

# Photographic survey of benthos provides insights into the Antarctic fish fauna from the Marguerite Bay slope and the Amundsen Sea<sup>†</sup>

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**Abstract:** We reviewed photographic images of fishes from depths of 381–2282 m in Marguerite Bay and 405–2007 m in the Amundsen Sea. Marguerite Bay fishes were 33% notothenioids and 67% non-notothenioids. Channichthyids (47%) and nototheniids (44%) were the most abundant notothenioids. The deep-living channichthyid *Chionobathyscus dewitti* (74%) and the nototheniid genus *Trematomus* (66%) were the most abundant taxa within these two families. The most abundant non-notothenioids were the macrourid *Macrourus whitsoni* (72%) and zoarcids (18%). Amundsen Sea fishes were 87% notothenioids and 13% non-notothenioids, the latter exclusively *Macrourus whitsoni*. Bathydraconids (38%) and artedidraconids (30%) were the most abundant notothenioids. We observed that *Macrourus whitsoni* was benthopelagic and benthic and infested by large ectoparasitic copepods. Juvenile (42 cm) *Dissostichus mawsoni* was not neutrally buoyant and resided on the substrate at 1277 m. *Lepidonotothen squamifrons* was seen near and on nests of eggs in early December. A *Pogonophryne* sp. from 2127 m was not a member of the deep-living unspotted *P. albipinna* group. *Chionobathyscus dewitti* inhabited the water column as well as the substrate. The pelagic zoarcid *Melanostigma gelatinosum* was documented in the water column a few metres above the substrate. The zoogeographic character of the Marguerite Bay fauna was West Antarctic or low-Antarctic and the Amundsen Sea was East Antarctic or high-Antarctic.

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## Introduction

The fish fauna of the Antarctic continental shelf and slope includes about 225 species and is unique in the marine realm because its diversity is greatly restricted at higher taxonomic levels. The fauna consists primarily of ray-finned fishes (superorder Acanthopterygii), including a large radiation of notothenioids (46% of species) that exhibit great morphological and ecological diversity, accompanied by smaller radiations of liparids (31%) and zoarcids (11%) (Gon & Heemstra 1990). Although notothenioids lack a swim bladder, they fill a host of niches ranging from small benthivores to a 2 m long, neutrally buoyant predator (Eastman 1993). They also dominate fish

abundance and biomass on the high-Antarctic continental shelves (Eastman 2005). Most collecting activity has been devoted to defining the shelf fauna, which is now reasonably well known from both taxonomic and ecological perspectives. The continental slopes of the Southern Hemisphere, however, are among the least-sampled marine habitats with respect to fishes (Eschmeyer *et al.* 2010), especially in the Antarctic region. Furthermore, the longline fishery for the Antarctic toothfish (*Dissostichus mawsoni* Norman, 1937) operates at slope depths of 1000–2000 m (Hanchet *et al.* 2012), and this has heightened interest in the composition of the slope fauna and the biology of bycatch species.

We had the opportunity to examine underwater photographic images of fishes obtained from two infrequently explored areas of West Antarctica: the slope of Marguerite Bay (68°30'S, 68°30'W), located between Adelaide and Alexander islands near the base of the Antarctic Peninsula, and the Amundsen Sea (73°00'S, 112°00'W) off

<sup>†</sup>This paper is dedicated to the memory of Rebecca Dickhut. Her management skills and boundless energy as co-chief scientist of our Oden cruise made it possible for us to capture the images of Amundsen Sea fauna highlighted here.

**Table 1.** Data for localities sampled and photographic images obtained with the towed vehicle SeaSled during December 2010 cruises of the RV *Nathaniel B. Palmer* and RVIB *Oden*. na = no data available.

Dive	Date	Begin °S	End °S	SeaSled Begin °W	End °W	At depth (h:min)	Imaging depth (m) min	Imaging depth (m) max	Distance SeaSled towed (km)	SeaSled images (n)	Area seafloor imaged (m <sup>2</sup> )	Water temp. at depth (°C) mean	Water temp. at depth (°C) min	Water temp. at depth (°C) max
<b>Marguerite Bay</b>														
NBP-1	1 Dec 10	66.4440	66.3830	71.3641	71.4747	5:19	469	1391	9.97	10 808	40 316	na	na	na
NBP-2	2 Dec 10	66.4098	66.4836	71.5025	71.5195	5:02	555	1534	9.99	9808	38 496	na	na	na
NBP-3	2 Dec 10	66.4845	66.4894	71.5190	71.6447	2:44	552	1306	6.1	5544	27 422	na	na	na
NBP-4	2 Dec 10	66.4900	66.5636	71.6107	71.7347	4:14	1032	1313	10.64	8714	32 403	0.994	0.797	1.183
NBP-5	3 Dec 10	66.6676	66.6841	71.8061	71.9945	3:26	620	1523	8.88	7074	26 064	0.997	0.721	1.153
NBP-6	4 Dec 10	66.7413	66.8667	72.1048	72.5129	10:44	1103	1396	23.46	22 066	56 004	0.799	0.753	0.883
NBP-7	4 Dec 10	66.9366	66.9702	72.6509	72.3872	5:25	381	639	13.24	11 140	29 235	1.530	1.026	1.598
NBP-8	5 Dec 10	66.8713	66.9416	72.6804	72.5196	4:21	383	2282	10.77	8952	27 861	0.893	0.425	1.586
Totals									93.05	84 106	277 801			
<b>Amundsen Sea</b>														
Oden-1	24 Dec 10	71.9128	71.9079	115.1321	115.1437	2:02	405	440	0.7	4154	9327	0.634	0.561	0.642
Oden-2	26 Dec 10	72.9793	72.9591	117.0009	116.9897	5:26	590	627	2.89	13 054	19 819	0.012	-0.132	0.124
Oden-3	27 Dec 10	72.1883	72.1933	118.9794	119.0029	2:26	660	714	1.01	6644	11 107	0.946	0.923	0.967
Oden-4	28 Dec 10	72.2235	72.2245	119.1352	119.1267	3:22	727	784	1.06	8094	11 022	0.854	0.838	0.875
Oden-5	28 Dec 10	71.9841	71.9885	119.5810	119.5823	0:43	1631	1665	0.52	1750	2646	0.659	0.657	0.661
Oden-6	29 Dec 10	71.9781	71.9792	120.0894	120.0874	3:20	1942	2007	1.27	4836	8064	0.504	0.501	0.571
Totals									7.45	38 532	61 985			

Marie Byrd Land. While the pelagic fish fauna of Marguerite Bay is well documented (Donnelly & Torres 2008, Cullins *et al.* 2011), the benthic fauna is under-sampled, especially along the steep bathymetric gradients of the slope deeper than 800 m. The remote and perpetually ice-covered Amundsen Sea is the least sampled area of the high Antarctic. Given the circum-Antarctic distribution of most high latitude notothenioids (Eastman 1993), the fish fauna of the Amundsen Sea would be expected to resemble that of the East Antarctic zoogeographic province, especially the Weddell and Ross seas. Nevertheless, sampling in the Amundsen Sea has been sufficiently sparse that Andriashev (1987) indicated its affinity with a question mark when mapping zoogeographic subdivisions of the Antarctic.

Underwater photography has previously been used in the Antarctic to document the abundance and ecology of fishes in the Weddell and Lazarev seas (Ekau & Gutt 1991, Gutt *et al.* 1994, Gutt & Ekau 1996), but, with the exception of the work of Yau *et al.* (2002) involving still and video cameras near South Georgia at depths to 1519 m, it has never been employed at slope depths. Here we present information on the depth ranges and approximate abundances of higher-level taxa, as well as some individual species, from the outer continental shelf to the lower continental slope of Marguerite Bay (MB) and the Amundsen Sea (AS). We also provide insights into the biology of notothenioid and non-notothenioid species derived from our images.

## Materials and methods

We conducted a photographic survey of sea floor communities in Marguerite Bay aboard the US Antarctic Program's RV *Nathaniel B. Palmer* (early December 2010), and we surveyed select sites in the Amundsen Sea (late December) aboard the Swedish RVIB *Oden* (Table 1). We obtained images of the sea floor communities using SeaSled (Singh *et al.* 2007), a towed vehicle with high-dynamic-range cameras mounted side-by-side. A 150 w-sec strobe was mounted aft of the cameras to minimize backscatter. Every three seconds, slightly overlapping, paired high-resolution (1.4 mpixel or 1360 x 1024 pixels) digital images recorded *c.* 10 m<sup>2</sup> of the sea floor (typical range 2–19 m<sup>2</sup>). Onboard sensors included an acoustic Doppler current profiler (ADCP; 1200 kHz Teledyne RD Instruments). The ADCP provided real-time navigation data via a standard conductivity-temperature-depth (CTD) cable. The navigation data enabled the SeaSled pilots to maintain the vehicle 3 m above the substrate to balance the trade-off between maximizing area coverage and maintaining good colour characteristics. Additional environmental data for every image were recorded with a Seabird SBE-49 Fast CAT 16-Hz CTD and a Paroscientific depth sensor.

We sampled in Marguerite Bay while the RV *Nathaniel B. Palmer* was underway and SeaSled was towed at ship speeds

of 2–4 knots (3.2–7.4 km hr<sup>-1</sup>). Benthic communities were imaged along eight transects on the continental shelf and continental slope between 381 and 2282 m depth (Table I). Logistical constraints aboard the RVIB *Oden* limited the photographic surveys to periods when the ship was anchored to ice and drifting at speeds never greater than 0.3 knots (0.56 km hr<sup>-1</sup>) over sea floor depths of 405–2007 m. Upon recovery of SeaSled, we downloaded images at full resolution. We used formulas to determine the width of the area photographed for each image in each pair, subtracted the area of overlap imaged by the two cameras and converted that to total area photographed in square metres. Several batch-processing steps following Kaeli *et al.* (2011) were used to correct for lens distortion and colour attenuation.

We measured the approximate sizes of subjects with Critter Gridder, a graphical user interface custom-designed by one of us (JWK). A measurement grid was superimposed on the image and the spacing between the grid lines was mathematically derived from the image-linked ADCP data, specifically, how far the camera was from the bottom (ideally 3 m). The dimensions of the grid spacings were specified to the nearest 0.01 m to fine-tune the measurements. This procedure is accurate when the fish to be measured are on the substrate. There is less accuracy when the fish are in the water column. Their sizes are slightly overestimated because they are closer to the camera lens and, therefore, appear to cover more of the grid on the substrate. Unless otherwise noted, we provide total lengths (TL) for fishes.

The surveys were designed to capture images of large swaths of the sea floor and its invertebrate benthos, the fishes were an incidental finding. Images captured from a camera located 3 m above the sea floor are not ideal for identifying small species that require close scrutiny to resolve key taxonomic details. Although we were able to identify some fishes to species, others were identified to genus, family or sometimes simply as “fish.” JTE and MLM reviewed images for the presence of fish and used Gon & Heemstra (1990) and more recent taxonomic literature to make identifications. We selected the best quality images for Figs 1 & 2. Some images had multiple fish and some individual fish were present in multiple images, thus, presence in an image is used as an approximation of abundance.

## Results

### *Approximate abundance of taxa*

The RV *Nathaniel B. Palmer* travelled 93 km in Marguerite Bay while the SeaSled was at depth, allowing the vehicle to image a total of 277 801 m<sup>2</sup> of the bottom. Similarly, while SeaSled was at depth in the Amundsen Sea, the RVIB *Oden* travelled a total of 7.5 km and the vehicle imaged a total of 61 985 m<sup>2</sup> (Table I). Tables II and III summarize the depths of occurrence and approximate abundances of the taxa that we identified. The 1944 images from Marguerite Bay

(Table II) included representatives of nine families, 15 genera, and 13 species; 33% were notothenioids and 67% were non-notothenioids. Among the notothenioids, channichthyids (47%) and nototheniids (44%) were the most abundant. The deep-living channichthyid *Chionobathyscus dewitti* Andriashev and Neelov, 1978 (74%) and species of the nototheniid genus *Trematomus* (66%) were the most abundant taxa within these two families. Among non-notothenioids, the macrourid *Macrourus whitsoni* (Regan, 1913) (at 72%) and zoarcids (at 18%) were most abundant. Twenty-nine percent of the images of fish lacked resolution and were not assigned to any taxon. The high proportion of normally deeper-living non-notothenioids may in part be attributable to the fact that 57% of the images we examined were from the outer shelf and slope at depths > 600 m where they are more common. Another possible influence, to be considered later, is the unique hydrography of Marguerite Bay, which facilitates the entry of offshore non-notothenioids onto the upper slope and shelf (Donnelly & Torres 2008, Parker *et al.* 2011).

The 365 images from the Amundsen Sea (Table III) were not as representative of the fauna because they were obtained primarily from depths of 435–785 m and included only five families, six genera, and six species. Eighty-seven percent of the images were notothenioids and 13% non-notothenioids, the latter exclusively *M. whitsoni*. Among the notothenioids, bathydraconids (38%) and artedidraconids (30%), especially the small *Dolloidraco longedorsalis* Roule, 1913 (28%) were the dominant elements. Only 4% of the total images of fish were unassigned to a taxon.

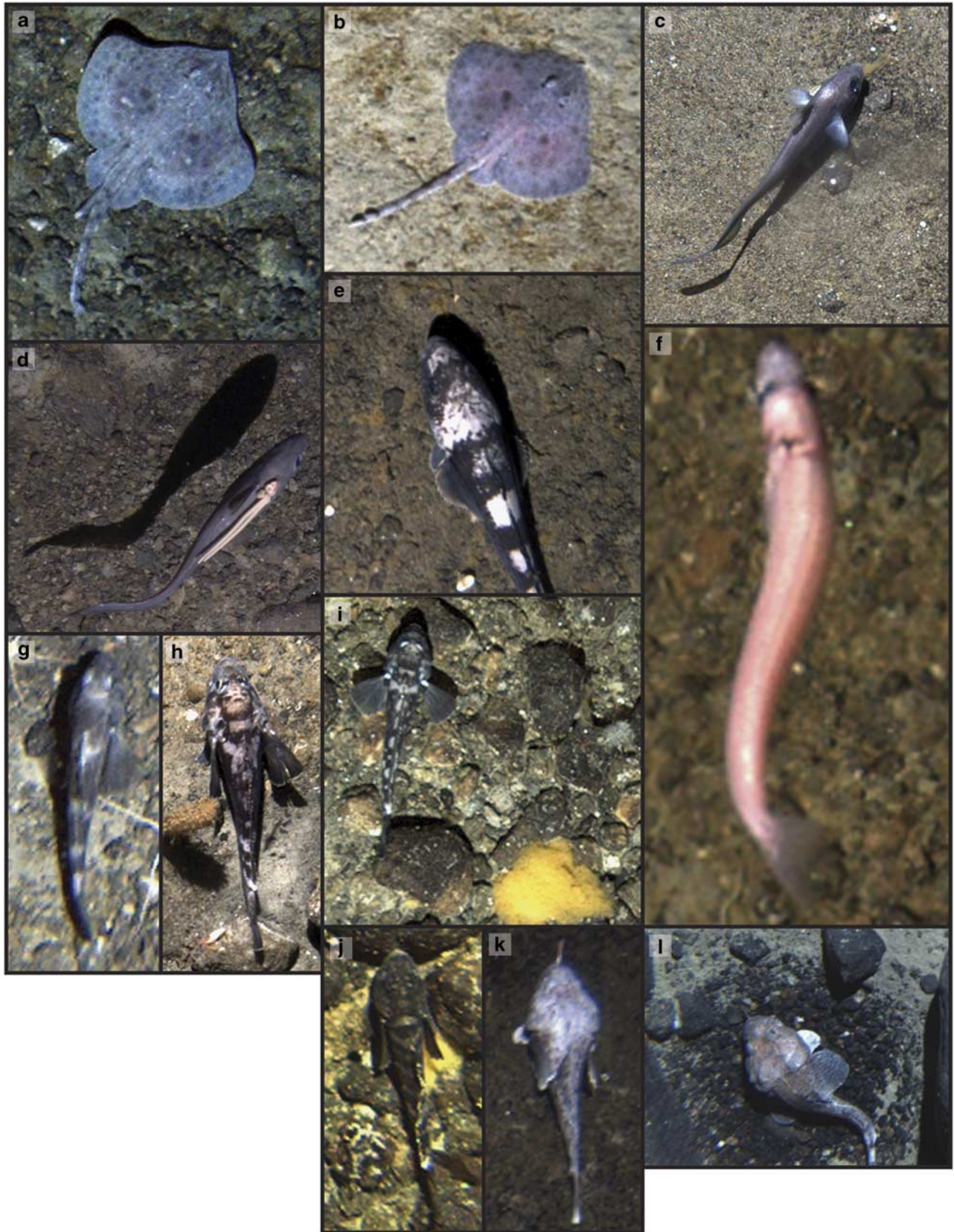
## Discussion

### *Comments on fish in images*

Rajidae (skates) (Fig. 1a & b). Six species of skates are the only chondrichthyan fishes in the Southern Ocean south of 60° (Stehmann & Bürkel 1990). *Bathyraja maccaini* Springer, 1971, *Bathyraja eatonii* (Günther, 1876) and *Amblyraja georgiana* (Norman, 1938) are known from the area of our images (Arana & Vega 1999, Kock *et al.* 2000). There are also undescribed species of *Bathyraja* in the Antarctic (Stehmann & Bürkel 1990, Smith *et al.* 2008). Identification is difficult and based partly on the size and pattern of thorns that requires handling of the specimens. We could not, therefore, identify most of our images to species and group them as *Bathyraja* spp. (Table II). A few images were sufficiently detailed, as exemplified by Fig. 1a & b, that we were able to identify male and female specimens of *B. maccaini*. Antarctic species of *Bathyraja* exhibit sexual dimorphism in the shape of the snout (Duhamel *et al.* 2005, p.77).

Our images of skates spanned depths from 389–1375 m in Marguerite Bay. *Bathyraja* are found as deep as 1700 m around Kerguelen (Duhamel *et al.* 2005), but most records from higher latitudes are from < 650 m





(Stehmann & Bürkel 1990). We also obtained images of several egg cases at depths of 397–412 m.

Macrouridae (grenadiers) (Fig. 1c & d). Macrourids have a worldwide marine distribution. There are four species in the genus *Macrourus* at slope depths in the sub-Antarctic and Antarctic (Iwamoto 1990), including, as revealed by nucleotide sequences of the cytochrome oxidase I gene, a cryptic species in the Ross Sea (Smith *et al.* 2011). In our images we encountered *M. whitsoni*, a circum-Antarctic species that is replaced by the sub-Antarctic and Magellanic species *Macrourus holotrachys* Günther, 1878 north of 65°S. Our identification is based on geographic location as well as the deep and angular head and snout, and larger eye than in *M. holotrachys*. *Macrourus whitsoni* was present in Marguerite Bay at depths of 422–2275 m. Only 5% of images were from <600 m whereas, 30% were from 600–1000 m and 65% were from >1000 m. Although the number of images of *M. whitsoni* from the Amundsen Sea was only 44, they covered a wide depth range of 702–1995 m, again with 65% of the images from depths >1000 m.

*Macrourus* are abundant in deep trawl catches from the Lazarev Sea, yet images have not been captured during photographic surveys in that area (Gutt *et al.* 1994, Zimmermann 1997). Our numerous images of *M. whitsoni* from both Marguerite Bay and the Amundsen Sea indicate that it is both benthopelagic and benthic, living within a few metres of the substrate or resting on the substrate. It is one of the few large (88–96 cm maximum TL) fish at these depths (Arana & Vega 1999, Marriott *et al.* 2003) and its abundance reflects its importance in the ecosystem of the slope. For example, in experimental longlining along the western Antarctic Peninsula and in the Bellingshausen Sea, *M. whitsoni* was the most abundant species and had the second highest biomass (Arana & Vega 1999). It is important in the diet of the Antarctic toothfish *D. mawsoni*. Examination of the stomachs of *D. mawsoni* taken by the longline fishery at slope depths in the Ross Sea has shown that *M. whitsoni* is the second most abundant dietary item, with a frequency of

occurrence of 36.9% (Fenaughty *et al.* 2003). Near Bouvetøya, *M. whitsoni* was the most important dietary item by both frequency of occurrence (82%) and wet weight (60%) in a sample of 376 *D. mawsoni* captured at 1300–1900 m (Petrov 2011a). The same is true at the South Sandwich Islands (Roberts *et al.* 2011). *Macrourus whitsoni* is a substantial bycatch species in the longline fishery for *D. mawsoni* in the Ross Sea (Smith *et al.* 2011) and, given that it is slow growing and long-lived (Marriott *et al.* 2003), it is susceptible to overfishing.

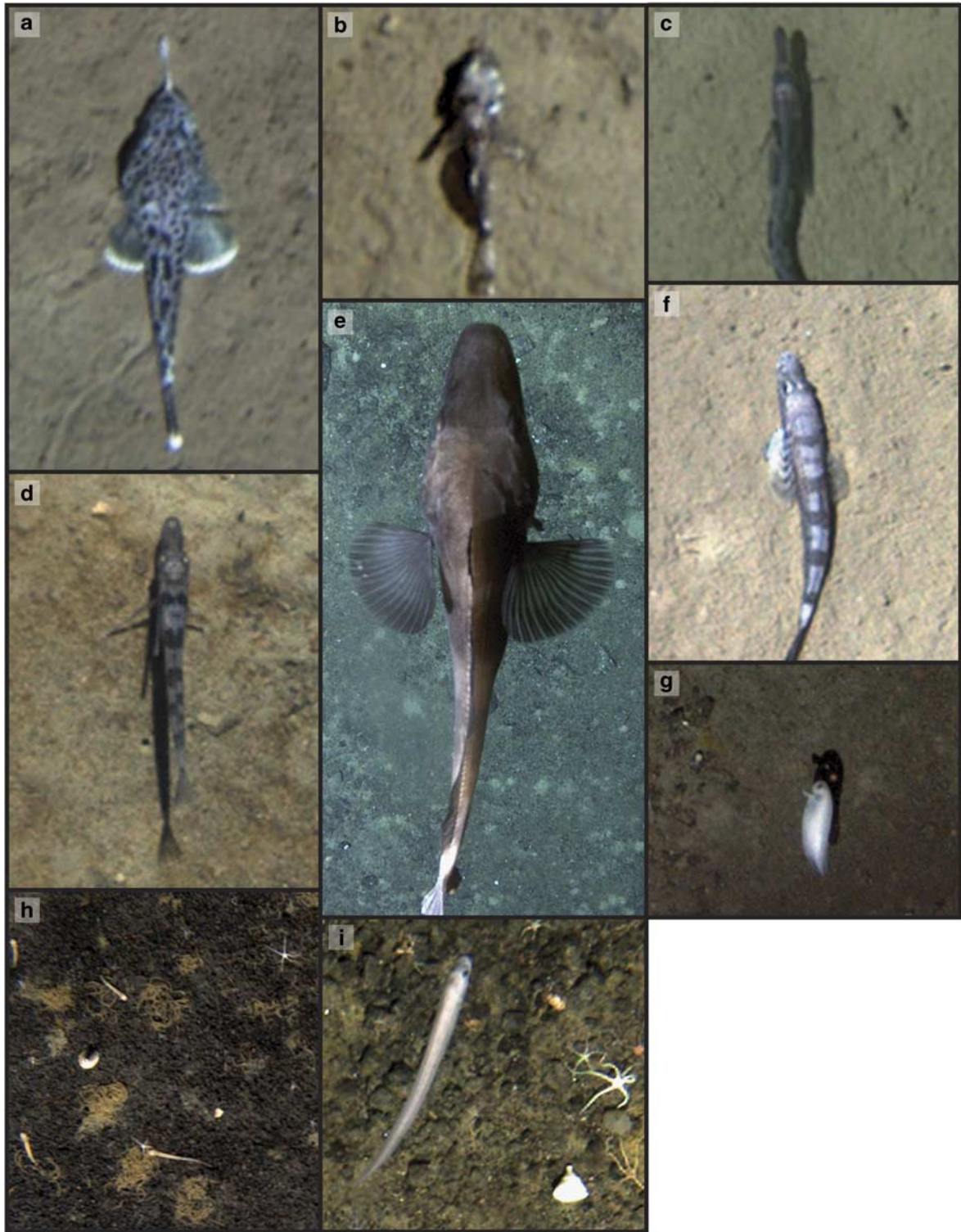
Six of our images of *M. whitsoni* showed specimens parasitized by large copepods attached along the posterior head or anterior trunk. In one instance the parasite was 36% the length of the host (Fig. 1d). Three species of copepods infest *M. whitsoni* (Walter *et al.* 2002) and we suspect that our images depict a member of the genus *Lophoura* because it is attached externally rather than in the oral or opercular cavities.

Nototheniidae (notothenes). *Dissostichus mawsoni* (Antarctic toothfish) (Fig. 1e). In an image taken 2.2 m off the bottom, we identified a fish resting on the substrate at 1277 m as *D. mawsoni*. We made the identification based on its wide head, large eyes, protruding lower jaw, and distinctive pattern of six dark vertical bars encompassing the dorsal and anal fins - a pattern first described in juveniles by Gon (1988). Having measured the head length in this specimen as 12 cm, and knowing that head length is 28.4% of total length for *D. mawsoni* (Eastman, personal observation), we estimated that this was a juvenile specimen, 42.2 cm TL and 3–5 yr old (Brooks *et al.* 2011). We encountered four other small specimens of *D. mawsoni* at depths of 565–1229 m.

Although exploratory longlining has documented its presence from Clarence Island (61°12'S) in the north to Peter I Island (68°49'S) and the Bellingshausen Sea (70°38'S) in the south (Arana & Vega 1999), *D. mawsoni* is not as abundant along the western Antarctic Peninsula as it is in higher latitudes like the Ross Sea. Nevertheless, juvenile specimens of *D. mawsoni* 10–50 cm TL are regularly collected around the South Shetland Islands

**Fig. 1.** Fish images from the slope of Marguerite Bay (MB) and the Amundsen Sea (AS). **a.** Male specimen of *Bathyraja maccai* showing claspers, identified on basis of rostral and snout morphology and overall colour pattern; body (disc) width = 15 cm, 543 m depth, MB. **b.** Female specimen of *Bathyraja maccai* with sexual dimorphism evident in rounded less angular snout than in male; body (disc) width = 14.5 cm, 418 m, MB. **c.** *Macrourus whitsoni* near the substrate; total length (TL) = 36 cm, 1215 m, MB. **d.** *Macrourus whitsoni* swimming above the substrate with an attached copepod parasite 16 cm long; TL = 44 cm, 1346 m, MB. **e.** Juvenile *Dissostichus mawsoni* on substrate, displaying negative buoyancy at this stage in the life history; TL = 42 cm, 1277 m, MB. **f.** Neutrally buoyant *Pleuragramma antarcticum* in the water column employing subcarangiform locomotion; TL = 27 cm, 720 m, MB. **g.** *Trematomus loennbergii* showing characteristic wide, blunt snout and extensive white reflective head skin over dorsal aspect of eye; TL = 24 cm, 813 m, MB. **h.** *Lepidonotothen squamifrons* on the substrate showing diagnostic characters including wide head, dark stripe on head skin over eye, and trunk pigmentation pattern; TL = 37 cm, 414 m, MB. **i.** *Lepidonotothen squamifrons*, showing strobe flare off white patch posterior to dark eye-skin stripe (h.), in vicinity of an egg mass 16 cm in horizontal diameter; TL = 33 cm, 579 m, MB. **j.** *Lepidonotothen squamifrons* on a nest of eggs; TL = 30 cm, 581 m, MB. **k.** Deep-living *Pogonophryne* spp. of the mentella group, possibly *P. bellingshausenensis*; TL = 24 cm, 2127 m, MB. **l.** *Pogonophryne scotti*, on a rock nest with strobe flare off right pectoral fin (not eggs) responsible for light-coloured area in nest; TL = 20 cm, 767 m, AS.





(M. La Mesa, personal observation), although a spawning location in this area is unknown. The significance of the specimen in Fig. 1e from the Marguerite Bay slope is that it offers a glimpse into the little-known life cycle of the major piscine predator in high-Antarctic waters, a species now subject to intensive commercial fishing. The image provides definitive proof that, unlike the neutrally buoyant adults (Eastman & DeVries 1981), small specimens of *D. mawsoni* are not neutrally buoyant (Eastman & Sidell 2002, Near *et al.* 2003) and are associated with the sea floor. The image is more clearly identifiable as *D. mawsoni* than that provided by Eastman & Barry (2002) of a larger juvenile resting on the substrate of the Ross Sea. Furthermore, it shows that small specimens can be found at considerable depths - in this case 1277 m.

*Pleuragramma antarcticum* Boulenger, 1902 (Antarctic silverfish) (Fig. 1f). Our cameras captured two images of *Pleuragramma*, including one large individual 27 cm TL (Fig. 1f), that we identified on the basis of the light-reflective integument, bluntly V-shaped and cartilaginous snout (appearing opaque), and partially visible eyes in dorsal view. *Pleuragramma* are neutrally buoyant and tend to hang motionless in the water column with their body axis straight. The image demonstrates that, when swimming, they employ trunk undulation rather than the pectoral stroking typical of most notothenioids. Given that their maximum depth of occurrence is 700–900 m (Gerasimchuk 1986, DeWitt *et al.* 1990), most of our survey was conducted below their depth range.

*Pleuragramma antarcticum*, a key species in the high-Antarctic food web for other fishes as well as for penguins, Weddell seals and some whales (La Mesa *et al.* 2004), are suspected of declining in abundance along the western Antarctic Peninsula as a result of rapidly warming seawater and the attendant loss of sea ice (Massom & Stammerjohn 2010). SCUBA divers observed *Pleuragramma* under sea ice at Anvers Island in 1975 (Daniels & Lipps 1982). *Pleuragramma* are associated with sea ice, perhaps obligatorily, for reproduction. In the Ross Sea *Pleuragramma* spawn beneath the sea ice. Its eggs and

early larvae float to incubate within the platelet ice, where the eggs are protected from freezing by the chorion (Vacchi *et al.* 2004, Cziko *et al.* 2006). Given the current warming along the western Antarctic Peninsula, the adult component of the population of *Pleuragramma* may be seasonally absent from Marguerite Bay. Although young stages of *Pleuragramma* constitute one of the most abundant species in the water column of Marguerite Bay (Donnelly & Torres 2008), it is also possible that the adult population is contracting to the south, where there is more sea ice.

*Trematomus loennbergii* Regan, 1913 (Fig. 1g). We encountered this species at depths of 493–882 m. The distinguishing features are the wide, blunt snout and the extensive light-coloured head skin over the dorsal portions of the eyes. Although it is a high-Antarctic species, it has previously been found both north and south of Marguerite Bay (Daniels & Lipps 1982, Matallanas & Olaso 2007), so its occurrence in Marguerite Bay is not surprising.

As documented by underwater still and video images (Ekau & Gutt 1991, Gutt & Ekau 1996), *T. loennbergii* is an epibenthic species, living on or in close proximity to the sea floor. It shares a circum-Antarctic distribution and epibenthic lifestyle with two other *Trematomus* spp., *Trematomus eulepidotus* Regan, 1914 and *Trematomus lepidorhinus* Pappenheim, 1911, although it is commonly found in deeper waters (Ekau 1990, Eastman & Hubold 1999).

*Lepidonotothen squamifrons* (Günther, 1880) (Fig. 1h–j). Figure 1h is a clear image of *L. squamifrons*, Fig. 1i shows another individual of this species near a nest of eggs, and Fig. 1j depicts a third individual on a nest of eggs. The main diagnostic characters included the wide head, dark stripe on head skin over the eye, and pigmentation pattern on the trunk.

According to Schneppenheim *et al.* (1994), the *L. squamifrons* group contains only one species, *L. squamifrons* (Günther, 1880), as *Lepidonotothen kempii* (Norman, 1937) and perhaps *Lepidonotothen macrophthalmia* (Norman, 1937) are considered junior synonyms. In the Bellingshausen Sea, *L. squamifrons* is one of the most abundant nototheniids, generally caught at depths > 350 m

**Fig. 2.** Fish images from the slope of Marguerite Bay (MB) and the Amundsen Sea (AS). **a.** *Pogonophryne* spp. of the mentella group, possibly *P. lanceobarbata*, showing mental barbel with a terminal expansion deployed horizontal to the substrate; total length (TL) = 17 cm, 618 m depth, AS. **b.** *Dolloidraco longedorsalis* with erect first dorsal fin casting long narrow shadow to left and posterior to head, long thin mental barbel, and pattern of dark and light (with strobe flare) blotches on body; TL = 10 cm, 614 m, AS. **c.** *Gerlachea australis* showing characteristic narrow, tubular snout; TL = 20 cm, 618 m, AS. **d.** *Chaenocephalus aceratus* showing a sub-adult perched on the substrate; TL = 27 cm, 405 m, MB. **e.** *Chionobathyscus dewitti* in the water column employing labriform locomotion, with the broad, square snout that is distinctive among channichthyids. Pattern of four to five thick, regularly spaced, dark cross-bars on trunk are also evident; TL not given as fish is too far off sea floor for accurate measurement, 1360 m, MB. **f.** *Chaenodraco wilsoni* on the sea floor showing a narrower and shorter snout than *C. dewitti* and a pattern of five dark cross-bars (but thinner than those of *C. dewitti*); TL = 27 cm, 617 m, AS. **g.** Unidentified liparid, probably genus *Paraliparis* or *Careproctus*, hovering above substrate in a characteristic head-down position; TL = 16 cm, 1344 m, MB. **h.** Four small, white, unidentified benthic zoarcids among an assemblage of unidentified invertebrates including brittlestars; TL = 6 cm, 1260 m, MB. **i.** Pelagic zoarcid *Melanostigma gelatinosum* in the water column, showing head and eyes, as well as diagnostic tapering of trunk to confluence of dorsal and anal fins with caudal fin. Translucent gelatinous layer beneath skin also evident; TL = 20 cm, 932 m, MB.

**Table II.** Depth ranges, new depth record (bold) and approximate abundances (as indicated by presence in an image) for benthic fishes photographed on or near the sea floor of the outer shelf and upper slope of Marguerite Bay.

Taxon	Minimum depth (m)	Maximum depth (m)	Number of images <sup>a</sup>	Representation among images <sup>b</sup> subtotal (%)	total (%)
Notothenioids					
Channichthyidae					
Unidentified	383	1358	50		
<i>Chionobathyscus dewitti</i>	495	<b>2025<sup>c</sup></b>	157		
<i>Chaenodraco wilsoni</i>	418	502	3		
<i>Chaenocephalus aceratus</i>	405	405	1		
<i>Chionodraco</i> spp.	407	407	1		
Nototheniidae					
Unidentified	385	604	28		
<i>Trematomus</i> spp.	381	882	109		
<i>T. loennbergii</i>	493	882	24		
<i>Lepidonotothen squamifrons</i>	406	651	31		
<i>Dissostichus mawsoni</i>	558	1277	5		
<i>Pleuragramma antarcticum</i>	583	720	2		
<i>Gobionotothen gibberifrons</i> (Lönnberg, 1905)	706	706	1		
Bathydraconidae					
Unidentified	388	1969	40		
<i>Gymnodraco acuticeps</i> Boulenger, 1902	706	706	1		
Arteidraconidae					
<i>Pogonophryne scotti</i>	418	418	1		
<i>Pogonophryne</i> spp.	2127	2127	1		
Subtotal (notothenioids)			455		33
Non-notothenioids					
Macrouridae					
<i>Macrourus whitsoni</i>	422	2275	662		72
Zoarcidae					
Unidentified	407	2001	141		18
<i>Melanostigma gelatinosum</i>	566	1339	25		
Rajidae					
<i>Bathyraja</i> spp.	389	1375	59		6
Liparidae					
Unidentified	482	1641	34		4
Paralepididae					
<i>Notolepis coatsi</i> Dollo, 1908	1693	1693	1		< 1
Subtotal (non-notothenioids)			922		67
Total (identified fish)			1377		
Other unidentified fish	381	992	567		29
Total			1944		

<sup>a</sup> A reasonably accurate approximation of the number of individual fish; some images had multiple fish and some individual fish were in multiple images.

<sup>b</sup> Not including "Other unidentified fish" category.

<sup>c</sup> New maximum-depth record based on previous records of 2000 m in Gon & Heemstra (1990) and 2012 m in Kock (2005).

(Matallanas & Olaso 2007). Its preference for deeper shelf waters is confirmed in our images from Marguerite Bay, where we recorded it at depths of 406–651 m. The several images showing adult *L. squamifrons* in the vicinity of and directly on clutches of eggs constitute the first substantial evidence of parental care by this species. This surmise is supported by previous studies, indicating that fertilized eggs of *L. squamifrons* are benthic and adhesive (Zaitsev 1989). The timing and location of the nesting behaviour we observed is consistent with what is known about the reproductive cycle

of *L. squamifrons*, which spawns on the slope in November and December near the Antarctic Peninsula (Kock & Kellermann 1991). Parental care is a common feature in the genus *Lepidonotothen*, as nest guarding has also been reported for *Lepidonotothen nudifrons* (Lönnberg, 1905) and *Lepidonotothen larseni* (Lönnberg, 1905) (Hourigan & Radtke 1989, Konecki & Targett 1989).

Arteidraconidae (plunderfishes), genus *Pogonophryne* (Figs 1k & 1 & 2a). Members of this genus are sedentary-benthic fishes with wide, triangular heads and distinctive



**Table III.** Depth ranges and approximate abundances (as indicated by presence in an image) for benthic fishes photographed on or near the sea floor of the Amundsen Sea.

Taxon	Minimum depth (m)	Maximum depth (m)	Number of images <sup>a</sup>	Representation among images <sup>b</sup>	
				subtotal (%)	total (%)
Notothenioids					
Nototheniidae					
Unidentified	434	622	20	26	
<i>Trematomus</i> spp.	435	624	42		
<i>T. loennbergii</i>	613	623	17		
Channichthyidae					
Unidentified	616	622	14	6	
<i>Chaenodraco wilsoni</i>	784	784	4		
Bathydraconidae					
Unidentified	613	1989	114	38	
<i>Gerlachea australis</i>	616	625	4		
Arteidraconidae					
<i>Dolloidraco longedorsalis</i>	613	627	87	30	
<i>Pogonophryne scotti</i>	764	767	4		
<i>Pogonophryne</i> spp.	618	618	1		
Subtotal (notothenioids)			307		87
Non-notothenioids					
Macrouridae					
<i>Macrourus whitsoni</i>	702	1995	44	100	
Subtotal (non-notothenioids)			44		13
Total (identified fish)			351		
Other unidentified fish	438	1593	14		4
Total			365		

<sup>a</sup> A reasonably accurate approximation of the number of individual fish; some images had multiple fish and some individual fish were in multiple images.

<sup>b</sup> Not including "Other unidentified fish" category.

mental barbels of various lengths and shapes. The genus is composed of 19 species that have experienced phyletic diversification unaccompanied by morphological and ecological diversification (Eakin *et al.* 2009). Although *Pogonophryne* is the most speciose genus of notothenioid fishes, many species are only known from a few specimens and little is known of their biology. They are difficult to identify because of their morphological similarity and the intraspecific variation in the length and appearance of the mental barbel. The barbel lacks taste buds but has free nerve endings and is thought to be a tactile device used to locate their prey (Eastman & Lannoo 2003), which consists primarily of amphipods and polychaetes (Olaso *et al.* 2000).

*Pogonophryne* spp., possibly *Pogonophryne bellingshausenensis* Eakin, Eastman & Matallanas, 2008 (Fig. 1k). Outside of *Pogonophryne immaculata* Eakin, 1981 from 2542 m (Eakin 1990), this specimen is the second-deepest record for a species in this genus (2127 m, slope of Marguerite Bay). The specimen is significant because the deepest-living species are largely confined to a group within the genus, referred to as the unspotted *Pogonophryne albipinna* group, consisting of four species (Eakin 1990). However, this specimen is spotted and not a member of that group. It is similar to

*P. bellingshausenensis* (Eakin *et al.* 2008), which has a similarly shaped mental barbel of a similar length (12–13% of SL), and is from a similar locality and depth (66°88'S, 72°66'W, 2127 m) as the holotype and only known specimen of *P. bellingshausenensis* (68°91'S, 78°23'W, 1947 m).

*Pogonophryne scotti* Regan, 1914 (Fig. 11). The fish is identifiable as *P. scotti* because the dorsum of the head is without dark markings, the posttemporal and supratemporal ridges are well developed, and the mental barbel is short and lacks a terminal expansion. It is a male because the anterior rays of the second dorsal fin are black and elongated. It occupies a rock nest with no eggs visible, although this is a potential site for laying eggs. Nesting and egg-guarding behaviour by males have recently been reported for this species at 240 m near the South Orkney Islands. This first record of nesting behaviour in the Arteidraconidae confirms the prevalence of the behaviour among all five Antarctic notothenioid families (Jones & Near 2012).

*Pogonophryne* sp. of the mentella group, possibly *Pogonophryne lanceobarbata* Eakin, 1987 (Fig. 2a). This species was identified as a member of the mentella group on the basis of the pattern of dark markings on the dorsum of the head, the lower jaw that projects beyond the upper,

a mental barbel about 20% of standard length and the terminal expansion of the mental barbel about 40% of the barbel length.

*Dolloidraco longedorsalis* (Fig. 2b). This small artedidraconid was common in the Amundsen Sea and is a typical representative of the East Antarctic or high-Antarctic fish fauna. The diagnostic characters include a long, narrow first dorsal fin, frequently projecting as a shadow on the substrate in our images, a relatively long barbel; and an irregular pattern of dark and light blotches on the body including the caudal fin.

*Bathydraconidae* (dragonfishes) (Fig. 2c). Bathydraconids were also common in the Amundsen Sea but their small size and generally similar morphology and colour patterns made species identification difficult. We were able to identify *Gerlachea australis* Dollo, 1900 (Fig. 2c), which is one of two bathydraconids with a long, tubular snout (the other is *Cygnodraco mawsoni* Waite, 1916). Our identification is based on the presence of four to five dark, vertical bars on trunk whereas *Cygnodraco* has a more irregular pattern of thinner bars and splotches (Gon & Heemstra 1990). *Gerlachea* is also found in the nearby Bellingshausen Sea (Matallanas & Olaso 2007) and occurs at the depth where our specimen was photographed.

Channichthyidae (icefishes) (Fig. 2d–f). As was the case with bathydraconids, we could not identify many of the channichthyid images to species. A few species were recognizable (Tables II & III), including *Chaenocephalus aceratus* (Lonnberg, 1906) (Fig. 2d). For this species we based our identification on the distinctive ratios of various parts of the head and relative length of the pelvic fins. We also identified *Chaenodraco wilsoni* Regan, 1914 (Fig. 2f) based on the relatively short snout and the pattern of five dark bars on the trunk. The bars are thinner than those of *Chionobathyscus dewitti* (see below).

*Chionobathyscus dewitti* (Fig. 2e) was the most distinctive and abundant channichthyid we encountered. Identification of *C. dewitti* is facilitated by its wide, bluntly rounded almost squarish snout, clearly shown in the original species description (Andriashev & Neyelov 1978, fig. 2) and in our image of the dorsum of the head (Fig. 2e). Furthermore, it is the only channichthyid that has a pattern of four to five thick, regularly spaced, dark bars on the trunk (Fig. 2e). At 2012 m, it is also the deepest-living channichthyid (Kock 2005), and one of our specimens from Marguerite Bay edges the record slightly deeper to 2025 m. Our images support the notion that *C. dewitti* dwells primarily on the upper slope. In Marguerite Bay, for example, *C. dewitti* spanned a depth range of 495–2025 m, with 6% of images from < 600 m, 12% from 600–1000 m and 82% from > 1000 m.

Among channichthyids, *C. dewitti* has a low percentage buoyancy (1.22%) on the notothenioid spectrum, where 0% represents neutrally buoyant species and 6% characterizes benthic species (Near *et al.* 2012, table S5). Many of our

images are similar to Fig. 2e and show *C. dewitti* in the water column, thus reflecting its low percentage buoyancy compared to the 3–4% range common for the more benthic channichthyids (Eastman & Sidell 2002, Near *et al.* 2012).

Until recently *C. dewitti* was the least known (Balushkin & Prut'ko 2006) of the 16 channichthyid species, but some of its biology has been revealed as the longline fishery for *D. mawsoni* has moved to slope depths and has taken *C. dewitti* either as bycatch or stomach contents from *D. mawsoni*. Along the Antarctic Peninsula and in the Bellingshausen Sea, *C. dewitti* is the second-most important bycatch species (Arana & Vega 1999). In the Ross Sea *C. dewitti* is the most common channichthyid taken as bycatch (Sutton *et al.* 2008) and its diet consists of a variety of mesopelagic and benthic fish and cephalopods (Kock 2005, Petrov 2011b). Although not identified to species, in the Ross Sea *C. dewitti* is probably the most important dietary item of *D. mawsoni* captured at slope depths by the longline fishery (Fenaughty *et al.* 2003). Being one of the larger channichthyids (Kock 2005), *C. dewitti* is of considerable importance in the food web of the upper slope. Its ecological role is corroborated by its abundance in our images.

Liparidae (snailfishes) (Fig. 2g). One of two major non-notothenioid components of the Antarctic fauna, liparids were present on the slope of Marguerite Bay. Many new species have come to light recently (Eschmeyer *et al.* 2010), especially at slope depths in the Antarctic (Stein 2012). They are difficult to identify, and we simply document their presence here. They frequently assume a head-down position with respect to the substrate (Stein *et al.* 2005) as demonstrated in Fig. 2g.

Zoarcidae (eelpouts) (Fig. 2h & i). Zoarcids are the second major non-notothenioid component of the Antarctic fish fauna. They were well-represented on the slope in Marguerite Bay, where they were second to the macrourids in abundance among non-notothenioids. We were unable to identify most zoarcids. The majority were benthic and solitary, however, we did encounter the unusual assemblage seen in Fig. 2h. There were six small zoarcids (6 cm TL; two have been cropped out of the figure) on total area of 1.56 m<sup>2</sup> of sea floor consisting of volcanic rubble with a dense assemblage of invertebrates including occasional brittlestars. Although zoarcids are most frequently seen on soft bottoms, this association on a hard bottom at 1260 m may be a feeding site, as the substrate appears richer in invertebrate taxa than most areas of the Marguerite Bay slope.

In addition to the benthic zoarcids, we encountered the pelagic species *Melanostigma gelatinosum* Günther, 1881 (Fig. 2i) in the water column a few metres above the substrate at depths of 566–1339 m (but usually > 800 m). They tended to “hang” in the water column with their body axis straight, suggesting that they are neutrally buoyant. We identified them (Fig. 2i) based on the short head, tapering trunk, confluence of the dorsal and anal fins with the caudal

fin, and presence of a clear-appearing gelatinous layer (probably a buoyancy agent) beneath the skin of the trunk. They could be easily misidentified as *P. antarcticum*, but the tapering trunk and absence of a distinct caudal fin distinguish *M. gelatinosum*. The species is expected in Marguerite Bay, as mid-water trawling has shown that they are an important component of the pelagic fish biomass (Donnelly & Torres 2008).

Many new zoarcid genera and species have been discovered recently in Antarctic waters (Matallanas 2010), but little is known about the life history of most species. As a group associated with extreme and ephemeral deep-sea habitats worldwide, it is not surprising that zoarcids are also present in the vicinity of the only known deep-sea hydrothermal vent system in the Southern Ocean (Rogers *et al.* 2012).

#### *Zoogeographic affinities of the fishes of the Marguerite Bay slope and the Amundsen Sea*

The western Antarctic Peninsula, including Marguerite Bay, belongs to the West Antarctic or low-Antarctic zoogeographic province and, therefore, has a fish fauna dominated by the nototheniid genera *Notothenia*, *Lepidonotothen*, and *Gobionotothen* and the channichthyid and bathydraconid genera *Champocephalus*, *Chaenocephalus*, and *Parachaenichthys*. There are relatively few of the 11 species of the primarily East Antarctic or high-Antarctic nototheniid genus *Trematomus* (Andriashev 1987, Kock 1992). Most of the common West Antarctic taxa occur in water < 250 m deep (Kock *et al.* 2000). Given that most of our images were captured at depths > 600 m and represent the slope fauna, we cannot offer any definitive zoogeographic analysis other than to say that the typically West Antarctic genera *Lepidonotothen* and *Gobionotothen* are present in our images. The only species of *Trematomus* we were able to identify, *T. loennbergii*, is a primarily a deep-water species that is expected to be in the area, as mentioned previously. Our images are unusual in documenting that offshore non-notothenioids, especially *Macrourus whitsoni* and zoarcids, extend into waters < 600 m deep and are the most abundant component of the sample at 67% (Table II). This may be due to the bias of our sampling toward deep-water sites, but it may also reflect the unusual hydrography of Marguerite Bay. A deep cross-shelf trough allows periodic intrusions of warm (+1–2°C) Circumpolar Deep Water onto the slope and shelf of Marguerite Bay and allows, in the case of pelagic fishes, mixing of offshore non-notothenioids with notothenioids typically found on the shelf (Donnelly & Torres 2008, Parker *et al.* 2011). Because the Marguerite trough is 1600 m deep (Meredith *et al.* 2010), it also offers a conduit into Marguerite Bay for offshore, deep-living benthic species like *M. whitsoni* and zoarcids.

The Bellingshausen Sea, located between Alexander and Thurston islands, is south of Marguerite Bay and, although

little studied, has been considered part of the West Antarctic Zoogeographic Province (Andriashev 1987). Recent collecting in this area, however, led Matallanas & Olaso (2007) to conclude that the nototheniid and channichthyid genera characteristic of the West Antarctic were absent, and that the fauna was instead East Antarctic because it contained trematomid, artedidraconid, bathydraconid, and channichthyid species typical of this province. Matallanas & Olaso (2007) also found that, unlike other East Antarctic areas, overall fish abundance and biomass at depths of 355–1947 m was dominated by zoarcids rather than notothenioids. They attributed this in part to their use of baited traps, which were more effective than trawls in catching the chemosensitive zoarcids.

To the south and west the Bellingshausen Sea is contiguous with the Amundsen Sea, so the latter would also be expected to have an East Antarctic fish fauna. Although we had relatively few images from the Amundsen Sea and the taxonomic diversity was low, the fish fauna is consistent with the East Antarctic Province. Bathydraconids are especially numerous in the coldest, deepest shelf waters at the highest latitudes (Eastman 1993), and their relatively high abundance in the Amundsen Sea supports the East Antarctic character of the fauna. For example, in our images bathydraconids and artedidraconids were 38% and 30% of nototheniid diversity, respectively (Table III). Moreover, aside from unidentified bathydraconids, the artedidraconid *D. longedorsalis* was the second-most abundant taxon. This is similar to the East Antarctic Weddell and Ross seas where *D. longedorsalis* is the most abundant artedidraconid and is especially numerous at depths > 600 m (Ekau 1990, Eastman & Hubold 1999).

Finally, our images from the Marguerite Bay and the Amundsen Sea also document the relatively high abundance of *M. whitsoni* and *C. dewitti* on the Antarctic slope, especially at 1000–2000 m. As discussed above, their presence has also been noted in other sectors of the Southern Ocean, primarily from the longline fishery for *D. mawsoni*, in which both species are major components of the bycatch and the stomach contents of *D. mawsoni*. As the largest and most abundant fishes in the ecosystem of the slope, their importance is just beginning to be appreciated.

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## References

- ANDRIASHEV, A.P. 1987. A general review of the Antarctic bottom fish fauna. In KULLANDER, S.O. & FERNHOLM, B., eds. *Proceedings of the fifth congress of European ichthyologists, Stockholm, 1985*. Stockholm: Swedish Museum of Natural History, 357–372.
- ANDRIASHEV, A.P. & NEYLOV, A.V. 1978. The new whiteblooded fish (*Chionobathyscus dewitti*, gen. et sp. n.; fam. Channichthyidae) from the continental slope of the East Antarctic. In SKARLATO, O.A., ANDRIASHEV, A.P., BARSUKOV, V.V., DOROFEEVA, E.A., KOROVINA, V.M. & NEYLOV, A.V., eds. *Morphology and systematics of fish*. Leningrad: Akademia Nauk SSSR, 5–12.
- 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.
- BALUSHKIN, A.V. & PRUT'KO, V.G. 2006. On occurrences of *Chionobathyscus dewitti* (Notothenioidei Channichthyidae) in the Ross Sea. *Journal of Ichthyology*, **46**, 271–273.
- BROOKS, C.M., ANDREWS, A.H., ASHFORD, J.R., RAMANNA, N., JONES, C.D., LUNDSTROM, C.C. & CAILLIET, G. 2011. Age estimation and lead-radium dating of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea. *Polar Biology*, **34**, 329–338.
- CULLINS, T.L., DEVRIES, A.L. & TORRES, J.J. 2011. Antifreeze proteins in pelagic fishes from Marguerite Bay (western Antarctica). *Deep-Sea Research II*, **58**, 1690–1694.
- CZIKO, P.A., EVANS, C.W., CHENG, C.-H.C. & DEVRIES, A.L. 2006. Freezing resistance of antifreeze-deficient larval Antarctic fish. *Journal of Experimental Biology*, **209**, 407–420.
- DANIELS, R.A. & LIPPS, J.H. 1982. Distribution and ecology of fishes of the Antarctic Peninsula. *Journal of Biogeography*, **9**, 1–9.
- DEWITT, H.H., HEEMSTRA, P.C. & GON, O. 1990. Nototheniidae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 279–331.
- DONNELLY, J. & TORRES, J.J. 2008. Pelagic fishes in the Marguerite Bay region of the West Antarctic Peninsula continental shelf. *Deep-Sea Research II*, **55**, 523–539.
- DUHAMEL, G., GASCO, N. & DAVAINÉ, P. 2005. *Poissons des îles Kerguelen et Crozet. Guide régional de l'Océan Austral*. Paris: Muséum National d'Histoire Naturelle, 419 pp.
- EAKIN, R.R. 1990. Artedidraconidae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 332–356.
- EAKIN, R.R., EASTMAN, J.T. & MATALLANAS, J. 2008. New species of *Pogonophryne* (Pisces, Artedidraconidae) from the Bellingshausen Sea, Antarctica. *Polar Biology*, **31**, 1175–1179.
- EAKIN, R.R., EASTMAN, J.T. & NEAR, T.J. 2009. A new species and a molecular phylogenetic analysis of the Antarctic fish genus *Pogonophryne* (Notothenioidei: Artedidraconidae). *Copeia*, **4**, 705–713.
- EASTMAN, J.T. 1993. *Antarctic fish biology: evolution in a unique environment*. San Diego, CA: Academic Press, 322 pp.
- EASTMAN, J.T. 2005. The nature of the diversity of Antarctic fishes. *Polar Biology*, **28**, 93–107.
- EASTMAN, J.T. & BARRY, J.P. 2002. Underwater video observation of the Antarctic toothfish *Dissostichus mawsoni* (Perciformes: Nototheniidae) in the Ross Sea, Antarctica. *Polar Biology*, **25**, 391–395.
- EASTMAN, J.T. & DEVRIES, A.L. 1981. Buoyancy adaptations in a swim-bladderless Antarctic fish. *Journal of Morphology*, **167**, 91–102.
- EASTMAN, J.T. & HUBOLD, G. 1999. The fish fauna of the Ross Sea, Antarctica. *Antarctic Science*, **11**, 293–304.
- EASTMAN, J.T. & LANNOO, M.J. 2003. Anatomy and histology of the brain and sense organs of the Antarctic plunderfish *Dolloidraco longedorsalis* (Perciformes: Notothenioidei: Artedidraconidae), with comments on the brain morphology of other artedidraconids and closely related harpagiferids. *Journal of Morphology*, **255**, 358–377.
- 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.
- EKAU, W. 1990. Demersal fish fauna of the Weddell Sea, Antarctica. *Antarctic Science*, **2**, 129–137.
- EKAU, W. & GUTT, J. 1991. Notothenioid fishes from the Weddell Sea and their habitat, observed by underwater photography and television. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology*, **4**, 36–49.
- ESCHMEYER, W.N., FRICKE, R., FONG, J.D. & POLACK, D.A. 2010. Marine fish diversity: history of knowledge and discovery (Pisces). *Zootaxa*, **2525**, 19–50.
- 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.
- GERASIMCHUK, V.V. 1986. Characteristics of Antarctic silverfish, *Pleuragramma antarctica* (Nototheniidae), from Olaf-Pruds Bay (Commonwealth Sea, eastern Antarctica) with notes on the identification of the species. *Journal of Ichthyology*, **26**, 10–17.
- GON, O. 1988. The fishes collected during the South African SIBEX I+II expeditions to the Indian Ocean sector of the Southern Ocean (60–66°S, 48–64°E). *South African Journal of Antarctic Research*, **18**, 55–70.
- GON, O. & HEEMSTRA, P.C., eds. 1990. *Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 462 pp.
- GUTT, J. & EKAU, W. 1996. Habitat partitioning of dominant high Antarctic demersal fish in the Weddell Sea and Lazarev Sea. *Journal of Experimental Marine Biology and Ecology*, **206**, 25–37.
- GUTT, J., EKAU, W. & GORNY, M. 1994. New results on the fish and shrimp fauna of the Weddell Sea and Lazarev Sea (Antarctic). *Proceedings of the National Institute of Polar Research Symposium on Polar Biology*, **7**, 91–102.
- HANCHET, S.M., TRACEY, D., DUNN, A., HORN, P.L. & SMITH, N. 2012. Mercury concentrations of two toothfish and three of its prey species from the Pacific sector of the Antarctic. *Antarctic Science*, **24**, 34–42.
- HOURLIGAN, T.F. & RADTKE, R.L. 1989. Reproduction of the Antarctic fish *Nothotheniops nudifrons*. *Marine Biology*, **100**, 277–283.
- IWAMOTO, T. 1990. Macrouridae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 192–206.
- JONES, C.D. & NEAR, T.J. 2012. The reproductive behaviour of *Pogonophryne scotti* confirms widespread egg-guarding parental care among Antarctic notothenioids. *Journal of Fish Biology*, **80**, 2629–2635.
- KAELI, J.W., SINGH, H., MURPHY, C. & KUNZ, K. 2011. Improving colour correction for underwater image surveys. *Proceedings IEEE/MTS Oceans '11, Kona, Hawaii, 19–22 September 2011*. New York: Institute of Electrical and Electronic Engineers, 805–810.
- KOCK, K.-H. 1992. *Antarctic fish and fisheries*. Cambridge: Cambridge University Press, 359 pp.
- KOCK, K.-H. 2005. Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, part I. *Polar Biology*, **28**, 862–895.

- KOCK, K.-H. & KELLERMANN, A. 1991. Reproduction in Antarctic notothenioid fish. *Antarctic Science*, **3**, 125–150.
- KOCK, K.-H., JONES, C.D. & WILHELMS, S. 2000. Biological characteristics of Antarctic fish stocks in the southern Scotia Arc region. *CCAMLR Science*, **7**, 1–41.
- KONECKI, J.T. & TARGETT, T.E. 1989. Eggs and larvae of *Nototheniops larseni* from the spongocoel of a hexactinellid sponge near Hugo Island, Antarctic Peninsula. *Polar Biology*, **10**, 197–198.
- LA MESA, M., EASTMAN, J.T. & VACCHI, M. 2004. The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biology*, **27**, 321–338.
- MARRIOTT, P.M., HORN, P.L. & McMILLAN, P. 2003. Species identification and age estimation for the ridge-scaled macrourid (*Macrourus whitsoni*) from the Ross Sea. *CCAMLR Science*, **10**, 37–51.
- MASSOM, R.A. & STAMMERJOHN, S.E. 2010. Antarctic sea ice change and variability - physical and ecological implications. *Polar Science*, **4**, 149–186.
- 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. & OLASO, I. 2007. Fishes of the Bellingshausen Sea and Peter I Island. *Polar Biology*, **30**, 333–341.
- MEREDITH, M.P., WALLACE, M.I., STAMMERJOHN, S.E., RENFEW, I.A., CLARKE, A., VENABLES, H.J., SHOOSMITH, D.R., SOUSTER, T. & LENG, M.J. 2010. Changes in the freshwater composition of the upper ocean west of the Antarctic Peninsula during the first decade of the 21st century. *Progress in Oceanography*, **87**, 127–143.
- 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.
- OLASO, I., RAUSCHERT, M. & DE BROYER, C. 2000. Trophic ecology of the family Artedidraconidae (Pisces: Osteichthyes) and its impact on the eastern Weddell Sea benthic system. *Marine Ecology Progress Series*, **194**, 143–158.
- PARKER, M.L., DONNELLY, J. & TORRES, J.J. 2011. Invertebrate micronekton and macrozooplankton in the Marguerite Bay region of the Western Antarctic Peninsula. *Deep-Sea Research II*, **58**, 1580–1598.
- PETROV, A.F. 2011a. Distribution and biological characteristics of two sister species of toothfishes of the genus *Dissostichus* (Fam. Nototheniidae) at Bouvet Island. *Journal of Ichthyology*, **51**, 813–818.
- PETROV, A.F. 2011b. New data on the diet of deep-sea icefish *Chionobathyscus dewitti* (Channichthyidae) in the Ross Sea in 2010. *Journal of Ichthyology*, **51**, 692–694.
- ROBERTS, J., XAVIER, J.C. & AGNEW, D.J. 2011. The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. *Journal of Fish Biology*, **79**, 138–154.
- ROGERS, A.D., TYLER, P.A., CONNELLY, D.P., COPLEY, J.T. & JAMES, R.E.A. et al. 2012. The discovery of new deep-sea hydrothermal vent communities in the Southern Ocean and implications for biogeography. *PLoS Biology*, **10**, e1001234.
- SCHNEPPENHEIM, R., KOCK, K.-H., DUHAMEL, G. & JANSEN, G. 1994. On the taxonomy of the *Lepidonotothen squamifrons* group (Pisces, Perciformes, Notothenioidei). *Archive of Fisheries and Marine Research*, **42**, 137–148.
- SINGH, H., ROMAN, C., PIZARRO, O. & CAN, A. 2007. Towards high-resolution imaging from underwater vehicles. *International Journal of Robotics Research*, **26**, 55–74.
- SMITH, P.J., STEINKE, D., McVEAGH, S.M., STEWART, A.L., STRUTHERS, C.D. & ROBERTS, C.D. 2008. Molecular analysis of Southern Ocean skates (*Bathyraja*) reveals a new species of Antarctic skate. *Journal of Fish Biology*, **73**, 1170–1182.
- SMITH, P.J., STEINKE, D., McMILLAN, P.J., STEWART, A.L., McVEAGH, S.M., DIAZ DE ASTARLOA, J.M., WELSFORD, D. & WARD, R.D. 2011. DNA barcoding highlights a cryptic species of grenadier *Macrourus* in the Southern Ocean. *Journal of Fish Biology*, **78**, 355–365.
- STEHMANN, M. & BÜRKELE, D.L. 1990. Rajidae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: JLB Smith Institute of Ichthyology, 86–97.
- STEIN, D.L. 2012. Snailfishes (family Liparidae) of the Ross Sea, Antarctica, and closely adjacent waters. *Zootaxa*, **3285**, 1–120.
- STEIN, D.L., FELLE, J.D. & VECCHIONE, M. 2005. ROV observations of benthic fishes in the Northwind and Canada Basins, Arctic Ocean. *Polar Biology*, **28**, 232–237.
- SUTTON, C.P., MANNING, M.J., STEVENS, D.W. & MARRIOTT, P.M. 2008. Biological parameters for icefish (*Chionobathyscus dewitti*) in the Ross Sea, Antarctica. *CCAMLR Science*, **15**, 139–165.
- VACCHI, M., LA MESA, M., DALU, M. & MACDONALD, J. 2004. Early life stages in the life cycle of Antarctic silverfish, *Pleuragramma antarcticum* in Terra Nova Bay, Ross Sea. *Antarctic Science*, **16**, 299–305.
- WALTER, T., PALM, H.W., PIEPIORKA, S. & RÜCKERT, S. 2002. Parasites of the Antarctic rattail *Macrourus whitsoni* (Regan, 1913) (Macrouridae, Gadiformes). *Polar Biology*, **25**, 633–640.
- YAU, C., COLLINS, M.A., BAGLEY, P.M., EVERSON, I. & PRIEDE, I.G. 2002. Scavenging by megabenthos and demersal fish on the South Georgia slope. *Antarctic Science*, **14**, 16–24.
- ZAITSEV, A.K. 1989. The reproductive biology of gray Notothenia, *Lepidonotothen squamifrons squamifrons*, of the Indian sector of Southern Ocean. *Journal of Ichthyology*, **29**, 9–17.
- ZIMMERMANN, C. 1997. On the demersal fish fauna of the Lazarev Sea (Antarctica): composition and community structure. In BATTAGLIA, B., VALENCIA, J. & WALTON, D.W.H., eds. *Antarctic communities: species, structure and survival*. Cambridge: Cambridge University Press, 26–32.