ORIGINAL PAPER

Population characteristics of benthopelagic *Gymnoscopelus nicholsi* (Pisces: Myctophidae) on the continental shelf of South Georgia (Southern Ocean) during austral summer

Ryan A. Saunders[1] · Philip R. Hollyman[1] · Sally E. Thorpe[1] · Martin A. Collins[1]

Abstract

Southern Ocean myctophid fish (Family Myctophidae) are an important conduit of energy through foodwebs and between the surface layers and mesopelagic depths. Species that reside in both pelagic and near-bottom environments of continental shelves, such as *Gymnoscopelus nicholsi* and *Gymnoscopelus bolini*, may also be important in benthopelagic coupling, although their ecology and role in such processes remain unresolved. Here, we examined inter-annual variation in the depth of occurrence, biomass and population dynamics of benthopelagic *G. nicholsi* on the South Georgia shelf (100–350 m) using bottom trawl data collected between 1987 and 2019. *Gymnoscopelus nicholsi* was a regular component of the local benthopelagic community, particularly northwest of South Georgia, but was patchily distributed. It appeared to enter a benthopelagic phase at ~ 3 years, with annual growth and recruitment of year classes between ~ 3 and 5 years. However, transition of cohorts into the benthopelagic zone was not annual. There was clear inter-annual variation in *G. nicholsi* biomass and depth of occurrence. Shallower depth of occurrence was significantly ($P < 0.05$) correlated with years of warmer summer sea surface temperatures, suggesting that inter-annual variation in local environmental conditions has an important influence on its migration behaviour and ecology. Our data also suggest that Antarctic krill is an important dietary component of the older *G. nicholsi* cohorts (~ 5 years) in the benthopelagic zone. We note that *Gymnoscopelus bolini* is rare in bottom trawl catches between 100 and 350 m, although Antarctic krill appears to dominate its diet from the available data. Our study provides important information on understudied myctophid species in a poorly investigated region of the water column that is relevant for Southern Ocean ecosystem studies, particularly in relation to understanding trophic connectivity between the pelagic and near-bottom realms.

Keywords Myctophidae · *Gymnoscopelus* · Benthopelagic ecology · South Georgia · Southern Ocean

Introduction

Myctophid fish (Family Myctophidae) are an important component of pelagic ecosystems in most oceans due to their relatively high biomass (Gjøsaeter and Kawaguchi 1980; Irigoien et al. 2014). They play a crucial role in food webs, being an intermediate link between primary consumers and higher trophic levels, and are an important vector in the transfer of energy through the water column via their extensive vertical migratory behaviour between the mesopelagic and surface layer (Pakhomov et al. 1996; Murphy et al. 2007b; Davison et al. 2013; Olivar et al. 2018; Saunders et al. 2019; Wang et al. 2019). In light of their ecological importance at both a regional and global scale, and the striking paucity of information that exists on the ecology of these fish, there has been much impetus for new research on myctophids to improve our understanding of how oceanic ecosystems operate and their sensitivities to environmental change (Irigoien et al. 2014; St. John et al. 2016; Saunders and Tarling 2018; Freer et al. 2019; Dornan et al. 2019; Belcher et al. 2020). However, there remain crucial knowledge gaps on most species, particularly in relation to their behaviour, population processes and habitat utilisation.

Myctophids typically reside at depths of 200–1000 m in open ocean waters during the daytime and many species

✉ Ryan A. Saunders
ryaund@bas.ac.uk

1   British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

undertake vertical migrations at night, although there are both intra- and inter-specific variations in vertical migratory behaviour, as well as seasonal and regional variations that could be related to underlying environmental characteristics, such as food availability and temperature (Klevjer et al. 2016; Olivar et al. 2017; Saunders et al. 2019). In most regions, myctophid abundance is generally elevated close to ocean fronts and along continental slopes (Gjøsaeter and Kawaguchi 1980; Koubbi 1993; Duhamel et al. 2014; Dornan et al. 2019). Several studies in continental slope regions around the globe have reported that certain species occur in both pelagic and demersal trawl samples, with the larger adult stages often found inhabiting the benthopelagic zone, indicating a possible switch between pelagic and benthopelagic modes (we describe individuals that reside near, but rarely on, the bottom as being "benthopelagic" in this context) during their lifecycles (Linkowski 1985; Stefanescu and Cartes 1992; Uchikawa et al. 2002; Olivar et al. 2012; Duhamel et al. 2014; Fanelli et al. 2014). The reasons for such a change in habitat utilisation remain unresolved, although it has been suggested that ontogenetic changes in feeding behaviour, vertical migration behaviour, energy conservation/growth strategies and competition avoidance are important mechanisms, with several studies hypothesising the importance of the benthic boundary layer (the layer of water extending a few tens of meters above the sediment of the sea floor) for deeper dwelling myctophids (Olivar et al. 2012; Fanelli et al. 2014; Bernal et al. 2015). However, to date, there have been few investigations on the ecology of myctophids in the benthopelagic zone (Stefanescu and Cartes 1992; Uchikawa et al. 2002; Fanelli et al. 2014). Regardless of the causal mechanisms, the possibility of a switch between pelagic and benthopelagic habitats in these relatively high biomass, mid-trophic level fish suggests that they could be important in transporting energy from surface productivity to higher trophic levels in demersal fish communities. Benthopelagic myctophids may therefore be important in bentho-pelagic coupling and crucial in the benthic ecosystem function (Dayton et al. 1994; Schnack-Schiel and Isla 2005; Colaço et al. 2013; Valls et al. 2014; Murphy et al. 2016; Drazen and Sutton 2017). However, little is known of their role in bentho-pelagic coupling and further ecological studies of myctophids in their benthopelagic habitats are warranted for improving our understanding of regional marine ecosystem dynamics in the context of ecosystem management and climate change (Murphy et al. 2016).

In the Southern Ocean, myctophids are the most diverse and biomass dominant group of mesopelagic fish, comprising around 35 species and an estimated biomass that may substantially exceed 200 million tonnes (Mt) (Hulley 1981; Lubimova et al. 1987). They are an important component of the Southern Ocean pelagic food web south of the Antarctic

polar front (APF), preying upon copepods, amphipods and euphausiids (Pakhomov et al. 1996; Pusch et al. 2004; Saunders et al. 2019), whilst being important prey for many pelagic predators, including seals, penguins, petrels, squid and large predatory fish (Rodhouse et al. 1992; Olsson and North 1997; Brown et al. 1999; Cherel et al. 2002; Reid et al. 2006; Collins et al. 2007). In a system otherwise dominated by Antarctic krill (*Euphausia superba*; hereafter krill), myctophids are considered to be a major alternative trophic pathway in periods and regions of low krill abundance, potentially being crucial for maintaining short- to medium-term ecosystem stability as krill stocks decline (or retreat southwards) under realistic scenarios of ocean-warming (Murphy et al. 2007a, b; Atkinson et al. 2004, 2019). However, questions remain regarding the resilience of myctophid populations to such change and their capacity to buffer the ecosystem in the longer-term, and further research focus is required as a priority (Murphy et al. 2007b; Saunders et al. 2019).

Gymnoscopelus nicholsi is an abundant species in the Southern Ocean myctophid community (Pusch et al. 2004; Collins et al. 2008). The data available indicate that it lives for approximately 7 years, attaining a size of around 170 mm standard length (SL), and is a sub-Antarctic to broadly Antarctic species with a circumpolar distribution between 36°S and the Antarctic continent (Hulley 1981; Linkowski 1985; Duhamel et al. 2014). The species is thought to have its core population centred between the sub-tropical front (STF) and the APF, with only non-reproducing expatriate populations occurring at higher latitudes (Hulley 1981; McGinnis 1982; Efremenko 1986; Saunders et al. 2017). Temperature appears to be a crucial factor that governs both the distribution pattern of *G. nicholsi* and the underlying macroecological tendency for larger (and older) body sizes to inhabit colder waters at higher latitudes (Saunders and Tarling 2018; Freer et al. 2019). The species is reported to have a pelagic association with Antarctic intermediate water and Sub-Antarctic mode water, occurring predominantly at depths shallower than 700 m, with pronounced diel vertical migration (DVM) behaviour apparent (Collins et al. 2008; Duhamel et al. 2014; Saunders et al. 2015). Furthermore, *G. nicholsi* is a species that may adopt a benthopelagic lifestyle in shelf regions south of the APF, with individuals thought to transition from the pelagic to benthopelagic realm between 3 and 5 years of age (Linkowski 1985; Duhamel et al. 2014). However, little is known of its ecology in this realm. *Gymnoscopelus nicholsi* appears to consume mostly copepods, small euphausiids (non-krill species) and amphipods, although the species can also consume substantial amounts of krill, suggesting that this myctophid may be important in bentho-pelagic coupling in the Southern Ocean ecosystem (Pakhomov et al. 1996; Pusch et al. 2004; Shreeve et al. 2009; Saunders et al. 2019). A recent study at the South

Shetland Islands (Atlantic sector) has also suggested a possible decline in *G. nicholsi* abundance between 2000 and 2015, together with a decline in the mean age of individuals since 2008 (Klemmedson et al. 2020). In contrast, very little is known of the ecology of *Gymnoscopelus bolini*. The species has a circumpolar distribution pattern that ranges generally between the STF and the APF, and it occurs in pelagic waters and in the benthopelagic zone along continental slopes (Hulley 1981). However, the species appears to be rare in the myctophid community south of the APF (Collins et al. , 2008, 2012). It appears to attain up to 280 mm SL in size and consumes mostly euphausiids and copepods based on the few data available (Hulley 1981; Gaskett et al. 2001). The species has been caught only rarely in pelagic surveys in the Scotia Sea region (Collins et al. 2012).

In this paper, we examined the ecology of *G. nicholsi* in its benthopelagic habitat at South Georgia using trawl data collected during regular demersal fish surveys conducted on the continental shelf (100–350 m depth) between 1987 and 2019. Our objectives were to assess the level of inter-annual variation in the species' depth of occurrence and biomass in summer in this region, and to examine patterns in these ecological characteristics in relation to inter-annual variations in temperature. The study also aimed to investigate inter-annual variations in population structure for the benthopelagic component of the local *G. nicholsi* population and gain new insight into its diet in this region of the water column. A further objective was to report, where possible, new data on the abundance, size structure and diet of the understudied species *G. bolini* in the benthopelagic zone. This study comprises the first comprehensive examination of the ecology of these species in their benthopelagic habitat to date and provides important information for ecosystem studies in the Southern Ocean.

Methods and materials

Study area

The island of South Georgia (54–55°S, 35–38°W) is located in the Scotia Sea, within the Atlantic sector of the Southern Ocean. The island has a large continental shelf with depths generally < 300 m (area 36,560 km^2). The shelf extends up to ~ 110 km offshore, with a steep continental slope from the shelf to abyssal depths > 3000 m (Fig. 1). South Georgia lies in the path of the Antarctic circumpolar current (ACC), the dominant ocean current of the Southern Ocean which comprises several circumpolar fronts (Orsi et al. 1995). The APF is located north of South Georgia while the Southern ACC front (SACCF) lies to the south, flowing anti-clockwise around the island's shelf before retroflecting to the east, and transporting waters of Antarctic origin from the Antarctic Peninsula region (Hofmann et al. 1998; Thorpe et al. 2002). The SACCF also plays an important role in bringing Antarctic krill to South Georgia, which is key in the operation of the local food web (Atkinson et al. 2001). In contrast to the generally low productivity of the open ocean of the Antarctic zone (AAZ) as a whole (generally < 2.5 mg chl a m^{-3}), the South Georgia region is highly productive, with both phytoplankton (blooms > 20 mg chl a m^{-3}) and zooplankton
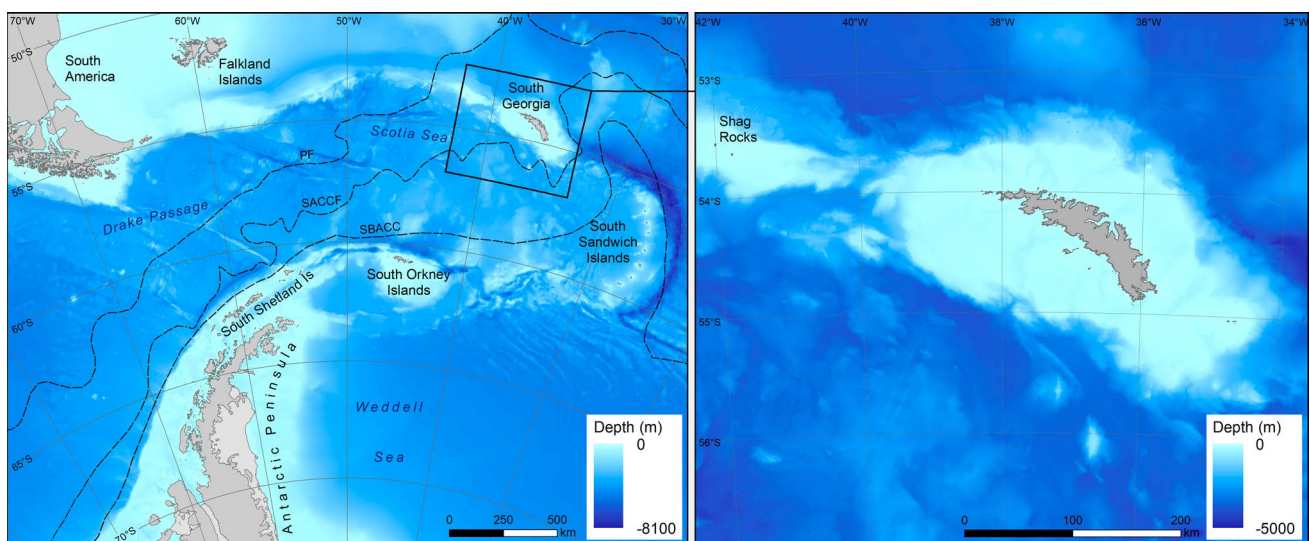
Fig. 1 Map of the Southwest Atlantic and the South Georgia and Shag Rocks study region. The main oceanographic features are the Antarctic polar front (PF), Southern Antarctic circumpolar current front (SACCF) and the Southern boundary of the Antarctic circumpolar current (SBACC). Southwest Atlantic and South Georgia bathymetry data are taken from the GEBCO 21 grid [GEBCO Compilation Group (2021), https://doi.org/10.5285/c6612cbe-50b3-0cff-e053-6c86abc09f8f] and Hogg et al. (2017), respectively

productivity (~4–5 times greater) notably higher than is typical for this region of the Southern Ocean (Atkinson et al. 2001).

Fish survey data

Distribution and relative biomass data were obtained for *G. nicholsi* from 24 demersal trawl surveys undertaken on the continental shelves of South Georgia and Shag Rocks [Commission for the Conservation of Antarctic marine living resources (CCAMLR) sub-area 48.3] between 1987 and 2019 (Fig. 1, Table 1). Although principally designed to provide data for stock assessment of commercially targeted finfish species, these surveys routinely provide data on the ecology of the wider demersal fish assemblage in the region, which includes large benthopelagic myctophids such as *G. nicholsi* and *G. bolini* (Gregory et al. 2017). With the exception of the September 1997, September 2007 and April 2008 surveys, all surveys were conducted in the middle of the austral summer (December to February; Table 1). Each survey followed a random design, stratified by depth zone (100–200 and 200–350 m, but with deeper trawls on occasion; see Everson et al. (1999) and Collins et al. (2004) for details), except the 2003 survey, where trawls were organised in a series of non-random transects radiating out from South Georgia from shallow to deep water (see Collins et al. 2004; Gregory et al. 2017). We omitted the 2003 survey from the biomass time-series to maintain comparability with the other surveys.

All surveys used a commercial sized otter trawl with a headline height of 4–6 m, a wingspread of approximately 18–22 m and a cod-end mesh of 40 mm. The net was fished on the seafloor during daylight hours for approximately 30 min at a speed of 3–4 knots. Although a number of different vessels were used throughout the survey time-series, we consider this to be a negligible source of bias given the use of large trawl vessels of similar power, identical Polyvalent trawl doors, and consistent trawl-warp to depth ratios coupled with the rough fishing grounds at South Georgia (Everson et al. 1999). The fish catch was sorted by species and weighed using motion compensated marine scales. The total catch of *G. nicholsi* was recorded (kg) and, where possible, individual *G. nicholsi* were measured using standard length (SL; rounded down to nearest 1 cm) during the 1987, 2002 to 2006 and 2008 surveys. Stomachs were also dissected from random subsamples of up to 10 fish per net trawl during the 2003 and 2005 surveys. All stomachs were frozen for subsequent microscopic analysis back at the laboratory. *Gymnoscopelus bolini* was encountered in deeper trawl nets (> 500 m) during some surveys (notably 2003) and catch weights of these specimens were recorded, together with their total length measurements (TL; rounded down to

nearest 1 cm). Stomachs were also collected from *G. bolini* during the 2003 and 2005 surveys.

Comparative data from two pelagic netting surveys conducted on-board RRS *James Clark Ross* around northwest South Georgia during March–April 2004 (cruise JR100) and January 2008 (JR177) were available for our study on *G. nicholsi* [see Collins et al. (2008) and Collins et al. (2012) for details]. In brief, depth-stratified samples of *G. nicholsi* were collected using a 25 m² rectangular midwater trawl net (RMT25; 5 mm mesh) deployed at discrete depth intervals of ~200–300 m between the surface and 1000 m. Towing speeds were ~2.5 to 3 knots, with hauls deployed during daytime and night-time. A total of 69 and 10 RMT25 hauls were undertaken during 2004 and 2008, respectively.

Relative biomass estimation

Biomass estimates were derived using catch densities based on area swept by the trawl (from wing-spread and tow distance). Seafloor areas were obtained from the South Georgia bathymetry dataset, based primarily on swath bathymetry (Fretwell et al. 2009). Biomass estimates and confidence limits were estimated using a bootstrap method (Main et al. 2009), which adjusts individual haul densities (*D*) to correct for different sampling intensities in different strata using the following equation:

$$D_C = D \times \frac{A_S}{A_T} \times \frac{H_T}{H_S}$$

where D_C is corrected density, A_S is stratum area, A_T is total area, H_T is total number of hauls and H_S is number of hauls in that stratum. The biomass estimate is obtained by multiplying the mean corrected density by the total seafloor area in that strata and confidence intervals are determined by a bootstrap re-sampling of the corrected densities, with 10,000 re-samples (Efron and Tibshirani 1993). The bootstrap was applied using 10 strata (five regions each with 100–200 and 200–350 m depth zones; Fig. 2). Since the demersal trawl gear samples to ~6 m above the seabed, it is unlikely to cover the full vertical extent of the species' benthopelagic habitat and so we consider our values of biomass to be underestimates and relative.

Population analyses

Component-fitting software (CMIX) (de la Mare 1994) was used to fit normal distributions to composite length-frequency data (in 1 cm bins) and identify cohort modes following the procedure detailed in Saunders et al. (2007). In brief, a series of runs were performed during the analysis based on the presence of one or more cohorts in the data. The best component fit to the observed data were determined

Table 1 Details of South Georgia demersal trawl surveys between 1987 and 2019

Survey code	Season	Survey vessel	Start date	End date	No. of trawls	Max. sampling depth (m)	No. trawls > 350 m	Mean biomass (tonnes)	Lower 95% C.I	Upper 95% C.I
SG87	1987	Professor Siedlecki	29-Nov-86	17-Dec-86	121	514	4	152	23	362
SG88	1988	Professor Siedlecki	19-Dec-87	12-Jan-88	113	420	6	1	0	3
SG89	1989	Professor Siedlecki	01-Feb-98	14-Feb-89	65	788	5	6	1	13
SG90	1990	Hill Cove	06-Jan-90	26-Jan-90	68	462	3	984	227	1942
SG91	1991	Falklands Protector	22-Jan-91	11-Feb-91	86	490	6	532	166	1006
SG92	1992	Falklands Protector	03-Jan-92	26-Jan-92	88	417	3	4	1	10
SG94	1994	Cordella	04-Jan-94	08-Feb-94	96	440	2	2068	847	3587
SG97	1998	Argos Galicia	02-Sep-97	29-Sep-97	71	900	17	6	1	13
SG00	2000	Argos Galicia	16-Jan-20	30-Jan-20	52	430	5	1077	178	2537
SG02	2002	Dorada	05-Jan-02	01-Feb-02	69	547	4	409	111	802
SG03	2003	Dorada	07-Jan-03	31-Jan-03	45	964	25	–	–	–
SG04	2004	Dorada	05-Jan-04	05-Feb-04	65	830	13	236	67	497
SG05	2005	Dorada	07-Jan-05	25-Jan-05	43	734	11	885	272	1788
SG06	2006	Dorada	03-Jan-06	01-Feb-06	66	410	2	510	23	1225
SG07	2007	Dorada	30-Aug-07	13-Sep-07	56	523	5	4	0	11
SG08	2008	Sil	17-Apr-08	30-Apr-08	70	355	3	2	0	6
SG09	2009	Sil	15-Jan-09	23-Jan-09	73	350	0	972	603	1414
SG10	2010	Sil	15-Jan-10	24-Jan-10	75	352	1	712	32	1583
SG11	2011	Sil	26-Jan-11	06-Feb-11	87	355	1	102	51	165
SG12	2012	New Polar	26-Jan-12	29-Jan-12	23	400	3	0	0	1
SG13	2013	Sil	22-Jan-13	29-Jan-13	70	362	1	192	39	447
SG15	2015	New Polar	13-Jan-15	23-Jan-15	77	356	2	2480	691	4817
SG17	2017	Sil	30-Jan-17	07-Feb-17	74	356	1	6	0	16
SG19	2019	Sil	27-Jan-19	05-Feb-19	73	352	1	29	3	65

Estimates of mean *Gymnoscopelus nicholsi* biomass (tonnes) between ~ 100 and 350 m depth at South Georgia are also presented, together with estimated 95% confidence intervals
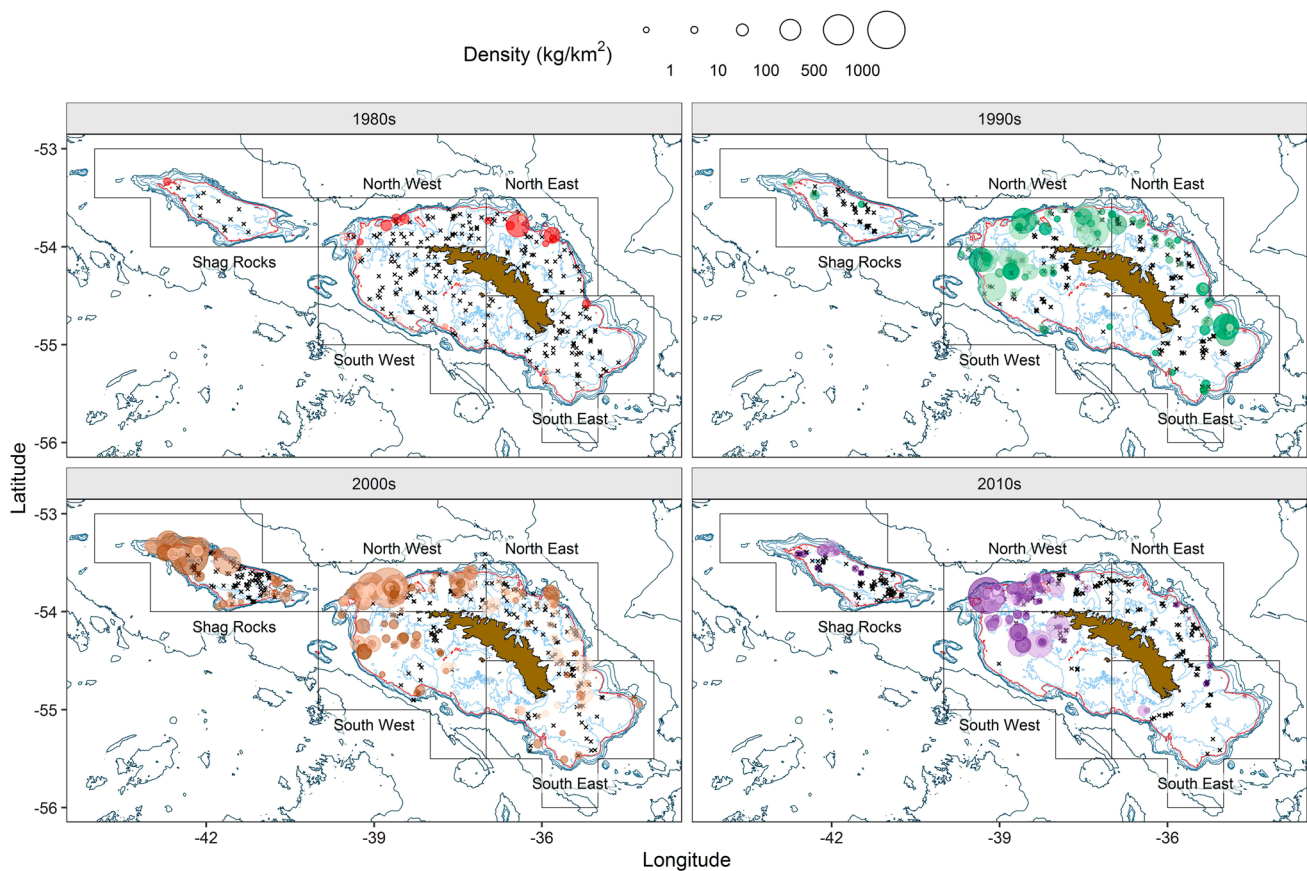
Fig. 2 Distribution of *Gymnoscopelus nicholsi* around South Georgia and Shag Rocks during demersal surveys between 1987 and 2019. Where the species was present, each colour shade represents a different year (survey), whilst trawls where the species was absent are shown as "x". Density (kg km^{-2}) is represented by circle size and the 5 standard statistical zones used in the biomass calculation are shown. Depth contours are 100, 200, 300, 500, 1000 and 3000 m. The main survey zone limit is shown by the red contour at 350 m depth

using a chi-squared test. No constraints were placed on the mean length, variance or proportions expected within each component when fitting the mixed distributions. Where possible, spatial variations (regional and pelagic vs benthopelagic) in length-frequency structures were examined using a series of Kolmogorov–Smirnov tests. We adhered to the growth and age-at-length criteria of Linkowski (1985) when identifying the observed population cohorts and interpreting our data. Although there could be size selectivity issues associated with the trawl net, which may have resulted in some *G. nicholsi* size classes being underrepresented in our data, we maintain that these proportions of the population would have been underrepresented consistently given that the same gear was used across the time-series. Therefore, our inter-annual comparisons of *G. nicholsi* population structure should still hold valid.

Diet analyses

Fish stomach contents were thawed and sorted to the lowest taxonomic level possible. Individual prey items were enumerated and weighed. During instances in which prey was highly disaggregated, the weights of component species were estimated as a proportion of the total stomach contents weight.

Diet composition was expressed using percentage frequency of occurrence (% *F*), percentage mass (% *M*), percentage number (% *N*) and percentage index of relative importance (% *IRI*) (Cortes 1997). The % IRI was calculated as:

$$\%IRI_i = \frac{\left(\%N_i + \%M_i\right) \times \%F_i}{\sum_{i=1}^{n} \left(\%N_i + \%M_i\right) \times \%F_i} \times 100$$

where *i* is prey item. The % IRI_{DC} was also calculated for the prey categories Amphipoda, Copepoda, Euphausiacea, Mysidae and unidentified crustaceans (Shreeve et al. 2009).

Environmental analyses

Mean monthly sea surface temperature (SST) for the northwest South Georgia region covering the period January

1986 to December 2019 was calculated from daily fields of high resolution (0.05° horizontal resolution) SST data from the operational sea surface temperature and ice analysis (OSTIA) (Donlon et al. 2012; Good et al. 2020). This is a gap-free product derived from in situ and satellite data. We calculated monthly spatial means from all grid cells within 53.5–54.5°S, 39.5–38.5°W, which encompasses the area of greatest *G. nicholsi* abundance observed around South Georgia (Fig. 2). SST anomalies were calculated relative to the long-term mean seasonal cycle derived from all data from January 1986 to December 2019. Here, we consider SST to be a proxy for inter-annual changes in the general environmental conditions in the local region during the main productive season (e.g. warmer vs. colder years), rather than surface temperature being the only driver of changes in benthopelagic fish population characteristics (Brandon et al. 2000; Meredith et al. 2005). Although *G. nicholsi* is a vertically migrating species, and could therefore be impacted directly by SST during surface migrations (Collins et al. 2008), we acknowledge that other environmental covariates could be correlated with warmer summer environmental conditions, which could act synergistically to affect the population characteristics of the species.

We used Pearson's Correlation Coefficient to relate both mean *G. nicholsi* depth of occurrence and biomass to mean monthly SST at the time of the survey across the available time-series. Since surveys in September 1997 and 2007 were conducted in early spring, we omitted these biomass estimates from the analysis to avoid seasonal aliasing following the unproductive winter season. We also omitted the 2012 estimate, as sampling was much reduced during this survey due to weather and logistic constraints (Table 1). Throughout the time-series net trawls were deployed mostly to depths < 350 m, although there were some surveys when our sampling occasionally extended to deeper depths, particularly in 2003 (Table 1). The number of trawls undertaken deeper than 350 m was predominantly < 10% per survey, with the exception of surveys in 1997 and between 2003 and 2005 (~ 20–56%). However, we only used data collected between 100 and 350 m in our analysis to avoid sampling bias between surveys.

Since very little is known about the thermal habitat of *G. nicholsi* in the benthopelagic environment, we used data from the Copernicus Marine Service global ocean eddy-resolving reanalysis, GLORYS12V1 (Global Monitoring and Forecasting Center 2018) to characterise the bottom water temperatures that the species inhabits in this region around South Georgia. GLORYS12 provides an estimate of the state of the ocean by assimilating ocean observations (sea level anomaly, sea surface temperature, sea ice concentration, and vertical profiles of in situ temperature and salinity) with a 1/12° horizontal resolution version of the Nucleus for European Modelling of the Ocean (NEMO)

platform that is forced at the surface with European Centre for Medium-Range Weather Forecasts ERA-Interim and ERA5 reanalysis data. Monthly mean data were available between 1993 and 2019. Mean and range in bottom water temperature were calculated for depths < 500 m on the South Georgia and Shag Rocks continental shelves for the summer period (December, January and February) for 1993 to 2019. To examine the thermal environment at which zero and non-zero catch densities of *G. nicholsi* were caught, bottom temperature from the monthly mean GLORYS12V1 field at the time of the survey was extracted for the nearest grid cell to each catch location. A comparison of GLORYS12V1 output with conductivity-temperature-depth (CTD) data collected on the South Georgia and Shag Rocks continental shelves in December 2004–January 2005 (Whitehouse et al. 2008) shows that while GLORYS12V1 tended to overestimate the temperature of surface waters, the temperatures at depths below 50 m were generally within ± 0.5 °C of the CTD data (Online Resource 1).

Results

Sea surface temperature and bottom water temperature at South Georgia

Clear seasonality in mean monthly SST was observed for the main area of *G. nicholsi* occurrence (Fig. 3) with peak summer temperatures occurring between January and March (~ 3–4 °C) and winter minima occurring between July and September (~ −0.5 to 0.5 °C). Clear inter-annual variation in mean SST was also apparent at congruent times of year. For example, temperatures in January reached ~ 4 °C in 1990, 1991, 2005, 2006 and 2011, but were below ~ 3 °C in 1992, 1998, 2014 and 2016.

Summer mean bottom water temperatures were generally between 0.5 and 2 °C around the South Georgia shelf, with higher temperatures at the western end of the Shag Rocks shelf and closer inshore to South Georgia (Fig. 4). Clear spatial variation in bottom water temperatures was apparent with temperatures generally warmer around Shag Rocks and the northeast sector of the South Georgia shelf (~ 1–2 °C) than for the northwest and southeast sectors (0.5–1 °C). In the oceanic waters off the continental shelf, water temperature increases beneath the near-surface layers to a maximum at ~ 200 m (Meredith et al. 2008; Saunders et al. 2013). Bottom waters in the canyons on the South Georgia shelf are warmer than shallower waters of the shelf, due to the incursion of this warmer subsurface water from off-shelf. The range in bottom temperature is also spatially variable, with a range in summer temperature of 0.5 to > 3 °C. The largest range in bottom temperature occurs over the southeast sector of the South Georgia continental shelf and in shallower

Fig. 3 Time-series of **A** mean monthly sea surface temperature averaged for a region to the northwest of South Georgia (see text for details) and **B** sea surface temperature anomaly in relation to **C** mean *Gymnoscopelus nicholsi* biomass caught between ~ 100 and 350 m during the survey time-series. See Table 1 for details on survey times in each year. Years where no survey was undertaken are denoted "**" and years where biomass estimates were not calculated due to incompatible sampling design are denoted "+ +"
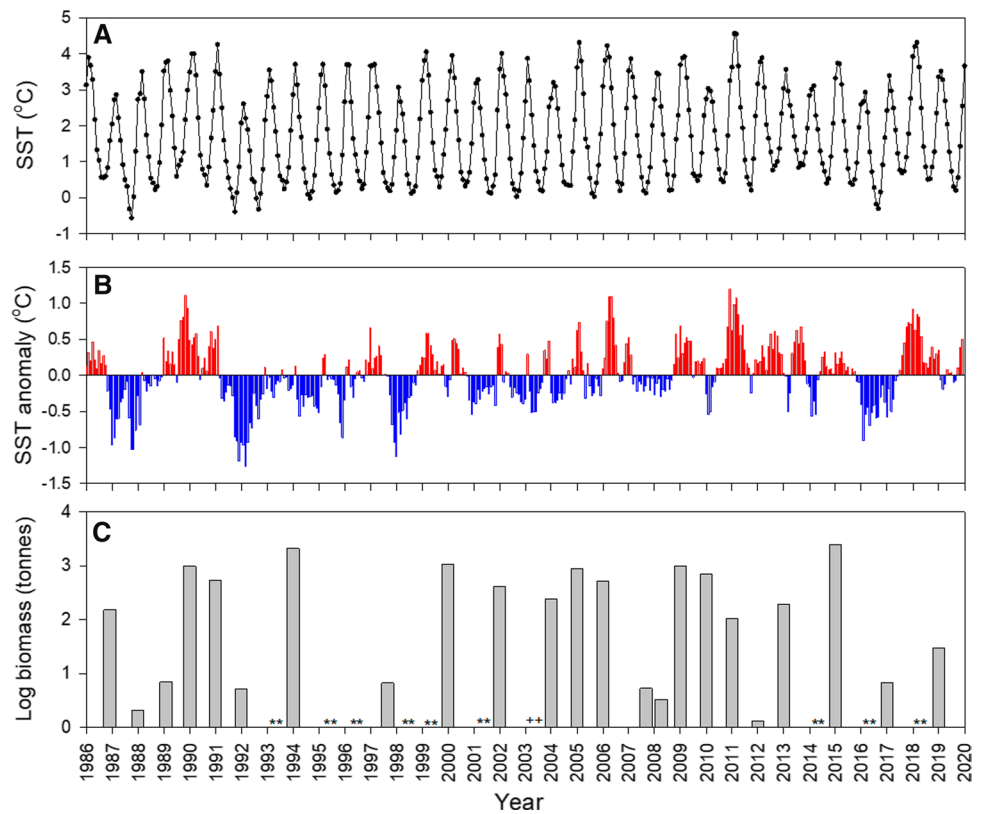
Distribution of biomass

Gymnoscopelus nicholsi was caught in 23% of the research trawls undertaken around the South Georgia shelf during 23 surveys between 1987 and 2019. In general, there was considerable between-haul and between-year variability in catches, but the species was present in most sectors around the island (Fig. 2). The greatest concentrations of the species were found consistently around the northwest region of South Georgia, whilst the concentrations were low around the southeast region (Fig. 2). The species also occurred at Shag Rocks, but predominantly during the 2000s.

Gymnoscopelus nicholsi was sampled predominantly at depths between 100 and 350 m on most demersal surveys during the time-series, although the species was relatively abundant at depths > 350 m and it occurred as deep as ~ 920 m during surveys when deep water trawling was undertaken during 2003 and 2004 (Fig. 5). Despite the differences in maximum sampling depths between surveys, there was evidence of inter-annual variation in the depth of occurrence of *G. nicholsi* across the 100–350 m sampling range that was sampled consistently across all surveys during the time-series. For example, there were years when *G. nicholsi* was spread across shallower depths between

150 and 350 m (1994, 2000, 2009, 2011, 2013, 2015 and 2019), but confined mostly to deeper waters between 300 and 350 m in other years (1987 to 1992, 2004 to 2008, 2010, 2012, 2017). Although there was relatively high variation in the data, analyses also revealed a significant correlation (Pearson's correlation coefficient: $r_{17} = 0.540$, $P = 0.017$) between the mean depth of *G. nicholsi* occurrence within the 100–350 m zone and SST during the available time-series, with summer depth of occurrence shallower in years with warmer summers (Fig. 6).

Gymnoscopelus bolini was caught only rarely during all surveys, except 2003 where sampling was predominantly deeper (Online Resource 2). Overall, the species was found at depths between 226 and 928 m, but it mostly occurred in waters > 350 m. The species was found in all sectors around South Georgia, including Shag Rocks, with maximum trawl densities of 95.71 kg km^{-2}.

Inter-annual variation in biomass

Estimates of *G. nicholsi* biomass between 100 and 350 m depth varied substantially between surveys (years), ranging from 1 to 2480 tonnes (Table 1; Fig. 3). Although low biomass (< 6 tonnes) could be attributed to possible seasonal effects in some instances from surveying in different months (spring 1997 and 2007, autumn 2008), low biomass was also observed during some years when surveys were conducted
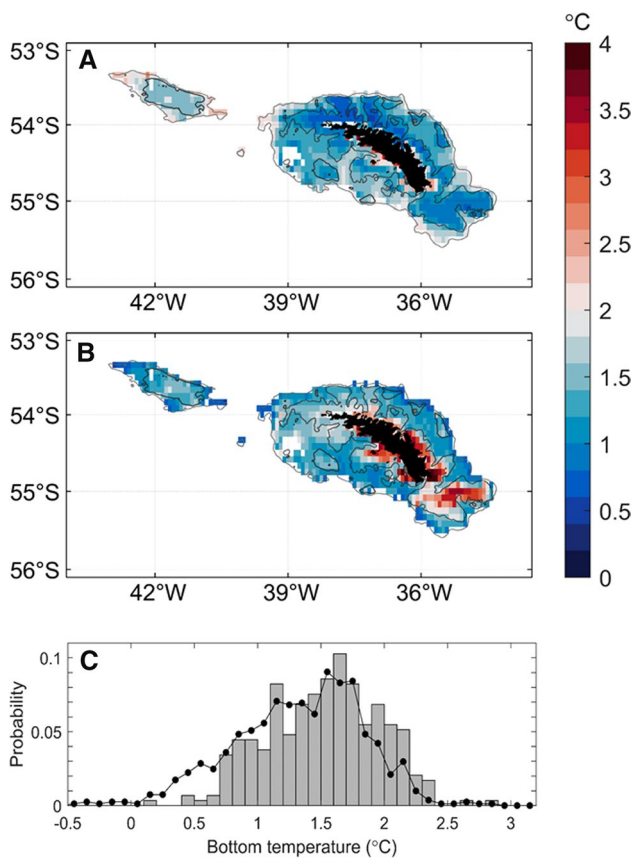
Fig. 4 **A** Mean and **B** range in bottom temperature (°C) around South Georgia and Shag Rocks during December–February between 1993 and 2019 for continental shelf regions shallower than 500 m. The 200 m isobath is also shown. **C** Bottom temperatures from locations of non-zero catches (histogram) and zero catches (line plot) of *G. nicholsi* between 1993 and 2019

during the summer (1988, 1992 and 2017). These low *G. nicholsi* biomasses (<6 tonnes) generally occurred when SST was <2.5 °C (Fig. 3), including years with summer SST anomalies (cooler summers in 1988, 1992 and 2017). However, there was no significant correlation (Pearson's correlation coefficient: $r_{17} = 0.435$, $P = 0.063$) between mean summer *G. nicholsi* biomass (within 100–350 m depth) and mean SST from the available time-series data. There was insufficient time-series data for a robust examination of biomass variation with bottom water temperature.

Thermal habitat of benthopelagic *G. nicholsi*

Although there was relatively high patchiness in *G. nicholsi* catch densities, the available data suggested that the species predominantly occupies a thermal range between ~0.5 and 2.5 °C in its benthopelagic habitat (Fig. 4). There was high overlap in the probability distributions of bottom temperatures from both non-zero and zero *G. nicholsi* catches, although there was a general tendency for an increased probability of *G. nicholsi* catches at temperatures >1.8 °C. Similarly, there was an increased probability of zero *G. nicholsi* catches at temperatures <0.8 °C.

Population structure

Gymnoscopelus nicholsi ranged from 50 to 180 mm SL during the surveys, with the majority of individuals between 100 and 170 mm (Fig. 7). Length-frequency histograms showed a single cohort in the benthopelagic populations in each year where data were available (1987, 2002 to 2006, and 2008). Based on the criteria of Linkowski (1985), we identified these cohorts as either 3, 4 or 5+ years old. Most
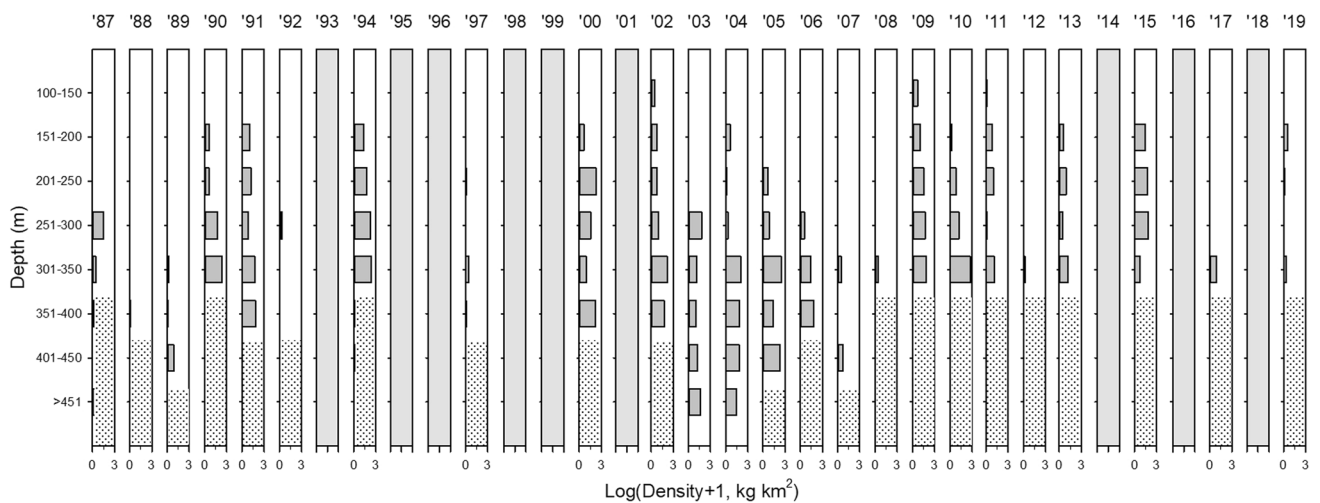
Fig. 5 Mean *Gymnoscopelus nicholsi* catch density (kg km^{-2}) by bathymetric depth zone around South Georgia during demersal surveys between 1987 and 2019 (dark grey bars). Years when no surveys were conducted in the time-series are masked by grey shade. Depth zones that were either not sampled, or had <3 trawls, during the surveys are blocked by dotted shading
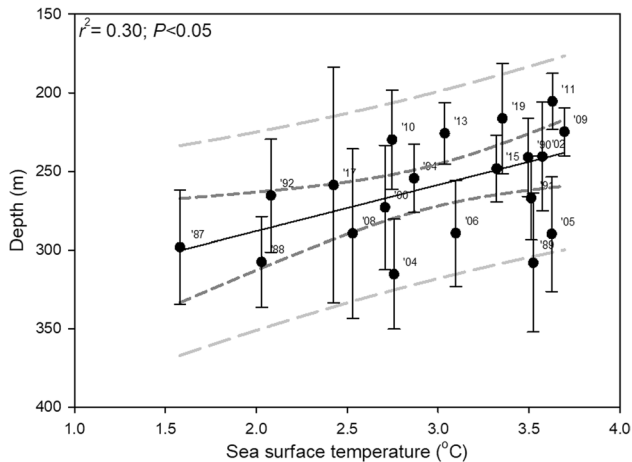
Fig. 6 Relationship between mean *Gymnoscopelus nicholsi* depth and mean monthly sea surface temperature for the northwest South Georgia region at the time of the demersal surveys between 1987 and 2019. The error bars are the 95% confidence intervals. Solid lines are the regression fits, short dashed lines are the 95% confidence intervals of the regression, and long dashed lines are 95% confidence intervals of the observations

of the length-frequency data were obtained from the northwest region of South Georgia, which limited spatial comparisons of population structure. Sufficient data were available for comparisons between South Georgia and Shag Rocks during 2002 and 2003, although there were no significant differences in population structure in either year (KS tests: $D_{505, 186} = 0.250$ $P = 0.699$ and $D_{131, 125} = 0.205$ $P = 0.699$ for 2002 and 2003, respectively). There was also no significant difference in population structure between the northwest and northeast regions of South Georgia during 1987 (KS test: $D_{1255, 278} = 0.125$ $P = 0.996$).

There was clear inter-annual variation in length-frequency distribution between consecutive years, consistent with annual growth and recruitment of year-class cohorts. For example, the 2004 population comprised a 3+ cohort which recruited to a 4+ cohort in 2005 and a 5+ cohort in 2006. Presumably, this 5+ cohort either died or moved out of the sampled range in 2007. This 3-year pattern of cohort growth and recruitment was consistent with the data from 2002 and 2003, with recruitment of 4+ and 5+ cohorts in 2002 and 2003, respectively. The 5+ cohort had also presumably died or moved out of the sampled population by 2004. No length data were available from 2007. Only data from pelagic samples were available in 2008, which showed the presence of a 4+ cohort in the pelagic population at this time.

Data available from 2004 allowed us to perform a preliminary comparison in the observed length-frequency distributions of *G. nicholsi* caught by pelagic and demersal trawls (Fig. 7), albeit sample sizes were relatively low in the pelagic data ($n = 73$). There was a slightly significant (KS

test, $D_{256, 73} = 0.50$, $P < 0.036$) difference with the pelagic population comprising a small 2+ cohort and a predominantly 4+ cohort, whilst the 3+ cohort that was present in the benthopelagic zone was largely absent in the pelagic zone. There was also a notable absence of 4+ specimens in the benthopelagic population compared to the pelagic population.

Based on measurements collected during the 1987, 2003 and 2005 surveys, *G. bolini* ranged between 150 and 360 mm TL in each year (Online Resource 3). As well as data being obtained in non-consecutive years, the sample sizes were also relatively small for this species (< 102 individuals) on each survey, which prohibited a robust analysis of its population dynamics. However, data from the 1987 survey suggest that two cohorts could be present in *G. bolini* populations in the benthopelagic realm around South Georgia (modes: 210 and 260 mm).

Diet

A total of 203 and 19 *G. nicholsi* stomachs from surveys undertaken in 2003 and 2005 contained prey items, respectively (Table 2). In 2003, the species' diet was dominated by Antarctic krill *Euphausia superba* (98%IRI), with minor proportions of the amphipod *Themisto gaudichaudii* (2%IRI). The *G. nicholsi* population comprised mostly larger 5+ specimens (~ 110–180 mm SL) during this time (Fig. 7). In contrast, the copepods *Rhincalanus gigas* (45%IRI) and *T. gaudichaudii* (15%IRI) dominated its diet in 2005, and *E. superba* was only a minor dietary component (2%IRI). The population in 2005 comprised mostly 4+ specimens between ~ 100–150 mm SL in size.

A total of 91 and 39 *G. bolini* stomachs were obtained in 2003 and 2005, respectively (Online Resource 4). The diet of this larger myctophid species (~ 160–300 mm TL) was dominated by Antarctic krill in both 2003 (76%F, 82%M, 58%N and 97%IRI) and 2005 (92%F, 97%M, 83%N and 99%IRI). Additional minor prey in 2003 included the mysid *Antarctomysis* spp. (3%IRI) and the small myctophid fish (~ 1%IRI) species *Krefftichthys anderssoni* and *Protomyctophum bolini*.

Discussion

Although *G. nicholsi* has previously been found in demersal trawls in shelf regions in the Southern Ocean (Linkowski 1985), this study comprises the first investigation into its occurrence and ecology in the benthopelagic realm using time-series data. Our results have shown that *G. nicholsi* is a regular component of the near-bottom community of the South Georgia continental shelf across multiple years and in different seasons, and the survey data indicate inter-annual

Fig. 7 Length-frequency distributions (standard length, mm) of *Gymnoscopelus nicholsi* in demersal and pelagic nets at South Georgia between 1987 and 2008
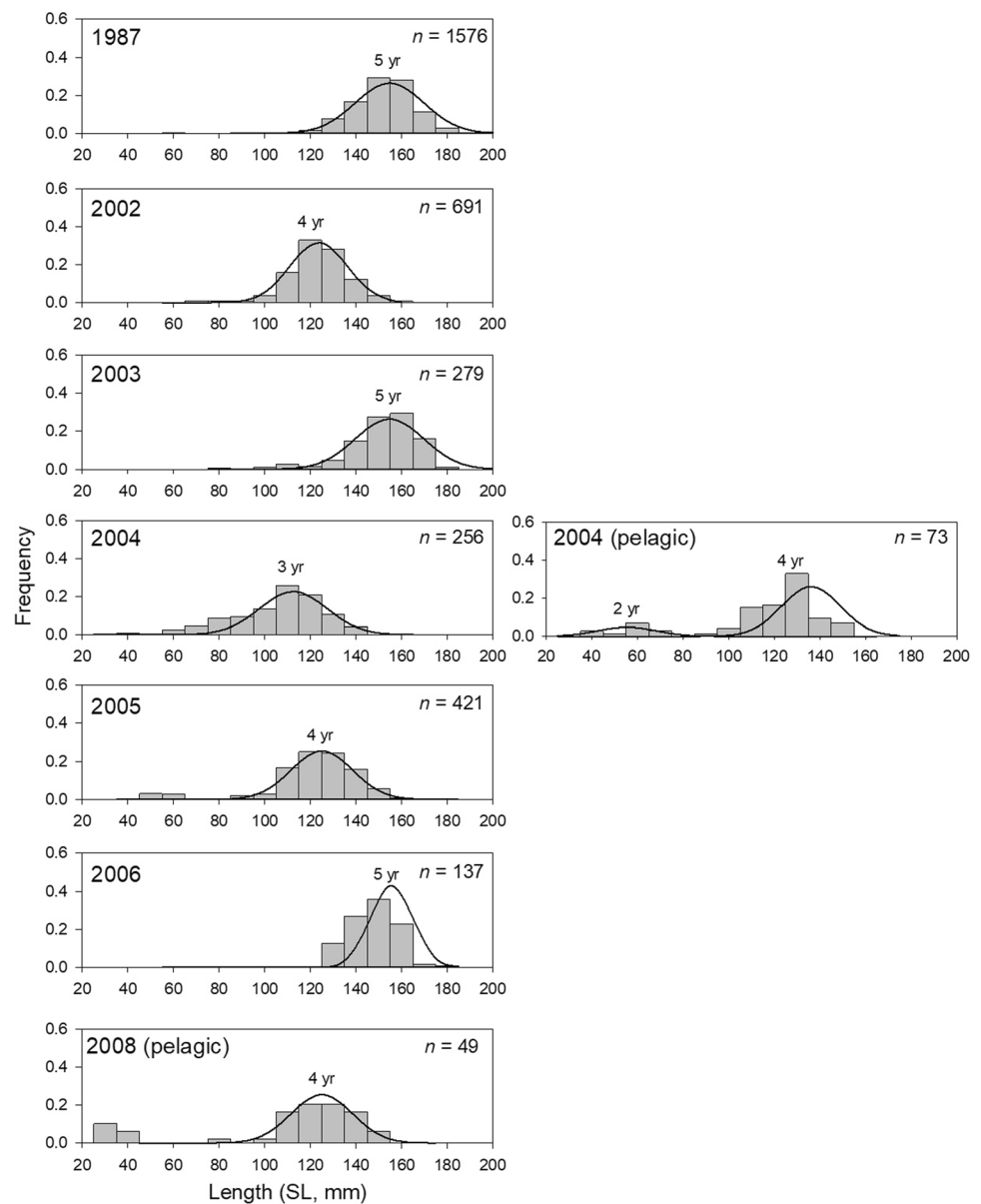
variations in its recruitment, depth of occurrence and abundance. However, it is important to recognise the limitations of the sampling depths in this study. Although the greatest concentrations of *G. nicholsi* are predominantly found above ~ 600 m in the pelagic realm, the species has a depth distribution that may extend to 1000 m (Piatkowski et al. 1994; Pusch et al. 2004; Collins et al. 2008; Saunders et al. 2015). The maximum depth that we considered in our analyses was 350 m, so rather than being representative of the entire depth range of the species, the data are limited to the shallower continental shelf regions around South Georgia. Based on local bathymetry data, we estimate that our sampling misses ~ 17% of the species' potential shelf slope habitat between 350 and 1000 m depth, assuming that the estimated area between 350 and 1000 m is 7738 km² and

the total area < 1000 m is 44,702 km² (Fretwell et al. 2009; Hogg et al. 2017). Nevertheless, this allows us to assess temporal and spatial changes in the distribution in this region, with the understanding that these changes may be linked to redistribution of the biomass to deeper areas at certain times.

Distribution

Our study suggests that, although there is high patchiness in *G. nicholsi* distribution around the South Georgia continental shelf (between 100 and 350 m depth), the greatest concentrations in the benthopelagic zone are to the northwest of the island. This pattern was consistent across the ~ 30 years time-series and accords with data from pelagic studies that also indicate that *G. nicholsi* is relatively abundant in this

Table 2 All prey items identified from *Gymnoscopelus nicholsi* stomachs collected in demersal trawls at South Georgia in 2003 and 2005

Prey	2003				2005			
	%F	%M	%N	%IRI	%F	%M	%N	%IRI
Amphipoda								
Themisto gaudichaudii	15.87	2.63	20.27	2.63	73.68	26.34	8.77	21.26
Unident. Amphipods	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	16.35	2.63	20.27	**2.35**	73.68	26.34	8.77	**15.16**
Copepoda								
Candacia falcifera	1.92	0.07	0.45	0.01	0.00	0.00	0.00	0.00
Paraeuchaeta spp.	0.00	0.00	0.00	0.00	21.05	1.52	1.62	0.54
Rhincalanus gigas	0.48	0.00	0.00	0.00	84.21	15.20	49.03	44.46
Unident. Copepods	0.00	0.00	0.00	0.00	57.89	2.88	31.82	16.51
Total	2.40	0.07	0.45	**0.01**	94.74	19.60	82.47	**56.66**
Euphausiacea								
Euphausia frigida	0.48	1.33	0.90	0.01	0.00	0.00	0.00	0.00
Euphausia superba	80.29	93.20	74.32	97.19	15.79	14.74	1.30	2.08
Euphausia triacantha	0.00	0.00	0.00	0.00	21.05	6.99	1.62	1.49
Thysanoessa spp.	0.48	0.00	0.00	0.00	10.53	2.36	1.62	0.35
Unident. Euphausiids	9.62	1.12	0.00	0.08	47.37	11.37	3.57	5.82
Total	90.87	95.65	75.23	**97.56**	89.47	35.46	8.12	**22.85**
Mysidacea								
Antarctomysis spp.	1.44	0.14	4.05	0.04	0.00	0.00	0.00	0.00
Total	1.44	0.14	4.05	**0.04**	0.00	0.00	0.00	**0.00**
Unident. Crustaceans	4.81	1.50	0.00	0.05	47.37	18.59	0.65	7.49
Total	4.81	1.50	0.00	**0.05**	47.37	18.59	0.65	**5.34**
No. of full stomachs	208				19			
Size range (SL, mm)	120–170				105–145			
Cohort age class	5+				4+			

Note that %IRI is not additive, so the sum of the individual species' IRI values is not the same as the prey categories %IRI$_{DC}$ (in bold) values

Unident unidentified

region (Collins et al. 2008; Saunders et al. 2015). The area to the northwest of South Georgia is often associated with high levels of summer productivity, and hence elevated zooplankton food resources, compared to other areas, which may be an important driver of this spatial distribution pattern in *G. nicholsi* (Atkinson et al. 2001; Matano et al. 2020). Furthermore, low *G. nicholsi* concentrations in the southeast sector broadly correspond with more variable seafloor temperatures, low mean summer productivity and greater cross-shelf transport velocities in this region (Matano et al. 2020). The relatively large variation in temperature in this region is possibly related to variability in the location of the SACCF around the southeast end of the South Georgian shelf (Boehme et al. 2008), with this frontal system bringing colder waters onto the shelf when it approaches more closely. Our data also suggest that the species can be periodically abundant at Shag Rocks during some decades, such as during the 2000s, although the reasons for this long-term temporal variability remain unclear and further data are required in the region.

Gymnoscopelus bolini was rare in the on-shelf bottom trawls around South Georgia and it was predominantly caught in regions deeper than 350 m. Similarly, the species was consistently rare in pelagic net samples (from 0 to 1000 m) in the region (Collins et al. 2008, 2012). However, individual catch densities in our study were also relatively high on occasion (up to 96 kg km^{-2}), suggesting that its abundance in the deeper slope regions could be consistent with other species of the local myctophid community (Collins et al. 2008), albeit with a high degree of patchiness, and mostly confined to the benthopelagic zone. Further data from the deeper slope regions are clearly required for this species.

Vertical distribution

Our results showed distinct inter-annual variations in the depth of occurrence of benthopelagic *G. nicholsi* at South Georgia over a relatively narrow range of seabed depths between 100 and 350 m. This is broadly consistent

with observations from acoustic studies of pelagic myctophid schools (albeit gas-bearing swimbladder species, unlike adult *G. nicholsi*) around northwest South Georgia between 0 and 500 m (Saunders et al. 2013), suggesting that such variation is common in this group of fish in the region. However, no discernible associations with pelagic myctophid school depth and environmental parameters, such as oxygen and temperature, were found in this previous study, possibly due to insufficient time-series data. It has been hypothesised that apparent seasonal variations in the depth distribution patterns of some vertically migrating Southern Ocean myctophids may be linked to seasonal variations in temperature (Collins et al. 2008, 2012; Lourenço et al. 2017). To some extent, this resonates with the findings in our study which suggest that inter-annual variations in water temperatures also influence the depth of occurrence of myctophids at South Georgia, including those that occupy the benthopelagic pelagic zone and undertake vertical migrations, such as *G. nicholsi* (Collins et al. 2008).

In the case of benthopelagic *G. nicholsi*, one possible explanation for its shallower depth of occurrence in warmer summers could be a change in vertical migration behaviour. As the species is predominantly of sub-Antarctic origins (Hulley 1981), individuals occurring in the colder waters of the Scotia Sea are likely to have a preference for thermal environments that are closer to the conditions that they are acclimated to at lower latitudes (Freer et al. 2019). We hypothesise that, in years with warmer water temperatures at South Georgia, *G. nicholsi* individuals alter their vertical range to penetrate the more productive surface layers more readily for feeding (Atkinson et al. 2001), as their metabolism and activity levels increase (Alewijnse et al. 2021). Conversely, they become less active and remain in deeper, relatively warm, sub-surface waters more during years when summer temperatures are lower, as their metabolic demands are reduced (Pearcy et al. 1979; Neighbours and Nafpaktitis 1982). Shoreward, horizontal migrations of individuals from more off-shelf waters may contribute to this effect (Saunders et al. 2013), as well as spatiotemporal fluctuations in cross-shelf oceanographic transport processes (Matano et al. 2020). Interestingly, *G. nicholsi* appears to have a lower metabolism than the other myctophids in the Scotia Sea community, which may necessitate its requirement for benthopelagic occupancy and modulation of its vertical migration behaviour (Belcher et al. 2019; Alewijnse et al. 2021). However, the biological mechanisms underpinning such behavioural patterns are likely to be multifaceted and more time-series data are required to assess the possible effects of other environmental variables. The application of dynamic state variable models are also likely to be informative regarding optimal life-history and vertical migration behaviour of Southern Ocean mesopelagic fish in relation to variations in environmental conditions (Langbehn et al. 2019).

Temporal variation in biomass

In this study, we found relatively high inter-annual variation in summer *G. nicholsi* biomass between 100 and 350 m at South Georgia, albeit our sampling did not cover the species' full vertical range. From the available time-series, our data also suggest the possibility of intra-annual variation in biomass, with reduced concentrations in spring and autumn. The mechanisms influencing such temporal variations in *G. nicholsi* biomass remain unclear from our data, but our study suggests that temperature, or environmental covariates associated with temperature, could be a factor since low biomass was observed generally in both seasons (September and April) and years of low summer SST (< 2.5 °C) at South Georgia. However, we found no direct correlation between biomass and temperature, which could possibly be due to insufficient time-series data across different seasons and years with SST anomalies. In addition, our correlation analysis only considered SST as a proxy for environmental variation in the region, which might not be sufficient for *G. nicholsi* populations that reside predominately in near-bottom environments, as changes in surface conditions may not be directly indicative of conditions in the circumpolar deep waters. We had insufficient observational data for robust analyses of changes in biomass in relation to bottom depth temperatures, but output from reanalysis products, such as GLORYS (Global Monitoring and Forecasting Center 2018), and ocean models could be insightful for future studies.

Population dynamics and migration hypotheses

Population dynamics data are limited for *G. nicholsi* across the Southern Ocean, including at South Georgia. However, those that exist indicate that multiple cohorts/year classes > 1 year old occur in populations at South Georgia (Linkowski 1985; Collins et al. 2008; Saunders et al. 2015). This is in contrast to waters further south at the South Shetland Islands where *G. nicholsi* populations are dominated by larger (~ 120–170 mm) and older (mostly 3–5 years old) fish (Linkowski 1985; Pusch et al. 2004; Klemmedson et al. 2020). Overall, our data are consistent with the findings of Linkowski (1985), in that the species appears to live for ~ 6 years and that it appears to enter a benthopelagic mode around South Georgia at ~ 3 years of age. Our data further showed distinct annual recruitment and growth of population cohorts between 3 and 5 years of age following its transition into the benthopelagic phase. However, our data suggest that the transition of ~ 3 years old *G. nicholsi* into the benthopelagic realm is sporadic at South Georgia rather than annual, as would be expected in a local population that is both

self-sustaining and has regular successful annual recruitment in most years. Given the marked absence of reproduction and year classes < 1 year old in *G. nicholsi* populations south of the APF compared to their counterparts at temperate latitudes, this suggests that recruitment of *G. nicholsi* into the benthopelagic, and at South Georgia generally, could be linked to immigration from other regions and/or changes in either local or remote environmental conditions. It has been proposed that *G. nicholsi* populations in the Scotia Sea are sustained by immigration from more temperate regions north of the APF to polar waters (Hulley 1981; McGinnis 1982; Linkowski 1985; Pusch et al. 2004; Saunders et al. 2017), with southward migrations across the APF possibly related to searching for food hotspots. Saunders and Tarling (2018) further proposed that the extent to which individuals can cross the APF and penetrate the colder waters at higher latitudes during such feeding migrations is determined by body size. For example, larger sized myctophids have a greater swimming and migration ability (Fuiman and Batty 1997), as well as greater body reserves to draw upon to reduce starvation stress during periods of reduced food availability in the highly seasonal Southern Ocean. *Gymnoscopelus nicholsi* individuals may therefore only have the capacity to cross the APF and reach South Georgia when they attain 1–2 years of age (~ 50–80 mm), whereupon they transition to the benthopelagic realm at ~ 3 years. However, our data still suggest that such southward migrations are episodic and possibly environmentally driven, and behavioural mechanisms are likely to be important, which require further examination.

Alternatively, Klemmedson et al. (2020) proposed that the eastward flowing ACC plays a crucial role in determining the population structure of *G. nicholsi* at the South Shetland Islands by regularly transporting larvae and early life stages eastwards on a ~ 3 years journey around the Southern Ocean to the South Shetland Islands, such that the local population becomes dominated by ~ 3–4 years old fish (Linkowski 1985; Pusch et al. 2004). However, this eastward transport hypothesis is incomplete, as *G. nicholsi* appears not to spawn in waters south of the APF but at more temperate latitudes. Therefore, there would still need to be southward transportation of the early life stages from these spawning grounds across the APF to enable transport to the Scotia Sea islands and there is little evidence that these early stages penetrate the ACC and survive (Saunders et al. 2017). Also, although there is evidence of near-surface transport of biological material from north of the APF to the South Shetland Islands (Fraser et al. 2018), consistent transport pathways for this route and their timescales have not yet been established. The effects of small to mesoscale variations in the flow field of the ACC clearly need to be accounted for in such pathways (Baudena et al. 2021; Murphy et al. 2021).

The eastward transport hypothesis further implies that the southwest Atlantic is the predominant spawning location for the species, with regions at longitudes equivalent to those of the South Shetlands (or South Georgia) being the entry point for larval entrainment in the ACC to enable the recorded age structure of the population. However, the available evidence suggests that spawning is circumpolar (Efremenko 1987) giving the potential for connectivity from various locations, which would manifest in both temporal variations in population structure at the islands and the presence of cohorts < 3–4 years old, given the difference in transit times relative to these endpoints. The situation is likely to be complicated further given that adult *G. nicholsi* are capable of directed horizontal movement. Consequently, there remains the possibility of directed southward and eastward migrations of *G. nicholsi*, to places such as South Georgia and the South Shetlands Islands, once they attain a sufficient body size for active displacement and starvation resistance in waters south of the APF.

Diet

In this study, the diet of *G. nicholsi* varied between surveys, with krill being the dominant prey during 2003 and copepods, amphipods and small euphausiids dominant in 2005. The high consumption of krill in the diet of *G. nicholsi* at South Georgia is consistent with observations of pelagic populations at the South Shetland Islands (Pusch et al. 2004), whilst the consumption of other zooplankton is consistent with previous studies at South Georgia (in autumn 2004) and in the northern Scotia Sea, which indicated that the species consumes mostly copepods, amphipods and other small euphausiids (Shreeve et al. 2009; Saunders et al. 2015). To some extent, the perceived inter-annual variations in diet in our study could be related to differences in *G. nicholsi* size, as specimens were predominantly larger and older in 2003 (5+ years) than in 2005 (4+ years). Large myctophids have a greater capacity for catching and handling larger sized prey, so they may have a greater preference for krill than smaller prey (Shreeve et al. 2009; Saunders et al. 2018). However, temporal variations in *G. nicholsi* diet are also likely to be associated with variations in the available prey field in the region, as Southern Ocean myctophids are largely opportunistic feeders (Saunders et al. 2018). Presently, there are insufficient data to resolve possible size-related differences in the diet between the pelagic and benthopelagic components of the *G. nicholsi* population at South Georgia. There is also evidence that krill interact frequently with the seabed (Schmidt et al. 2011), suggesting that krill could be available to *G. nicholsi* in the benthopelagic realm without the need for *G. nicholsi* to migrate to surface waters to feed on krill. Indeed, krill have been found in the diet of demersal skates (*Amblyearaja georgiana*) in the region (Main and Collins 2011). Nevertheless, our data raise the possibility that there are important concentrations of *G. nicholsi* in the

benthopelagic realm consuming more krill in the region than previously thought, and that recent estimates of krill consumption by myctophids in the Scotia Sea are underestimated due to a lack of data on benthopelagic populations around the continental shelves (Saunders et al. 2019). The trophic relationship between *G. nicholsi* and krill is dynamic and complex, as it appears to be a process that is dependent upon the life stage of both the myctophid predator (large vs small fish and/or pelagic vs benthopelagic mode) and krill (larval and juvenile vs large adults). Nested in these ontogenetic interactions, there are also multiscale, temporal variations in both predator and prey vertical distribution patterns to consider, which occur through diurnal, seasonal and environmentally related changes in vertical migration behaviour. Further studies are required to more fully resolve the diet and behaviour of both benthopelagic and pelagic *G. nicholsi* at appropriate temporal scales around South Georgia, particularly regarding its trophodynamics in relation to krill.

Diet data on *G. bolini* are rare in the Southern Ocean, particularly south of the APF. Limited data from pelagic hauls around Macquarie Island (Pacific Ocean sector) showed that its diet was comprised predominantly of unidentified fish species, although more data are required to substantiate its diet composition and resolve spatial, temporal and ontogenetic variations (Gaskett et al. 2001). Nevertheless, the high portion of krill in its diet in our study emphasises the requirement for new data on *G. bolini* to better quantify its contribution to the level of krill demand by myctophids in the region, and to understand its wider role in Southern Ocean food webs.

Benthopelagic and pelagic coupling

Given the inherent caveats with our sampling methodology, it is not possible to compare our estimates of *G. nicholsi* abundance or biomass with estimates from pelagic studies in the region (Collins et al. 2008; Saunders et al. 2015). It therefore remains unclear whether *G. nicholsi* abundance and biomass is greater in the benthopelagic realm than in the pelagic around South Georgia. The extent and frequency of exchange of *G. nicholsi* between these two environments, due to their DVM behaviour, also remains unclear. However, our data raise the possibility that there are important concentrations of *G. nicholsi*, and potentially other large myctophids, such as *G. bolini*, residing in near-bottom environments at South Georgia that are being missed in ecosystem analyses. Since benthopelagic *G. nicholsi* consumes zooplankton (including Antarctic krill) that occur mostly in the upper water column around South Georgia (Atkinson et al. 2001; Ward et al. 2006), and is an important part of the diet of demersal fish species, such as Patagonian toothfish *Dissostichus eleginoides* (Collins et al. 2007), the species is

potentially important in transporting energy from secondary surface productivity to higher trophic levels in demersal fish communities. *Gymnoscopelus nicholsi* could therefore be crucial to the operation of benthic ecosystems, but there remain many uncertainties in the ecology of *G. nicholsi*. Our study demonstrates the utility of time-series data from annual bottom trawl surveys for examining the ecology and trophodynamics of myctophids around South Georgia, which will contribute to an improved understanding of their role in local ecosystem and food web function.

Conclusions

Sampling myctophids in both the pelagic and benthopelagic zones is both practically and logistically challenging, particularly in the remote Southern Ocean. Our study, based on annual bottom trawl surveys, provides useful insight for future ecosystems studies in the region. *Gymnoscopelus nicholsi* occurs regularly in the benthopelagic zone at South Georgia and potentially plays an important role in the transfer of energy from secondary producers in the upper water column to higher trophic levels in the demersal fish community. However, there remain many uncertainties in the ecology of the species in both the pelagic and benthopelagic realm. This study highlights the necessity for greater consideration of benthopelagic myctophids, such as *G. nicholsi* and *G. bolini*, in future Southern Ocean ecosystem studies, as well as the need for more data to resolve their role in benthopelagic coupling. This will help to improve our ability to better understand how sensitive both pelagic and demersal food webs are to possible broad-scale environmental change in the region.

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Data availability The data will be made available upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest Authors declared that they have no conflict of interest.

Ethical approval All research was conducted after a preliminary environmental assessment and under permits issued by the UK Foreign and Commonwealth Office and the Government of South Georgia and South Sandwich Islands. Fishes were collected as part of faunal surveys and no animal experiments were conducted. Therefore, no ethical approval was required.

Consent to participate All authors consent to participation.

Consent for publication All authors and British Antarctic Survey consent for publication.

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