

Zonation of demersal fishes off Anvers Island, western Antarctic Peninsula

MARGARET O. AMSLER¹, JOSEPH T. EASTMAN², KATHRYN E. SMITH³, JAMES B. MCCLINTOCK¹, HANUMANT SINGH⁴, SVEN THATJE⁵ and RICHARD B. ARONSON³

¹Department of Biology, University of Alabama at Birmingham, Birmingham, AL 35294, USA

²Department of Biomedical Sciences, Ohio University, Athens, OH 45701, USA

³Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901, USA

⁴Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

⁵Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK
mamsler@uab.edu

Abstract: The Antarctic fish fauna from outer continental shelf/upper slope depths is under-sampled compared to that of the inner shelf, and there are limited quantitative data available on absolute abundance and taxonomic change with depth. A photographic survey of demersal fishes was conducted along a depth-gradient of 400–2099 m on the outer shelf and upper slope west of Anvers Island, Palmer Archipelago. A total of 1490 fishes were identified at least to the family level. Notothenioids composed 52.7% of absolute abundance and non-notothenioids 47.3%. The most abundant families were Nototheniidae (39.4%), followed by Macrouridae (28.9%), Zoarcidae (16.9%), and Channichthyidae (12.1%). The most abundant species were the notothenioids *Lepidonotothen squamifrons* (30.5%) and *Chionobathyscus dewitti* (11.7%), and the non-notothenioid *Macrourus* spp. (29.5%). The absolute abundance of all fishes peaked at 400–599 m. Depths of maximum abundance were 400–599 m for *L. squamifrons*, 700–1499 m for *Macrourus* spp., and 900–1499 for *C. dewitti*. At 700–999 m the abundance shifted from primarily notothenioids to the non-notothenioids *Macrourus* spp. and zoarcids. Fishes of the outer shelf and upper slope are not provincialized like those of the inner shelf and are circum-Antarctic.

Received 11 May 2015, accepted 25 August 2015, first published online 5 October 2015

Key words: *Chionobathyscus dewitti*, *Lepidonotothen squamifrons*, *Macrourus*, notothenioid, zoarcid

Introduction

The endemic notothenioids are the most prominent component of the fish fauna in all Antarctic shelf waters, and species composition differs between the seasonal pack ice of West Antarctica and the permanent pack ice of East Antarctica (Andriashev 1965). Ichthyologists have also noted some unusual aspects of the bathymetric distribution of these fishes (Andriashev 1965, 1987, DeWitt 1971). For example, whereas the depth of maximum species diversity is at 100–200 m in most continental shelf areas of the world, shelf diversity peaks at 400–600 m in East Antarctica (Andriashev 1965, DeWitt 1971), a phenomenon attributable to glacial isostasy (Andriashev 1987). Given the larger ice sheet, the deeper depth of maximum diversity is more pronounced in East than West Antarctica, where diversity is greatest at 200–400 m. There are also changes in the taxonomic composition of the fauna with depth. In both East and West Antarctica, the dominant notothenioid species differ between the inner and outer shelf, and some notothenioids extend onto the slope (Andriashev 1965, 1987, DeWitt 1971) to depths, in the

case of a few species, of 2500–3000 m (Gon & Heemstra 1990). Bathymetric zonation of benthic species, including fishes, has also been considered to be the result of niche separation by physiological and ecological adaptations (for a review see Brown & Thatje 2014).

Although notothenioids evolved *in situ*, the Antarctic fish fauna also contains representatives of cosmopolitan non-notothenioid groups of northern origin, such as zoarcids, liparids and macrourids (Andriashev 1987, Anderson 1990a). Zoarcids (Anderson 1990b) and liparids (Stein & Andriashev 1990, Andriashev 2003) are found on the shelf and slope, and high-Antarctic macrourids of the genus *Macrourus* are primarily mid-slope and seamount species (Iwamoto 1990, Clark *et al.* 2010). The abundance and diversity of these three taxa increase at depths greater than 500–600 m, and, at least in the Bellingshausen Sea, zoarcids are the dominant element (Matallanas & Olasso 2007). However, our knowledge of most aspects of the biology of these three groups is far less comprehensive than that for notothenioids.

Recent bottom-trawling and trapping at depths below 1000 m have yielded many new species of non-notothenioids, especially zoarcids (Matallanas 2010, 2011,

Matallanas *et al.* 2012) and liparids (Chernova & Prut'ko 2011, Stein 2012). Nevertheless, depths greater than 1000 m remain under-sampled (Duhamel *et al.* 2014, p. 331) and there are few quantitative data on taxonomic changes with depth. The 1000–2000 m interval in the Ross Sea is a notable exception because the longline fishery for Antarctic toothfish, *Dissostichus mawsoni* Norman, operates in this depth range and results in a significant bycatch of notothenioids and non-notothenioids (O'Driscoll *et al.* 2012, Hanchet *et al.* 2013). There is a bias associated with this bycatch in that it captures primarily scavenging fishes that are attracted to an odour plume.

A camera system towed along the outer shelf and slope provided an opportunity to compile higher level taxonomic identification and abundance data for demersal fishes in an area west of Anvers Island in the Palmer Archipelago. We have previously demonstrated the feasibility of identifying fishes in photographs obtained with our towed camera-system in transects in

Marguerite Bay and the Amundsen Sea (Eastman *et al.* 2013). Our photographic data are not comparable to that obtained with a bottom-trawl because small species ($\leq 15\text{--}20$ cm total length) are missed or unidentifiable in the photographs; however, our data provide insight into the largest and most conspicuous elements of the fauna and their depth distributions. By analysing photographs from this survey relative to bathymetry, we i) provide data for family level taxonomic composition, absolute abundance and areal abundance, and ii) discuss the potential homogeneity of the fauna on the outer continental shelf and upper slope around Antarctica.

Materials and methods

A photographic survey of benthic communities on the continental shelf and slope west of Anvers Island, Antarctica, was conducted aboard the RV *Nathaniel B. Palmer* in November 2013 (cruise NBP 13-10: 63.53°S,

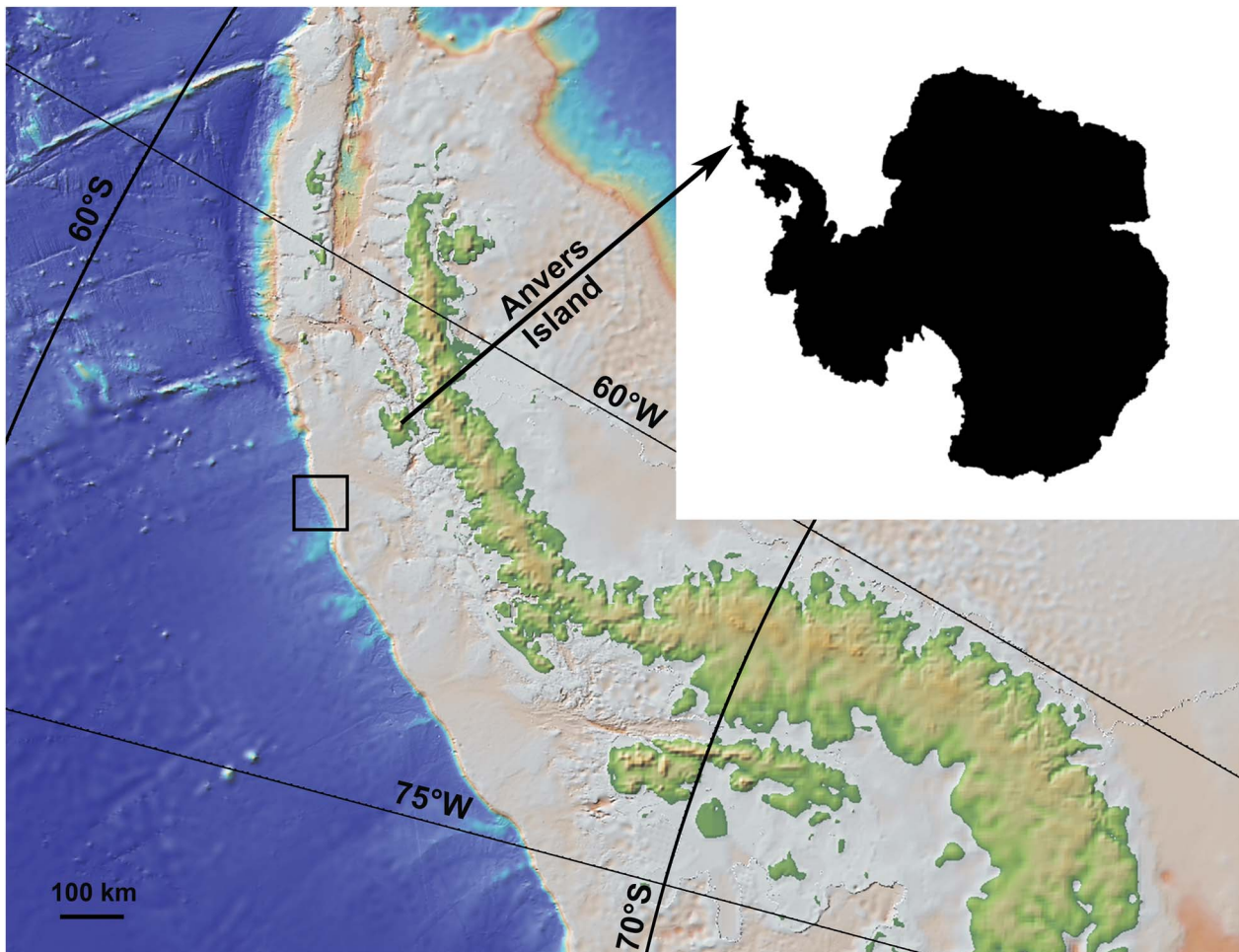


Fig. 1. Location of the 100-by-100 km photographic survey (box) encompassing the outer continental shelf and upper slope off Anvers Island, Antarctica. The upper right silhouette indicates the Antarctic continent and the arrow points from Anvers Island to its location along the western Antarctic Peninsula. Bathymetry constructed in GeoMapApp 3.5.1. based on data from Smith & Sandwell (1997).

Table I. Absolute abundances of demersal fishes by depth and taxon on the shelf and slope west of Anvers Island, Palmer Archipelago, Southern Ocean (63.53°S, 66.05°W to 64.30°S, 67.43°W).

Depth interval (m)	Number of individuals						Not identified	Total Count	%
	Notothenioids			Non-notothenioids					
	Bathydraconidae	Channichthyidae	Nototheniidae	Macrouridae	Zoarcidae	Liparidae			
400–499	1	2	280	0	0	0	4	287	18.9
500–599	0	3	276	1	0	0	1	281	18.5
600–699	0	0	3	2	0	0	0	5	0.3
700–799	1	2	33	98	1	0	4	139	9.2
800–899	0	0	4	52	0	1	1	58	3.8
900–999	1	18	0	55	43	0	3	120	7.9
1000–1099	0	4	0	12	90	1	0	107	7.1
1100–1199	0	5	0	6	2	0	0	13	0.9
1200–1299	0	28	0	42	29	0	1	100	6.6
1300–1399	0	68	0	67	30	0	5	170	11.2
1400–1499	0	16	0	23	11	0	2	52	3.4
1500–1599	0	1	0	0	0	0	0	1	0.1
1600–1699	–	–	–	–	–	–	–	–	–
1700–1799	0	1	0	1	0	0	0	2	0.1
1800–1899	0	10	0	13	4	0	1	28	1.9
1900–1999	1	21	1	46	37	6	5	117	7.7
2000–2099	0	4	1	21	9	2	0	37	2.4
Total by taxon									
Count	4	183	598	439	256	10	27	1517	
% of identifiable	0.3	12.3	40.1	29.5	17.2	0.6	–		100.0
Total %		52.7			47.3				

66.05°W to 64.30°S, 67.43°W). SeaSled, a towed camera vehicle, imaged nine benthic transects, each approximately 8 km long. The 100-by-100 km survey area incorporated

both the shelf-break at 450–500 m and the slope, which in this area of the peninsula descended steeply to 2000 m and then flattened between 2500 and 3000 m (Fig. 1).

Table II. Areal densities of demersal fishes by depth and taxon (based on data in Table I) on the shelf and slope west of Anvers Island, Palmer Archipelago, Southern Ocean (63.53°S, 66.05°W to 64.30°S, 67.43°W).

Depth interval (m)	Area (m ²)	Density (ind m ⁻²)						Not identified	Total
		Notothenioids			Non-notothenioids				
		Bathydraconidae	Channichthyidae	Nototheniidae	Macrouridae	Zoarcidae	Liparidae		
400–499	24 291	0.0000	0.0001	0.0115	0.0000	0.0000	0.0000	0.0002	0.0118
500–599	3721	0.0000	0.0008	0.0742	0.0003	0.0000	0.0000	0.0003	0.0755
600–699	1575	0.0000	0.0000	0.0019	0.0013	0.0000	0.0000	0.0000	0.0032
700–799	18 702	0.0001	0.0001	0.0018	0.0052	0.0001	0.0000	0.0002	0.0074
800–899	6139	0.0000	0.0000	0.0007	0.0085	0.0000	0.0002	0.0002	0.0094
900–999	10 033	0.0001	0.0018	0.0000	0.0055	0.0043	0.0000	0.0003	0.0120
1000–1099	2014	0.0000	0.0020	0.0000	0.0060	0.0447	0.0005	0.0000	0.0531
1100–1199	2691	0.0000	0.0019	0.0000	0.0022	0.0007	0.0000	0.0000	0.0048
1200–1299	11 430	0.0000	0.0024	0.0000	0.0037	0.0025	0.0000	0.0001	0.0087
1300–1399	22 687	0.0000	0.0030	0.0000	0.0030	0.0013	0.0000	0.0002	0.0075
1400–1499	8115	0.0000	0.0020	0.0000	0.0028	0.0014	0.0000	0.0002	0.0064
1500–1599	482	0.0000	0.0021	0.0000	0.0000	0.0000	0.0000	0.0000	0.0021
1600–1699	–	–	–	–	–	–	–	–	–
1700–1799	2223	0.0000	0.0004	0.0000	0.0004	0.0000	0.0000	0.0000	0.0009
1800–1899	11 102	0.0000	0.0009	0.0000	0.0012	0.0004	0.0000	0.0001	0.0025
1900–1999	21 384	0.0000	0.0010	0.0000	0.0022	0.0017	0.0003	0.0002	0.0055
2000–2099	3315	0.0000	0.0012	0.0003	0.0063	0.0027	0.0006	0.0000	0.0112
Total area	149 903								
Total by taxon									
Ind m ⁻²		0.0002	0.0197	0.0904	0.0485	0.0598	0.0015	0.0020	0.2221
% of identifiable		0.09	8.95	41.07	22.04	27.17	0.68	–	100
Total %			50.11			49.89			

Four depth ranges were chosen for this survey: 400–700 m, 700–1100 m, 1100–1600 m and 1600–2100 m. An additional ‘vertical’ transect cut across depth contours in a depth range of 400–1500 m. Details of SeaSled imaging and environmental sampling specifications are described in Amsler *et al.* (2015).

The results of our counts are expressed as absolute abundances (Table I) and areal densities (Table II) by 100 m depth intervals from the cumulative transects and by taxon. The area for each depth zone was determined by combining the area covered by each image within the depth zone. Overlap in images was accounted for using the distance travelled between each image. There was considerable variation in the area photographed for each depth interval; the 1500–1599 m interval was notably under-sampled and there was no photography within the 1600–1699 m interval. Because the 1500–1700 m intervals were under-sampled in our survey, normalized counts are presented as areal densities (Table II).

The identification of fishes in photographs relied upon our familiarity with the Antarctic fauna gained from previous trawling and trapping during fieldwork around the continent, and on our prior experience identifying Antarctic fish in photographs (Eastman *et al.* 2013). Gon & Heemstra (1990) and more recent taxonomic literature were also consulted. Four species of the macrourid genus *Macrourus* occupy slope depths in the sub-Antarctic and Antarctic, including the recently described cryptic species, *M. caml* McMillan, Iwamoto, Stewart & Smith. This species is found in the area of our survey and is geographically and bathymetrically sympatric with *M. whitsoni* (Regan) in the Antarctic (McMillan *et al.* 2012, Pinkerton *et al.* 2013). Because these two species are morphologically similar and were indistinguishable in our images, they were collectively identified as *Macrourus* spp.

Depth was not a factor in our ability to identify fishes in photographs because the camera array was towed at ≤ 10 m above the substrate regardless of the depth of the water column above, and this provided uniform lighting of the photographic field. Lighting consisted of paired 150 w-sec strobes mounted aft of the cameras to minimize backscatter. Although several images did show a cloud of disturbed substrate suggesting that an animal on the bottom had moved away rapidly, in general alarm reactions or escape responses by fish were not detected in response to the strobe flash.

Results

The nine transects imaged on the outer continental shelf and slope off Anvers Island yielded 35 437 images that were analysed for fishes. All images analysed were ≤ 10 m off the seafloor and collectively visualized approximately 149 903 m² of the benthos. A total of 1277 images had single fish in them and 32 had multiple fish. Near-bottom

water temperatures increased with depth from 0.46°C at 2000 m to 1.55°C at 700 m, while 1.39°C at 400 m.

Tables I & II provide absolute abundances and areal densities by depth and taxon. Our focus in this paper is on absolute abundance; hence, we simply note that the values for areal density were low (Table II) and will not be considered in additional detail except to mention that notothenioids, especially nototheniids, accounted for 50.1% of the areal density. Non-notothenioids accounted for 49.9%, with zoarcids and macrourids overwhelmingly dominant.

Absolute abundance

Our images contained a total of 1517 fishes. Of these, 1490 were identified at least to the level of the family. The four most abundant families were Nototheniidae, Macrouridae, Zoarcidae and Channichthyidae (Table I). Of the fish identified, 52.7% individuals counted were notothenioids, predominantly species of the families Nototheniidae and Channichthyidae, and 47.3% were non-notothenioids, mostly macrourids and zoarcids. The most abundant species were *Lepidonotothen squamifrons* (Günther) at 30.5%, *Macrourus* spp. at 29.5%, and *Chionobathyscus dewitti* Andriashev and Neelov at 11.7%. Absolute abundance peaked at 400–599 m. Minor peaks in several other depth intervals may simply reflect the larger area imaged at these depths (Table II).

Taxa across depths

Nototheniids were most abundant at 400–599 m. Most individuals were *L. squamifrons* or species of *Trematomus*, especially *T. loennbergii* Regan. *Lepidonotothen squamifrons* was approximately three-fold more abundant than *T. loennbergii*. The abundance of nototheniids fell off abruptly at depths > 599 m, although two relatively small individuals of *D. mawsoni* were seen resting on the substrate at depths of 1949 and 2002 m.

A few channichthyids (*Chaenocephalus aceratus* (Lonnberg) and *Chaenodraco wilsoni* Regan) were present at the shallow ends of transects between 400–599 m. At greater depths, the channichthyids were almost exclusively *C. dewitti*. This species appeared at 704 m, was most abundant at 900–1499 m and persisted to 2007 m (Table I).

The transition in dominance from notothenioids to non-notothenioids, specifically *Macrourus* spp. and zoarcids, occurred between 700 and 999 m. *Macrourus* spp. began to appear at 704 m and were most abundant at 700–1499 m. Allowing for gaps in sampling, they were continuously present into the deepest intervals of the survey with an observed maximum of 2045 m (Table I).

Benthic and pelagic zoarcids appeared at 740 m, were most abundant at 900–1099 m and persisted to 2099 m (Table I). Approximately two-thirds of the zoarcids were

the pelagic *Melanostigma gelatinosum* Günther, known to be common in the area of our survey. They frequently occurred in groups of 2–3, and up to 10, widely spaced individuals, and exhibited anguilliform locomotion when swimming a few metres above the substrate. We were not able to identify the benthic zoarcids even to the level of genus although, as previously mentioned, they have recently been recognized as an important but underestimated component of fish biomass in high-Antarctic localities.

Liparids, of several different morphotypes including tadpole-like forms, were sparse and encountered mostly at depths of 1900–2099 m.

Discussion

Abundant species

Lepidonotothen squamifrons, *Macrourus* spp. and *C. dewitti* were the most abundant species of demersal fishes encountered in our transects. The fishes identified in our photographic transects are the same species that have been collected elsewhere in the Antarctic at outer shelf/upper slope depths or, in the case of *L. squamifrons* (Clark *et al.* 2010, Hanchet *et al.* 2013), at shallower depths and around seamounts. This previous information was obtained during research trawling, acoustic surveys and as bycatch from longline fishery for the Antarctic toothfish *D. mawsoni*. For example, there are data with absolute abundance values similar to ours for *Macrourus* spp. plus *C. dewitti* and/or *L. squamifrons* near the Antarctic Peninsula and in the Bellingshausen Sea in the Atlantic Sector (Arana & Vega 1999). There is comparable information for the Indian Ocean Sector off Adélie Land (Koubbi *et al.* 2010, Causse *et al.* 2011) and for the Ross Sea in the Pacific Sector (Clark *et al.* 2010, O'Driscoll *et al.* 2012, Hanchet *et al.* 2013). It is estimated that *Macrourus* may constitute over 65% of the total fish biomass on the Ross Sea slope and seamounts to the north (Hanchet *et al.* 2013).

Abundant species are trophically linked to Dissostichus mawsoni

Macrourus spp., *L. squamifrons* and *C. dewitti* are integral components of the food web of the upper continental slope around Antarctica and, as such, are important prey for *D. mawsoni*, the largest predatory fish at these depths (Fenaughty *et al.* 2003, Stevens *et al.* 2014). More specifically, in longline catches at depths of 1157–1798 m in the Lazarev Sea (Atlantic Ocean Sector), *C. dewitti* and *Macrourus* spp. were the most important fish in the stomach contents of *D. mawsoni*, with *C. dewitti* being two-fold greater by both frequency of occurrence and weight (Petrov & Tatarnikov 2011). *Lepidonotothen*

squamifrons is also found in the stomachs of *D. mawsoni* caught by the longline fishery at depths of 1500–2033 m around Bouvet Island, again in the Atlantic Sector (Petrov 2011). At 786–1552 m in the Weddell Sea, also within the Atlantic Sector, *M. whitsoni* and *C. dewitti* were first and fourth most important dietary items by weight at 55% and 8.6%, respectively (Petrov & Gordeev 2015). In catches at slope depths in the Ross Sea, *Macrourus* spp. were *c.* 40% of stomach contents by weight compared to 27% for *C. dewitti*, the most important channichthyid in the diet of *D. mawsoni* (Pinkerton *et al.* 2012, 2013, Stevens *et al.* 2014). Although early juveniles of *D. mawsoni* are pelagic (Hanchet *et al.* 2008), later juveniles and subadults have reduced buoyancy (Eastman & Sidell 2002, Near *et al.* 2003) and, as confirmed by our images, live demersally.

Is the fish fauna of the circum-Antarctic slope homogeneous in taxonomic composition?

Kaiser *et al.* (2011) considered whether or not the Antarctic slope harbours a 'distinct' invertebrate fauna, and concluded that there was not a 'homogenous and unique' fauna that was restricted to the slope. Is this also true in the case of Antarctic slope fishes? In the high-latitude shelf areas of the Antarctic, there are notable differences in the taxonomic composition of notothenioids at the specific and generic levels that are sufficient to recognize East and West Antarctic biogeographic provinces (Andriashev 1987). Based on the data from our photographic survey and on the trawl and fishery data cited above, the fish fauna at slope depths of 1000–2000 m is more homogeneous and circum-Antarctic in character than that of the shelf and is not assignable to a province. This statement, however, refers to only the largest and most conspicuous elements of the fish fauna, and to fishes living within the range of our camera array at ≤ 10 m above the substrate.

Although the fish fauna of the slope appears geographically homogeneous, unlike the situation for invertebrates, the fish fauna is not confined to the slope. Both *Macrourus* spp. and *C. dewitti* are also present on the outer shelf, but are less abundant there than on the slope. Given the limited spatial coverage, our data may underestimate the number of slope taxa found in the area under investigation. For example, members of the gadiform families Muraenolepididae and Moridae do inhabit the Antarctic slope (Gon & Heemstra 1990), but they possess swim bladders and live in the water column above the depth of our camera array. Although documented in a previous survey (Eastman *et al.* 2013), species of Rajiidae were not encountered in the Anvers Island transects. The most likely explanation is that they are spotty in occurrence and that most of our photography was conducted at depths greater than their preferred range of < 650 m (Gon & Heemstra 1990).

At least two factors may contribute to the taxonomic homogeneity of the fish fauna at upper slope depths and make provincialization less likely. First, water temperatures are warm enough at slope depths that fishes do not require antifreeze compounds to protect them from freezing. Bottom water minimum and maximum temperatures along our transects were 0.46 and 1.55°C, well above the freezing point of seawater at -1.9°C. This is especially relevant in the case of macrourids, which are not known to possess antifreeze compounds; they do not live on the high-Antarctic shelf but are not excluded from living in the warmer waters of the slope. *Lepidonotothen squamifrons* and all channichthyids studied to date do possess antifreeze compounds (Near *et al.* 2012, table S4), which are vital for survival in shelf waters where temperatures may be also low as -1.9°C. However, these species are not excluded from living in the warmer waters of the slope, if the greater slope depths are within their bathymetric ranges.

A second characteristic contributing to homogeneity of the slope fauna may be the relatively broad depth tolerances of the slope fishes. Eurybathy of *c.* 900 m to nearly 2800 m is documented for each of the three most abundant species in our survey, a feature facilitating habitation of the outer shelf and slope. For example, *M. whitsoni* is found from 400–3185 m, a range of 2785 m (Iwamoto 1990), *M. caml* from 350–2080 m, a range of 1730 m (McMillan *et al.* 2012), and *C. dewitti* from 460–2025, a range of 1565 m (Miller 1993, Eastman *et al.* 2013). Although most of our specimens of *L. squamifrons* were from 400–599 m, this species is known from 5–900 m, a range of 895 m (Gon & Heemstra 1990, Miller 1993, Petrov 2011).

Conclusions

The Antarctic notothenioid fishes of the outer shelf/upper slope have not received much attention. The notothenioids *L. squamifrons* and *C. dewitti* and the non-notothenioid *Macrourus* spp. were identified as the most abundant large demersal species in our photographic survey of the outer slope and upper shelf, although *L. squamifrons* was found at considerably shallower depths than the other two species. Our results are consistent with abundance data obtained from the limited demersal trawling that has taken place at similar depths elsewhere around Antarctica. The photographic transect provides precise data on the depths at which these species are maximally abundant, and on the depth interval at which the abundance shifts from primarily notothenioids to non-notothenioids, which is 700–999 m. Finally, the slope habitat is receiving increased attention as the fishery for *D. mawsoni* becomes centred at 1000–2000 m. The three abundant species are the most important fish prey in the diet of *D. mawsoni* during the portion of its life spent on the slope, and they also constitute a major component of the bycatch of the

longline fishery. Despite the recognition of this trophic linkage between *D. mawsoni* and its prey species, much remains to be learned about the biology of *Macrourus* spp., *L. squamifrons* and *C. dewitti*.

Acknowledgements

The authors thank J. Anderson, C.J. Brothers, A. Brown, D. Ellis and S.C. Vos for assistance with the image analysis and E. Barrero-Oro and an anonymous reviewer for valuable comments. We are grateful to the captain and crew of the RV *Nathaniel B. Palmer*, along with representatives of the US Antarctic Support Contractor, Lockheed Martin, for assistance at sea. Our research was supported by collaborative grants from the National Science Foundation's Office of Polar Programs to RBA (ANT-0838846 and ANT-1141877) and JBM (ANT-0838844 and ANT-1141896). JTE was supported by a National Science Foundation grant ANT-0436190. This paper is Contribution No. 137 from the Institute for Research on Global Climate Change at the Florida Institute of Technology.

Author contribution

Margaret O. Amsler conducted the majority of the image analysis, fish identification, data analysis and manuscript writing and editing. Joseph T. Eastman provided the conceptual framework for the manuscript, verified fish identification and wrote a major portion of the manuscript. Kathryn E. Smith assisted with field component, image analysis and manuscript editing. James B. McClintock provided the funding for the photographic survey, contributed intellectual input and edited the manuscript. Hanumant Singh assisted with the field component providing the technological expertise necessary to conduct the photographic survey. Sven Thatje contributed to the conceptual framework of the funded proposal. Richard B. Aronson provided the funding for the photographic survey, contributed intellectual input and edited the manuscript.

References

- AMSLER, M.O., SMITH, K.E., MCCLINTOCK, J.B., SINGH, H., THATJE, S., VOS, S.C., BROTHERS, C.J., BROWN, A., ELLIS, D., ANDERSON, J. & ARONSON, R.B. 2015. *In situ* observations of a possible skate nursery off the western Antarctic Peninsula. *Journal of Fish Biology*, **86**, 1867–1872.
- ANDERSON, M.E. 1990a. The origin and evolution of the Antarctic ichthyofauna. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 28–33.
- ANDERSON, M.E. 1990b. Zoarcidae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 256–276.
- ANDRIASHEV, A.P. 1965. A general review of the Antarctic fish fauna. In VAN OYE, P. & VAN MIEGHEM, J., eds. *Biogeography and ecology in Antarctica, Monographiae Biologicae*, Vol. XV. The Hague: Junk, 491–550.

- ANDRIASHEV, A.P. 1987. A general review of the Antarctic bottom fish fauna. In KULLANDER, S.O. & FERNHOLM, B., eds. *Fifth Congress of European Ichthyologists, Proceedings, Stockholm, 1985*. Stockholm: Swedish Museum of Natural History, 357–372.
- ANDRIASHEV, A.P. 2003. *Liparid fishes (Liparidae, Scorpaeniformes) of the Southern Ocean and adjacent waters*. St. Petersburg: Russian Academy of Sciences, Zoological Institute, 476 pp. [Russian].
- ARANA, P.M. & VEGA, R. 1999. Exploratory fishing for *Dissostichus* spp. in the Antarctic region (subareas 48.1, 48.2 and 88.3). *CCAMLR Science*, **6**, 1–17.
- BROWN, A. & THATJE, S. 2014. Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. *Biological Reviews*, **89**, 406–426.
- CAUSSE, R., OZOUF-COSTAZ, C., KOUUBI, P., LAMY, D., ELAUME, M., DETTAÏ, A., DUHAMEL, G., BUSSON, F., PRUVOST, P., POST, A., BEAMAN, R.J. & RIDDLE, M.J. 2011. Demersal ichthyofaunal shelf communities from the Dumont d'Urville Sea (East Antarctica). *Polar Science*, **5**, 272–285.
- CHERNOVA, N.V. & PRUT'KO, V.G. 2011. Two new species of *Paraliparis* (Scorpaeniformes: Liparidae) from the Ross Sea (Antarctica). *Journal of Ichthyology*, **51**, 293–302.
- CLARK, M.R., DUNN, M.R., McMILLAN, P.J., PINKERTON, M.H., STEWART, A. & HANCHET, S.M. 2010. Latitudinal variation of demersal fish assemblages in the western Ross Sea. *Antarctic Science*, **22**, 782–792.
- DEWITT, H.H. 1971. Coastal and deep-water benthic fishes of the Antarctic. In BUSHNELL, V.C., ed. *Antarctic map folio series, Folio 15*. New York, NY: American Geographical Society, 1–10.
- DUHAMEL, G., HULLEY, P.-A., CAUSSE, R., KOUUBI, P., VACCHI, M., PRUVOST, P., VIGETTA, S., IRISSON, J.-O., MORMÈDE, S., BELCHIER, M., DETTAÏ, A., DETRICH, H.W., GUTT, J., JONES, C.D., KOCK, K.-H., LOPEZ ABELLAN, L.J. & VAN DE PUTTE, A.P. 2014. Biogeographic patterns of fish. In DE BROYER, C. & KOUUBI, P., eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 328–362.
- EASTMAN, J.T. & SIDELL, B.D. 2002. Measurements of buoyancy for some Antarctic notothenioid fishes from the South Shetland Islands. *Polar Biology*, **25**, 753–760.
- EASTMAN, J.T., AMSLER, M.O., ARONSON, R.B., THATJE, S., MCCLINTOCK, J.B., VOS, S.C., KAELI, J.W., SINGH, H. & LA MESA, M. 2013. Photographic survey of benthos provides insights into the Antarctic fish fauna from the Marguerite Bay slope and the Amundsen Sea. *Antarctic Science*, **25**, 31–43.
- FENAUGHTY, J.M., STEVENS, D.W. & HANCHET, S.M. 2003. Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (Subarea 88.1). *CCAMLR Science*, **10**, 113–123.
- GON, O. & HEEMSTRA, P.C. eds. 1990. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 462 pp.
- HANCHET, S.M., RICKARD, G.J., FENAUGHTY, J.M., DUNN, A. & WILLIAMS, M.J.H. 2008. A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science*, **15**, 35–53.
- HANCHET, S.M., STEWART, A.L., McMILLAN, P.J., CLARK, M.R., O'DRISCOLL, R.L. & STEVENSON, M.L. 2013. Diversity, relative abundance, new locality records, and updated fish fauna of the Ross Sea region. *Antarctic Science*, **25**, 619–636.
- IWAMOTO, T. 1990. Macrouridae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 192–206.
- KAISER, S., GRIFFITHS, H.J., BARNES, D.K.A., BRANDÃO, S.N., BRANDT, A. & O'BRIEN, P.E. 2011. Is there a distinct continental slope fauna in the Antarctic? *Deep-Sea Research II - Topical Studies in Oceanography*, **58**, 91–104.
- KOUUBI, P., OZOUF-COSTAZ, C., GOARANT, A., MOTEKI, M., HULLEY, P.-A., CAUSSE, R., DETTAÏ, A., DUHAMEL, G., PRUVOST, P., TAVENIER, E., POST, A.L., BEAMAN, R.J., RINTOUL, S.R., HIRAWAKE, T., HIRANO, D., ISHIMARU, T., RIDDLE, M. & HOISE, G. 2010. Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys. *Polar Science*, **4**, 115–133.
- MATALLANAS, J. 2010. Description of two new genera, *Santelmoa* and *Bentartia* and two new species of Zoarcidae (Teleostei, Perciformes) from the Southern Ocean. *Polar Biology*, **33**, 659–672.
- MATALLANAS, J. 2011. Description of two new species of *Ophthalmolycus* (Teleostei: Zoarcidae) from the Southern Ocean and key to species of the genus. *Journal of the Marine Biological Association of the United Kingdom*, **91**, 561–567.
- MATALLANAS, J. & OLASO, I. 2007. Fishes of the Bellingshausen Sea and Peter I Island. *Polar Biology*, **30**, 333–341.
- MATALLANAS, J., CORBELLA, C. & MØLLER, P.R. 2012. Description of two new species of *Santelmoa* (Teleostei, Zoarcidae) from the Southern Ocean. *Polar Biology*, **35**, 1395–1405.
- McMILLAN, P., IWAMOTO, T., STEWART, A. & SMITH, P.J. 2012. A new species of grenadier, genus *Macrourus* (Teleostei, Gadiformes, Macrouridae) from the southern hemisphere and a revision of the genus. *Zootaxa*, **3165**, 1–24.
- MILLER, R.G. 1993. *History and atlas of the fishes of the Antarctic Ocean*. Carson City, NV: Foresta Institute for Ocean and Mountain Studies, 792 pp.
- NEAR, T.J., RUSSO, S.E., JONES, C.D. & DeVRIES, A.L. 2003. Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biology*, **26**, 124–128.
- NEAR, T.J., DORNBERG, A., KUHN, K.L., EASTMAN, J.T., PENNINGTON, J.N., PATARNELLO, T., ZANE, L., FERNÁNDEZ, D.A. & JONES, C.D. 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 3434–3439.
- O'DRISCOLL, R.L., HANCHET, S.M. & MILLER, B.S. 2012. Can acoustic methods be used to monitor grenadier (Macrouridae) abundance in the Ross Sea region? *Journal of Ichthyology*, **52**, 700–708.
- PETROV, A.F. 2011. New data on depths inhabited by striped-eyed rock cod *Lepidonotothen kempfi* (Norman) (Nototheniidae) off Bouvet Island. *Journal of Ichthyology*, **51**, 683–685.
- PETROV, A.F. & GORDEEV, I.I. 2015. Distribution and biological characteristics of Antarctic toothfish *Dissostichus mawsoni* in the Weddell Sea. *Journal of Ichthyology*, **55**, 166–172.
- PETROV, A.F. & TATARNIKOV, V.A. 2011. Results of investigation of the diet of Antarctic toothfish *Dissostichus mawsoni* (Nototheniidae) in the Lazarev Sea. *Journal of Ichthyology*, **51**, 131–135.
- PINKERTON, M.H., FORMAN, J., STEVENS, D.W., BURY, S.J. & BROWN, J. 2012. Diet and trophic niche of *Macrourus* spp. (Gadiformes, Macrouridae) in the Ross Sea region of the Southern Ocean. *Journal of Ichthyology*, **52**, 787–799.
- PINKERTON, M.H., McMILLAN, P., FORMAN, J., MARRIOTT, P., HORN, P., BURY, S. & BROWN, J. 2013. Distribution, morphology and ecology of *Macrourus whitsoni* and *M. caml* (Gadiformes, Macrouridae) in the Ross Sea region. *CCAMLR Science*, **20**, 37–61.
- SMITH, W.H.F. & SANDWELL, D.T. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. *Science*, **277**, 1956–1962.
- STEIN, D.L. 2012. Snailfishes (family Liparidae) of the Ross Sea, Antarctica, and closely adjacent waters. *Zootaxa*, **3285**, 1–120.
- STEIN, D.L. & ANDRIASHEV, A.P. 1990. Liparididae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 231–255.
- STEVENS, D.W., DUNN, M.R., PINKERTON, M.H. & FORMAN, J.S. 2014. Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the continental slope and oceanic features of the Ross Sea region, Antarctica. *Antarctic Science*, **26**, 502–512.