull-mounted thermosalinograph (depth 4 m), provided additional surface data for fluorescence, salinity and temperature.

The Macroplankton trawl has a nominal mouth opening of 36 m^2 and net mesh of 3 mm (7 mm when stretched) from mouth opening including the cod-end (Krafft et al. 2010, 2018). Oblique trawls deployed both on- and off-shelf, aimed to sample 2 stations per day as close to 12 am or 12 pm (UTC) as possible. The South Orkney stations were sampled 25 nautical miles apart independent of time of day (see Table ESM1 for trawl details). The trawl was deployed rapidly to depth of ~ 200 m depending on bottom depth and fished in an oblique tow to the surface (mean max. trawl depth 201.00 m, range 249.44–55.69). The trawl was assumed not to be fishing whilst deploying the trawl to depth. Trawls were carried out at a mean vessel speed of 1.46 knots (range 0.83–2.61), and mean trawl duration was 8.99 min (range 1.62–18.30). The number of fish observed per trawl was standardised to number of individuals per 1000 m^3 (hereafter standardised abundance).

Volume of water filtered was calculated based on the trawl mouth opening of ~ 36 m^2 and oblique distance the trawl net travelled from maximum fishing depth to surface, using Pythagoras' theorem. Horizontal distance was calculated from latitude and longitude data obtained via the vessel's navigation system (GPS) held in the Scanmar custom built log files along with Scanmar NMEA telegrams received from the trawl attached speed/symmetry sensors.

Once on deck, fish larvae plus the juveniles of benthic adult taxa were separated from the rest of the catch and identified to the lowest taxonomic resolution possible. All meso- and bathypelagic species (Bathylagidae, Paralepididae, Myctophidae) used in the current analysis were larvae (transparent or only partly pigmented body, photophores not fully developed, telescopic eyes), as were the Congridae (leptocephali) and most of the Notothenioidei (transparent or only partly pigmented body). Some of the Notothenioidei and the gadiform Muraenolepididae and Macrouridae were likely newly transformed juveniles but are included here as their adult habitat is benthic or benthopelagic (Table 3). For convenience we have described this as "early life stage".

Molecular analyses

Several specimens from all genera were frozen (-20°C) and genetic samples preserved in ethanol for further onshore genetic analysis to verify and supplement the morphological identification.

DNA was isolated using removed larval eyes (preferred) or a piece of larval tissue placed into individual wells containing 75 µL of a solution 5% Chelex 100 Resin (BioRad, CA, USA) and 15 µL of Proteinase K (Qiagen, Germany). Samples were then incubated at 56 °C for 1 h followed by 10 min at 96 °C.

PCR was amplified following the procedure described by Mateos-Rivera et al. (2020) targeting the mitochondrial COI gene in 12 µL reactions containing 2.4 µL 5 × buffer, 1 µL of $MgCl_2$ [25 mM], 1.92 µL dNTPs [1.25 mM], 1.44 µL 10 µM primer pair combination with the M13F sequence incorporated in the forward primers (Ivanova et al. 2007), 0.07 µL GoTaq G2 DNA polymerase (Promega, WI, USA), 3.17 µL dH_2O and 2 µL template DNA. The PCR conditions were i) an initial denaturation of 2 min at 95°C, followed by ii) 35 cycles of amplification (denaturation 30 s at 94°C, annealing at 52°C for 30 s and an extension of 1 min at 72°C), and iii) a final extension of 10 min at 72°C. The products were then cleaned using 5 µL of the PCR product and 2 µL ExoSap-IT PCR product Cleanup (ThermoFisher, MA, USA) followed by an incubation at 37°C for 15 min and 80°C for 15 min. Sequencing was performed using 1 µL of M13F primer [0.35 µM].

The resulting sequences (of ca. 600–700 bp) were manually checked for quality control in Geneious v8.0.5 (Kearse et al. 2012) and used as queries for BLASTn in GenBank using the default parameters and individually compared to reference sequences to determine its taxonomic identity.

Statistical analyses

Multivariate statistical analyses were carried out using the analytical package PRIMER 7 (version 7.0.13, Primer-E, Plymouth, UK), with standardised abundance as the response variable. Whilst 58 predetermined sample locations were trawled, only stations ($n = 39$) containing early life stage fish were used in the analysis (see Fig. 1 and Online Resource 1). Statistical analysis was carried out on the lowest taxonomic resolution available for individual taxa. In some cases, visual identification was possible only to genus level and genetic analysis of a subset of individuals provided species-level identification. For each genus where only a subset was identified to species level, the statistical analysis was carried out at genus level to prevent the introduction of artificial spatial boundaries in the community. Specifically, *Artedidraco skottsbergi* was analysed as *Artedidraco* spp., *Bathylagus antarcticus* as *Bathylagus* spp., *Electrona antarctica* as *Electrona* spp., *Muraenolepis marmorata* as *Muraenolepis* spp. and *Notolepis coatsorum* (syn. *Notolepis coatsi*) as *Notolepis* spp.. For these five genera, it is possible that multiple species were present, however, in each of the genetically analysed subsamples only a single species was recorded.

Standardised abundance data were square root transformed to allow for a more even contribution of rare and abundant taxa, and a Bray–Curtis resemblance matrix calculated for each pair of trawl samples. Hierarchical agglomerative cluster analysis using group averages and non-metric multidimensional scaling (nMDS with added 5% metric contribution, see Clarke et al. (2014)) were used to identify group clusters within the trawl samples from the resemblance matrix. Significance of clusters was tested using a similarity profile (SIMPROF) routine with a significance level of 5%. To identify the dominant taxa contributing to group differences, a similarity percentage (SIMPER) routine was applied to the SIMPROF groups. Shannon–Wiener diversity indices were calculated for each trawl with a fish sample size ≥ 5.

Environmental variables

Abiotic environmental variables were investigated to identify which best explained the early life stage fish community structure using a PRIMER BEST (Bio-Env) routine applied to the taxa resemblance matrix (see Table 1 for data sources). Continuous variables were latitude, longitude, water depth, sea surface temperature, primary productivity, salinity (at 4 m depth), fluorescence (at 4 m depth), dynamic height (a proxy for frontal positions) and geostrophic current speed. We also included the factor of sampling time of day. CCAMLR subareas, which divide the region into smaller units for fishery management and reporting purposes

(Fig. 1), and the 1000m bathymetric contour (on-shelf versus off-shelf, defined as depth < 1000m and ≥ 1000 m respectively) were used to visualise spatial patterns (GEBCO Compilation Group 2019). Based on exploratory histogram and density plots of environmental data, variables were transformed to approximate normality (see Table 1 for transformations applied) and normalised to a common scale using the PRIMER normalise operation, where the values for each variable have their mean subtracted and are divided by their standard deviation. The BEST routine compares the rank correlation coefficients between the communities' Bray–Curtis resemblance matrix and environmental data Euclidean distance matrix. Considering various combinations of environmental variables, BEST matches patterns in the community abundance data to patterns in environmental matrices, by maximising rank correlation between the resemblance matrices such that the routine finds the 'best fitting' suite of environmental variables. As is common in satellite derived products, primary productivity had two missing data points for sampling stations (1 and 8), however, this has limited influence on the analysis as PRIMER automatically applies correction factors to compensate for missing data in resemblance matrices when carrying out BEST routines, using pairwise elimination of missing variables (Clarke et al. 2014). Sunrise and sunset were calculated for each trawl sample based on the trawl time midway through the trawl event (UTC), using a modified sunriseset function in R package 'maptools' (Bivand and Lewin-Koh 2018). Samples were classified as 'Day', 'Night', or 'Twilight' using sunrise, sunset and nautical twilight (where sun is 012° below the horizon).

Results

Community composition

Of 58 non-target Macroplankton trawls undertaken as part of the survey, 39 trawls contained early life stage fish (see Table 2). A total of 347 early life stage fish were sampled, representing 10 families. The Paralepididae, Channichthyidae, Nototheniidae, Myctophidae and Muraenolepididae families accounted for 90% of the early life stage fish sampled.

Paralepididae dominated the early life stage fish community catch (number of individuals $n = 121$, percentage contribution of standardised abundance to the study community = 33.01%) and were entirely comprised of *Notolepis* species. Of the 121 early life stage *Notolepis* spp. sampled, 23 were identified to species level and all were *N. coatsorum*.

The icefishes, Channichthyidae ($n = 61$, 18.77%), were the second most abundant family, and consisted of multiple species including *Chaenocephalus aceratus* ($n = 23$, 8.25%),

Table 1 Environmental variables included in the BEST (Bio-Env) routine and data sources

Variable *Transform*	Abbreviation	Units	Resolution	Product/Source
Sea surface temperature *log(SST)*	SST	°C	0.01° grid Daily	GHRSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis (v4.1) (JPL MUR MEaSUREs Project 2015)
Absolute Dynamic Height (proxy for frontal positions) *log(ADT+0.15)*	ADT	m	0.25° grid daily	E.U. Copernicus Marine and Environment Monitoring Service (CMEMS) Product SEALEVEL_GLO_PHY_L4_NRT_OBSERVA-TIONS_008_046
Geostrophic current speed *log(CurrSpeed)*	CurrSpeed	m s^{-1}		
Primary Productivity *log(PP)*	PP	mg C m^{-2} d^{-1}	1/6° grid 8 day mean	Ocean productivity (Behrenfeld & Falkowski 1997) Available at: http://orca.science.oregonstate.edu/ 1080.by.2160.8day.hdf.vgpm.m.chl.m.sst.php
Fluorescence *log(F)*	F	mg m^3	Trawl duration specific	Hull mounted thermosalinograph at 4 m depth. Mean values were calculated for each trawl location during trawling (1 record every 10th second)
Temperature *log(T)*	T	°C		SCANMAR data was used to identify trawl deployment window
Salinity	S	ratio		
Time of day	DNT	Day Night Twilight		Sunrise, sunset and twilight calculated using R package 'maptools' (Bivand & Lewin-Koh 2018)
Latitude **Longitude**		°		Latitude and Longitude indicate location at the start of the trawl as measure in decimal degrees WG84
Water depth (bathymetry) *sqrt(Depth)*	Depth	m	15 arc-second grid	GEBCO_2019 grid (GEBCO Compilation Group 2019)
Shelf		On Off		On-shelf water depth < 1000 m Off-shelf water depth ≥ 1000 m
CCAMLR Subarea				CCAMLR subareas in region 48 48.1—Antarctic Peninsula region 48.2—South Orkney region 48.3—South Georgia region 48.4—South Sandwich Islands region

Bold variables were used in the BEST analysis, non-bold were used for visualisation of trends. Transform indicates any applied data transformation prior to BEST analysis

Chionodraco rastrospinosus ($n = 27$, 7.50%), *Cryodraco antarcticus* ($n = 5$, 1.28%), *Pseudochaenichthys georgianus* ($n = 4$, 1.32%) and *Chaenodraco wilsoni* ($n = 2$, 0.42%).

Nototheniidae ($n = 40$, 17.65%), were also represented by multiple species, with *Nototheniops larseni* (syn. *Lepidonotothen larseni*, $n = 33$, 10.76%), *Notothenia coriiceps* ($n = 9$, 2.66%), and *N. rossii* ($n = 9$, 2.00%), making up the majority. Early life stage *Lepidonotothen squamifrons* ($n = 3$), *Trematomus loennbergii* ($n = 2$), *Trematomus newnesi* ($n = 1$), *Trematomus eulepidotus* ($n = 1$) and *Dissostichus mawsoni* ($n = 1$) however were rare, and each accounted for less than 1% of all samples.

The Myctophidae ($n = 38$, 11.90%), consisted of a single genus, *Electrona*, of five individuals identified to species level by genetic analysis all were *E. antarctica*.

Muraenolepididae ($n = 40$, 8.64%) consisted of a single genus *Muraenolepis*, of which five were identified to species level, all of which were *M. marmorata*. See Fig. 2, and Table 3 for a breakdown of taxa sampled. The most frequently encountered genera in on-shelf and off-shelf trawls were *Chionodraco* and *Notolepis* (observed in 9 and 16 trawls) respectively, whilst the most widespread genus overall was *Notolepis* (observed in 21 trawls).

Patterns in community assemblage

Diversity

Shannon–Wiener (log *e*) diversity, H' index, was calculated for each trawl station containing 5 or more early life stage fish (see Fig. 3 and Online Resource 2). On-shelf stations ($n = 9$), had the highest maximum taxonomic diversity, indicated by H' index (H' range = 0–1.748), with a mean H' index of 1.232. Off-shelf locations ($n = 13$) had a lower taxonomic diversity (H' range = 0–1.061), mean H' index of 0.770, despite a higher sampling intensity.

Sampling was most intensive on the South Orkney shelf where the highest maximum H' index of 1.748 was recorded. This contributed to a mean H' index of 1.075 for subarea 48.2. Subarea 48.3, encompassing South Georgia,
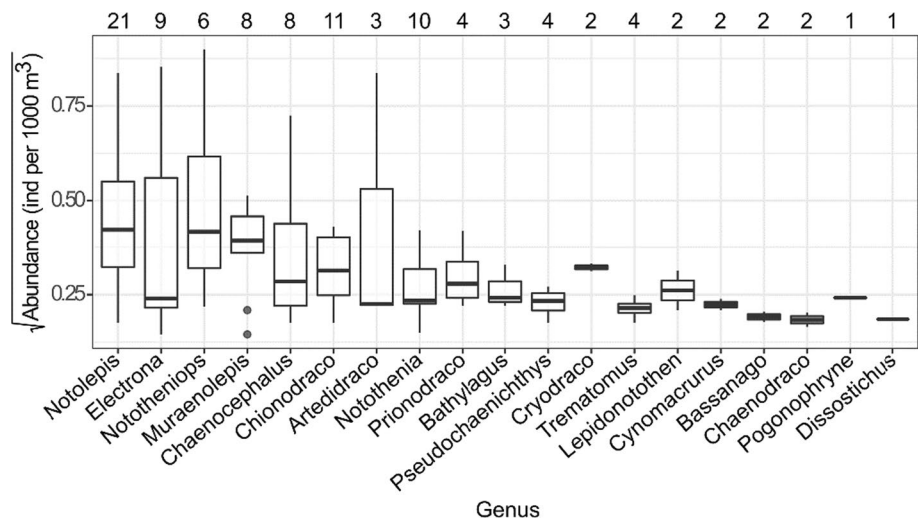
Table 2 Numbers of sampling stations that contained early life stage (ELS) fish subdivided by day, night or twilight, and total ELS fish sampled, in four CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) subareas. Shelf On = water depth < 1000 m, Off = water depth ≥ 1000 m

Subarea	Shelf	Number of stations			Total ELS fish
		Day	Night	Twilight	
48.1	On	3			5
	Off	1			8
48.2	On	8		4	130
	Off	7	2	1	70
48.3	On				
	Off	5	5		107
48.4	On				
	Off	2	1		27
Totals (S_{tot})	All	26 (39)	8 (11)	5 (8)	347

Total ELS fish = number of individual early life stage fish in trawls (not standardised for volume filtered). Totals contains the sum of columns. 'S_{tot}' is the number of sampled stations including stations that did not capture ELS fish. A full summary of all trawl data, which includes trawls with no fish in catch, can be found in Online Resource 1

had a mean H' index of 0.898 (range 0.820–1.012), which was based on 7 stations from off-shelf locations. Estimated H' indices between subareas may not be directly comparable as most on-shelf sampling was restricted to the South Orkney shelf in Area 48.2. Areas 48.1 and 48.4 each had only a single station with 5 or more fish, with relatively low individual H' index values of 0.662 and 0.185 respectively. An overview of trawl sample stations and fish abundance can be found in Online Resource 1.

Taxon distribution

To ensure that rarely occurring taxa were represented, all 39 trawls containing early life stage fish were included to identify spatial patterns in taxonomic assemblages. Figure 4 illustrates the spatial distribution of the early lie stage fish taxa by family throughout the study region.

Group similarity

Hierarchical cluster analysis of the early life stage fish abundance Bray–Curtis similarity matrix generated a number of clusters (Fig. 5). SIMPROF analysis applied to this structure identified 5 significantly different groups at the 5% level. The coherence of these 5 groups was further emphasised by a subsequent nMDS analysis where each showed spatial coherence in n-dimensional space (Fig. 6). Each of these five groups comprised of stations that were predominantly from a single bathymetric region (on- or off-shelf).

Spatial variability

A SIMPER routine was used to assess the taxa contributing to the five groups (Fig. 7). Group 'c', the largest cluster ($n = 16$ sampling stations), was predominantly off-shelf and geographically dispersed. Group 'c' was dominated by pelagic to bathypelagic taxa, principally *Notolepis* spp., with abundant *Muraenolepis* spp., and *Electrona* spp. (see Table 4 for taxa contribution). This group included just 1 on-shelf station, in the Bransfield Strait, that contained only *Notolepis* spp..

Group 'd' was the second largest cluster ($n = 14$ sampling stations) containing a diverse group of taxa that was predominantly on-shelf and generally restricted to the South Orkney's shelf, the main focus of on-shelf sampling. This group was dominated by *C. rastrospinosus*,

Fig. 2 Spread of abundance of each early life stage fish genus (square root transformed, individuals per 1000 m.^{3}) in macroplankton trawls. Box spans interquartile range (IQR), horizontal line is the median, whiskers include values up to 1.5×IQR, outlying values plotted as points. Numbers above each box are the number of individual trawl stations containing a specified genus. Taxa are ordered by total standardised abundance, summed across all trawls (see Table 3)

Table 3 Contribution of each genera to total standardised abundance of early life stage fish observed in the study, percentage is based on abundance standardised for volume of water filtered

Genus (Family) ADULT HABITAT	Taxa breakdown	Contribution (%)	Cumulative percent	N	Presence (%)
Notolepis (Paralepididae) MESOPELAGIC/ BATHYPELAGIC	*Notolepis* spp.	26.37			
	Notolepis coatsorum	6.64			
	Notolepis	33.01	33.01	21	53.85
Electrona (Myctophidae) MESOPELAGIC	*Electrona* spp.	10.14			
	Electrona antarctica	1.75			
	Electrona	11.90	44.91	9	23.08
Nototheniops (Nototheniidae) BENTHIC	*Nototheniops larseni*	10.76			
	Nototheniops	10.76	55.66	6	15.38
Muraenolepis (Muraenolepididae) BENTHOPELAGIC	*Muraenolepis* spp.	7.06			
	Muraenolepis marmorata	1.58			
	Muraenolepis	8.65	64.31	8	20.51
Chaenocephalus (Channichthyidae) BENTHIC	*Chaenocephalus aceratus*	8.25			
	Chaenocephalus	8.25	72.56	8	20.51
Chionodraco (Channichthyidae) BENTHIC	*Chionodraco rastrospinosus*	7.50			
	Chionodraco	7.50	80.06	11	28.21
Artedidraco (Artedidraconidae) BENTHIC	*Artedidraco* spp.	0.30			
	Artedidraco skottsbergi	4.63			
	Artedidraco	4.93	84.99	3	7.69
Notothenia (Nototheniidae) BENTHIC	*Notothenia coriiceps*	2.67			
	Notothenia rossii	2.00			
	Notothenia	4.67	89.66	10	25.64
Prionodraco (Bathydraconidae) BENTHIC	*Prionodraco evansii*	2.35			
	Prionodraco	2.35	92.00	4	10.26
Bathylagus (Bathylagidae) MESOPELAGIC/ BATHYPELAGIC	*Bathylagus* spp.	0.97			
	Bathylagus antarcticus	0.36			
	Bathylagus	1.33	93.33	3	7.69
Pseudochaenichthys (Channichthyidae) BENTHIC	*Pseudochaenichthys georgianus*	1.32			
	Pseudochaenichthys	1.32	94.65	4	10.26
Cryodraco (Channichthyidae) BENTHIC	*Cryodraco antarcticus*	1.28			
	Cryodraco	1.28	95.93	2	5.13
Trematomus (Nototheniidae) BENTHIC	*Trematomus loennbergii*	0.46			
	Trematomus newnesi	0.38			
	Trematomus eulepidotus	0.30			
	Trematomus	1.14	97.06	4	10.26
Lepidonotothen (Nototheniidae) BENTHIC	*Lepidonotothen squamifrons*	0.87			
	Lepidonotothen	0.87	97.94	2	5.13
Cynomacrurus (Macrourinae) BATHYPELAGIC	*Cynomacrurus piriei*	0.62			
	Cynomacrurus	0.62	98.56	2	5.13
Bassanago (Congridae) BATHYDEMERSAL*	*Bassanago albescens*	0.45			
	Bassanago	0.45	99.01	2	5.13
Chaenodraco (Channichthyidae) BENTHIC	*Chaenodraco wilsoni*	0.42			
	Chaenodraco	0.42	99.43	2	5.13
Pogonophryne (Artedidraconidae) BENTHIC	*Pogonophryne scotti*	0.36			
	Pogonophryne	0.36	99.79	1	2.56
Dissostichus (Nototheniidae) ENGIBENTHIC	*Dissostichus mawsoni*	0.21			
	Dissostichus	0.21	100.00	1	2.56

Contribution was the sum of taxon-specific standardised abundance (individuals per 1000 m^3) across all nets, divided by the sum of standardised abundance across all taxa and all nets. N denotes the number of trawls each genus was found in. Presence indicates the percentage of trawls each genus was found in, based on the 39 trawls containing early life stage fish. Adult habitat classifications are based on descriptions in Gon and Heemstra (1990) except that for Bassanago (denoted *) which is taken from FishBase (Froese and Pauly 2023)

Fig. 3 Shannon–Wiener diversity index (H') of early life stage taxa of the Scotia Sea. The highest region of diversity is clustered around the South Orkney on-shelf region (dark blue squares) subarea 48.2. Diversity Index calculated only for trawls with 5 or more early life stage samples
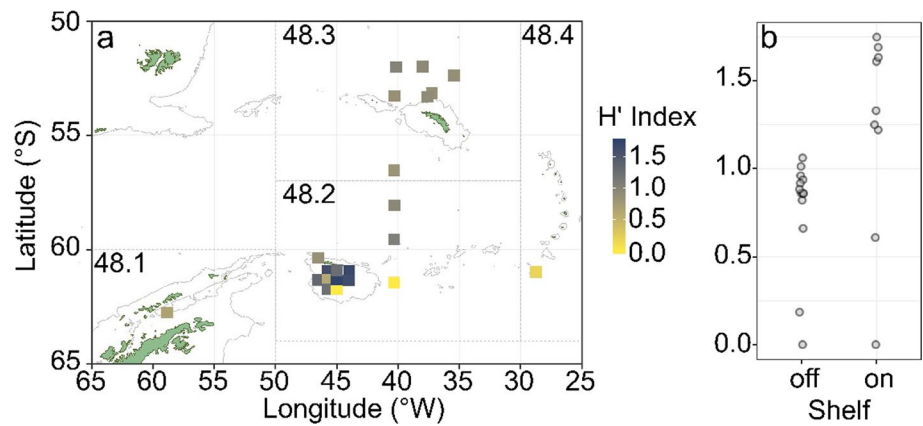

Fig. 4 Spatial distribution of the relative abundance of early life stage fish taxa collected across the study area **a** Antarctic Peninsula/Bransfield Strait region **b** South Orkney region **c** South Georgia and South Sandwich Islands (SSI) regions. For ease of visualisation the two southernmost trawl stations to the southwest of the South Sandwich Islands are shown as an inset in plot c. Radius of circles are proportional to standardised catch abundance with scale maintained across all plots. Note differing axis scales
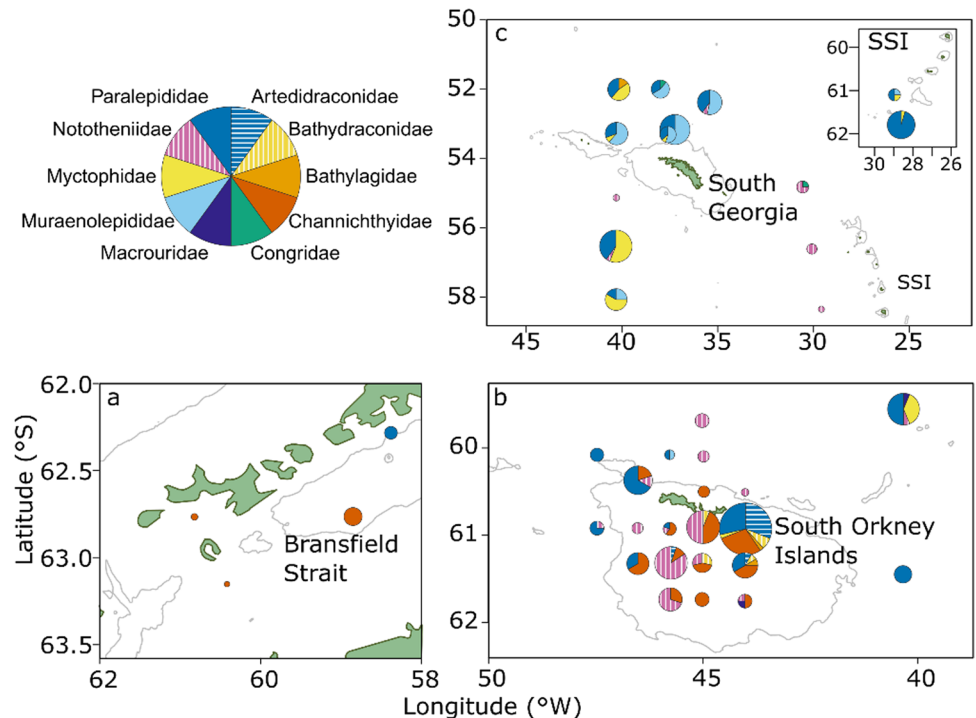
C. aceratus, *N. larseni* and *Notolepis* spp.. One off-shelf station (no. 8, Fig. ESM1) in group 'd' was located in the Bransfield Strait, comprising solely of *C. rastrospinosus* and *C. aceratus*, whilst a second station (no. 18) was located on north-western edge of the South Orkney shelf slope and comprised of *C. rastrospinosus*, *N. larseni*, *Notolepis* spp..

Groups 'a' and 'b', were both entirely off-shelf. Group 'a' ($n=4$ sampling stations), were comprised solely of *N. coriiceps* and were geographically dispersed, occurring throughout the study region, with the exception of subarea 48.1. Group 'b' samples ($n=2$), were predominantly comprised of *N. rossii*, though one station to the north-west of the South Sandwich Islands (SSI) also contained a single individual of *Bassanago albescens* (Congridae). It is worth noting the

both *N. coriiceps* and *N. rossii* occurred in small quantities in additional off-shelf mixed taxa samples from group 'c'.

Group 'e' was comprised of 3 stations, which each contained a single species. On-shelf stations 3 and 4 in the Bransfield strait contained the only records of *C. wilsoni* in the study, these were grouped with one off-shelf station in subarea 48.4, which contained the only record of *D. mawsoni* in the study.

Environmental conditions BEST

To explore the relationships between community assemblage and the prevailing environmental conditions, a BEST (Bio-Env) routine was applied to the taxa resemblance matrix. As highlighted in both cluster analysis and nMDS,

Fig. 5 Hierarchical cluster analysis (HCA) of the early life stage abundance Bray–Curtis similarity matrix. All individuals captured in the survey were included in the analysis. HCA indicates the early life stage community is split into 5 distinct groups, at 5% significance level
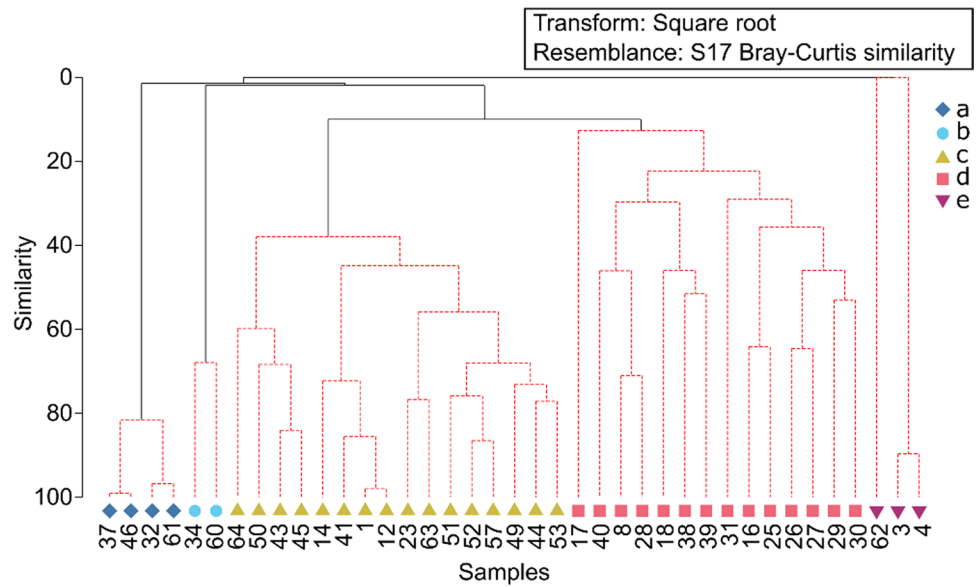

Fig. 6 Non-metric multidimensional scaling (nMDS) plots of early life stage taxa Bray–Curtis similarity between sampling stations. Colour and shape indicate sample SIMPROF group (a–e). Filled shape indicates on-shelf station (water depth < 1000 m), open shape indicates off-shelf station (≥ 1000 m) location. Points are numbered by sample station. Plot demonstrates a clear community split based on whether the sample station was on- or off-shelf
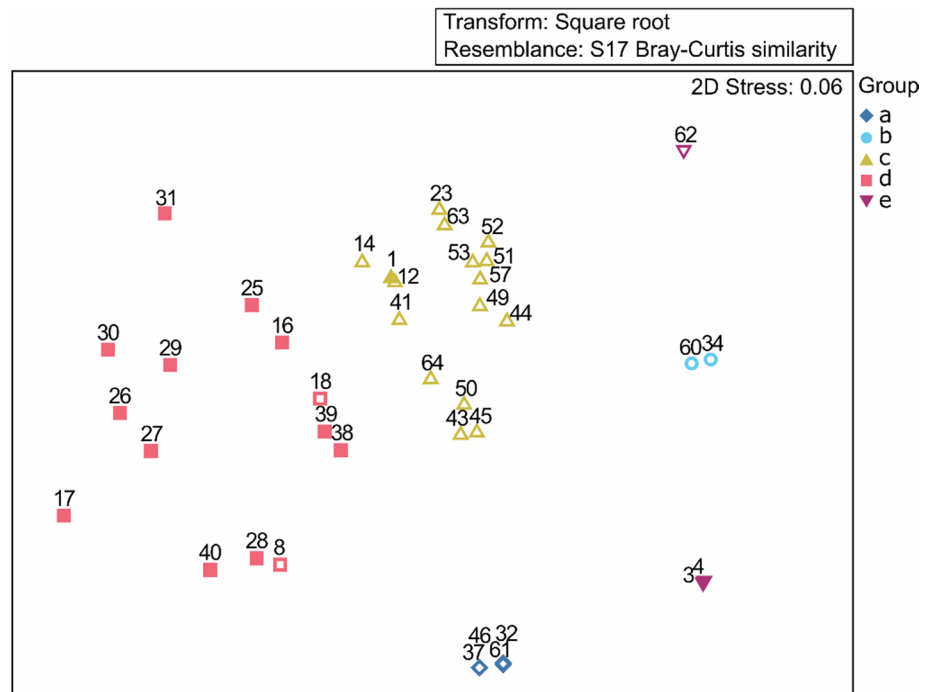
a combination of water depth coupled with longitude best explained community assemblage (Spearman rank correlation $\rho = 0.396$). Temporarily removing latitude and longitude from the potential suite of explanatory variables and analysing the group within the factor of 'shelf' (on or off) revealed that whilst depth was still the single best variable explaining the community structure ($\rho = 0.231$), a combination of depth, primary productivity and dynamic height provided the best match to community assemblage ($\rho = 0.265$).

Focussing on the South Orkney region (station numbers 11–40, see Fig. ESM1), we applied a BEST routine to assess how local conditions may drive community structure at a smaller scale. Water depth was still the single largest correlated variable to early life stage fish assemblage $\rho = 0.491$. However, a combination of depth, latitude, longitude, surface temperature and dynamic height resulted in a $\rho = 0.565$. Individually, whilst water depth explained 49.1% of community variation, latitude and longitude explained 40.6%, surface temperature 28.6% and dynamic height 20.5%, indicating that community structure was linked most strongly to bathymetry and physical

Fig. 7 SIMPROF groups, all early life stage data included. Colours indicate SIMPROF groups. Coastlines are green, 1000 m depth contour in grey delimiting on or off shelf classifications
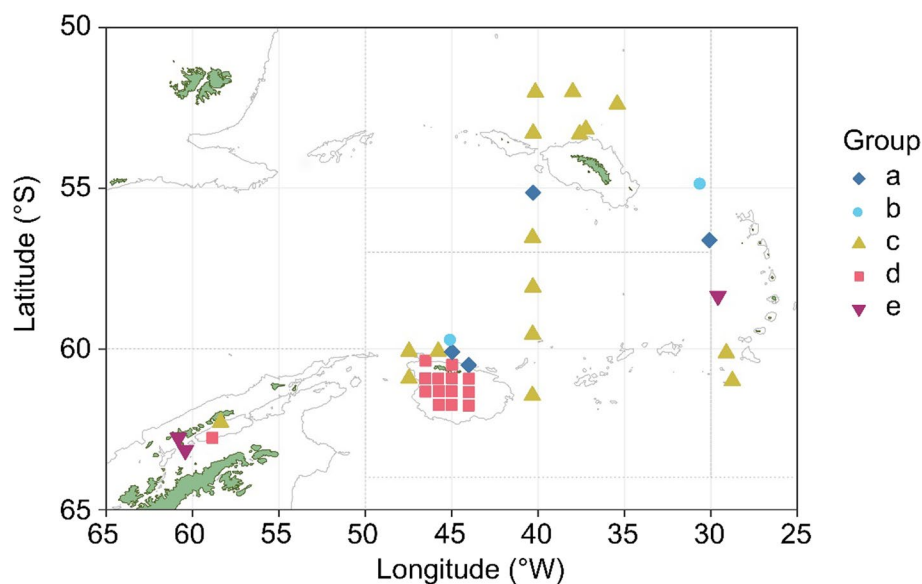
Table 4 Clusters identified by SIMPROF routine

	Cluster				
	a	b	c	d	e
Notothenia coriiceps	**100.00**				
Notothenia rossii		**100.00**			
Notolepis			**75.39**	7.53	
Muraenolepis			14.80		
Electrona			9.35		
Chionodraco rastrospinosus				**48.14**	
Chaenocephalus aceratus				19.45	
Nototheniops larseni				15.45	
Pseudochaenichthys georgianus				3.50	
Prionodraco evansii				2.69	
Artedidraco				1.15	
Cryodraco antarcticus				0.97	
Lepidonotothen squamifrons				0.81	
Chaenodraco wilsoni					100.00*
Shelf	Off	Off	Off	On	On (Off)
Region	48.2	48.2	48.1	48.1	48.1
	48.3	48.3	48.2	48.2	(48.4)
			48.3		
			48.4		
Stations	4	2	16	14	2 (1)

Values indicate percentage contribution of each taxon to the group, with the dominant taxon in bold. Shelf indicates predominant bathymetric region for the group. Stations is number of sampling stations contributing to the group. SIMPER analysis of cluster 'e' identifies the dominant taxon as 100%* Chaenodraco wilsoni, based on 2 sampling stations each containing a single individual of C. wilsoni, however cluster 'e' is also grouped with a single individual of Dissostichus mawsoni from a third station

location, with local water mass and surface temperature contributing significantly but to a lesser extent.

Discussion

This survey was the first to produce concurrent basin-scale data on the early life stage fish community in the Scotia Sea region. It sampled 19 fish genera in the upper 200 m of the water column and has highlighted a hotspot of early life stage fish biodiversity on the previously data poor South Orkneys shelf.

Basin scale spatial structure of early life stage fish community

The Scotia Sea early life stage fish assemblages were strikingly and consistently structured by the bathymetry of both the sampling location and the habitat preference of adults (Tables 3 and 4). Of the five distinct groupings of early life stage taxa, the most common were an assemblage of genera with both pelagic (*Notolepis*, *Electrona*) and benthopelagic (*Muraenolepis*) adults which was mainly found in oceanic waters (depth ≥ 1000 m) and an assemblage of genera with benthic adults (*Chionodraco*, *Chaenocephalus* and *Nototheniops*) mainly found in shelf waters. Diversity was higher on-shelf than in oceanic waters and bathymetric depth was the main environmental determinant of community structure. These findings are consistent with earlier observations (Loeb et al. 1993). In our study, taxa with pelagic adults were largely absent from on-shelf samples, whereas some taxa with shelf-associated adults (*Notothenia* and *Muraenolepis*) were most common in off-shelf samples. This corroborates the interpretation that the genus *Notothenia* relies

on ocean currents as a larval dispersal mechanism (Loeb et al. 1993; Young et al. 2015).

We found that off-shelf groups were dominated by the mesopelagic taxa *Notolepis*, *Electrona* and the benthopelagic *Muraenolepis*. Whilst *Notolepis* was common and widespread across both open-ocean and shelf regions, *Electrona* samples were most abundant in open-ocean only, and *Muraenolepis* was typically found in the highest densities to the north of the South Georgia shelf. Few data exist on the reproductive strategy of *Muraenolepis*. However, it is interesting to note that our genetic analysis indicated that the majority were *M. marmorata*, a species that is associated with sub-Antarctic shelf regions including South Georgia, Crozet, Kerguelen and Heard Island (Duhamel et al. 2014; Priede 2017).

All of the 20% of *Notolepis* identified to species level using genetic analysis were *N. coatsorum*. This widespread distribution of *Notolepis* agrees with the findings of Efremenko (1983), who identified larval *N. coatsorum* across the region south of the Polar Front. The early life history of *Notolepis* is poorly understood. However, adults of this genus are regularly found throughout the Scotia Sea region and are known to have a circum-Antarctic distribution (Post 1990; Duhamel et al. 2014). The widespread occurrence of *Notolepis* suggests that this taxon might play an important role in the Scotia Sea ecosystem. *Notolepis* diet varies with individual size and location, with smaller individuals targeting copepods and chaetognaths, switching to consuming krill of various life stages as they grow (Kock et al. 2012). In turn, *Notolepis* are important in the diets of King penguins, Emperor penguins (*Aptenodytes forsteri*), and Antarctic fur seals (Klages 1989; Olsson and North 1997; Daneri et al. 2008), therefore occupying an important mid-trophic position.

Although an abundant and diverse community of adult myctophids exists in the Scotia Sea (Saunders et al. 2017), our larval myctophid specimens were all from the genus *Electrona* and all that were identified to species level were *E. antarctica*. This low larval diversity is consistent with the observations of Belchier and Lawson (2013) and Saunders et al. (2017). The former report two *Electrona* species (*E. antarctica* and *E. carlsbergi)* plus *Krefftichthys anderssoni* and *Gymnoscopelus*, identified only to genus level, from seven years of weekly sampling in Cumberland Bay, South Georgia. The latter report larval *E. antarctica, K. anderssoni* and *Protomyctophum bolini* from Scotia Sea surveys at different times of year with the majority of larval myctophids captured north of the polar front, supporting the conclusion that most myctophid species in the Scotia Sea are expatriates from populations further north (Saunders et al. 2017). Only the polar specialist *E. antarctica*, has been found to breed in the sea-ice sector of the Southern Ocean (Moteki et al. 2017a). *E. antarctica* are

assumed to have a relatively short larval phase of 30–47 days from hatching to juvenile transformation (Greely et al. 1999). In our study larval *E. antarctica* were found ranging from the southern edge of the Scotia Arc, northwards into the open ocean and onto the north-west of South Georgia. Given that *E. antarctica* were sampled within this relatively short larval phase it seems plausible that *E. antarctica* may have hatched in the vicinity of the sea ice zone of the southern Scotia Sea and were drifting north and into their mesopelagic adult habitat. As it is unknown how long the incubation period is for *E. antarctica*, further research will be required to identify potential spawning locations.

There is a potentially high biomass of myctophids in the Scotia Sea (Dornan et al. 2022), that, with the exception of *E. antarctica*, is supported by expatriated myctophids from further north (Saunders et al. 2017). This suggests the most vulnerable fish larvae occupying the upper ~ 200 m are often cold-adapted endemic fish species that depend on Antarctic temperatures for sustained population recruitment, and for the maintenance of Antarctic ecosystem fish diversity. Thus, these species could certainly be affected by rising sea temperatures and potential by-catch in the krill fishery.

Spatial structure of Scotia Sea early life stage fish community—South Orkney shelf region

Our on-shelf sampling stations were largely restricted to the South Orkney Island shelf and slopes. However, our research indicates that this region had a relatively high species richness in comparison to the surrounding open-ocean and was dominated by shelf associated taxa including *C. rastrospinosus*, *C. aceratus*, *N. larseni* and *Notolepis* spp.. Adult *C. rastrospinosus* are known to be closely associated with the Antarctic continental shelf, but also occur in relatively high abundance at the South Orkney Islands, along with *C. aceratus* and *N. larseni* (Kock & Jones 2005). Larval *N. larseni*, *C. rastrospinosus* and *C. aceratus* have previously been identified as common ichthyoplankton in the Bransfield Strait region of the Antarctic Peninsula (Loeb et al. 1993; La Mesa et al. 2016). *C. rastrospinosus* and *C. aceratus* in this study were located only in the Bransfield Strait or confined to the South Orkney shelf suggesting that if adult *C. rastrospinosus* and *C. aceratus* are also spawning at the South Orkneys, there is potentially a high degree of site fidelity amongst these early life stage fish. The Nototheniidae *N. larseni* is relatively abundant at neritic shelf locations around the Scotia Arc (Duhamel et al. 2014). The presence of relatively abundant *N. larseni* in our catches is unsurprising as it is thought to spawn at the South Orkneys in July–August, with fish only becoming demersal at the end of year one (Kock & Jones 2005).

Spatial structure in a Southern Ocean context

The spatial distribution patterns of early life stage fish that we found within the Scotia Sea accords well with other regions of the Southern Ocean. Similar low diversity in the off-shelf larval fish community is seen in Indian Ocean sector (Hoddell et al. 2000; Van de Putte et al. 2010) and the Lazarev Sea region (Flores et al. 2008), where mesopelagic *Notolepis* and *E. antarctica* also dominate. Larval *N. coatsorum* have also been found at shelf break and oceanic waters north of the Ross Sea (Vacchi et al. 1999). There is also a high degree of genetic diversity and lack of differentiation amongst mesopelagic *E. antarctica* at the circumpolar scale, suggesting a high degree of gene flow and connectivity across the Southern Ocean (Van de Putte et al. 2012).

Benthic taxa are largely restricted to the island shelves they occupy as adults, with the Nototheniidae and Channichthyidae community commonly thought to rely on the pelagic larval phase for connectivity between populations (Eastman 2005). However, connectivity and dispersal varies amongst species. *C. rastrospinosus* and *C. aceratus*, dominant in our larval sampling, are restricted to the Atlantic Sector of the Southern Ocean (Gon and Heemstra 1990), suggesting a limit to larval dispersal. Analysis of otolith chemistry indicates that *C. aceratus* populations in the Scotia Sea are connected along the southern Scotia Arc but distinct at South Georgia (Ashford et al. 2010). The circumpolar *N. larseni*, are known to have a long pelagic larval phase that should facilitate connectivity, however, genetic analysis reveals that local communities may be more structured than previously thought (Damerau et al. 2014).

Environmental drivers

Our analyses revealed that bathymetry was the most important environmental driver of community structure both at the scale of the Scotia Sea and on the South Orkney Island shelf, with early life stage fish showing a high degree of correspondence with their adult habitats. Given that larval fish are likely to have limited horizontal swimming capability it is interesting to note the lack of influence of geostrophic velocity had on the community structure and how coupled some taxa are to the shelf break. Predicting the speed at which larvae actually swim in the ocean is complex, larvae make decisions depending on a variety of factors, including feeding and the avoidance of predators and obstruction (marine snow). Different taxa are likely to have evolved different larval swimming patterns, body orientation, vertical depth of occupation and settlement speeds based on the environmental conditions that enable them to settle in their adult habitat (Leis 2010, 2020).

However, some early life stage fish of shelf-associated *Notothenia* and *Muraenolepis* were most common in off-shelf samples. *N. rossii* larvae are known to reach the Falkland Islands north of the Antarctic Polar Front (Gritsenko et al. 2006), supporting the interpretation that *Notothenia* rely on ocean currents for larval dispersal (Loeb et al. 1993; Young et al. 2018).

We also considered the effect of time of day in our analysis as many adult pelagic fish exhibit daytime net avoidance behaviour and perform diel vertical migration (DVM) (Collins et al. 2012). Initial data exploration indicated that our catches of early life stage fish were broadly independent of when the sample was taken (Fig. ESM3), and so all data was pooled for the current study. In addition, Time of Day (Day, Night or Twilight) was included as a factor in examining the environmental drivers of early life stage community structure and was not found to be correlated to the community assemblage. This is not surprising as most of our samples were larval fish, which are likely to have limited ability to migrate out of the epipelagic sampling zone (Moteki et al. 2017a, b). However, we do recognise that a small proportion of larval fish may have occurred in deeper water (Morales-Nin et al. 1995).

Climate change has already resulted in poleward shifts of marine fauna globally (Poloczanska et al. 2013). Models predict that within the Southern Ocean there will be a poleward shift for many fish, with high latitude specialists likely to experience a reduction in available habitat as they meet the Antarctic continent (Freer et al. 2019). Whilst subantarctic fish may also shift further south into the Southern Ocean, this may still result in a reduction in fish biomass as Southern Ocean mesopelagic fish comply with Bergmann's rule, where smaller fish inhabit warmer water (Saunders and Tarling 2018; Dornan et al. 2022). Warming seas and the loss of sea ice are particularly likely to impact taxa that are cold adapted and rely on sea ice in their early life histories (Constable et al. 2014; Moteki et al. 2017a, b; Caccavo et al. 2021), including both benthic and pelagic taxa in our study.

Challenges and future work

We recognise that our survey conducted in late summer is likely to have missed a number of larval and juvenile fishes that had either not yet spawned at that time of year or had already begun ontogenetic migrations into deeper waters. All net systems have an inherent degree of selectivity and hence sampling bias. Whilst the 3 mm mesh size on our macroplankton net was small enough to sample larval fish, we do recognise that it may have missed fish close to the surface or more mobile juveniles that were able to evade capture due to relatively slow towing speeds, and so the standardised abundances we present should be viewed as relative to the net system rather than absolute.

We also recognise that other important shelf areas beyond the South Orkneys, including around South Georgia, were

not well represented. Constraints on our sampling effort were required to complete a large-scale survey with multiple objectives. Thus, our key recommendation is for more effort to increase coverage both spatially and temporally by adding dedicated early life stage sampling to planned surveys and through data rescue and compilation efforts such as Myctobase (Woods et al. 2022).

Conclusion

Our results indicate that, for many demersal taxa, their epipelagic young are likely to exhibit a high degree of settlement site fidelity in the first year of their lives. The concentration of the Antarctic krill fishery in epipelagic waters at shelf-break locations (Krafft et al. 2015; Kawaguchi and Nicol 2020) puts early life stage fish at risk of being included in bycatch. In addition, as environmental conditions change, species exhibiting strong site fidelity in early life may be less able to shift to habitats where conditions are more suitable. In the face of environmental change and under increasing pressure from a potentially expanding krill fishery, we recommend dedicated monitoring of early life stage fish to understand how these assemblages change seasonally and inter-annually.

Declarations

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