Vol. 633: 55–69, 2020
https://doi.org/10.3354/meps13176

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 9

Variability in age of a Southern Ocean myctophid (*Gymnoscopelus nicholsi*) derived from scat-recovered otoliths

Angela D. Klemmedson[1,*], Christian S. Reiss[2], Michael E. Goebel[2], Ronald S. Kaufmann[1], Emmanis Dorval[3], Tomasz B. Linkowski[4], Renato Borras-Chavez[5]

[1]Department of Environmental and Ocean Sciences, University of San Diego, San Diego, CA 92110, USA
[2]Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, NOAA Fisheries, La Jolla, CA 92037, USA
[3]Ocean Associates Inc. under contract with National Marine Fisheries, Southwest Fisheries Science Center, La Jolla, CA 92037, USA
[4]Department of Fisheries Oceanography and Marine Ecology, National Marine Fisheries Research Institute, 81-332 Gdynia, Poland
[5]Center of Applied Ecology and Sustainability, Pontificia Universidad Católica de Chile, 8331150, Santiago, Chile

ABSTRACT: Myctophids are ecologically important in the Southern Ocean, where they occupy a central trophic position and are a key energy resource for top predators. However, understanding their population dynamics is limited by a paucity of data due to sampling challenges. Antarctic fur seal *Arctocephalus gazella* scats provide large collections of otoliths and other prey remains that can be used to form time series for important mesopelagic taxa such as *Gymnoscopelus nicholsi* (*Gn*). Examination of otoliths from scats allowed for a reconstruction of *Gn* age and length structure from 8 selected sample years between 2000 and 2015. While mean reconstructed length did not change significantly over the time series, mean age declined. Older age classes were scarce in scat samples, and age-6 animals were not found after 2008. During the same time period, *Gn* otoliths in fur seal scats declined from approximately 2000 to fewer than 200. The decline in the number of otoliths in Antarctic fur seal scat samples coupled with the negative trend in mean age suggests declines in the availability of *Gn* on the South Shetland Island slope region between 2000 and 2015. This study demonstrates the utility of central-place foragers in assessing populations of unfished but ecologically important mesopelagic fishes, thus allowing evaluation of hypotheses about their population structure and dispersal.

KEY WORDS: Myctophidae · *Gymnoscopelus nicholsi* · Otolith · Mesopelagic · Southern Ocean · Antarctic fur seal · Krill

1. INTRODUCTION

Myctophid fishes (family Myctophidae) are a critical component of the Southern Ocean pelagic food web, owing to their large biomass and their intermediate trophic position between primary consumers and higher trophic levels (Collins et al. 2008, Cherel et al. 2010, Saunders et al. 2015). Myctophids have high lipid and nutrient content, making them an important energy resource for top predators, including marine mammals, seabirds, and other fishes (Saito & Murata 1996, Van de Putte et al. 2006, Catul et al. 2011). Despite their ecological importance, there is a conspicuous lack of biological and population information (e.g. lifespan, growth rate, recruitment, age structure) for myctophid populations both globally (Irigoien et al. 2014) and for the Southern Ocean (Linkowski 1985, Greely et al. 1999, Kock et al. 2012, Saunders et al. 2017). This is in striking contrast to another important Southern Ocean prey item and target of commercial fisheries, Antarctic krill *Euphausia superba* (hereafter ‘krill’), for which life his-

---

*Corresponding author: aklemmedson@sandiego.edu

tory and population dynamics are regularly documented (Siegel 2016).

The lack of data for myctophid life history exists because these species are not commercially fished and are challenging to sample using traditional methods such as acoustic and trawl surveys. Acoustic methods fail to provide the physical specimens necessary to obtain biological information (e.g. species, age, and size) and trawl-based sampling introduces biases related to net avoidance and escapement (Gjøsaeter & Kawaguchi 1980, Lancraft et al. 1989, Kaartvedt et al. 2012). Thus, in contrast to krill or commercially fished species, there are no time series from which to examine trends in the population dynamics, distribution, or relative abundance of mesopelagic fish populations.

Limited data from occasional trawl surveys suggest that *Gymnoscopelus nicholsi* (Gilbert, 1911) (hereafter '*Gn*') is one of the most abundant myctophid species in the Southern Ocean. Analysis of trawl-caught specimens indicates that *Gn* lives approximately 7 yr (Linkowski 1985), has a maximum recorded standard length (SL) of 174 mm (Williams & McEldowney 1990), and is a broadly Antarctic species with a circumpolar distribution between the Antarctic continent and 36° S (Duhamel et al. 2014). *Gn* are thought to be most abundant between the Sub-Tropical Front and Polar Front (PF) and to have a pelagic association with Antarctic Intermediate Water and Sub-Antarctic Mode Water (Duhamel et al. 2014). Larvae and juveniles are found in the open ocean and are mesopelagic; however, adults typically adopt a benthopelagic lifestyle in slope regions further south where the southern Antarctic Circumpolar Current front approaches the continent (Hulley 1990, Duhamel et al. 2014; Fig. 1a).

The absence of *Gn* eggs or larvae south of the PF (Linkowski 1985, Pakhomov et al. 1996, Pusch et al. 2004, Flores et al. 2008, Saunders et al. 2015) has led to the hypothesis that *Gn* spawn in the western South Atlantic and then migrate south to more polar waters with age, length, or maturity (Saunders et al. 2015), yet the mechanism of movement is unknown. A number of hypotheses exist to explain the population structuring mechanisms in the Southern Ocean (Ashford et al. 2008, Saunders et al. 2015, Caccavo et al. 2018, Zhu et al. 2018) including southward migration (Saunders et al. 2015) and advection around the Antarctic continent (Ashford et al. 2008). There is merit to the southward migration hypothesis in that it is the most direct path from the northern spawning area and the slope regions around Antarctica where adult *Gn* are found. However, the hypothesis does not explain how larvae and young fishes can be transported south without also being advected in the eastward circulation of the Antarctic Circumpolar Current (ACC). Eastward advection of larvae and juveniles around the Antarctic continent in the ACC has been observed for similar Southern Ocean mesopelagic fishes (Ashford et al. 2008, Zhu et al. 2018), and it is reasonable to hypothesize that *Gn* may use a similar method of transport to arrive in Antarctic slope regions. Testing these hypotheses is difficult because of the paucity of time series of *Gn* age and length distributions from which to infer how patterns of distribution are related to the transport pathway. Thus, although there is a basic understanding of *Gn* ecology, there is poor understanding of their distribution and migration patterns, population dynamics, and links to other components of the pelagic ecosystem.

Piscivorous marine predators, such as pinnipeds, can be effective samplers of fish populations and can provide information for assessing population dynamics of fish prey (Lowry & Carretta 1999, Reid & Croxall 2001, Field et al. 2007). While indigestible prey parts (e.g. fish otoliths and crustacean carapaces) are frequently used to infer predator foraging habits (Davis et al. 2006), they can also be useful in providing information about age and length distributions for fish and zooplankton species (Campana 1999, Begg et al. 2005, Goebel et al. 2007). Similar to trawl sampling, there are inherent biases associated with using marine mammals to sample prey because of their size selectivities. For example, it is unlikely that predators sample the entire age or size distribution of prey populations; however, examining remains of prey from piscivorous marine predators can provide valuable data describing poorly sampled prey species, like mesopelagic fishes.

Antarctic fur seals *Arctocephalus gazella* (family Otariidae; hereafter 'fur seals') are particularly useful biological samplers of mesopelagic taxa because they are numerous in the Southern Ocean (Davis et al. 2006), are significant predators of mesopelagic fishes including myctophids (Cherel et al. 1997, Osman et al. 2004, Polito & Goebel 2010) such as *Gn*, and females are central-place foragers during their perinatal period of December through March, allowing consistent collection of regional prey (Davis et al. 2006). Also, fur seals reliably return to the same colonies annually where they can be easily monitored (Hucke-Gaete et al. 2004). Fur seals are an important indicator species for the CCAMLR Ecosystem Monitoring Program (Agnew 1997), and multiple long-term monitoring programs regularly collect fur seal scats and foraging data in the Antarctic and Sub-Antarctic islands

(Agnew 1997). Myctophids comprise the second most abundant prey item by mass, after krill, in the diets of fur seals around the South Shetland Islands (Osman et al. 2004, Polito & Goebel 2010) and *Gn* is the most dominant myctophid in terms of biomass and abundance among myctophids collected in fur seal diets in this region (Daneri 1996, Casaux et al. 2003, Osman et al. 2004, Polito & Goebel 2010). Owing to these biological characteristics of fur seals, they may be an effective sampler that can provide information on *Gn* population characteristics.

The purpose of this study is to use otoliths derived from fur seal scats to examine the utility of central-place foragers for assessing populations of unfished, and difficult to sample, but ecologically important mesopelagic fishes. Specifically, we use sagittal otoliths recovered from long-term monitoring of fur seal diets conducted at Cape Shirreff, South Shetland Islands, Antarctica by the US Antarctic Marine Living Resources (AMLR) Program from 2000 to 2015 to examine patterns in the age structure and reconstructed length distributions of *Gn*. We then discuss the importance of central-place foragers as a source of information on changes in mesopelagic fish population structure and recruitment variability in relation to hypotheses about transport and recruitment pathways.

2. MATERIALS AND METHODS

2.1. Study area

Cape Shirreff (62° 28′ S, 60° 46′ W) is an ice-free peninsula (Osman et al. 2004) on the north side of Livingston Island in the South Shetland Islands separated from the Antarctic Peninsula by the Bransfield Strait (Fig. 1). Cape Shirreff has the largest breeding colony of fur seals in the Antarctic Peninsula region (14 842 estimated in 2002; Hucke-Gaete et al. 2004) and has been surveyed by the US AMLR Pinniped Research Program each austral summer/autumn (late October through early March) since 1997/98.

The continental shelf (<500 m depth) is approximately 30 km wide around Cape Shirreff (Goebel et al. 2000), and then the shelf slope transitions quickly into deeper water (1000 to 5000 m; Fig. 1b). The bathymetry near Cape Shirreff includes 2 submarine canyons, one on either side of the Cape (Fig. 1b), that may make mesopelagic species readily available to foraging fur seals at Cape Shirreff. Over the last 20 yr, 95% of fur seal foraging trips have occurred within ~60 km of the colony (Hinke et al. 2017; Fig. 1b). Fur seals forage both on the shelf and over the shelf slope region, and occasionally offshore of the southern boundary of the Antarctic Circumpolar Current front (Fig. 1b). Although fur seal daytime foraging (40–75 m; Croxall et al. 1985) is shallower than the typical depths mesopelagic species occupy during the day (>200 m; Duhamel et al. 2014), the majority of fur seal dives take place at night (Croxall et al. 1985) when meso-

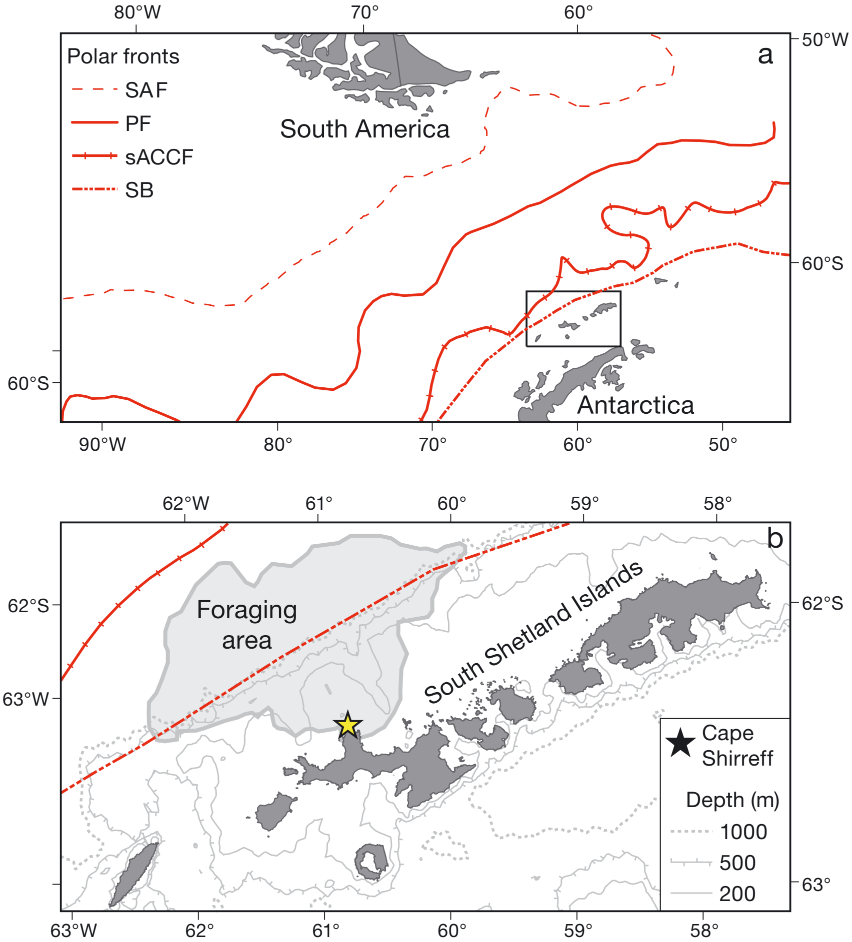

Fig. 1. (a) Location of the South Shetland Islands (boxed) relative to Antarctica and South America, with the average locations of the Antarctic Polar Fronts (Orsi et al. 1995); and (b) the location of Cape Shirreff (starred; 62° 28′ S, 60° 46′ W), Livingston Island, with the 200, 500 and 1000 m isobaths (Ryan et al. 2009), and the 95% foraging area for Antarctic fur seals *Arctocephalus gazella* during January and February between 2009 and 2014 (Hinke et al. 2017). SAF: Subantarctic Front; PF: Polar Front; sACCF: southern Antarctic Circumpolar Front; SB: southern boundary of the Antarctic Circumpolar Front

pelagic species make vertical migrations to the surface. At night, the dive depth of fur seals (<30 m; Croxall et al. 1985) overlaps with the nighttime depth of myctophids (<20 m; Duhamel et al. 2014).

2.2. Scat collection

Field work for the US AMLR fur seal monitoring program began the third week of December (2000 through 2015) and lasted 10 to 11 wk each field season. Weekly surveys of female fur seal suckling sites resulted in the collection of up to 10 scats per week, with approximately 100 scats collected annually (Table 1). This sample size is greater than what Trites & Joy (2005) report to be the required sample size of scats to identify principal prey remains and to monitor effects over time. The suckling sites were searched for fresh (i.e. same day and not trampled or picked through by seabirds) fur seal scats by walking in an outward concentric pattern around female harem groups. To avoid bias associated with more highly-visible, brightly-colored krill scats, researchers collected all fresh scats (regardless of the contents; krill or fish) immediately in front of them (~1 m on either side) as they walked around each harem group and across suckling sites. In order to collect 10 fresh scats, surveys of the entire suckling area typically took 1 to 2 d, but on occasion, up to a full week.

In the field, each scat was washed through a 3-tiered sieve (1 mm, 0.5 mm and 0.25 mm mesh size) under running water and all otoliths and other prey parts were removed. Fish otoliths of principal taxa are sufficiently large that they are retained in one of the 3 mesh sieves, and *Gn* otoliths, which are greater than 1 mm regardless of age (Williams & McEldowney 1990), are easily collected with the mesh sizes used. Otoliths and other hard parts (i.e. krill carapaces or squid beaks) were cleaned and counted, and identified to species according to Hulley (1981) and Hecht & Hecht (1987). Additionally, a reference otolith collection created from locally-caught fish species during offshore US AMLR oceanographic surveys facilitated identification of otoliths to species. *Gn* otoliths were also characterized as left side or right side. The present study is only concerned with the ageing of archived *Gn* otoliths. All samples recovered from scats, including otoliths from other species and other prey parts, were archived at the NOAA Laboratory in La Jolla, CA. For more detailed collection methodology see Polito & Goebel (2010).

2.3. *Gn* otolith analysis

2.3.1. Scat selection

Otoliths were retrospectively subsampled from the US AMLR archives to be analyzed for age and length. To maximize temporal coverage, we selected otoliths from 8 years spanning the 16 yr sampling period. The samples were spaced approximately every other year (Table 1) to quantify variability over the span of the available time series. From these selected years, we identified scats that had >30 *Gn* otoliths to ensure there were sufficient numbers of *Gn* otoliths for analyses. Scats with only a few *Gn* otoliths may not be representative of *Gn* in the region and could reflect biases with individual seal foraging preferences. Fur seals are thought to consume an increased proportion of myctophids in the second half of their breeding season (Polito & Goebel 2010), thus for this study we focused our sampling on the second half of the field season when high *Gn* contents were more common. We randomly subsampled *Gn* otoliths from 6 to 10 randomly sampled scats each sampling year (approximately 2 scats per week; Table 1), over the 6 wk between January and February.

Table 1. Summary of sampling information for *Gymnoscopelus nicholsi* (*Gn*) sagittal otoliths selected from Antarctic fur seal *Arctocephalus gazella* scats collected at Cape Shirreff

Year	Collection dates		Scats (n)		*Gn* otoliths (n)		
			Collected	Sampled	Identified	Sampled	Analyzed
2000	26 Jan 00	2 Mar 00	114	10	2160	130	109
2002	24 Jan 02	28 Feb 02	115	10	1340	130	122
2004	26 Jan 04	1 Mar 04	112	10	2066	130	127
2006	24 Jan 06	24 Feb 06	95	6	565	108	97
2008	27 Jan 08	1 Mar 08	111	10	1386	130	124
2010	30 Jan 10	1 Mar 10	108	8	501	112	96
2012	21 Jan 12	19 Feb 12	90	10	1449	130	127
2015	25 Jan 15	22 Feb 15	100	10	778	130	120

2.3.2. Otolith selection and preparation

Otoliths were randomly selected from the previously identified scats with high fish content. All *Gn* otoliths of each selected scat were arranged on a numbered grid and randomly generated numbers (without replacement) identified otoliths to select. Sampling and analyzing otoliths is a time and labor intensive process, so it was necessary to limit sampling based on our available resources. We selected between 108 and 130 *Gn* sagittal otoliths per sampling year using the random selection procedure above (Table 1). A 1-way ANOVA power calculation using $\alpha = 0.05$, $\beta = 0.9$, $k = 8$, and a moderate effect size $f = 0.25$ produced a sample size of N = 37 for each year (R software; pwr package; Champely et al. 2018), thereby corroborating the sample sizes used in this study.

Several quality control measures were performed before analyzing the otolith ages. Only left sagittal otoliths were analyzed to prevent double-counting individual fish. It was assumed that there was no systematic bias in growth patterns between left and right otoliths. Otoliths that were severely eroded from digestion (i.e. otoliths with smooth ventral margins and no denticles) were excluded from analyses because the poor condition reduced the ability to withstand polishing or to yield accurate age estimates as annuli were likely removed by erosion. A numeric scale was developed to quantify erosion and was used to categorize each otolith (1 = no erosion; 2 = mild erosion/pointed denticles; 3 = moderate erosion/rounded denticles; 4 = high erosion/few denticles present; 5 = severe erosion/smooth margin and no denticles). We omitted erosion level-5 otoliths from analysis. There may be biases associated with removing eroded otoliths (i.e. if different sized/aged otoliths erode at varying rates); however, it was important for us to collect quality age estimates. The method used to select otoliths was consistent throughout the time series; therefore, any biases should be systematic and should not affect trends derived from the otolith time series.

2.3.3. Otolith analysis

Otoliths were randomly aged across years and with no knowledge of collection date to minimize reader bias. All otolith age-estimations were performed by a single reader. To visualize annuli (i.e. growth rings), otoliths were wet-polished on the proximal surface of each otolith, by hand using 30 µm lapping film, until the mid-sagittal plane was exposed and following the protocol in Matta & Kimura (2012). Preliminary experiments demonstrated that after polishing, all *Gn* annuli were visible from the proximal surface and outer annuli were not removed during polishing. Otoliths were submerged in water atop a Sedgewick-Rafter slide (1 mm grid size) using reflected light, and a digital camera (Leica MC170 HD) attached to a dissecting microscope (Leica S6D) was used to capture images using ImagePro Plus (version 6.2, Media Cybernetics). A stage micrometer was used to calibrate the software before each imaging session and a 1 mm background grid was used to provide further measurement confidence. Each image was assigned an index so that sample information would be unknown to the reader during analysis.

Otolith length (mm) and width (mm) along the anterior-posterior axis and dorso-ventral axis was measured, respectively, to the nearest 0.01 mm intersecting perpendicularly through the nucleus (Fig. 2). This technique is consistent with previously published studies of this species, making our results more comparable to existing otolith–fish length regressions (Williams & McEldowney 1990).

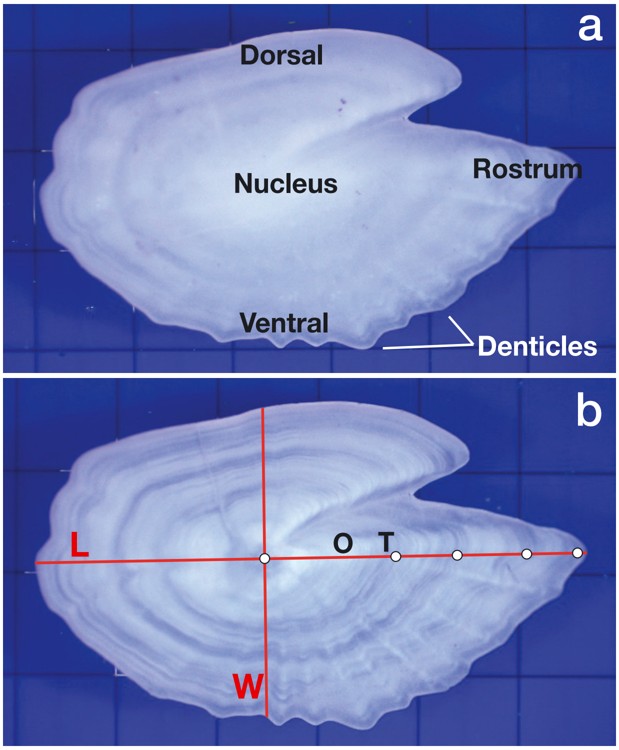

Fig. 2. Proximal surface of left *Gymnoscopelus nicholsi* sagittal otolith (a) before and (b) after polishing (age-4, erosion-2, 1 mm grid); showing otolith length (L; here 5.45 mm), width (W; here 3.09 mm), the first opaque (O) and translucent (T) zones, and each assigned annulus (marked with white circles)

Ages of fish in scats were determined from the analysis of 922 *Gn* sagittal otoliths (Table 1) by enumerating continuous and concentric annuli along the axis from the nucleus to the rostrum (Fig. 2). An annulus was defined as an opaque zone followed by a translucent (i.e. hyaline) zone. We regarded the first, and often faint, translucent ring (~0.5 mm from the nucleus; Fig. 2b) as an auxiliary larval ring and did not count it as an annulus (Zurbrigg & Scott 1972, Linkowski 1985, Gartner. 1991). The first annulus counted was the translucent zone following the larval zone. The outer annulus was only counted if complete. Proper age validation (Stevenson & Campana 1992) has not been published for *Gn*, as this species has not been reared in a laboratory or been the subject of any mark-recapture experiments. However, ageing myctophids using otoliths has been well documented (Odate 1966, Smoker & Pearcy 1970, Halliday 1970, Gjøsaeter 1973, Hecht & Hecht 1981).

2.3.4. Ageing reproducibility

To better quantify ageing consistency, 2 preliminary studies were conducted and age bias plots constructed following methods reported in Campana et al. (1995). First, a subset of the Linkowski (1985) *Gn* otoliths were aged and bias was analyzed between different readers (Fig. 3a). Age estimates had 89% agreement and a mean CV = 9.6% (N = 47; Fig. 3a). Then, repeated age measurements were performed for a random sample of the otoliths analyzed in this study to evaluate precision and bias for an individual reader (Fig. 3b). Our duplicated age estimates also had 89% agreement and a mean CV = 22.6%, with the second estimate of the same otolith (Estimate 2) biased to under-estimate age-5 and age-6, and slightly over-estimate age-2 (N = 100; Fig. 3b).

2.4. Data analysis

2.4.1. Fur seal diet

To examine whether fur seals exhibited any trends in prey switching that could impact our interpretation of the otolith data in fur seal scats, the percent occurrence of krill, fish, and cephalopods (indicated by the presence of carapaces, otoliths, and beaks, respectively) in fur seal scats were calculated for each year between 2000 and 2015. The number of *Gn* otoliths and other otoliths (i.e. remaining otoliths of other fish species) in fur seal scats each year between 2000 and 2015 were normalized for 100 scats (to adjust for varying sampling sizes among years) as an estimate of relative fish availability. Ordinary least squares (OLS) regressions with slopes significantly different from zero at $p < 0.05$ were used to examine trends in prey occurrence and the number of otoliths in fur seal scats among years. A series of Durbin-Watson (DW) tests suggested there was no temporal autocorrelation for krill occurrence (DW = 1.72, p = 0.19), fish occurrence (DW = 1.69, p = 0.17), squid occurrence (DW = 1.70, p = 0.18), or *Gn* otoliths (DW = 1.92, p = 0.32), while there was slight autocorrelation for otoliths of other species (DW = 1.22, p = 0.02).

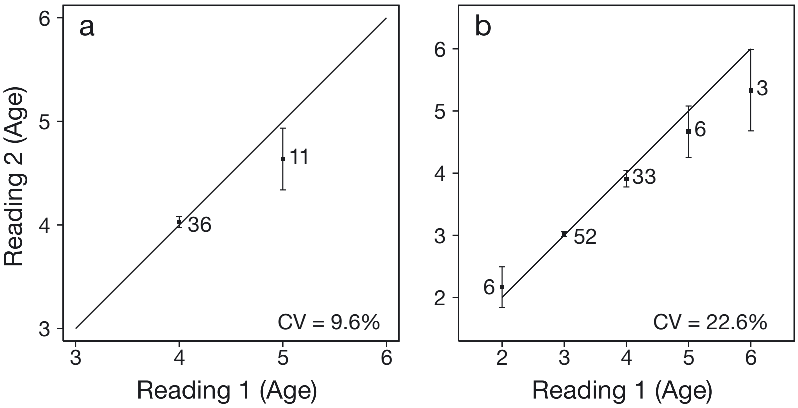

Fig. 3. Bias between pairwise age estimates of *Gymnoscopelus nicholsi* otoliths performed by (a) different readers (T. B. Linkowski and A. D. Klemmedson, respectively) on a subset of otoliths from Linkowski (1985) (n = 47), and (b) the same reader (Klemmedson) on a random sample (n = 100) of the otoliths analyzed in this study (each otolith read twice). Each point represents the mean of Estimate 2 (± 95% CI), grouped by Estimate 1, and is labelled with sample size. The reference line has a slope of 1 and represents zero bias

2.4.2. *Gn* age and length from otoliths

Age data were grouped by sampling year and age class to compare the proportions of each age class among years (see Table 2). To account for the possibility of inaccurate age estimation, ages were also grouped into 'younger' and 'older' groups (age-2 and -3, and age-4, -5 and -6). To examine whether relative proportions of age classes in the population varied over time, an indication of either increased relative recruitment or decreased availability of older age classes in the region, OLS regressions of the proportions of each age, and combined ages, were used.

To test whether there were any significant temporal effects on estimated ages in this study, a linear model was developed, based on the multi-stage sampling of otoliths. Samples of otoliths were categorized and analyzed by year and time of collection (i.e. ~every fortnight) within each sampling season, following the linear model:

$$y_{i,j} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{i,j} + e_{i,j} \qquad (1)$$

where $y_{i,j}$ was the mean age of *Gn* collected in year i during collection period j, μ the mean age of the observed fish population, α_i the year effect with i varying 1 to 8, β_j the time of collection with j varying from 1 to 3, $(\alpha\beta)_{i,j}$ the interaction between year and time of collection, and $e_{i,j}$ the sampling error. The age data was log-transformed to better approximate normality and equality of variance within year and time.

As only the year effect was significant in Eq. 1 (see Table 3), we plotted the mean estimated age for each sampling year with a 95% confidence interval (CI) and fit a weighted least squares (WLS) regression to the means. Weights were the inverse of the variance and were used to account for different sample sizes (and resulting variance) among years. Analysis of the residuals of mean ages from the weighted linear regression and a Durbin-Watson test (DW = 3.51, p = 0.99) suggested there was no sign of temporal autocorrelation.

Fish lengths (mm, SL) were reconstructed from otolith lengths (mm, OL; Fig. 2b), using the otolith–fish length regression (SL = 28.6 OL – 20.8; R^2 = 0.89; N = 140; from fish 31–174 mm SL) reported by Williams & McEldowney (1990), and WLS regression analysis of mean SL by sampling year was conducted to test for a temporal trend in mean size from 2000 to 2015.

Statistical analyses were performed using the Statistical Analysis Software (SAS, version 9.1) and R (version 3.5.1).

3. RESULTS

3.1. Diets of fur seals at Cape Shirreff

Fur seal diets inferred from analysis of scats at Cape Shirreff showed presence of krill, fish, and cephalopods each year of the study. When averaged over the time series, krill, fish, and cephalopods occurred in 93%, 41%, and 10% of scats, respectively (Fig. 4). Although variable, there was no significant trend in the occurrence of krill or cephalopods over time (p = 0.38 and p = 0.21, respectively). In contrast, fish, which made up a large component of fur seal diet, exhibited a significant decline in the percent occurrence in fur seal scats over the time series (p = 0.01), suggesting that fish availability to fur seals declined at Cape Shirreff.

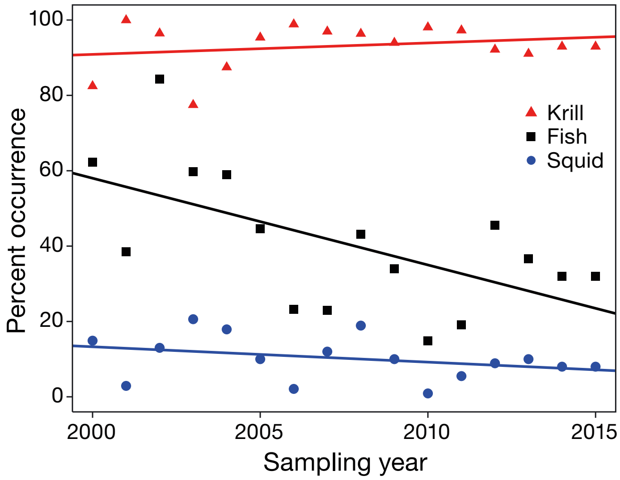

Fig. 4. Trends in the percent occurrence of principal taxa in diets of Antarctic fur seals (*Arctocephalus gazella*) from carapaces, otoliths, and beaks recovered from scats collected at Cape Shirreff (n = 16 years)

The number of otoliths of the most abundant fish taxa in the diets of fur seals declined over the study period (Fig. 5). The number of *Gn* otoliths declined (slope of linear regression: p = 0.01) from 2160 in 2000 to a minimum of 146 in 2015 (Fig. 5). For species other than *Gn* (predominantly *Electrona antarctica* and *E. carlsbergi*) a decline was also observed (slope of linear regression: p = 0.08) and the number of otoliths decreased from 827 in 2000 to 126 in 2015, with a minimum of 35 in 2011 (Fig. 5).

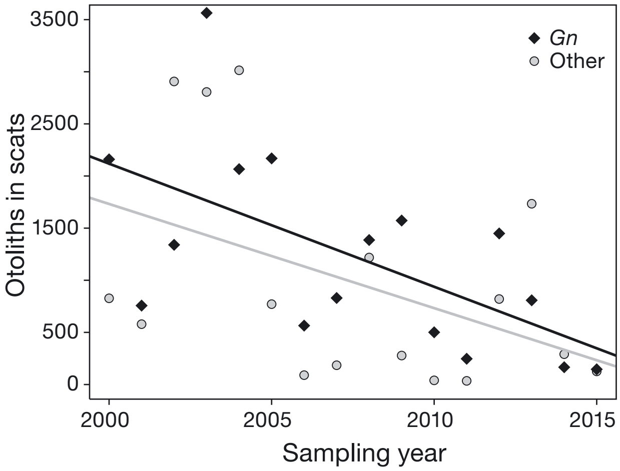

Fig. 5. Trends in the number of *Gymnoscopelus nicholsi* (*Gn*) otoliths and otoliths of other fish species in Antarctic fur seal *Arctocephalus gazella* scats at Cape Shirreff (n = 16 years)

3.2. Changes in *Gn* age distribution

Age composition of *Gn* in diets of fur seals varied over the 16-year time series (Table 2). Fur seals foraging around the South Shetland Islands consumed *Gn* age-2 through -6 (Table 2). Fish age-2 through -5 were present in fur seal diets in all sampling years, and fish aged 3 and 4 comprised 88% of the *Gn* consumed. The 2 ages occurred in similar proportions to each other throughout the study period, with age-3 and -4 making up on average 48% ± 6% SD and 40% ± 5% SD, respectively. There was a significant increase in the proportion of age-3 (p = 0.03) and a significant decrease in the proportion of age-5 (p = 0.02) fish in fur seal diet during this time period. Age-6 *Gn* were absent from 4 of the 8 sampling years (2006, 2010, 2012, 2015), including the 3 most recent sampling years (Table 2). Although age-6 fish made up a small proportion of the samples (0.5% of the otoliths analyzed), their absence in recent years coincided with the decline in the prevalence of age-5 *Gn* in fur seal diets, and the combined proportion of age-5 and age-6 fish declined significantly during the study period (p = 0.02).

The mean age of *Gn* in the diets of fur seals declined between 2000 and 2015 (Fig. 6). Over the time series, mean age declined from ~3.66 yr in 2004 to ~3.38 yr in 2015. A 2-way ANOVA (year × time of collection) of age showed no significant effect of time of collection (i.e. intra-annual variation in sampling dates) or of the interaction between year and time of collection (Table 3). There was, however, a significant effect of year of collection on the age of *Gn* from fur seal scats at Cape Shirreff between 2000 and 2015 (p = 0.04).

Table 2. Proportions of *Gymnoscopelus nicholsi* ages in Antarctic fur seal *Arctocephalus gazella* scats collected at Cape Shirreff

Year	Age-2	Age-3	Age-4	Age-5	Age-6
2000	0.06	0.40	0.41	0.12	0.01
2002	0.07	0.49	0.37	0.07	0.01
2004	0.02	0.39	0.50	0.08	0.01
2006	0.06	0.47	0.41	0.05	0.00
2008	0.04	0.48	0.40	0.07	0.02
2010	0.02	0.55	0.36	0.06	0.00
2012	0.06	0.50	0.41	0.04	0.00
2015	0.06	0.55	0.35	0.04	0.00

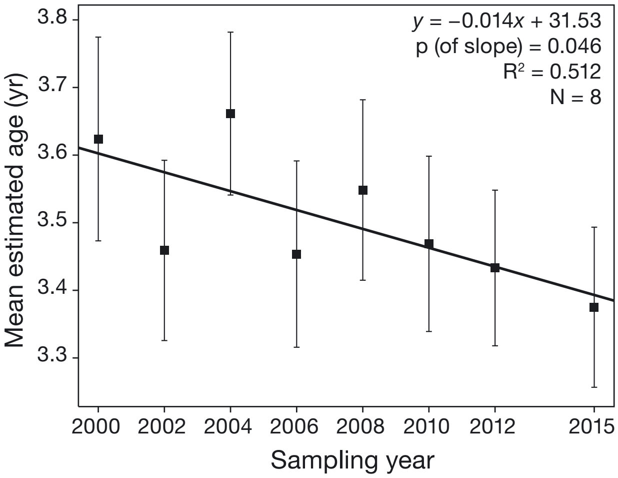

Fig. 6. Trend in the mean estimated age (error bars represent ± 95% CI) of *Gymnoscopelus nicholsi* consumed by Antarctic fur seals (*Arctocephalus gazella*) at Cape Shirreff from 2000 through 2015 (n = 8 years). Linear regression weighted by the inverse of the variance. Each mean represents approximately 100 otoliths

Table 3. Two-way ANOVA comparing the effects of year (α) and week (β) of collection on log age of *Gymnoscopelus nicholsi* otoliths collected from Antarctic fur seal *Arctocephalus gazella* scats at Cape Shirreff between 2000 and 2015

	df	Type-III SS	MS	*F*	p
α	7	0.64	0.09	2.14	0.04
β	2	0.07	0.04	0.83	0.43
$\alpha\beta$	13	0.88	0.07	1.59	0.08

3.3. Variability in reconstructed length distribution

Although there was a decline in *Gn* mean age over the course of this study, there was no significant change in reconstructed lengths (p = 0.77). Over the time series, otolith lengths ranged from 4.13 to 6.19 mm, and reconstructed lengths of *Gn* based on Williams & McEldowney (1990) ranged from 97 to 156 mm SL (Fig. 7).

4. DISCUSSION

The lack of directed studies on many ecologically important taxa means that alternative methods are required to provide data on the status and trends of these critical components of the pelagic ecosystem. In this study, we developed a time series of age and reconstructed length for an important Southern Ocean myctophid, *Gymnoscopelus nicholsi*, using otoliths collected as part of long-term monitoring of fur seal diets at a site in the Antarctic Peninsula region, among the fastest changing environments on the planet (Gille 2008, Whitehouse et al. 2008). Al-

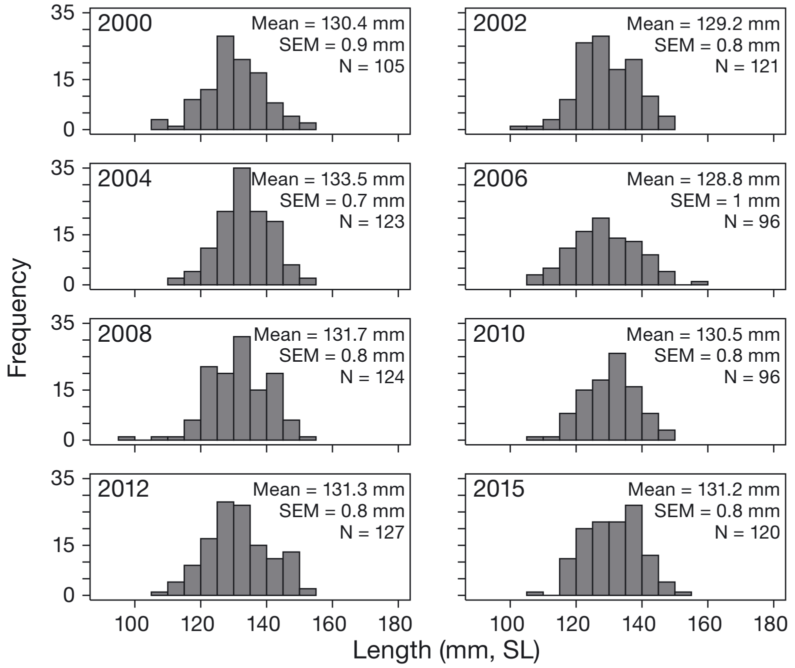

Fig. 7. Reconstructed length distributions of *Gymnoscopelus nicholsi* collected from Antarctic fur seal *Arctocephalus gazella* scats at Cape Shirreff (N = 912). Mean length, SEM, and sample size printed for each year. SL measurements reconstructed using the fish–otolith length regression reported by Williams & McEldowney (1990). Lengths of fractured otoliths were removed

though there are caveats and biases to any sampling strategy (i.e. fishing, acoustics, diets), we show that substantial information can be recovered about certain population features of difficult to sample taxa using analysis of diets of their predators. Our results indicate that scats are an effective source of otoliths, which can be used to examine *Gn* population structure fluctuations around the Antarctic Peninsula when data from traditional sampling methods are not readily available.

The presence and/or quantity of specific prey remains (i.e. otoliths, carapaces, and beaks) provides relative availability information for principal prey taxa (Agnew 1997, Davis et al. 2006) and the analysis of otoliths from scats provides high quality information on the age distributions of fish available to fur seals foraging at Cape Shirreff. During this study period, a decline was observed in the number of otoliths (of all species and of *Gn*) and in the occurrence of fish in fur seal scats. Over the same time period, a decline was also observed in the mean age of *Gn,* represented by fewer older individuals in the second half of the study period. The concurrent declines of *Gn* age and *Gn* in diets, combined with the consistent presence of younger age groups, suggests continual recruitment of *Gn* to the South Shetland Island slope region during the study period (i.e. 2000 through 2015) but local declines after recruitment.

4.1. Variability in *Gn* age

The mean age of *Gn* in diets of fur seals showed considerable interannual variability, with a negative trend over time, suggesting a change in the age of *Gn* consumed by fur seals in the slope region during this time. The proportions of older *Gn* (age-4, -5, and -6) all decreased, while the proportions of younger *Gn* increased (age-3) or stayed the same (age-2). Although the absolute decline in mean age was small (0.28 yr), this is a large change for a short-lived species. Assuming the maximum age of *Gn* is 6 yr, this decline in mean age represents ~5 % of their lifespan. Other studies of fish population structure have found similar declines in mean age along with age truncation for depleted or exploited populations (Berkeley et al. 2004, Hsieh et al. 2006, Charbonneau et al. 2019), suggesting changes comparable to fishing effects are occurring for *Gn* in the South Shetland Island slope region.

The negative trend in mean age appears robust considering the efforts and analyses made to minimize and quantify ageing bias. Firstly, otoliths were randomized across years for age analysis and a consistent ageing method was used. Second, when ages were grouped to account for the possibility of inaccurate age estimates, a decrease in the proportion of older (i.e. age-4, -5, and -6 combined) *Gn* was observed. Finally, the reproducibility between readers and precision were high, further strengthening our conclusion that mean age declined.

4.2. Decoupled *Gn* age and length

It is interesting that the observed decline in mean age was decoupled from the trend of mean reconstructed fish length. The absence of a significant change in mean length may be explained by several factors including foraging selectivity, variability in the allometric relationship, sexual dimorphism, and a change in the growth of *Gn* over time. First, fur seals have been found to select for larger krill (Reid & Arnould 1996), and it is reasonable to assume they have some size-selectivity for other available prey items, such as fish. Regardless of any size-selectivity that may exist, fur seals are not able to select for fish age. Second, the lack of a signal in changes in lengths during a period when mean age declined could result from the inherent variability in the relationship between otolith lengths and fish lengths. Due to variability in growth among individuals, variability exists within allometric equations. Length differences among adult *Gn* may be too small to detect given the variability in the reconstruction of SLs from otolith lengths. Third, there is some evidence of size-related sexual dimorphism in *Gn*, with females generally growing larger than males, especially in older age classes (Linkowski 1985, Saunders et al. 2015). Variability in sex ratios among years might also explain some of the difference between trends in mean age and reconstructed length. However, since sex information was not available for our specimens, it was not possible for us to determine whether changes in sex composition occurred during the study period and whether such changes might explain the lack of variability in the reconstructed length-frequency distributions. Finally, fish growth has high plasticity (Conover et al. 2005, Ward et al. 2017) and changes in size-at-age are common for populations exposed to size-selective fishing (Sullivan et al. 2018). Young *Gn* might grow faster as a density-dependent response to increased mortality of older/larger *Gn*, thereby explaining the decoupled trends of mean age and SL. Detailed size-at-age analyses and otolith increment data would contribute to our understanding of temporal *Gn* growth patterns. Consequently, the explanation for the decoupled age and reconstructed SL trends is unknown but may be a product of the factors listed above.

4.3. Biases from using predators to sample fish populations

There are inevitably biases involved with using otoliths collected from predator diets to understand whether changes in ages and lengths reflect the population dynamics of the prey. For example, otoliths may be partially or completely eroded from digestion (Pierce & Boyle 1991), thus causing inaccurate age estimates or length reconstructions. We accounted for potential bias owing to erosion by omitting severely eroded otoliths from analysis, but we assumed that the age distributions of omitted otoliths appeared in the scats in the same relative proportions as those retained for analysis. We have no evidence that this is not the case, and the relatively few otoliths that were rejected from the analysis suggests that any biases would be small.

Another concern is that predators may not feed on the entire prey population; in other words, their feeding behavior may introduce availability and selectivity biases. Similar types of biases exist for all other sampling strategies. For example, mesopelagic fishes are known to avoid nets (Kaartvedt et al. 2012) and spatially restricted surveys (e.g. Pusch et al. 2004) are unlikely to sample the entire population if the life history of the animal has a spatial component (Saunders et al. 2017). Fur seals forage continuously along a path over multiple-day trips (Davis et al. 2006) and are not limited to sampling at a designated location (as is the case for net sampling), suggesting availability bias from location selectivity is minimal. As central-place foragers, fur seals are effective samplers of fish populations in the vicinity of their sampled breeding sites; thus, our study is useful for following trends in the portion of the *Gn* population available to (i.e. residing within the spatial range of) and consumed by fur seals at Cape Shirreff.

4.4. Local processes affecting myctophid consumption by fur seals

The temporal patterns in the occurrence of prey items and the declines in fish in the diets of fur seals suggest that *Gn* and other myctophids (i.e. *E. antarctica* and *E. carlsbergi*) have become less available to fur seals foraging in the South Shetland Islands. Over time, the occurrence of krill and cephalopods in scats did not show any significant trends; however, during the same time period otoliths were found in fewer scats and in lower quantities. There are a number of hypotheses that may explain the observed decline in *Gn* otoliths in fur seal scats and variability of *Gn* ages consumed by fur seals over the study period. Some hypotheses include changes to fur seal behavior, predator abundance, krill availability, and *Gn* life history.

4.4.1. Changes to fur seal behavior

Changes in fur seal behavior like changing foraging location or prey switching could explain the decline of fish in fur seal diets. However, there is no evidence that foraging location changed significantly among years during our study. As for prey switching, female fur seals appear to increase the distance of foraging trips during lactation periods in order to feed on energy-rich myctophids, thereby maximizing the energy delivered upon returning to their pups (Ichii et al. 2007, Staniland et al. 2007). Prey switching during lactation likely was not responsible for fewer fish in fur seal diet unless decreased pup production (Hinke et al. 2017) caused fur seals to return to feeding predominantly on krill sooner. However, we are not able to test that hypothesis with the existing data.

4.4.2. Changes to predator abundance

Another factor that may explain the observed decline in *Gn* otoliths in fur seal scats, and also the variability of *Gn* ages consumed by fur seals over the study period, is predator abundance. Predator populations have changed dramatically over the last century (Trivelpiece et al. 2011). Southern Ocean cetacean (Zerbini et al. 2010) and pinniped (Davis et al. 2006) populations have recovered from near-extinctions that resulted from commercial exploitation in the 19th century. The population of fur seals at Cape Shirreff has also increased rapidly since the 1950s (Hucke-Gaete et al. 2004), potentially increasing predation pressure on fishes and krill in this region during the summer season. Increased predation pressure can decrease prey availability and affect population demography (Crozier & Hutchings 2014). Fur seals presumably consume the largest (and likely oldest) prey available, which could lead to a decline in mean SL and age over time, as evident in our age data. This would be more likely with mesopelagic fish like *Gn* that exhibit a benthopelagic life history as adults (Duhamel et al. 2014) and may be less likely to move long distances after recruiting to this area. Increased predation pressure from increasing predator abundances provides a plausible explanation for the observed demographic changes to the *Gn* consumed by fur seals at Cape Shirreff.

4.4.3. Changes to krill availability

Decreasing krill availability may be another cause for the observed decline of otoliths in fur seal scats and variability in ages of *Gn* consumed by fur seals over the study period. In the Southern Ocean and the Antarctic Peninsula region, krill are major prey items for fur seals (Casaux et al. 2003, Osman et al. 2004; this study). Decreases in the abundance, biomass, or availability of this important trophic link could result in increased predation pressure on alternative trophic pathways, including myctophids, as predators consume larger numbers of fishes when krill availability is lower (Murphy et al. 2007, Collins et al. 2008, Iwami et al. 2011). Changes in krill abundance are not reflected in our diet data, because the relative occurrence of krill carapaces cannot be accurately quantified from scats. However, fluctuations (Reiss et al. 2008, Cox et al. 2018) and declines in krill abundance have been reported in recent decades (Atkinson et al. 2004, 2019), and declines in the mean size of krill (Atkinson et al. 2019), all may contribute to increased predation on myctophids and other mesopelagic fishes.

4.4.4. Changes to *Gn* life history

Increased recruitment of younger age groups and/or increased mortality of older age groups may also provide an explanation for the declining trend in mean age. The overall decline in the fish portion of fur seal diets suggests that increased recruitment of younger fish is not occurring, otherwise percent occurrence of fish, and/or number of otoliths would increase or remain constant. The absence of age-6 fish from the 3 most recent sampling years, despite increased sampling effort (fewer otoliths available from scats and consistent sample size of ~100 otoliths per sampling year), supports the hypothesis that fewer older *Gn* were consumed by fur seals in recent years. Our results provide evidence for a change to the population of *Gn* that coincides with the decreased numbers of *Gn* otoliths in fur seal scats collected in this region. The combination of declining mean age and declining numbers of otoliths in scats suggests reduced availability of *Gn* to fur seals in the South Shetland Island region. If the decline in *Gn* otoliths is related to the decline in older *Gn*, we might expect that the faster-growing young fish would be a larger proportion of the diets. The increased growth rates of younger fishes is an outcome of predation removing the larger/older individuals and allowing the younger individuals greater access to resources that facilitate more rapid growth. Consequently, examining growth rate changes using size-at-age data would be helpful for understanding trends in myctophid growth rates, especially given the consistent size selectivity of fur seals on *Gn*.

4.5. Southern migration hypothesis

The age range of *Gn* in this study corroborates previous studies that suggest *Gn* move from the northern reproductive populations in the western South Atlantic to the Antarctic slope south of the Antarctic Polar Front between 3 and 5 yr of age (Linkowski 1985). The *Gn* available to fur seals at Cape Shirreff were age-2 to age-6, but were predominately age-3 and age-4. This is the same age range of fish found in trawl surveys (Linkowski 1985, Pusch et al. 2004). The consistency of the younger ages of animals found in this study allows us to begin to compare hypotheses regarding recruitment pathways from northern spawning areas to southern areas around the Peninsula.

Hulley (1981), McGinnis (1982), and Linkowski (1985) observed different size-groups of *Gn* had different distribution patterns. Saunders et al. (2015, 2017) built on these previous observations and suggested most Southern Ocean myctophids, including *Gn*, are expatriates and adults migrate from their reproductive populations for higher latitudes, where spawning does not take place. If this is the mechanism of recruitment to the slope region, it suggests a relatively consistent southward movement of life stages that would take ~3 yr. Barring a direct southward migration, such recruitment would likely be episodic because there is no known direct southward transport mechanism. A consequence of the episodic nature of such a mechanism might result in highly variable ages in diets among years as cohorts are recruited to the region. The consistent presence of younger ages in fur seal diets suggests that this southward migration hypothesis for *Gn* and other myctophids is incomplete.

In contrast to the southward direct migration hypothesis, Ashford et al. (2008, 2012), Caccavo et al. (2018), and Zhu et al. (2018) have shown the importance of longitudinal transport to explain the population structuring of fish species in the Southern Ocean. These studies highlight the potential transport of life stages with the prevailing circulation as a principal mechanism. The relatively continuous occurrence of animals ~3 yr of age in our study area, regardless of the number of fish in diet, suggests age at recruitment to the slope region is fairly constant, and suggests that transport around the Antarctic in the ACC could be an alternative mechanism to explain recruitment of animals. The current within the ACC is between 20 and 50 cm s^{-1} (Hofmann 1985) and the distance around the Antarctic at a latitude of 60° S is ~40 000 km. Given this speed and distance, it might take between 2.5 and 5 yr to be transported around the Antarctic, which is roughly equal to the age of occurrence at the South Shetland Islands.

With the direct southward migration hypothesis, we should expect much more variability in ages. While our data are not a direct test of this hypothesis, the differences between these models are certainly testable in the future. For example, stable isotope chemistry on otoliths can reveal the temporal scale at which fish experience changes in ocean environment (Ashford et al. 2008, Zhu et al. 2018). Such results would provide evidence for the timing of fish being exposed to strong gradients in the environment (especially temperature), and might clarify the timing and pathway of their movement. Similarly, otolith increment analysis among cohorts could be used to provide evidence of growth rate variability, therefore reflecting changing environments with age.

4.6. Conclusions

Although we have not identified a clear cause for the change in the availability of myctophids to predators and the observed variability in mean age of *Gn* among years, these changes appear robust and suggest variability within the mesopelagic fish community, indicating a significant trend between 2000 and 2015. The combination of a decline in the number of *Gn* in fur seal scats with a decline in mean age of *Gn* consumed by fur seals suggests there are fewer *Gn* available to fur seals near the South Shetland Islands than in the past. The consistent presence of younger *Gn* in our samples suggests continual recruitment to the Antarctic slope region, which may result from transport mechanisms involving the ACC, instead of episodic migration events. Once age-2 and age-3 have recruited to the slope, various local processes likely contributed to the decline in the overall availability of *Gn*, particularly older individuals.

Obtaining age and length data for the intervening years in this time series will serve as an excellent next step and could facilitate an examination of correlations between observed age trends and environmental drivers. Another approach will be to employ additional analytical methods, including otolith increment analysis, to understand changes in somatic growth (Jones 1992), and stable isotope analysis, to understand water mass association (Campana 1999, Dorval et al. 2011) and transport rates. Employing these methods will increase our knowledge of myctophid life history, growth rates, and transport/

migrations. Given the important ecological role of myctophids, especially as a krill alternative in the changing Southern Ocean pelagic food web (Murphy et al. 2007), priority should be placed on studies that increase our comprehension of myctophid population dynamics (Hill et al. 2007, Watters et al. 2013).

This study demonstrates the power of using archived otoliths, collected by long-term ecological monitoring programs that study predator diets, to investigate temporal trends in unfished populations. This method of monitoring produces large sample sizes and can be sustained inexpensively over the long term, compared to ship-based surveys, which are expensive and infrequent. For the South Shetland Islands, there is an ongoing multi-decadal archive of fur seal scats, but no equivalent time series from net samples, making fur seals the most available sampler of mesopelagic fishes in the region. Other diet studies already exist in many locations where myctophids comprise a large proportion of predator diets (Casaux et al. 2003), including the South Shetland (Osman et al. 2004, Davis et al. 2006, Daneri et al. 2008, Polito & Goebel 2010), South Orkney (Daneri & Coria 1993), South Sandwich (Reid & Arnould 1996), Kerguelen (Cherel et al. 1997), McDonald (Green et al. 1991), and Prince Edward Islands (Klages & Bester 1998), suggesting that studies similar to ours can be expanded across the Antarctic, and to other areas where large predator monitoring studies occur (Lowry & Carretta 1999, Sydeman et al. 2001). Such studies can help to elucidate the status of myctophids and other fishes over large temporal and spatial scales, thereby expanding our understanding of the Southern Ocean pelagic ecosystem.

Acknowledgements. The authors are grateful to the numerous US AMLR field- and ship-based scientists for collecting and processing fur seal scats and identifying otoliths. Thank you to Dr. John Field, Dr. Julian Ashford, Jennifer Walsh, Anthony Cossio, Dr. Douglas Krause, and 2 anonymous reviewers for thoughtful comments. Special recognition to the late Dr. Adrian Dahood-Fritz for her valuable contributions to this manuscript through many constructive revisions and detailed maps of the study area. This work was supported by the US AMLR Program and the Antarctic Wildlife Research Fund. All marine mammal studies were conducted under the Marine Mammal Protection Act Permit #16074 and Antarctic Conservation Act Permits. All research and protocols were independently reviewed by the Southwest Fisheries Science Center Institutional Animal Care and Use Committee (SWPI-2014-03R). The last year of the diet portion of this study was jointly funded by NOAA and the Chilean Antarctic Institute through a grant to Mr. Borras-Chavez (INACH Grant No. DT_02-15) and to CONICYT 'Capital Humano Avanzado' (Grant No. 21130059 and CONICYT/PIA/BASAL FB0002).

LITERATURE CITED

Agnew DJ (1997) Review — The CCAMLR Ecosystem Monitoring Programme. Antarct Sci 9:235–242

Ashford JR, Jones CM, Hofmann EE, Everson I, Moreno CA, Duhamel G, Williams R (2008) Otolith chemistry indicates population structuring by the Antarctic Circumpolar Current. Can J Fish Aquat Sci 65:135–146

Ashford J, Dinniman M, Brooks C, Andrews AH and others (2012) Does large-scale ocean circulation structure life history connectivity in Antarctic toothfish (*Dissostichus mawsoni*)? Can J Fish Aquat Sci 69:1903–1919

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103

Atkinson A, Hill SL, Pakhomov EA, Siegel V and others (2019) Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nat Clim Chang 9:142–147

Begg GA, Campana SE, Fowler AJ, Suthers IM (2005) Otolith research and application: current directions in innovation and implementation. Mar Freshw Res 56:477–483

Berkeley SA, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries (Bethesda, MD) 29:23–32

Caccavo JA, Papetti C, Wetjen M, Knust R, Ashford JR, Zane L (2018) Along-shelf connectivity and circumpolar gene flow in Antarctic silverfish (*Pleuragramma antarctica*). Sci Rep 8:17856

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297

Campana SE, Annand MC, McMillan JI (1995) Graphical and statistical methods for determining the consistency of age determinations. Trans Am Fish Soc 124:131–138

Casaux RJ, Baroni AV, Ramón A (2003) Diet of Antarctic fur seals *Arctocephalus gazella* at the Danco Coast, Antarctic Peninsula. Polar Biol 26:49–54

Catul V, Gauns M, Karuppasamy PK (2011) A review on mesopelagic fishes belonging to family Myctophidae. Rev Fish Biol Fish 21:339–354

Champely S, Ekstrom C, Dalgaard P, Gill J and others (2018) pwr: basic functions for power analysis. R package version 1.2-2. https://CRAN.R-project.org/web/packages/pwr/index.html

Charbonneau JA, Keith DM, Hutchings JA (2019) Trends in the size and age structure of marine fishes. ICES J Mar Sci 76:938–945

Cherel Y, Guinet C, Tremblay Y (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croy, Kerguelen. Polar Biol 17:87–90

Cherel Y, Fontaine C, Richard P, Labat JP (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol Oceanogr 55: 324–332

Collins MA, Xavier JC, Johnston NM, North AW and others (2008) Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biol 31:837–851

Conover DO, Arnott SA, Walsh MR, Munch SB (2005) Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Can J Fish Aquat Sci 62:730–737

Cox MJ, Candy S, de la Mare WK, Nicol S, Kawaguchi S, Gales N (2018) No evidence for a decline in the density of Antarctic krill *Euphausia superba* Dana, 1850, in the Southwest Atlantic sector between 1976 and 2016. J Crustac Biol 38:656–661

Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW (1985) Fur seal diving behaviour in relation to vertical distribution of krill. J Anim Ecol 54:1–8

Crozier LG, Hutchings JA (2014) Plastic and evolutionary responses to climate change in fish. Evol Appl 7:68–87

Daneri GA (1996) Fish diet of the Antarctic fur seal, *Arctocephalus gazella*, in summer, at Stranger Point, King George Island, South Shetland Islands. Polar Biol 16: 353–355

Daneri GA, Coria NR (1993) Fish prey of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Laurie Island, South Orkney Islands. Polar Biol 13:287–289

Daneri GA, Carlini AR, Harrington A, Balboni L, Hernandez CM (2008) Interannual variation in the diet of non-breeding male Antarctic fur seals, *Arctocephalus gazella*, at Isla 25 de Mayo/King George Island. Polar Biol 31:1365–1372

Davis D, Staniland IJ, Reid K (2006) Spatial and temporal variability in the fish diet of Antarctic fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. Can J Zool 84:1025–1037

Dorval E, Piner K, Robertson L, Reiss CS, Javor B, Vetter R (2011) Temperature record in the oxygen stable isotopes of Pacific sardine otoliths: experimental vs. wild stocks from the Southern California Bight. J Exp Mar Biol Ecol 397:136–143

Duhamel G, Hulley PA, Causse R, Koubbi P and others (2014) Biogeographic patterns of fish. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz C (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, p 328–362

Field JC, Dick EJ, Lucero Y (2007) Population dynamics of an unexploited rockfish (*Sebastes jordani*) in the California Current. In: Heifetz J, DiCosimo J, Gharrett AJ, Love MS, O'Connell VM, Stanley RD (eds) Biology, assessment, and management of North Pacific rockfishes. Report no. AK-SG-07-01, Alaska Sea Grant College Program, Fairbanks, AK, p 451–472

Flores H, Van de Putte AP, Siegel V, Pakhomov EA, van Franeker JA, Meesters EHWG, Volckaert FAM (2008) Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea, Southern Ocean. Mar Ecol Prog Ser 367:271–282

Gartner JV Jr (1991) Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. Mar Biol 111:11–20

Gille ST (2008) Decadal-scale temperature trends in the Southern Hemisphere ocean. J Clim 21:4749–4765

Gjøsaeter J (1973) Age, growth and mortality of the myctophid fish, *Benthosema glaciale* (Reinhardt), from western Norway. Sarsia 52:53–58

Gjøsaeter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish. Food and Agriculture Organization of the United Nations, Rome

Goebel ME, Costa DP, Crocker DE, Sterling JT, Demer DA (2000) Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island, Antarctica. In: Davision W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences Press, Christchurch, p 47–50

Goebel ME, Lipsky JD, Reiss CS, Loeb VJ (2007) Using carapace measurements to determine the sex of Antarctic krill, *Euphausia superba*. Polar Biol 30:307–315

Greely TM, Gartner JV Jr, Torres JJ (1999) Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Mar Biol 133:145–158

Green K, Williams R, Burton HR (1991) The diet of Antarctic fur seals during the late autumn and early winter around Heard Island. Antarct Sci 3:359–361

Halliday RG (1970) Growth and vertical distribution of the glacier lanternfish, *Benthosema glaciale*, in the Northwestern Atlantic. J Fish Res Board Can 27:105–116

Hecht T, Hecht A (1981) A descriptive systematic study of the otoliths of the Neopterygean marine fishes of South Africa. IV. Siluriformes and Myctophiformes. Trans R Soc S Afr 44:401–440

Hecht T, Hecht A (1987) A guide to the otoliths of Southern Ocean fishes. S Afr J Antarct Res 17:1–87

Hill SL, Reid K, Thorpe SE, Hinke J, Watters GM (2007) A compilation of parameters for ecosystem dynamics models of the Scotia Sea — Antarctic Peninsula Region. CCAMLR Sci 14:1–25

Hinke JT, Cossio AM, Goebel ME, Reiss CS, Trivelpiece WZ, Watters GM (2017) Identifying risk: concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. PLOS ONE 12:e017013

Hofmann EE (1985) The large-scale horizontal structure of the Antarctic Circumpolar Current from FGGE drifters. J Geophys Res 90:7087–7097

Hsieh CH, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G (2006) Fishing elevates variability in the abundance of exploited species. Nature 443:859–862

Hucke-Gaete R, Osman LP, Moreno CA, Torres D (2004) Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica. Polar Biol 27:304–311

Hulley PA (1981) Results of the research cruises of FRV 'Walther Herwig' to South America. LVIII. Family Myctopidae (Osteichthyes, Mychophiformes). Arch Fisch Wiss 31:1–300

Hulley PA (1990) Family Myctophidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, p 146–178

Ichii T, Bengtson JL, Boveng PL, Takao Y and others (2007) Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Mar Ecol Prog Ser 344:277–297

Irigoien X, Klevjer TA, Røstad A, Martinez U and others (2014) Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat Commun 5:3271

Iwami T, Naganobu M, Taki K, Kiyota M (2011) Annual changes in species composition and abundance of myctophid fish in the north of South Georgia (Subarea 48.3), Antarctica during austral winters from 2002 to 2008. CCAMLR Sci 18:155–165

Jones CM (1992) Development and application of the otolith increment technique. In: Stevenson DK, Campana SE (eds) Otolith microstructure examination and analysis. Can Spec Publ Fish Aquat Sci 117:1–11

Kaartvedt S, Staby A, Aksnes DL (2012) Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. Mar Ecol Prog Ser 456:1–6

Klages NTW, Bester MN (1998) Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. Mar Biol 131:559–566

Kock KH, Barrera-Oro E, Belchier M, Collins MA and others (2012) The role of fish as predators of krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. CCAMLR Sci 19:115–169

Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biol 9: 225–233

Linkowski TB (1985) Population biology of the myctophid fish *Gymnoscopelus nicholsi* from the Western South Atlantic. J Fish Biol 27:683–698

Lowry MS, Carretta JV (1999) Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in Southern California (1981–1995). CalCOFI Rep 40:196–207

Matta ME, Kimura DK (eds) (2012) Age determination manual of the Alaska Fisheries Science Center Age and Growth Program. NOAA Professional Paper NMFS 13

McGinnis RF (1982) Summary of distributions. In: McGinnis RF (ed) Biogeography of lanternfishes (Myctophidae) south of 30° S. American Geophysical Union, Washington, DC, p 66–67

Murphy EJ, Watkins JL, Trathan PN, Reid K and others (2007) Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. Philos Trans R Soc B Biol Sci 362:113–148

Odate S (1966) Study on the fishes of the family Myctophidae in the northeastern sea area along the Pacific coast of Japan. III. Determination of the age and growth of the susukihadaka, *Myctophum affine* (Lutken). Bull Tohoku Reg Fish Res Lab 26:35–43

Orsi AH, Whitworth T III, Nowlin WDJ Jr (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep Sea Res I 42:641–673

Osman LP, Hucke-Gaete R, Moreno CA, Torres D (2004) Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. Polar Biol 27:92–98

Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. Mar Ecol Prog Ser 134:1–14

Pierce GJBPR, Boyle PR (1991) A review of methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol Annu Rev 29:409–486

Polito MJ, Goebel ME (2010) Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. J Exp Mar Biol Ecol 395:1–9

Pusch C, Hulley PA, Kock KH (2004) Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). Deep Sea Res I 51:1685–1708

Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. Polar Biol 16:105–114

Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proc Biol Sci 268:377–384

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. ICES J Mar Sci 65:497–508

Ryan WBF, Carbotte SM, Coplan JO, O'Hara S and others (2009) Global Multi-Resolution Topography (GMRT) synthesis data set. Geochem Geophys Geosyst 10:Q03014

Saito H, Murata M (1996) The high content of monoene fatty acids in the lipids of some midwater fishes: family Myctophidae. Lipids 31:757–763

Saunders RA, Collins MA, Ward P, Stowasser G, Shreeve R, Tarling GA (2015) Distribution, population structure and trophodynamics of Southern Ocean *Gymnoscopelus* (Myctophidae) in the Scotia Sea. Polar Biol 38:287–308

Saunders RA, Collins MA, Stowasser G, Tarling GA (2017) Southern Ocean mesopelagic fish communities in the Scotia Sea are sustained by mass immigration. Mar Ecol Prog Ser 569:173–185

Siegel V (ed) (2016) Biology and ecology of Antarctic krill. Adv Polar Sci Vol 1. Springer, Cham

Smoker W, Pearcy WG (1970) Growth and reproduction of the lanternfish *Stenobrachius leucopsarus*. J Fish Res Board Can 27:1265–1275

Staniland IJ, Boyd IL, Reid K (2007) An energy-distance trade-off in a central-place forager, the Antarctic fur seal (*Arctocephalus gazella*). Mar Biol 152:233–241

Stevenson DK, Campana SE (eds) (1992) Otolith microstructure examination and analysis. Can Spec Publ Fish Aquat Sci 117

Sullivan JY, Kruse GH, Mueter FJ (2018) Do environmental and ecological conditions explain declines in size-at-age of Pacific halibut in the Gulf of Alaska? In: Mueter F, Baker M, Dressel S, Hollowed A (eds) Impacts of a changing environment on the dynamics of high-latitude fish and fisheries. Alaska Sea Grant, University of Alaska Fairbanks, AK, p 103–121

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. Prog Oceanogr 49: 309–329

Trites AW, Joy R (2005) Dietary analysis from fecal samples: How many scats are enough? J Mammal 86:704–712

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108: 7625–7628

Van de Putte A, Flores H, Volckaert F, van Franeker JA (2006) Energy content of Antarctic mesopelagic fishes: implications for the marine food web. Polar Biol 29:1045–1051

Ward HGM, Post JR, Lester NP, Askey PJ, Godin T (2017) Empirical evidence of plasticity in life-history characteristics across climatic and fish density gradients. Can J Fish Aquat Sci 74:464–474

Watters GM, Hill SL, Hinke JT, Matthews J, Reid K (2013) Decision-making for ecosystem-based management: evaluating options for a krill fishery with an ecosystem dynamics model. Ecol Appl 23:710–725

Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. Deep Sea Res I 55:1218–1228

Williams R, McEldowney A (1990) A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. ANARE Research Notes 75, Kingston

Zerbini AN, Clapham PJ, Wade PR (2010) Assessing plausible rates of population growth in humpback whales from life-history data. Mar Biol 157:1225–1236

Zhu G, Duan M, Ashford JR, Wei L, Zhou M, Bestley S (2018) Otolith nucleus chemistry distinguishes *Electrona antarctica* in the westward-flowing Antarctic Slope Current and eastward-flowing Antarctic Circumpolar Current off East Antarctica. Mar Environ Res 142:7–20

Zurbrigg RE, Scott WB (1972) Evidence for expatriate populations of the lanternfish *Myctophum punctatum* in the Northwest Atlantic. J Fish Res Board Can 29:1679–1683

Editorial responsibility: Franz Mueter,
Juneau, Alaska, USA

Submitted: August 20, 2018; Accepted: October 25, 2019
Proofs received from author(s): December 22, 2019