



Spatial distribution and habitat preferences of demersal fish assemblages in the southeastern Weddell Sea (Southern Ocean)

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Abstract

Our knowledge on distribution, habitats and behavior of Southern Ocean fishes living at water depths beyond scuba-diving limits is still sparse, as it is difficult to obtain quantitative data on these aspects of their biology. Here, we report the results of an analysis of seabed images to investigate species composition, behavior, spatial distribution and preferred habitats of demersal fish assemblages in the southern Weddell Sea. Our study was based on a total of 2736 high-resolution images, covering a total seabed area of 11,317 m², which were taken at 13 stations at water depths between 200 and 750 m. Fish were found in 380 images. A total of 379 notothenioid specimens were recorded, representing four families (Nototheniidae, Artedidraconidae, Bathydraconidae, Channichthyidae), 17 genera and 25 species. Nototheniidae was the most speciose family, including benthic species (*Trematomus* spp.) and the pelagic species *Pleuragramma antarctica*, which was occasionally recorded in dense shoals. Bathydraconids ranked second with six species, followed by artedidraconids and channichthyids, both with five species. Most abundant species were *Trematomus scotti* and *T. lepidorhinus* among nototheniids, and *Dolloidraco longedorsalis* and *Pagetopsis maculatus* among artedidraconids and channichthyids, respectively. Both *T. lepidorhinus* and *P. maculatus* preferred seabed habitats characterized by biogenous debris and rich epibenthic fauna, whereas *T. scotti* and *D. longedorsalis* were frequently seen resting on fine sediments and scattered gravel. Several fish species were recorded to make use of the three-dimensional structure formed by epibenthic foundation species, like sponges, for perching or hiding inside. Nesting behavior was observed, frequently in association with dropstones, in species from various families, including Channichthyidae (*Chaenodraco wilsoni* and *Pagetopsis macropterus*) and Bathydraconidae (*Cygnodraco mawsoni*).

Keywords Photographic survey · Notothenioids · Benthic communities · Weddell Sea

Introduction

From a zoogeographic perspective, the Southern Ocean is divided into three subregions (Kock 1992): (1) Ice-free zone, between the Antarctic Convergence and the northern limit

of the Antarctic pack-ice in winter/spring, which is almost exclusively inhabited by meso- and bathypelagic fishes; (2) Seasonal Pack-ice Zone (and the islands north of it) between the boundaries of the pack-ice extension in winter/spring and autumn/summer, respectively, where mesopelagic species and a coastal fish fauna dominated by nototheniids of the genera *Lepidonotothen* and *Notothenia*, harpagiferids and some channichthyids occurs; and (3) High-antarctic Zone,

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around the Antarctic continent that is covered by sea ice for most of the year, characterized by a few mesopelagic species and a coastal fish fauna composed of nototheniids, mostly *Trematomus* spp., and many species of artemidraconids, bathydraconids and channichthyids.

As part of the East Antarctic Province in the High-Antarctic zone, the Weddell Sea is a deep embayment situated between 70–78°S and 20–60°W (Fig. 1). It has a wide, relatively deep (200–500 m) continental shelf, deepening in the southeastern part in the Filchner Trough (> 1500 m depth), with the shelf break located at 600 m. The circulation in the Weddell Sea is dominated by a cyclonic, oceanic wind-driven gyre, with a southern branch flowing as Modified Warm Deep Water (mWDW) along the shelf ice edge to

the southwest splitting into two branches, one following the shelf break and the other heading south towards the Filchner and Ronne Ice Shelves (Ryan et al. 2016). Two other water masses characterize the continental shelf of the Weddell Sea, i.e. the cold and less saline Eastern Shelf Water (ESW) with temperatures ranging between -2 and -1.6 °C, and the ice shelf water (ISW) located along both sides of the Filchner Trough at 700–1000 m depth, with temperatures between -2.4 and -2 °C (e.g. Nicholls et al. 2009).

At a large spatial scale, the demersal fish fauna of the southern and eastern Weddell Sea has been thoroughly investigated during bottom trawling surveys (Kock et al. 1984; Schwarzbach 1988; Eka 1990). The fish assemblage inhabiting the continental shelf is dominated by nototheniids

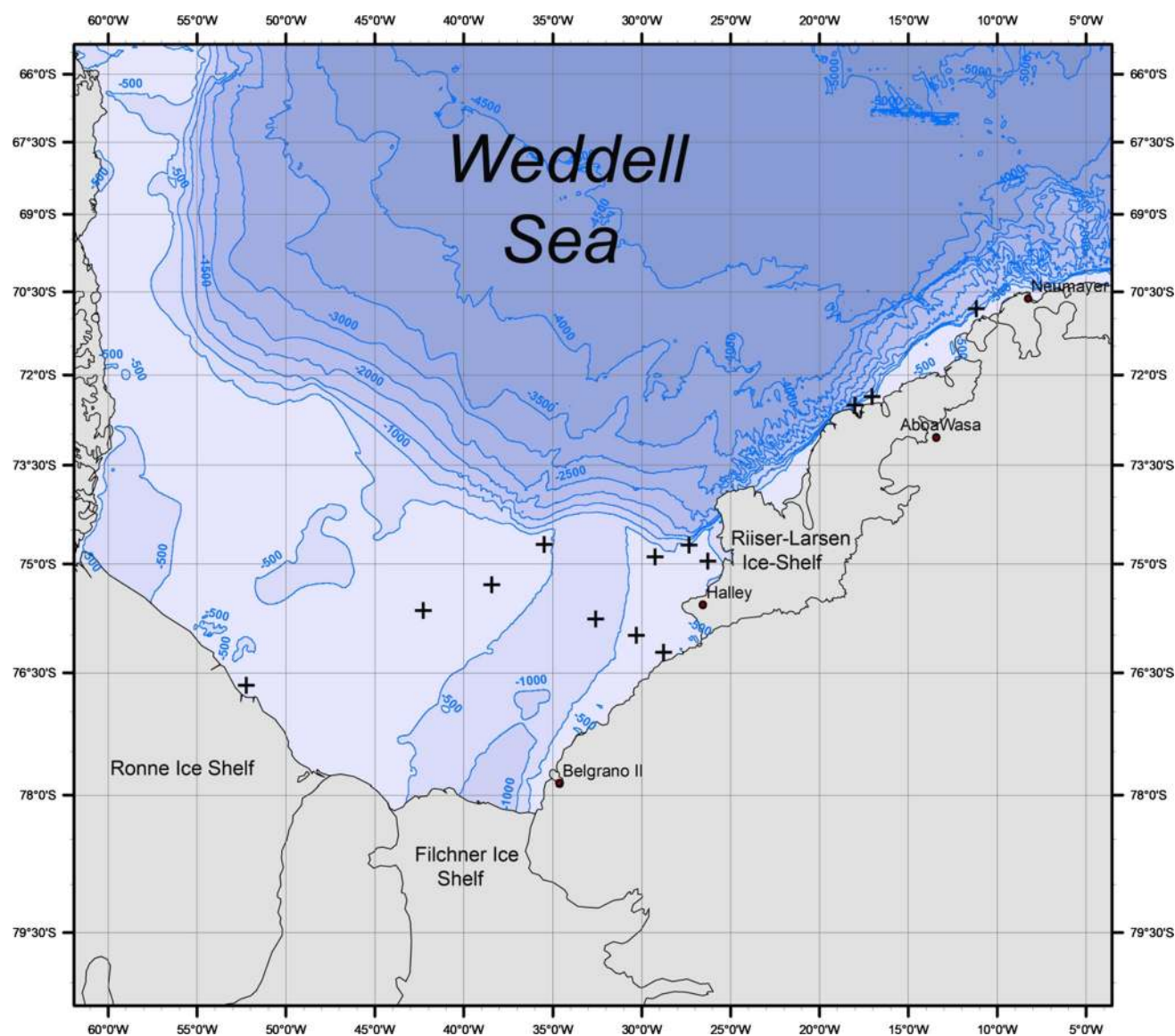


Fig. 1 Map of the Weddell Sea, showing the geographic positions (*crosses*) where the Ocean Floor Observation System (OFOS) was deployed during the *Polarstern* cruise ANTXXXI/2 (PS 96) from December 2015 to February 2016

(*Trematomus scotti*, *T. lepidorhinus* and *T. eulepidotus*), followed in decreasing importance by channichthyids (*Chionodraco myersi* and *Pagetopsis maculatus*) and artedidraconids (*Artedidraaco* spp.), whereas bathydraconids are negligible. The fish fauna inhabiting the deep waters of the Filchner Trough is different and composed primarily of bathydraconids (*Akarotaxis nudiceps* and *Gerlachea australis*) and artedidraconids (*Dolloidraco longedorsalis*), and to a lesser extent by the nototheniid *Trematomus loennbergii* (Schwarzbach 1988; Ekau 1990).

There is a long history of employing seabed photography to investigate composition, spatial distribution and habitat preferences of benthic communities (e.g. Bohnsack 1979), but it was rarely used in the Southern Ocean. It is a non-destructive and effective survey method, allowing a fine-scale description of benthic assemblages while minimizing the impacts of direct sampling. Using both still and video cameras mounted on remotely operated vehicles, species composition, relative abundance and behavior of benthic fish communities have been reported from the Weddell Sea and Lazarev Sea (Ekau and Gutt 1991; Gutt et al. 1994; Gutt and Ekau 1996). More recently, photographic surveys targeting the benthic communities of the continental shelf and upper slope of Marguerite Bay, the Amundsen Sea and the Antarctic Peninsula provided insights into the local fish fauna (Eastman et al. 2013; Amsler et al. 2016).

Within the framework of the research project Dynamics of Antarctic Marine Shelf Ecosystems (DynAMo), aimed at assessing the change and quality of benthos and endotherms in stable high-Antarctic environments not yet affected by climate change, a seabed imaging survey was carried out in the southeastern Weddell Sea using the ocean floor observation system (OFOS) developed at the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research in Bremerhaven (AWI). In the present study, we analyzed the seabed images for the fish fauna they show to: (1) investigate species composition, relative abundance and spatial distribution of the demersal fish (2) obtain insights on their habitat preferences and the parental care behavior observed in some species, and (3) explore the relationships between fish and some putative abiotic and biotic drivers by multivariate analyzes.

Materials and methods

Field sampling

A seabed imaging survey to investigate the epibenthic communities and their habitats was carried out during the ANT-XXXI/2 (PS96) cruise of RV *Polarstern* in the Weddell Sea from December 2015 to February 2016 (for more details, see Schröder 2016). Seafloor images were obtained using the

Ocean Floor Observation System (OFOS), which consisted of two downward-looking cameras mounted side-by-side: a high-resolution, wide-angle still camera (Canon®EOS 5D Mark III) and a high-definition color video camera (Sony®FCBH11).

The system was vertically lowered over the stern of the vessel with a broadband fiber-optic cable down to about 1.5 m above the seabed, then towed along transects at a speed of 0.5 km (0.25 m s⁻¹). The proper position of the system above the seafloor was monitored by the live video feed and by occasionally operating the winch to compensate for small-scale bathymetric variations. The height above the seafloor and water depth were continuously recorded by means of OFOS sensors. Three lasers placed beside the still camera, emitting parallel beams producing three equidistant (50 cm from each other) red light points on the seafloor, allowed for precise determination of the entire seabed area pictured in each image. A seabed photo, showing on average an area of about 3.45 m², was automatically taken every 30 s to obtain a series of stills along the transect. Overall, OFOS was deployed along 13 stations located in the southeastern and southern Weddell Sea. From east to west, a single station was located off Austasen, two stations were situated on the edge of the Riiser-Larsen Ice Shelf, five stations were located on the shelf east of the Filchner Trough, one station was within the Filchner Trough at about 750 m depth, and the remaining four stations were situated on the broad shelf west of the Filchner Trough (Fig. 1). For more details on the construction and operation of OFOS during the PS96 cruise see Piepenburg et al. (2017).

Image analysis

All images recorded during the survey were examined, and those showing fishes were subject to scrutiny. With the exception of zoarcids, all fishes were identified to the species level, using morphological diagnostic characters useful for identification (Gon and Heemstra 1990 and references therein). For each image, abundance of epibenthic invertebrate fauna at taxonomic unit and feeding guild level, as well as sediment characteristics were recorded and used to describe the epibenthic fauna accompanying all fish specimens. When appropriate, we classified benthic communities based on the previously described macrozoobenthic communities of the Weddell Sea (Voß 1988). For each fish species, the number of specimens and the standardized abundance (individuals 100 m⁻²) was determined for each transect.

Multivariate analyzes

Spatial distribution and species composition patterns of the fish fauna were explored by means of multivariate analyzes. Complete-linkage cluster analysis, based on Euclidean

distances quantifying the faunistic similarities between stations, was used to create a dendrogram visualizing the spatial resemblance pattern of the fish fauna. In addition, we used non-metric multidimensional scaling (MDS) of the similarity matrix as an ordination approach, representing the faunistic resemblance pattern through the distances between stations in a two-dimensional MDS plot. Moreover, we investigated the relationship between the fish fauna and a number of parameters also recorded for each transect, which are thought to potentially drive the distribution and composition of fish assemblages: water depth, bottom type, and type of macrobenthic epifauna co-occurring with the fish. These factors were categorized as follows:

- (1) Water depth (using mean depth of photo transect): 100–200, 200–300, 300–400, 400–500 and 750 m.
- (2) Bottom type: (a) fine sediment (b) spicule mats (c) fine sediment with drop stones (d) fine sediment with gravels.
- (3) Type of accompanying macrobenthic epifauna [using the seabed-community classification proposed for the Weddell Sea by Voß (1988)]: (a) Eastern Shelf Community (ESC) (b) Southern Shelf Community (SSC), and (c) Southern Trench Community (STC).

The affiliation of each station with one category each of these three factors was visualized with separately superimposing them in the MDS plot showing the fish-based resemblance pattern. Moreover, using a more formalized approach, BIO-ENV analysis (Clark and Warwick 1994) was employed to explore the degree of multivariate correlation between the fish-based faunistic similarities among stations and the resemblance pattern according to the three environmental factors.

Finally, to assess differences in fish biodiversity among the environmental factor gradients, Shannon diversity (H'), species richness (Margalef, d) and evenness (Pielou, J') indices were computed for each category. All statistical analyzes were performed using the PRIMER v5 software packages (Clarke and Gorley 2001).

Results

Photographic survey overview

Photographic surveys were conducted at 13 stations at water depths of 200 to 750 m, yielding 110 to 292 seabed images collected along drift transects of 0.9 to 2.6 km length (Table 1). Out of a total of 2736 still images analyzed, covering an overall area of 11,317 m², a total of 380 (13.9%) showed fishes. Most images showed a single specimen (93.6%), and rarely two (6.1%) or three (0.3%) specimens of

Table 1 Ocean Floor Observation System (OFOS) stations in the Weddell Sea during *Polarstern* cruise ANT-XXXI/2 (PS96) in December 2015 to January 2016

Station	Area	Date	Transect start			Transect end			Transect data		
			Latitude (S)	Longitude (W)	Depth (m)	Latitude (S)	Longitude (W)	Depth (m)	Duration (h)	Length (km)	No. of photos
001-4	Austasen	23/12/15	70.88656	11.10862	315	70.89597	11.14651	293	01:36	1.74	204
007-1	Filchner east	25/12/15	74.65717	26.94170	412	74.66767	26.99817	414	01:47	2.58	239
008-2	Filchner east	30/12/15	74.91990	29.42032	398	74.90734	29.40633	402	01:56	1.49	258
010-3	Filchner east	01/01/16	74.94354	26.03907	291	74.95666	26.08317	290	02:03	1.94	266
026-3	Filchner west	08/01/16	75.28338	37.91191	414	75.26742	37.91914	412	02:03	1.87	281
027-2	Ronne Depot	14/01/16	76.71955	52.19319	292	76.71915	52.15999	293	00:59	0.85	110
037-3	Filchner west	16/01/16	75.72218	42.46356	386	75.71473	42.44772	386	01:12	0.93	137
048-2	Filchner west	18/01/16	74.77064	35.30750	490	74.75814	35.34624	479	02:02	1.81	271
057-3	Filchner east	21/01/16	76.31746	29.03351	238	76.32195	29.00603	243	01:06	0.90	131
061-1	Filchner east	21/01/16	76.09967	30.30060	469	76.09070	30.33800	480	01:30	1.41	219
072-4	Filchner Trough	23/01/16	75.86119	32.38293	751	75.85799	32.33833	747	01:24	1.24	194
090-4	Rampen	29/01/16	72.43428	17.03233	281	72.44379	17.08049	302	02:14	1.95	292
106-2	Christmas Tree Inlet	31/01/16	72.60807	17.87568	194	72.60767	17.90184	211	01:02	0.90	134

different species. A total of 379 notothenioid fish specimens from four families, 17 genera and 25 species were recorded in the seabed images (Table 2). Most fish specimens were identified to species (98.7%) or genus (1.3%) level. Only three were unidentifiable zoarcids. Average fish species densities recorded along the transects ranged between 0.09 (for *Trematomus hansonii*) and 3.04 (for *T. scotti*) individuals 100 m^{-2} (Table 3). Raw count data of fish recorded in seabed images are presented in Online Resource 1.

Species composition and habitat preferences

Nototheniidae

Nototheniidae (notothens) was the most speciose fish family recorded in the Weddell Sea (Table 2), encompassing benthic and epibenthic species of the genus *Trematomus* and the pelagic species *Pleuragramma antarctica*.

Pleuragramma antarctica Boulenger, 1902 (Fig. 2a). This species was encountered primarily off the Riiser-Larsen Ice shelf (station 090-4; Table 2), forming dense shoals swimming in the water column near the seafloor. In addition, single specimens were occasionally observed in waters as deep as 750 m (station 072-4) in close proximity of the bottom, characterized by a seafloor covered by

Table 2 Numbers of fish specimens counted in seabed photos taken along Ocean floor observation system (OFOS) transects in the Weddell Sea during *Polarstern* cruise ANT-XXXI/2 (PS96)

Species/Station	001-4	007-1	008-2	010-3	026-3	027-2	037-3	048-2	057-3	061-1	072-4	090-4	106-2
Nototheniidae													
<i>Pleuragramma antarctica</i>							4				1	School	
<i>Trematomus eulepidotus</i>	1	5	7	2	1	7		1	1	2			
<i>Trematomus hansonii</i>												1	
<i>Trematomus lepidorhinus</i>	2	2		17					3	1		5	
<i>Trematomus loennbergii</i>		6											
<i>Trematomus pennellii</i>	8			2									
<i>Trematomus scotti</i>	3	1	29	25	1	4		4		6		14	1
<i>Trematomus tokarevi</i>											2		
<i>Trematomus</i> sp.				3	1	1							
Artedidraconidae													
<i>Artedidraco loennbergii</i>							1	1					
<i>Artedidraco orianae</i>		1											
<i>Dolloidraco longedorsalis</i>			17		1		1	10		11	2		
<i>Histiodraco velifer</i>													1
<i>Pogonophryne scotti</i>			4	1			3				1		
Bathydraconidae													
<i>Akarotaxis nudiceps</i>							3			2	15		
<i>Bathydraco macrolepis</i>							3	2		1	1		
<i>Cygnodraco mawsoni</i>	1	6		5								2	
<i>Gerlachea australis</i>								1		1	17		1
<i>Gymnodraco acuticeps</i>									1	2			
<i>Prionodraco evansii</i>	7			2		2							
<i>Racovitzia glacialis</i>	2		6		1			2		1			1
Channichthyidae													
<i>Chaenodraco wilsoni</i>			1			1					1		
<i>Chionodraco hamatus</i>		4	5	4	1		1						
<i>Cryodraco antarcticus</i>		1	1	1	1	2				1	2		
<i>Pagetopsis macropterus</i>									1				
<i>Pagetopsis maculatus</i>	1	3	3	17	2	2		2	3	1			
Zoarcidae													
Unidentified		2	1										

Table 3 Fish species density (individuals 100 m⁻²) determined in seabed photos taken along Ocean floor observation system (OFOS) transects in the Weddell Sea during *Polarstern* cruise ANT-XXXI/2 (PS96)

Species/station	001-4	007-1	008-2	010-3	026-3	027-2	037-3	048-2	057-3	061-1	072-4	090-4	106-2
Nototheniidae													
<i>Pleuragramma antarctica</i>							0.77				0.13	School	
<i>Trematomus eulepidotus</i>	0.10	0.59	0.73	0.21	0.09	1.53		0.10	0.10	0.21			
<i>Trematomus hansonii</i>												0.09	
<i>Trematomus lepidorhinus</i>	0.20	0.24		1.79					0.31	0.11		0.43	
<i>Trematomus loennbergii</i>		0.71											
<i>Trematomus pennellii</i>	0.82			0.21									
<i>Trematomus scotti</i>	0.31	0.12	3.04	2.63	0.09	0.87		0.41		0.64		1.20	0.15
<i>Trematomus tokarevi</i>											0.26		
<i>Trematomus</i> sp.				0.31	0.09	0.22							
Artedidraconidae													
<i>Artedidraco loennbergii</i>							0.19	0.10					
<i>Artedidraco orianae</i>		0.12											
<i>Dolloidraco longedorsalis</i>			1.78		0.09		0.19	1.03		1.18	0.26		
<i>Histiodraco velifer</i>													0.15
<i>Pogonophryne scottii</i>			0.42	0.10			0.57				0.13		
Bathydraconidae													
<i>Akarotaxis nudiceps</i>							0.57			0.21	1.92		
<i>Bathydraco macrolepis</i>							0.57	0.21		0.11	0.13		
<i>Cygnodraco mawsoni</i>	0.10	0.71		0.53								0.17	
<i>Gerlachea australis</i>								0.10		0.11	2.17		0.15
<i>Gymnodraco acuticeps</i>									0.10	0.21			
<i>Prionodraco evansii</i>	0.72			0.21		0.44							
<i>Racovitzia glacialis</i>	0.20		0.63		0.09			0.21		0.11			0.15
Channichthyidae													
<i>Chaenodraco wilsoni</i>			0.10			0.22					0.13		
<i>Chionodraco hamatus</i>		0.47	0.52	0.42	0.09		0.19						
<i>Cryodraco antarcticus</i>		0.12	0.10	0.10	0.09	0.44				0.11	0.26		
<i>Pagetopsis macropterus</i>									0.10				
<i>Pagetopsis maculatus</i>	0.10	0.35	0.31	1.79	0.17	0.44		0.20	0.31	0.11			
Zoarcidae													
Unidentified		0.24	0.10										

fine sediments and a benthic fauna dominated by motile deposit feeders, such as echinoids and crustaceans, and tube-forming polychaetes.

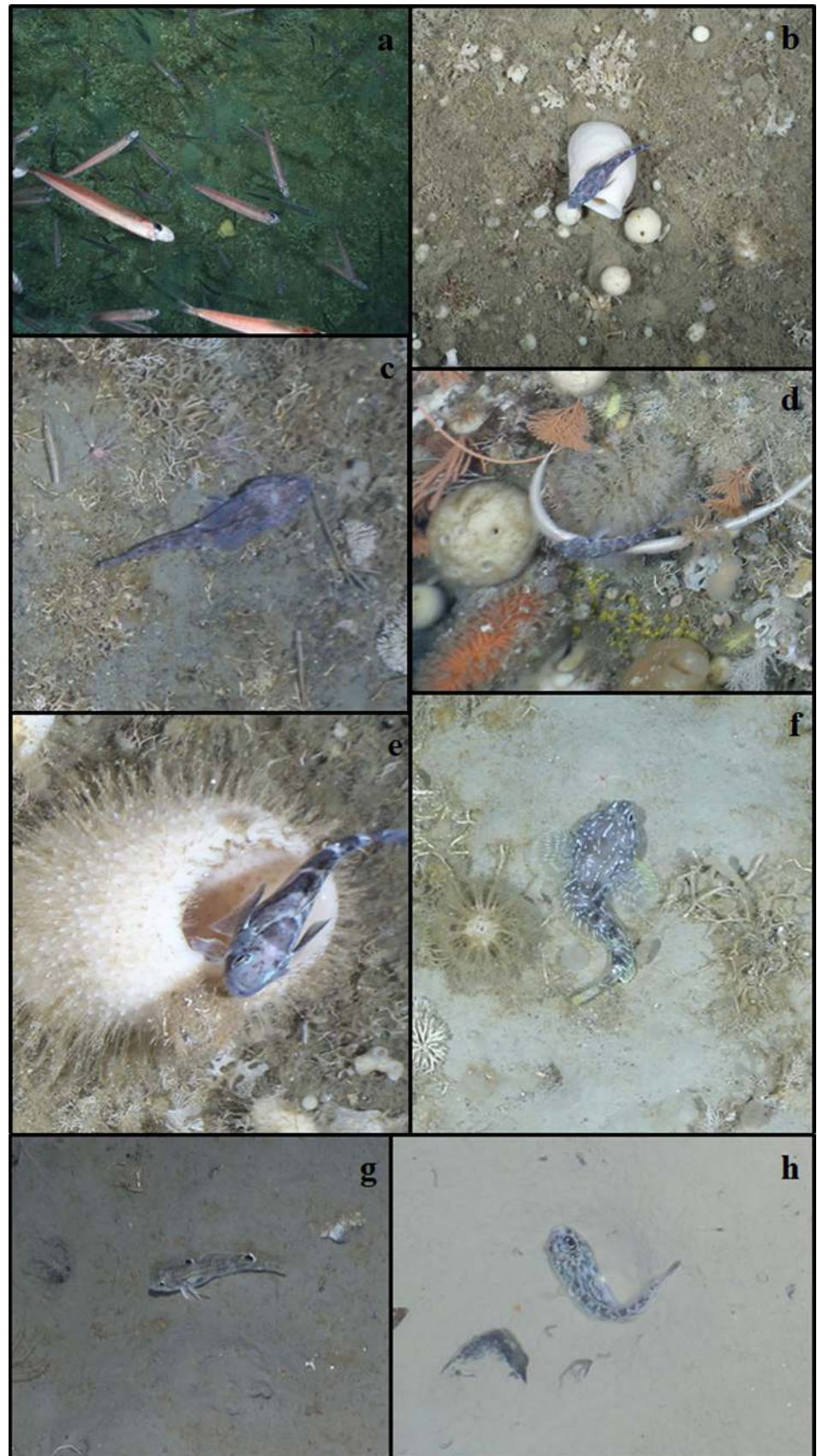
Trematomus eulepidotus Regan, 1914 (Fig. 2b). This epibenthic species was relatively common, being recorded at nine out of 13 stations and at depths of 249–484 m (Table 2). The majority of specimens were encountered in close association with the eastern shelf benthos community sensu Voß (1988), also accompanied by various motile organisms like ophiuroids, and sessile polychaetes and sponges living either on fine sediment (stations 008-2 and 010-3), or dispersed on spicule mats (station 007-1). Interestingly, some specimens were resting on the sponges, or hiding in the cavities. This species was also abundant off the Ronne Ice Shelf (station 027-2), dwelling on fine sediment populated

by deposit (ophiuroids) and patchy sessile suspension feeders (ascidians).

Trematomus hansonii Boulenger, 1902 (Fig. 2c). This species was very rare, as only a single specimen was found off the Riiser-Larsen Ice Shelf (station 090-4) at a depth of 281 m (Table 2). The benthos at this station was characterized by a mixture of eastern and southern shelf communities sensu Voß (1988), composed of abundant sessile organisms (bryozoans and sponges) living on fine sediment with sparse gravel.

Trematomus lepidorhinus (Pappenheim, 1911) (Fig. 2d). This species was the most abundant epibenthic nototheniid, recorded at depths of 240 to 468 m at almost one-half of stations surveyed (Table 2). Most specimens were encountered at station 010-3, where the benthos was characterized by a

Fig. 2 Photographic images of nototheniids from the continental shelf of southeastern Weddell Sea. **a** *Pleuragramma antarctica*, forming a dense shoal close to the seabed. **b** *Trematomus eulepidotus*, resting on a cup-shaped sponge. **c** *Trematomus hansonii*, showing the characteristic striped caudal fin useful for their identification. **d** *Trematomus lepidorhinus*, swimming slowly among a rich epibenthic fauna. **e** *Trematomus loembergii* resting on a large glass sponge. **f** gravid female of *Trematomus pennellii*, swimming slowly just above the substrate. **g** *Trematomus scotti* on fine sediment, easily recognizable by the obvious black spots on dorsal fins. **h** *Trematomus tokarevi*, found in deep water resting on fine sediments



patchily distributed eastern shelf benthic community sensu Voß (1988). It was less frequently found in association with epibenthic communities on dense spicule mats and dominated by sponges of the genus *Rossella* (station 007-1), or in association with mixed eastern and southern shelf benthic communities sensu Voß (1988), composed of bryozoans and sponges living on fine sediments with scattered gravels (station 57-3). This species was generally observed swimming just above the bottom, often hiding in close proximity to sponges or other macrobenthic invertebrates.

Trematomus loennbergii Regan, 1913 (Fig. 2e). This epibenthic species was less common, and the few specimens encountered were found at a single station (007-1) at 412 to 417 m depth (Table 2). The benthic community here consisted almost exclusively of sponges of the genus *Rossella* inhabiting dense spicule mats.

Trematomus pennellii Regan, 1914 (Fig. 2f). This benthic species was occasionally encountered, but almost exclusively in the easternmost sampling site (station 001-4) at depths ranging from 268 to 313 m (Table 2). The benthic community was dominated by a mixture of motile (crinoids, holothuroids and ophiuroids) and sessile invertebrates (bryozoans, polychaetes) inhabiting fine sediments, gravel patches or dropstones. Most fish specimens were probably adult females in spawning condition, with a rounded swollen abdomen.

Trematomus scotti (Boulenger, 1907) (Fig. 2g). It was the most abundant and widespread notothenioid species, which occurred at 10 of 13 stations at water depths of 197 to 487 m (Table 2). *T. scotti* is a small demersal fish, which was found in different habitats dominated by several motile benthic organisms (crinoids, holothuroids, ophiuroids) living on fine sediments, as well as sessile invertebrates (bryozoans, sponges, polychaetes and ascidians) on fine sediments with gravel. *Trematomus scotti* specimens were always observed resting directly on the sediment.

Trematomus tokarevi Andriashev, 1978 (Fig. 2h). Only two specimens of this rare species were observed at the deepest sampling site located in the Filchner Trough (station 072-4; Table 2), characterized by fine sediments mostly inhabited by motile deposit feeders, such as echinoids and crustaceans.

Artedidraconidae

Artedidraconidae (plunderfishes) were represented with five benthic species belonging to all four genera in the family (*Artedidraco*, *Dolloidraco*, *Histiodraco* and *Pogonophryne*) (Table 2).

Artedidraco loennbergi Roule, 1913 (Fig. 3a). Only two specimens were recorded on the shelf west of the Filchner Trough (stations 037-3 and 048-2) at 386 to 487 m depth (Table 2). They were resting on the fine sediment populated

by deposit-feeding benthos (polychaetes, ophiuroids) and by patchily distributed sessile suspension feeders (ascidians).

Artedidraco oriana Regan, 1914 (Fig. 3b). A single specimen was found at 418 m (station 007-1, Table 2), within a dense population of sponges (*Rossella*) on spicule mats.

Histiodraco velifer (Regan, 1914) (Fig. 3c). A single specimen of this species was recorded off the Riiser-Larsen Ice Shelf (station 106-2) in relatively shallow waters (197 m) (Table 2), in a curled-up position on a substratum dominated by ophiuroids, and patchily distributed small sponges and bryozoans.

Dolloidraco longedorsalis Roule, 1913 (Fig. 3d). This was the most abundant species among artedidraconids, being encountered in almost one-half of the stations across a depth range of 388 to 751 m (Table 2). Most specimens were observed at station 008-2, hosting an extremely patchily distributed eastern shelf benthos community sensu Voß (1988), which also consisted of motile organisms (mainly ophiuroids) living on fine sediments. *Dolloidraco longedorsalis* was also abundant at two other stations (048-2 and 061-1), which were dominated by deposit feeders (ophiuroids, echinoids and polychaetes) and sessile suspension feeders (sponges) sparsely distributed on fine sediments with occasional dropstones.

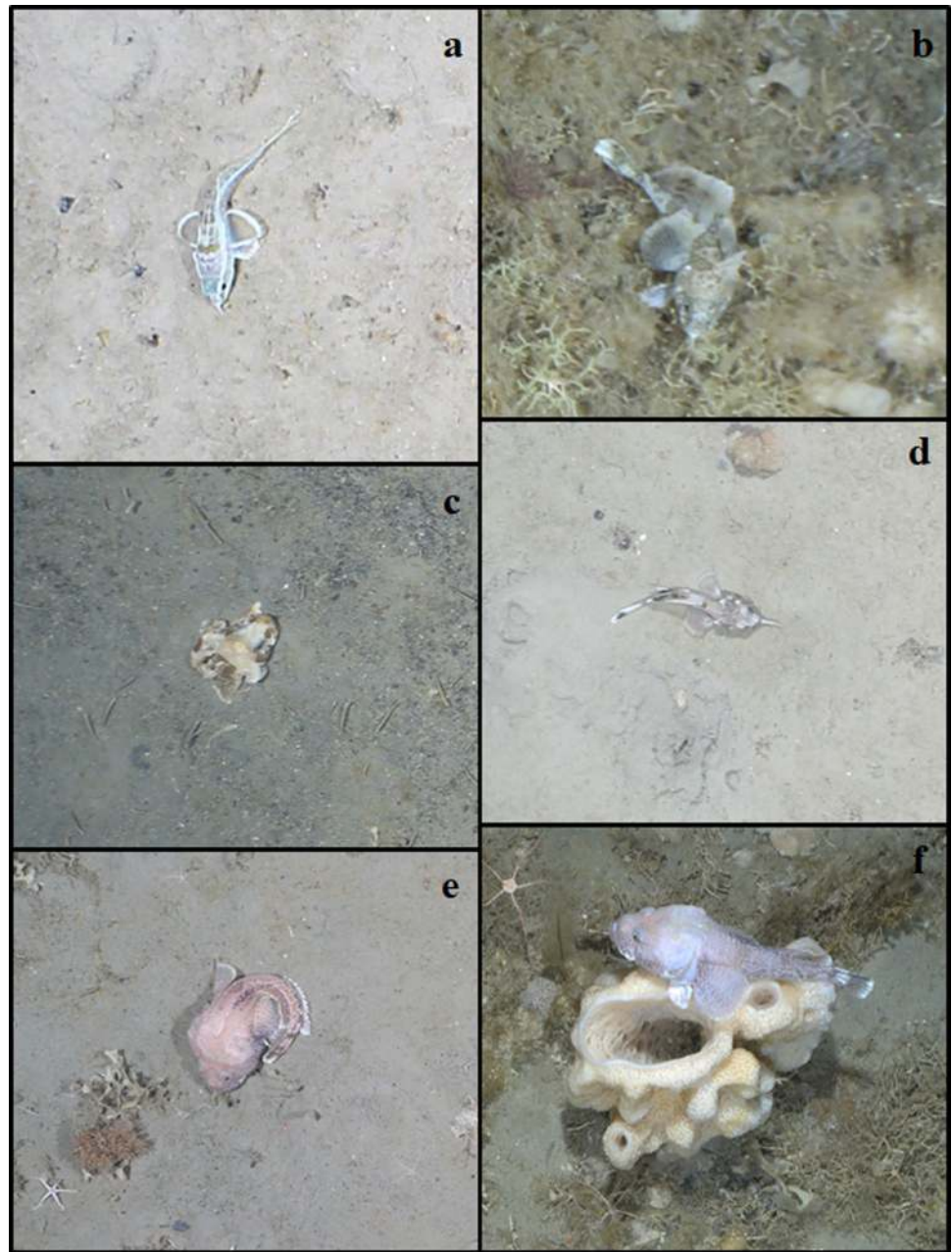
Pogonophryne scotti Regan, 1914 (Fig. 3e, f). This was the only species from the speciose genus *Pogonophryne* encountered in the Weddell Sea. The specimens occurred over a wide depth range (274 to 754 m; Table 2), generally resting on fine sediments inhabited by a benthic community mainly composed of motile (ophiuroids) species and occasional sessile invertebrates (sponges, bryozoans and polychaetes). One specimen of *P. scotti* was found resting on top of a glass sponge.

Bathydraconidae

Bathydraconidae (dragonfishes) were represented by seven species (Table 2) from seven genera (*Akarotaxis*, *Bathydraco*, *Cygnodraco*, *Gerlachea*, *Gymnodraco*, *Prionodraco* and *Racovitzia*) of the total of eleven genera belonging to this family.

Akarotaxis nudiceps (Waite, 1916) (Fig. 4a). This was one of the most abundant and deep living bathydraconids, although most specimens were documented in the Filchner Trench (station 072-4) at 750 m depth (Table 2). At this site, the benthic fauna was composed primarily of motile deposit feeders, such as echinoids (*Sterechinus*) and crustaceans. A few other specimens were found in shallower stations (037-3 and 061-1), dominated by deposit feeders (polychaetes and ophiuroids) and sessile suspension feeders (ascidians) sparsely distributed on fine sediments.

Fig. 3 Photographic images of artedidraconids from the continental shelf of southeastern Weddell Sea. **a** *Artedidraco loennbergii* on fine sediment, showing a short pointed mental barbel. **b** *Artedidraco oriana*, resting on a substrate composed of a dense spicule mat. **c** *Histiodraco velifer*, showing a light brown body with lateral dark blotches on cheeks and lips. **d** *Dolloidraco longedorsalis* on soft bottom, showing a long bi-colored caudal fin and a thin, long mental barbel. **e** *Pogonophryne scotti* curled-up on the substrate, characterized by the dorsum of head without dark markings. **f** A large specimen of *Pogonophryne scotti* resting above a sponge



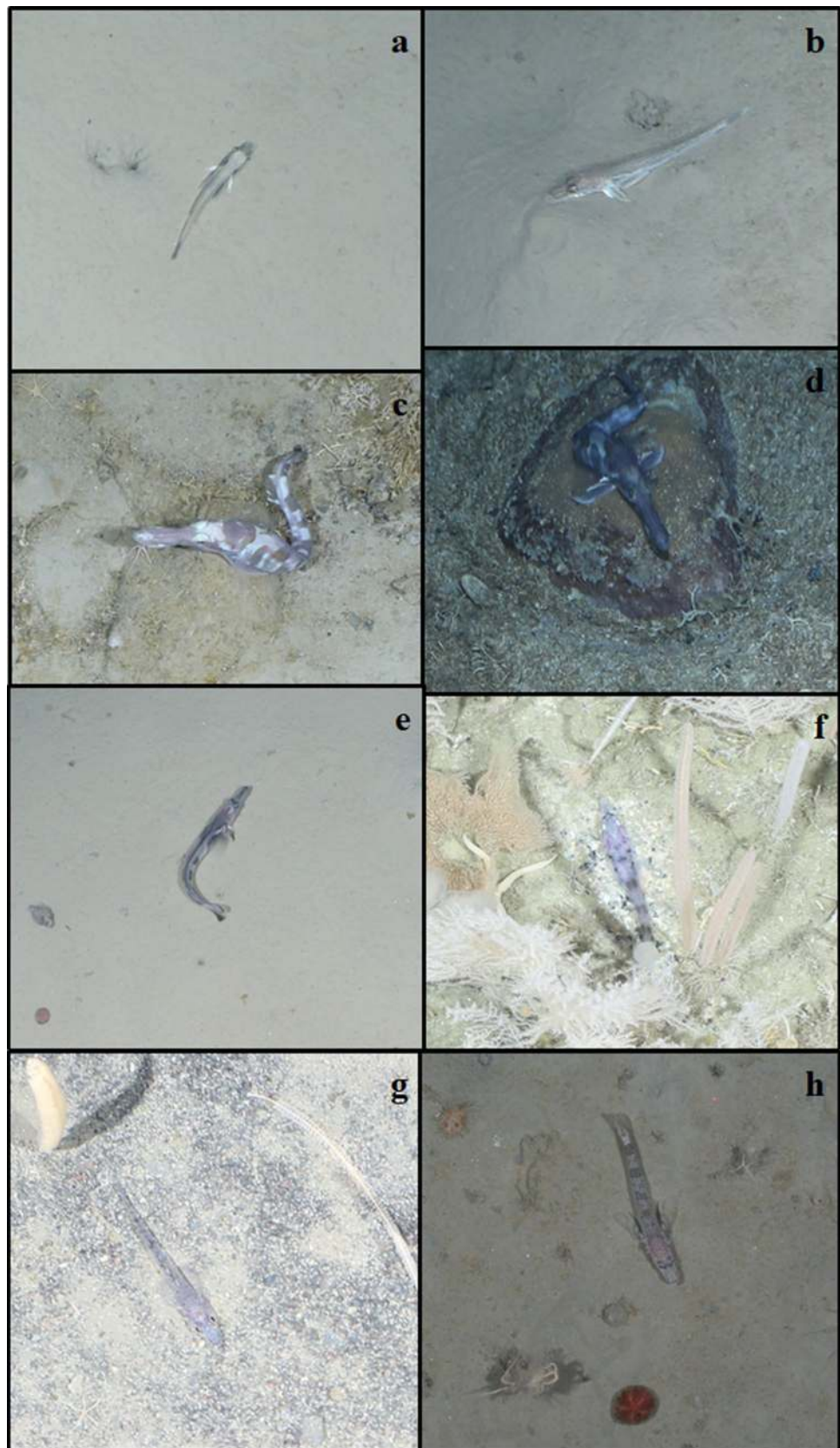
Bathydraco macrolepis Boulenger, 1907 (Fig. 4b). As the only representative of the genus *Bathydraco*, this species was occasionally encountered at four different stations at 386 to 751 m depth (Table 2). The seafloor at the sampling sites was inhabited by deposit feeders (ophiuroids, echinoids and polychaetes) and sessile suspension feeders (ascidians and sponges) scattered on fine sediments with dropstones.

Cygnodraco mawsoni Waite, 1916 (Fig. 4c, d). This was a common species, occurring at four stations (001-4, 007-1, 010-3, 090-4) at depths of 270–417 m off the Riiser-Larsen Ice Shelf (Table 2). The seabed at these stations hosted a typical eastern shelf benthos community sensu Voß (1988), mainly consisting of motile (ophiuroids) or sessile

invertebrates (sponges, ascidians and polychaetes) patchily distributed on fine sediments or sponge spicule mats. The *C. mawsoni* specimens frequently settled on the substrate, assuming a characteristic S-shaped body conformation. Remarkably, a single specimen was photographed guarding eggs laid on a flat stone (Fig. 4d).

Gerlachea australis Dollo, 1900 (Fig. 4e). This species was particularly abundant in the Filchner Trench at 754 m depth (Table 2). It was seldom recorded in shallower waters (station 106-2, 197 m). The benthic community consisted mainly of motile deposit feeders, and was dominated by echinoids and crustaceans living on fine sediment with scattered dropstones.

Fig. 4 Photographic images of bathydraconids from the continental shelf of southeastern Weddell Sea. **a** *Akarotaxis nudiceps* swimming slowly on fine sediment, showing light pelvic fins and dark gill chamber. **b** *Bathydraco macrolepis* resting on sandy bottom, with a dark caudal fin. **c** *Cygnodraco mawsoni* resting on the substrate with the typical s-shaped body position. **d** *Cygnodraco mawsoni* curled-up on a nest of eggs deposited on flat dropstone. **e** *Gerlachea australis* resting on fine sediment, showing the characteristic dark bands on the trunk. **f** *Gymnodraco acuticeps*, partially hidden by a rich epibenthic fauna, easily recognizable by the pointed snout. **g** *Prionodraco evansii* resting on fine sediment with pebbles, characterized by a fusiform body shape and narrow interorbital width. **h** *Racovitzia glacialis* dwelling on the substrate, with a typical mottled colouration and a black spot at base of uppermost caudal fin rays



Gymnodraco acuticeps Boulenger, 1902 (Fig. 4f). Compared to other bathydraconids, this species was relatively rare, occurring only at two stations situated east of the Filchner Trench between 237 and 476 m (Table 2). Two specimens were encountered on fine sediments populated mainly by motile deposit feeders (ophiuroids and echinoids), although another specimen was associated with sessile organisms (sponges, bryozoans) living on spicule mats and biological debris.

Prionodraco evansii Regan, 1914 (Fig. 4g). This small species was primarily recorded off the Riiser-Larsen Ice Shelf (stations 001-4, 010-3), as well as off the Ronne Ice Shelf (station 027-2) at depths of 273 to 324 m (Table 2). Most specimens were found in association with sparse motile benthic fauna (crinoids, holothuroids, ophiuroids) or occasionally with sessile invertebrates (ascidians, bryozoans and polychaetes) on fine sediments.

Racovitzia glacialis Dollo, 1900 (Fig. 4h). This species had a wide distribution, occurring on the eastern and western side of the Filchner Trench, as well as off the Riiser-Larsen Ice Shelf at 197 to 484 m depth (Table 2). The benthic community consisted of motile (crinoids, ophiuroids) and sessile organisms (sponges, bryozoans and polychaetes) sparsely distributed on fine sediment with dropstones.

Channichthyidae

From the family Channichthyidae (icefishes) five primarily benthic species, representing four of the eleven genera of this family (*Chaenodraco*, *Chionodraco*, *Cryodraco* and *Pagetopsis*), were identified in the images (Table 2).

Chaenodraco wilsoni Regan, 1914 (Fig. 5a). Single specimens of this species were encountered in three stations located in the Filchner Trench, at the eastern side, and off the Ronne Ice Shelf at depths of 293 to 752 m (Table 2). The benthic community at these stations was characterized by deposit feeders (polychaetes, crustaceans and ophiuroids) and patchily distributed sessile suspension feeders (sponges and ascidians) living on fine sediments. A single male *C. wilsoni* was photographed while swimming just above the bottom in close proximity of a nest with thousands of eggs.

Chionodraco hamatus (Lönnerberg, 1906) (Fig. 5b, c). It was a rather common channichthyid, occurring both in the shelves east (stations 007-1, 008-2, 010-3) and west (stations 026-3, 037-3) of the Filchner Trench at 286 to 415 m (Table 2). The seabed fauna at the eastern side of the Trench was characterized by a typical eastern shelf benthic community sensu Voß (1988), formed by motile taxa (e.g. ophiuroids) on fine sediments and sessile invertebrates (sponges, bryozoans and polychaetes) on spicule mats. At the western side of the Trench, the benthos community consisted of deposit feeders (polychaetes and ophiuroids) and patchily

distributed sessile suspension feeders (ascidians) living on fine sediments.

Cryodraco antarcticus Dollo, 1900 (Fig. 5d). This species was recorded at slightly more than one-half of sampling stations over a wide depth range (289–752 m), although usually as single or a few individuals (Table 2). It was found across various benthic communities, including deposit (ophiuroids, echinoids, crustaceans and polychaetes) and sessile suspension feeders (sponges, ascidians) on fine sediments with dropstones or rarely on spicule mats. The specimens were often observed resting on the substrate on the long pelvic fins.

Pagetopsis macropterus (Boulenger, 1907) (Fig. 5e). A single specimen guarding a nest with eggs was encountered east of the Filchner Trench at 238 m (Table 2), in association with sponges and bryozoans living on spicule mats and biological debris.

Pagetopsis maculatus Barsukov & Permitin, 1958 (Fig. 5f). This was by far the most abundant and widespread channichthyid species, encountered at nine out of 13 stations at depths of 244 to 483 m (Table 2). While most specimens were recorded on the shelf east of the Filchner Trench, a few specimens were found also on the shelves west and north of the Ronne Ice Shelf. The benthic community consisted of several taxa, encompassing mainly motile organisms (ophiuroids) living on fine sediments, and sessile suspension feeders (mainly sponges and ascidians) on spicule mats.

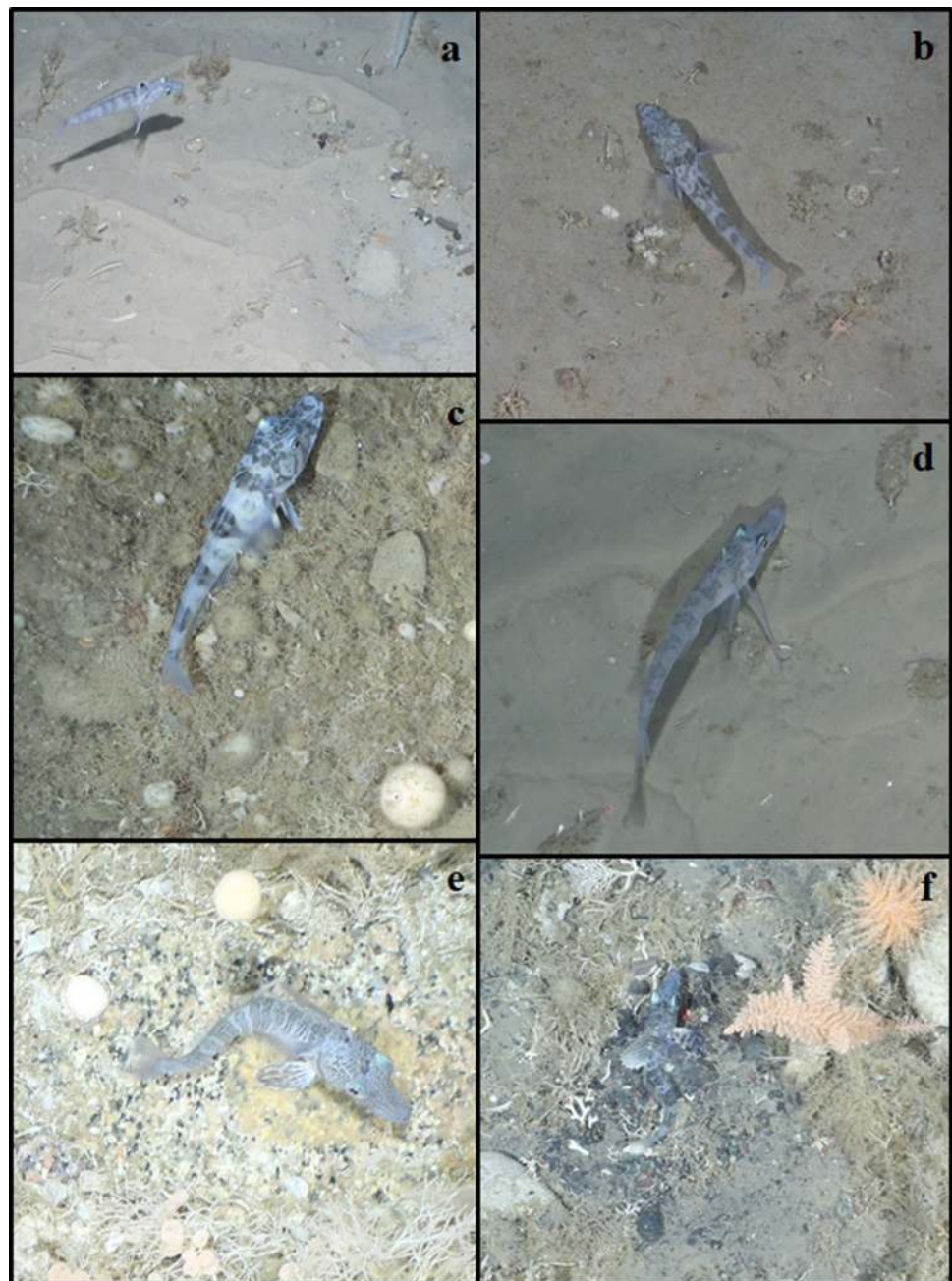
Zoarcidae

From this family, only three unidentified specimens were encountered at two stations located east of the Filchner Trench at 404 to 417 m depth (Table 2), in association with sessile invertebrates (sponges) inhabiting spicule mats.

Fish community structure in relation to environmental factors

With regard to their resemblance in fish fauna, stations were clustered in four main groups, mainly characterized by water depth and location (Fig. 6a). There were two small clusters, with only two stations each. The first featured stations on the narrow north-eastern shelf (stations 090-4 and 106-2), while the second encompassed the station in the deep Filchner Trough and a station located on the western shelf (072-4 and 037-3, respectively). A third cluster included the deep stations located on the wide shelves east and west of the Filchner Trough (008-2, 026-3, 048-2, and 061-1). The largest cluster was formed by the shallower stations distributed along the eastern shelf (001-4, 007-1, 010-3 and 057-3) and off the Ronne Ice Shelf (station 027-2). The ordination of stations in the MDS plot showed largely the same spatial resemblance pattern (Fig. 6b).

Fig. 5 Photographic images of channichthyids from the continental shelf of southeastern Weddell Sea. **a** *Chaenodraco wilsoni*, male swimming above a sandy bottom in close proximity of its nest with eggs. **b** *Chionodraco hamatus* dwelling on fine sediment. **c** *Chionodraco hamatus* resting on the pelvic fins above a dense spicule mat. **d** *Cryodraco antarcticus*, characterized by elongated pelvic fins used to position itself above the fine sediment of the substrate. **e** *Pagetopsis macrop-terus* guarding eggs laid directly on a spicule mat. **f** *Pagetopsis maculatus* dwelling within a rich epibenthic fauna, characterized by irregular dark blotches on the trunk and striped pelvic fins

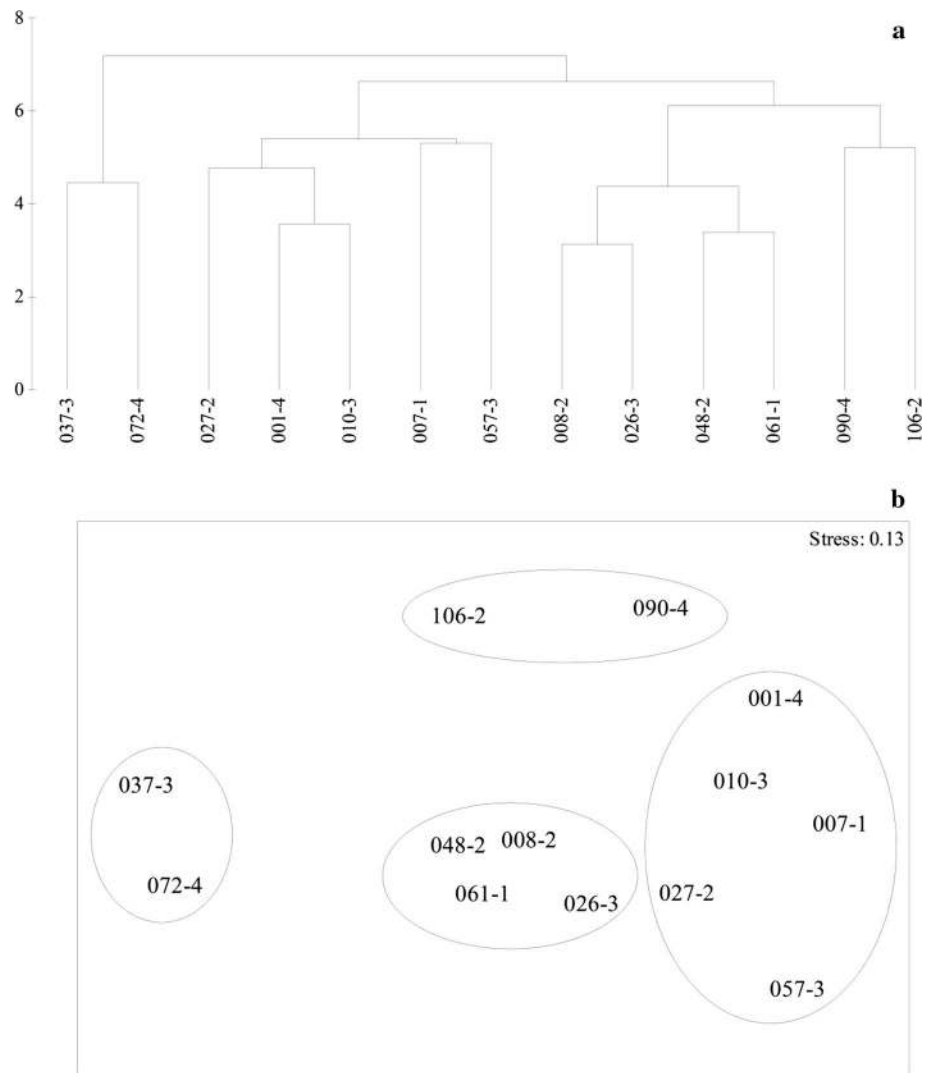


Superimposing the three environmental categorical factors on the station configuration in the MDS plot (Fig. 7a–c) revealed that all of them did not match well with the stations clusters based on faunistic resemblances, suggesting that these three factors had only little influence on the spatial distribution of the fish fauna. The results of the BIO-ENV analysis corroborated this impression, yielding correlations (ρ values) between the biotic fish-based station-similarity pattern and three- to one-factor combinations of environmental resemblance patterns that were 0.24 at maximum (for water depth and type of accompanying epifauna, see Table 4). This is a further clear indication that the three

factors considered in our study had only minor influence on the distribution of the fish fauna.

With regard to diversity (Shannon, Margalef, and Pielou indices), computed for all classes of each environmental category (Fig. 8a–c), evenness (J) was rather similar across all classes for each factor. In contrast, both Shannon diversity (H') and Margalef species richness (d) increased with water depth (except for the last depth class (> 750 m) that encompassed, however, only one station in the Filchner Trough) and decreased from fine sediment to gravel. With regard to the type accompanying epibenthic fauna, fish diversity and species richness were similar between the Eastern Shelf

Fig. 6 Dendrogram (a) and two-dimensional MDS plot (b) of sampling stations investigated in the southeastern Weddell Sea, to visualize the between-station resemblances according to fish fauna composition



Community (ESC) and Southern Shelf Community (SSC), but clearly lower for the Southern Trench Community (STC) (please note again that the latter was represented only by the single station in the Filchner Trough).

Discussion

Taxonomic composition, spatial distribution and behavior

The high resolution and definition of the OFOS cameras allowed, with the exception of zoarcids, species-level identification of even the smallest fish specimens recorded along the transects. Only five *Trematomus* specimens were identified to genus level only, owing to the poor quality of some images (blurred or dark photographs).

Previous trawl and photographic surveys conducted in the Weddell Sea (e.g. Ekau 1990; Ekau and Gutt 1991; Hubold

1992) documented the genus *Chionodraco* as represented by two species, *C. hamatus* and *C. myersi*, which are distributed over a largely overlapping depth range. We have tentatively identified all our specimens as *C. hamatus*, based on their narrower eye diameter and wider interorbital width respect to the head length, as well as to their relatively large body size (Miller 1993). All *Cryodraco* specimens have been provisionally identified as *C. antarcticus*, although the sister species *C. atkinsoni* has been recently recognized as valid through morphological and molecular genetic characters (La Mesa et al. 2002; Dornburg et al. 2016), and both are likely to be present in the Weddell Sea.

The rare nototheniid species *Trematomus tokarevi* was recorded for the first time in the deep shelf waters of the Weddell Sea. It can be easily confused with *Trematomus nicolai* (Kuhn et al. 2009), a similar species rarely encountered in shallow waters of the Weddell Sea (Hubold 1992). Based on the recent revision of the bathymetric distribution of notothenioid fishes (Eastman 2017), the minimum depths

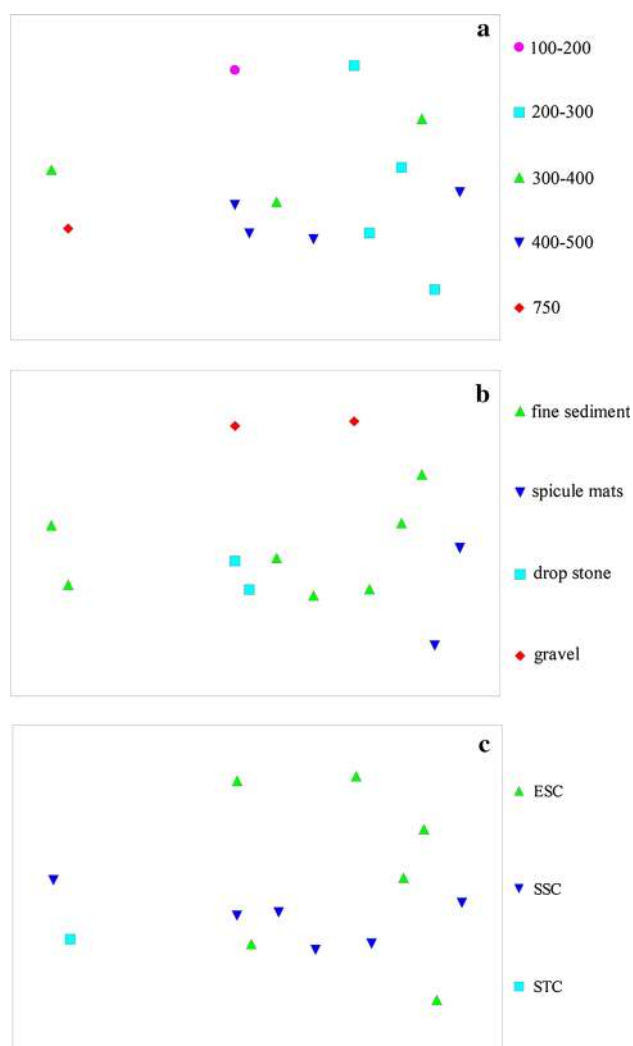


Fig. 7 Two-dimensional MDS plots with stations superimposed with categorized environmental factors: **a** mean water depth; **b** bottom type; **c** accompanying macrobenthic epifauna: Eastern Shelf Community (ESC), Southern Shelf Community (SSC), and Southern Trench Community (STC)

Table 4 Spearman rank correlation values (ρ) between the biotic fish-based station-similarity pattern and combinations of environmental factors from the BIO-ENV analysis; 1 = water depth; 2 = bottom type; 3 = accompanying macrobenthic epifauna

Environmental factors	p values
1, 3	0.241
3	0.235
1, 2, 3	0.230
2,3	0.187
1	0.166
1, 2	0.137
2	0.066

of occurrence of *Bathyraco macrolepis* and *Racovitzia glacialis* have now been documented as somewhat shallower at 386 m and 197 m, respectively.

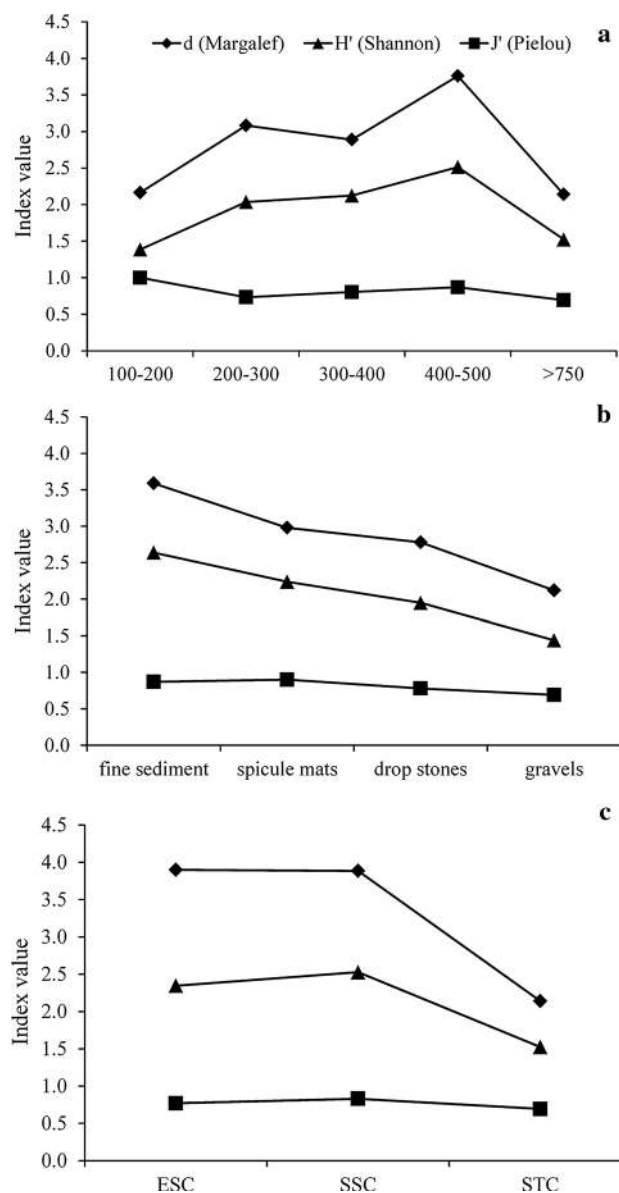


Fig. 8 Diversity indices (Shannon diversity H' , Margalef species richness d , and Pielou evenness J') computed for each categorized environmental factor: **a** water depth; **b** bottom type; **c** accompanying macrobenthic epifauna: Eastern Shelf Community (ESC), Southern Shelf Community (SSC), and Southern Trench Community (STC)

Seabed photography also provided insights into the behavior of some species. As expected, the majority of species were primarily benthic, resting on the substrate. The most common epibenthic species, such as *Trematomus eulepidotus* and *T. lepidorhinus*, were generally found to swim slowly a few centimeters above the substrate, or sometimes to perch on or inside large cup-shaped sponges, displaying a “sit, -observe and hide” strategy (Gutt and Ekau 1996). In contrast to previous direct observations made with a video camera in the Ross Sea, documenting loose

aggregations of *Pleuragramma antarctica* in the upper layers of the water column (Fuiman et al. 2012), we observed strikingly dense shoals of this species in the deepest reaches of the water column < 20 m above the seafloor.

Nesting behavior was observed in three species of different families. Males of *Chaenodraco wilsoni*, characterized by an obvious black blotch in the center of the first dorsal fin, guarded eggs deposited on a flat stone, as previously reported from both the southern and northern Weddell Sea (Kock et al. 2008; Riginella et al. 2014). Among bathydraconids, parental care was observed for the first time in *Cygnodraco mawsoni*, which was photographed directly on a nest assuming a typical defense posture (Ekau and Gutt 1991), as well as in *Gymnodraco acuticeps*, whose spawning behavior has been described in considerable detail (Evans et al. 2005). With our new observations, there are now about a dozen species of high-Antarctic notothenioids known to exhibit nesting or egg-guarding behavior. Therefore, with the exception of the few pelagic species that are likely broadcast spawners, this behavior may be a characteristic feature of many demersal notothenioids.

Comparison with previous studies and other areas

As reported in previous studies (Ekau and Gutt 1991; Gutt et al. 1994; Gutt and Ekau 1996), seabed photographic surveys are useful for documenting and describing demersal fish assemblages of the Weddell Sea, revealing differences in species composition and relative abundance among neighboring areas. In agreement with previous results, the fish assemblage of the shelf north of Halley Bay (including stations 007-1, 008-2 and 010-3) was by far the richest, in terms of both total fish abundance and number of species (Table 2). The fish assemblage was dominated by nototheniids (particularly *Trematomus scotti* and *T. lepidorhinus*), followed by channichthyids (*Chionodraco hamatus*) and bathydraconids (*Dolloidraco longedorsalis*). The Filchner Trough (station 072-4) was the second most populated area, consisting mainly of deep-water species such as bathydraconids and *Trematomus tokarevi*. Nevertheless, both diversity (Shannon) and species richness (Margalef) were lower in the Filchner Trough than in other areas, as individuals were unequally distributed among the species (Table 2). Finally, the wide and moderately deep continental shelf west of the Filchner Trough (including stations 026-3, 027-2 and 037-3) hosted a relatively poor fish community, in agreement with previous photographic surveys conducted in the southwestern Weddell Sea off Gould Bay and Vahsel Bay (Ekau and Gutt 1991).

Within the four groups of stations derived by the cluster analysis, the mean depth and the macrobenthic epifauna influenced the fish composition primarily at small spatial scales, providing food resources, protection from predators

or suitable breeding sites. Considering the most abundant species, *Trematomus lepidorhinus* and *Pagetopsis maculatus* preferred areas with biogenous debris and a rich epibenthic invertebrate fauna forming a three-dimensional habitat, which provided a suitable environment for settling or hiding. On the other hand, *Trematomus scotti* and *Dolloidraco longedorsalis* were recorded primarily in areas characterized by fine sediments with sparse gravels, where they were resting on and camouflaged by the substrate.

The relatively low values of correlation between the biotic fish-based station-similarity patterns and the selected environmental factors clearly indicate that several other parameters may play a role in determining species composition and distribution, all contributing to a more complex network of abiotic and biological interactions. Other factors like bottom temperature and food availability (Schwarzbach 1988; Ekau and Gutt 1991), or the impact of iceberg scouring (e.g. Brenner et al. 2001) may considerably affect fish distribution at small spatial scale in the Weddell Sea. In addition, the highly patchy distribution of benthic assemblages and substratum found along the transects did not allow to unambiguously determine their relationships with the local fish fauna.

Our photographic survey also provides further evidence that ice-rafted dropstones are important as sites of benthic diversity. In a photographic survey off the western Antarctic Peninsula at water depths of 437 to 724 m, Ziegler et al. (2017) found that although dropstones occupied < 1% of the total seafloor area surveyed, they contributed 20% of the megabenthic invertebrate species diversity. Ziegler et al. (2017) also captured images of the channichthyid *Chaenodraco wilsoni* guarding nests of eggs laid on dropstones. Notothenioids were also found in the vicinity of or directly on dropstones in many of our images. On the relatively barren seafloor characterizing outer shelf and upper slope environments, dropstones increase benthic habitat diversity by enhancing topographic heterogeneity and, when occupied by invertebrates, trophic complexity. Benthic notothenioids are frequently associated with dropstones, as these represent favorable habitats for feeding and hard substrates for nesting.

In terms of species composition and relative abundance, the demersal fish community of the southern Weddell Sea described in the present study closely resembled those reported from other areas, such as the Lazarev Sea (e.g. Gutt and Ekau 1996; Zimmermann 1997) and Ross Sea (Eastman and Hubold 1999; Donnelly et al. 2004). Therefore, as noted already by other authors (e.g. Andriashev 1965; DeWitt 1971), the benthic fish fauna of the Weddell Sea is a component of the East Antarctic or Greater Antarctic zoogeographical province.

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