



Aspects of the biology of the Antarctic dragonfish *Gerlachea australis* (Notothenioidei: Bathydraconidae) in the Weddell Sea, Antarctica

Mario La Mesa¹ · Federico Cali² · Fortunata Donato¹ · Emilio Riginella² · Carlotta Mazzoldi²

Received: 23 May 2017 / Revised: 13 December 2017 / Accepted: 16 December 2017
© Springer-Verlag GmbH Germany, part of Springer Nature 2017

Abstract

The Antarctic dragonfish *Gerlachea australis* is one of the most common bathydraconid species within the fish community of the Filchner Depression in the Weddell Sea. Nevertheless, several biological aspects of this species remain poorly known. The aim of this study was to provide new data on its population structure in terms of size, sex and age through sagittal otolith readings, as well as some reproductive traits based on macroscopic and histological analyses of gonads. The sex ratio in the sampled population was 1:1, with males being significantly smaller than females. Both sexes attained maximum age estimates of 14 years. Based on a von Bertalanffy growth model, females showed a higher asymptotic length than males at a comparable growth rate, thus reaching a higher growth performance. The spawning season was spread over a relatively long period, lasting at least from late December through late February. The reproductive effort in terms of fecundity and egg size diameter was similar to that of other bathydraconids, ranging from 739 to 1260 eggs/female and 3.2 mm after hydration, respectively. The fish size at first spawning (TL₅₀) was 18.5 and 22.5 cm in males and females, corresponding to 80% of their maximum size. *G. australis* exhibited a combination of life history traits found in other high-Antarctic notothenioids, such as long gametogenesis, large eggs associated with low fecundity, relatively rapid body growth until reaching a delayed sexual maturity, moderate longevity and maximum size, and overall low growth performance.

Keywords Bathydraconids · Age and growth · Reproductive biology · Weddell Sea

Introduction

Antarctic dragonfishes or bathydraconids are small benthic fishes endemic to the Southern Ocean, mainly distributed over the Antarctic continental shelf and slope, but also off the Antarctic and sub-Antarctic Islands (Gon 1990). The family Bathydraconidae includes 11 genera and 16 species (Eastman and Eakin 2000) of elongated, slender fishes occurring from shallow, inshore waters down to about 3000 m depth. Adult sizes range from 13 to 59 cm SL, although most are less than 25 cm (Eastman 1993). All genera in the family are morphologically well distinguished. Among the unique apomorphies, the genus *Gerlachea* is characterized by the presence of tubular scales in both dorsal and anal lateral

trunk lines (Balushkin and Voskoboinikova 1995). *Gerlachea australis* Dollo, 1900 is a monotypic, relatively rare species with a circum-Antarctic distribution. It is a bottom-dwelling fish, inhabiting the continental shelf between 200 and 670 m depth (Gon 1990). Although rare in general, at a regional scale this species is widely distributed on the southern shelf of the Weddell Sea, dominating the fish fauna of the Filchner Depression (Schwarzbach 1988; Ekau 1990).

Although sparse, most data on biological traits of *G. australis* have been reported from the Weddell Sea population. This species was frequently observed off Halley Bay and Gould/Vahsel Bay using underwater photography (Ekau and Gutt 1991). The area investigated was characterized by sandy sediment with small stones, scarcely populated by bryozoans, hydrozoans, sponges and ophiurids. Based on stomach content analysis, *G. australis* is predominantly a zooplankton feeder, relying in decreasing order of importance on euphausiids (*Euphausia crystallorophias*), hyperiids (*Hyperietta antarctica*), mysids and copepods (*Euchaeta* sp.), with no variation during the ontogeny (Kock et al. 1984; Schwarzbach 1988; Hubold and Ekau 1990). Length

✉ Mario La Mesa
m.lamesa@ismar.cnr.it

¹ CNR, Institute of Marine Sciences, UOS Ancona, Largo Fiera della Pesca 1, 60125 Ancona, Italy

² Department of Biology, University of Padova, Via U. Bassi 58/B, 35131 Padua, Italy

at sexual maturity is reached at 18–20 cm TL, corresponding approximately to 75% of maximum size (Kock et al. 1984; Duhamel et al. 1993). Based on a single specimen, total and relative fecundity of *G. australis* was estimated as 1143 oocytes/female and 20.8 oocytes/g, respectively (Duhamel et al. 1993). The lack of oil droplets and the large amount of yolk in oocytes, as well as the thickness of the chorion, suggests that eggs are benthic, as commonly found in other notothenioids (Kock and Kellermann 1991; Van der Molen and Matallanas 2003). The spawning period of *G. australis* is currently uncertain, likely occurring in late summer or in late winter–early spring (Duhamel et al. 1993; Van der Molen and Matallanas 2003).

Compared to other families of notothenioids, the life history traits of the small, deep living species of bathydraconids are still poorly known (Gon 1990), and only recently the biology of rare species of dragonfish, such as *Vomeridens infuscipinnis* (Khun et al. 2011), has received attention. Bottom trawling during two recent summer cruises carried out in the southern Weddell Sea provided a reasonable number of *G. australis*, representing the most abundant species of bathydraconids in total catches. The aim of the present study was to improve the current knowledge of this species, and provide more insight into the following life history traits: (1) reproductive biology, through the macroscopic and histological analyses of gonads and (2) population structure in terms of size, sex and age, through the microscopic analysis of annulation pattern in the sagittal otoliths.

Materials and methods

Field activities

Specimens of *G. australis* (Fig. 1) were collected by Agassiz trawl and bottom trawl during two summer expeditions of the RV *Polarstern* to the southern Weddell Sea (PS82, ANT-XXIX/9 in December 2013–March 2014; PS96, ANT-XXXI/2 in December 2015–February 2016). The main study area was located in front of the Filchner Ice Shelf in the southernmost part of the Weddell Sea (Fig. 2). The Agassiz



Fig. 1 Live specimen (male, 13.5 cm TL) of *Gerlachea australis* from the Weddell Sea collected during the PS96 *Polarstern* cruise

trawl (AGT) was equipped with 10-mm mesh in the cod end, and towed at 1 knot for 10–30 min, whereas the bottom trawl (BT) was equipped with 40-mm mesh in the cod end, and was towed at 3 knots for 30 min (Knust and Schröder 2014; Schröder 2016).

Fish were sorted, measured as total length (TL, 0.1 cm) and weighed as total body weight (TW, g). After dissection, each specimen was sexed and macroscopically staged according to the scale of gonad development reported for notothenioids (Kock and Kellermann 1991). Gonads were excised and weighed with a precision balance (GW, mg) and preserved in Dietrich solution (900 ml of distilled water, 450 ml of 95% ethanol, 150 ml of 40% formaldehyde and 30 ml of acetic acid) for further analyses. Sagittal otoliths were removed, cleaned and stored dry in vials.

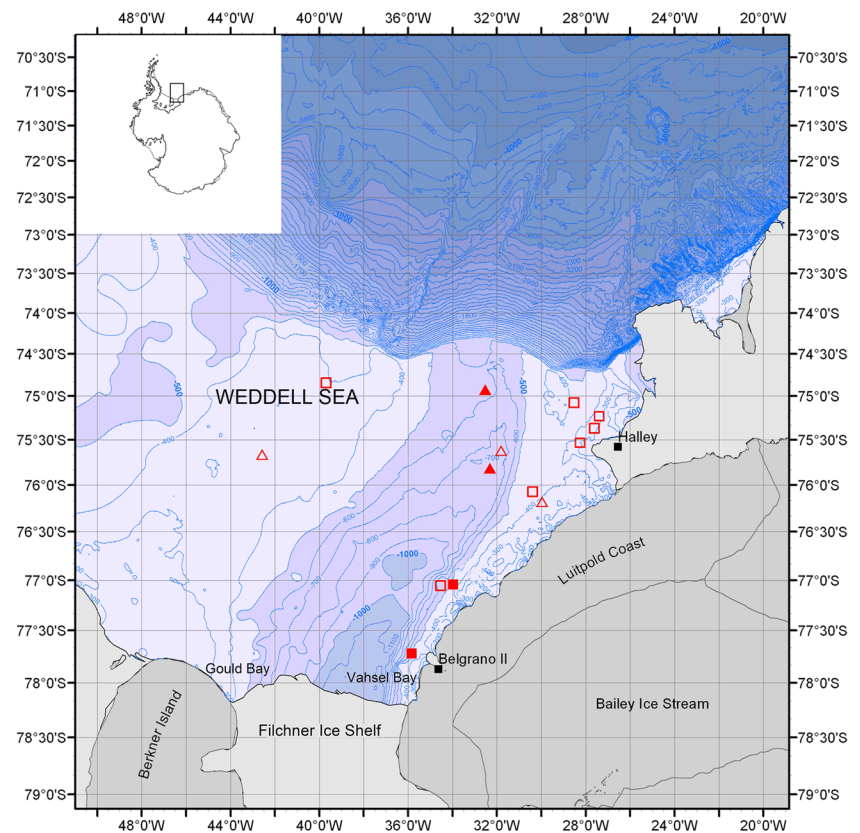
Laboratory activities

Paired ovaries were separated, and the left or right portion was randomly selected to estimate egg size and number at different stages of development. The selected portion was dissected and all oocytes were manually separated and soaked in a Petri dish. Oocytes were put under a stereomicroscope and photographed with a LEICA DFC 420 video camera. Pictures were then analysed using the LAS (Leica Application Suite) software to record number and size (μm) of oocytes. As gametogenesis in Antarctic fish is a biennial process (Kock and Kellermann 1991), only larger oocytes ($> 750 \mu\text{m}$) were considered to be spawned in the current season and counted to estimate individual fecundity.

To better define the stage of gonad development, histological analyses were carried out for most specimens of both sexes (28 females and 29 males). Following a standard protocol, gonads were dehydrated through increasing concentrations of ethanol and embedded in paraplast. Serial transverse sections ($7 \mu\text{m}$ thick) were obtained using a microtome, mounted on slides and stained with Harrys' haematoxylin and eosin (Pearse 1985). Histological sections were examined under a light microscope (Leica DM4000B) at $\times 5$ – 100 magnification. Based on cell structure and morphology, ovaries and testes were classified into five phases of development (Brown-Peterson et al. 2011). As notothenioids generally exhibit group synchronous ovaries (sensu Wallace and Selman 1981), each specimen was staged based on the most advanced stage of development observed in the gonad sections.

As commonly found in notothenioids (e.g. White 1991), sagittal otoliths of *G. australis* had a dense and opaque calcareous structure, thus needed to be sectioned to reveal the annulation pattern. Either right or left otolith from each specimen was randomly selected, burned in an oven at 350°C and embedded into Crystalbond resin on glass slides. Transverse sections were obtained by grinding and

Fig. 2 Map of the south-western Weddell Sea, showing positive sampling stations for *Gerlachea australis* made by Agassiz trawl (PS 82, filled squares; PS 96, filled triangles) and bottom trawl (PS 82, squares; PS 96, triangles) and the scientific Bases (small filled squares)



polishing procedures in order to improve readability of presumed annual rings from the core to otolith margin. Sections were soaked in fresh water to enhance the contrast between translucent and opaque zones and analysed under reflected light using a Leica M205C stereomicroscope at $\times 25$ – 80 . Individual age was estimated by counting annuli formed by contiguous translucent and opaque zones assumed to be deposited once a year. Each otolith was read twice by an experienced reader (MLM) and the mean value taken as individual age estimate. If blind readings differed by more than one year, a third reading was performed.

Data processing

The size–frequency distributions of sexes were compared by applying a Kolmogorov–Smirnov two-sample test. Departure from the expected 1:1 sex ratio was tested using a χ^2 goodness-of-fit test. The length–weight relationship was estimated for each sex through the exponential function $TW = aTL^b$, where TW is the total body weight (g) and TL is the total length (cm). Isometric growth (i.e. $b = 3$) departure was tested using a t test applied to the equation $t = (b - 3) SE^{-1}$, where SE is the standard error of b . The allometric indices (b) calculated for males and females were compared by applying an F test.

As a measure of reproductive investment, the gonadosomatic index (GSI) was calculated for each specimen as the percentage of gonad weight (GW) to total body weight (TW). Following the gravimetric method (Murua et al. 2003), total fecundity (F_{tot}) was estimated as the product of total gonad weight and oocyte density. Oocyte density was the number of oocytes in advanced vitellogenesis (i.e. those larger than $750 \mu m$) per gram of ovarian tissue. Relative fecundity (F_{rel}) was calculated as the number of oocytes per gram of total body weight (Witthames et al. 2009). Length at first spawning (sensu Kock 1989) was assessed for the whole population by fitting a logistic model to the proportion of specimens at gonad developmental phases 3–5 per size class, with TL_{50} representing the total body length at which 50% of population attain first spawning.

The precision of otolith readings was estimated by calculating the average percentage error (APE) and the coefficient of variation (CV) (Beamish and Fournier 1981; Chang 1982). The body growth for each sex and for the whole population was modelled by applying the von Bertalanffy growth function to the age–length data pairs, and estimated parameters compared using a likelihood ratio test (Kimura 1980). A growth performance index ($\Phi' = 2 \log L_{\infty} + \log k$) (Pauly and Munro 1984) was used to compare this species with other notothenioids. Fish length-at-age data estimated for each sex were compared

by applying a *t* test for paired comparison. Lacking a validation, however, age estimates have to be regarded as putative.

Statistical analyses were performed using the PAleontological STatistics (PAST, version 3.14) software (Hammer et al. 2001), which uses the Levenberg–Marquardt optimization for non-linear least squares parameter estimation. All tests were applied according to Sokal and Rohlf (1995).

Results

Fish samples

Overall, samples of *G. australis* consisted of 32 females (14–28 cm TL, 6–88 g TW), 32 males (13.5–22 cm TL, 5–34 g TW) and a single unsexed juvenile (11.5 cm TL, 2 g TW). Fish were collected by bottom and Agassiz trawls from 14 stations located in the south-eastern Weddell Sea, over a depth range of 372–763 m (Fig. 2; Table 1).

The length–frequency distribution (LFD) of *G. australis* sampled in the Weddell Sea was roughly unimodal, with a modal size of 21 cm TL (Fig. 3). LFDs differed significantly between sexes (Kolmogorov–Smirnov test, $p < 0.01$), with females attaining larger size than males. The length–weight relationships estimated for males and females are set out in Fig. 4. Both sexes exhibited positive allometric growth (*t* test, $t = 5.78$, $df = 30$, $p < 0.01$, males; $t = 4.65$, $df = 30$, $p < 0.01$, females), with no difference between the isometric parameters *b* (*F* test, $F_{1,60} = 0.03$, $p > 0.5$). Sex ratio did not differ from 1:1 (goodness-of-fit test, $\chi^2 = 0$, $p = 1$).

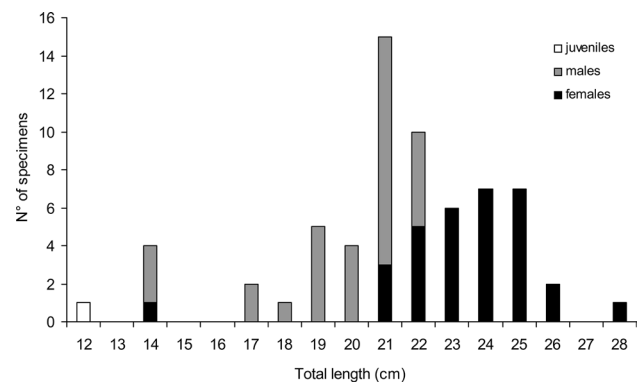


Fig. 3 Length–frequency distribution of *Gerlachea australis* collected in the Weddell Sea during summer *Polarstern* cruises PS 82 and PS 96

Reproductive cycle

Macroscopic and histological gonad developmental phases were individually assigned and compared to each other. Gonad developmental phases were generally underestimated by the macroscopic determination, though 40% of specimens completely matched. Nevertheless, the presence of four out of five developmental phases enabled almost the whole gonad cycle and gametogenesis for both sexes to be described.

Females had paired, often asymmetric ovaries fused posteriorly to form the oviduct. Ovaries followed a group synchronous development, consisting of larger oocytes in spawning condition during the current breeding season (determined fecundity), and more numerous smaller oocytes stored as a reserve for future breeding seasons. A distinct bimodal size–frequency distribution of oocytes was

Table 1 Sampling data of *Gerlachea australis* collected during PS82 and PS96 *Polarstern* summer cruises in the southern Weddell Sea

Station	Lat (S)	Long (W)	Date	Gear	Depth (m)	Specimen
PS82/018-1	75° 12.03′	27° 32.56′	04/01/2014	BT	391	1
PS82/039-1	76° 06.16′	30° 18.80′	07/01/2014	BT	453	3
PS82/073-1	77° 00.28′	34° 09.34′	11/01/2014	AGT	570	18
PS82/078-1	77° 01.25′	34° 26.47′	12/01/2014	BT	699	2
PS82/097-1	77° 43.45′	35° 58.84′	15/01/2014	AGT	572	2
PS82/129-1	75° 21.47′	27° 44.57′	20/01/2014	BT	372	9
PS82/244-1	74° 48.94′	39° 42.21′	02/02/2014	BT	415	3
PS82/296-1	75° 32.06′	28° 42.84′	08/02/2014	BT	396	3
PS82/306-1	75° 06.95′	28° 45.01′	09/02/2014	BT	422	4
PS96/016-3	74° 56.77′	32° 27.85′	04/01/2016	AGT	623	8
PS96/039-1	75° 40.49′	42° 27.79′	17/01/2016	BT	388	1
PS96/059-2	76° 11.16′	30° 02.90′	21/01/2016	BT	395	1
PS96/072-1	75° 51.23′	32° 22.91′	23/01/2016	AGT	748	6
PS96/073-3	75° 38.83′	31° 54.75′	24/01/2016	BT	763	4

BT bottom trawl, AGT Agassiz trawl

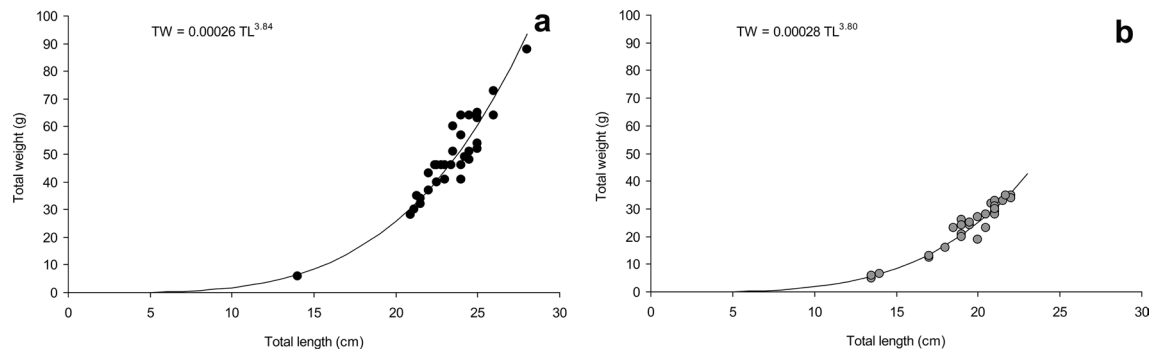


Fig. 4 Length–weight relationships of *Gerlachea australis* females (**a**) and males (**b**) collected in the Weddell Sea during summer *Polarstern* cruises PS 82 and PS 96

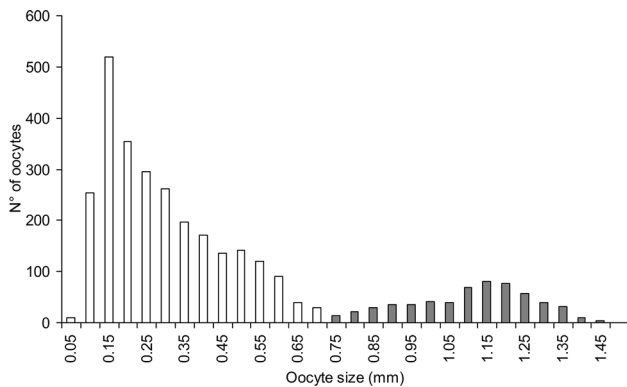


Fig. 5 Size–frequency distribution of oocytes within the ovaries of a spawning capable female (24.5 cm TL) of *Gerlachea australis*, showing previtellogenic (white bars) and vitellogenic (grey bars) oocytes separated by a threshold size of 0.75 mm

observed in specimens at stage 3 of gonad development (i.e. developing females), separated from each other by a “threshold” size of approximately 750 μm . Based on the histological analysis, the larger oocytes (> 750 μm) were in advanced vitellogenesis, whereas the smaller ones (< 750 μm) were in a pre- or early vitellogenic stage (Fig. 5). According to the classification scheme described by Brown-Peterson et al. (2011), females were found in the following phases of gonad development.

1. Immature (never spawned): small ovaries with a thin wall, ovigerous lamellae filled with oogonia and primary growth (Pg) oocytes (at chromatin nucleolar and perinucleolar stages) smaller than 100 μm (Fig. 6a).
2. Developing (ovaries beginning to develop): enlarging ovaries, consisting of smaller oocytes at primary growth phase and cortical alveoli oocytes (Ca) as large as 200–650 μm (Fig. 6b); Ca oocytes are characterized by large nucleus with small nucleoli located at its periphery, and by an eosinophilic cytoplasm, with a granular appear-

ance in the perinuclear and cortical zone and a conspicuous presence of chromophobic vesicles (cortical alveoli) in the middle; the cytoplasm is surrounded by the zona radiata and a thick granulosa cell layer (Fig. 6c); some atretic oocytes were occasionally present.

3. Spawning capable (female able to spawn within the current reproductive cycle): large ovaries, filling most of abdominal cavity; presence of Pg and Ca oocytes, but most volume is occupied by oocytes at different stages of vitellogenesis (Vtg 1, 2 and 3) (Fig. 6d); larger oocytes (700–1200 μm) undergo coalescence of yolk granules, as well as germinal vesicle migration and breakdown (Fig. 6e).
4. Regressing (cessation of spawning): flaccid ovaries with a thick ovarian wall, consisting of many post-ovulatory follicles (POFs) in varying stages of degeneration, Pg and Ca oocytes, and a few atretic oocytes (Fig. 6f).
5. Regenerating (sexually mature, reproductively inactive): not present.

Males had paired elongated testes posteriorly fused in the sperm duct, with a cystic lobular structure associated to the unrestricted spermatogonial type (sensu Grier et al. 1980), being spermatogonia distributed randomly along the lobules. According to Brown-Peterson et al. (2011), males were found in the following phases of gonad development.

1. Immature (never spawned): small testes, consisting of interstitial connective tissue and lobules without an evident lumen, filled with cysts containing exclusively spermatogonia (Sg); the spermatogenic activity is restricted to a few sparse spermatogonial mitotic divisions (Fig. 7a).
2. Developing (testes beginning to develop): testes increased in size, evident spermatocysts along the lobules containing mainly spermatogonia, and a few scattered spermatocytes (Sc) and spermatids (St); lumen

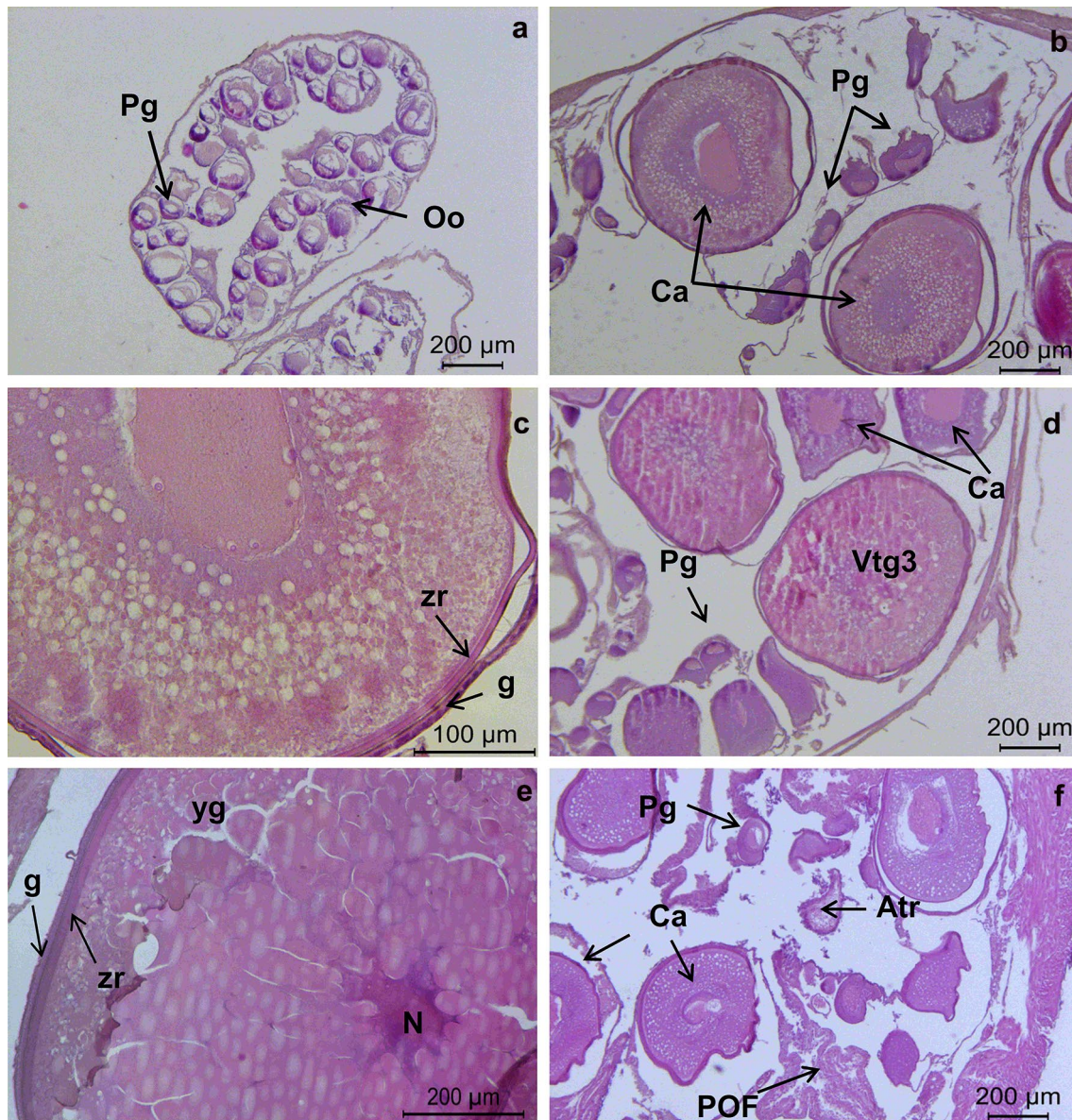


Fig. 6 Histological sections of ovaries of *Gerlachea australis* at different developmental phases: **a** immature; **b** and **c** developing; **d** and **e** spawning capable; **f** regressing. Abbreviations: *Oo* oogonia, *Pg* pri-

mary growth, *Ca* cortical alveoli, *Vtg 3* tertiary vitellogenic oocyte, *POF* post-ovulatory follicles, *Atr* atresia, *N* nucleus, *yg* yolk granules, *zr* zona radiata, *g* granulosa layer

of lobules and sperm duct devoid of spermatozoa (Sz) (Fig. 7b).

3. Spawning capable (male able to spawn within the current reproductive cycle): testes large and firm, lumen of lobules and sperm duct completely filled with spermatozoa; a few scattered cysts of spermatids and cysts of spermatogonia located exclusively at the periphery of the testis (Fig. 7c).
4. Regressing (cessation of spawning): small and flaccid testes, residual spermatozoa are mainly present in the sperm duct and in the lumen of lobules in proximity of the sperm duct; presence of few scattered spermatocysts

and great amount of connective tissue within lobules, lumen of lobules of decreasing size (Fig. 7d).

5. Regenerating (sexually mature, reproductively inactive): not present

Reproductive investment

The reproductive investment in terms of GSI was calculated for both sexes within each phase of gonad development (Fig. 8). The GSI was consistently larger in females than in males. In both sexes, GSI increased until gonad maturity and declined afterwards. In females, total

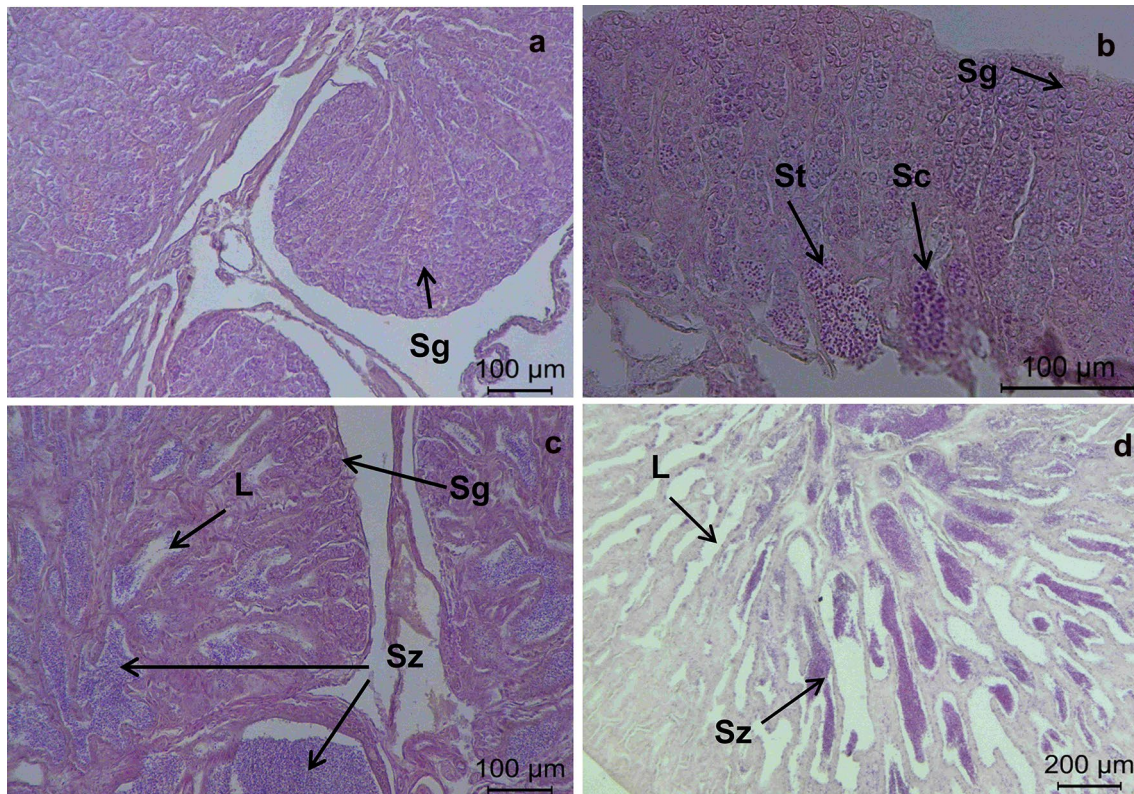


Fig. 7 Histological sections of testes of *Gerlachea australis* at different developmental phases: **a** immature; **b** developing; **c** spawning capable; **d** regressing. Abbreviations: Sg, primary spermatogonia; St, spermatid; Sc, spermatocyte; Sz, spermatozoa; L, lumen of lobule

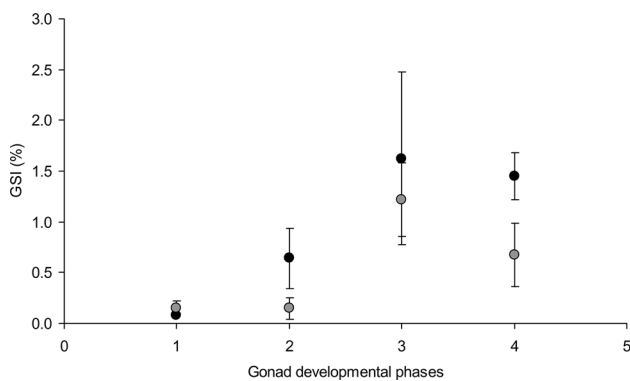


Fig. 8 Gonadosomatic index (GSI, mean \pm SD) in females (black dots) and males (grey dots) of *Gerlachea australis* at different developmental phases

fecundity ranged between 739 and 1260 eggs/female (mean \pm SD, 1026 ± 194 , $n = 8$), whereas relative fecundity ranged between 8.4 and 21.3 eggs/g (16.5 ± 4.2 , $n = 8$). No significant relationship was found between total and relative fecundity and fish size ($r^2 = 0.19$, $p > 0.1$; $r^2 = 0.02$, $p > 0.5$). The maximum size of yolked oocytes

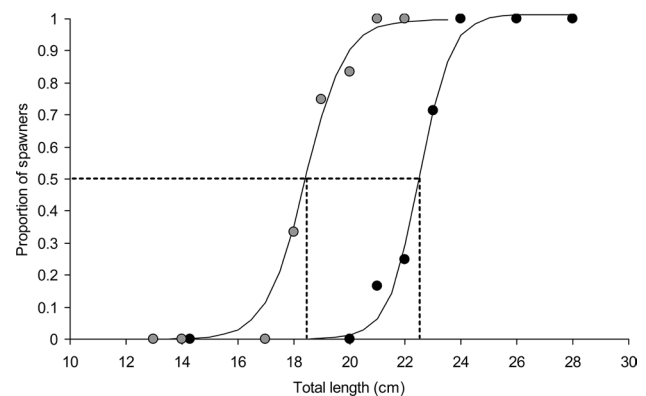


Fig. 9 Logistic curves fitted to the proportion of spawners in females (black dots) and males (grey dots) of *Gerlachea australis*; dotted lines indicate the length at first spawning (TL_{50})

ranged between 1.1 and 1.7 mm (mean \pm SD, 1.4 ± 0.2). A single hydrated oocyte found in a regressing female measured 3.2 mm. Based on the logistic curves fitted to the proportion of spawners in relation to fish size (Fig. 9), the length at first spawning was 18.5 and 22.5 cm for males and females, respectively.

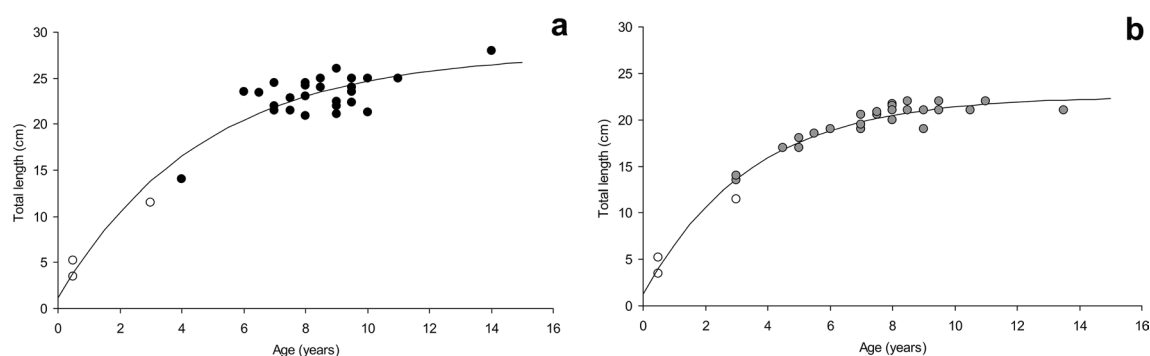


Fig. 10 von Bertalanffy growth curves estimated for females (**a**) and males (**b**) of *Gerlachea australis*; empty dots indicate juvenile specimens

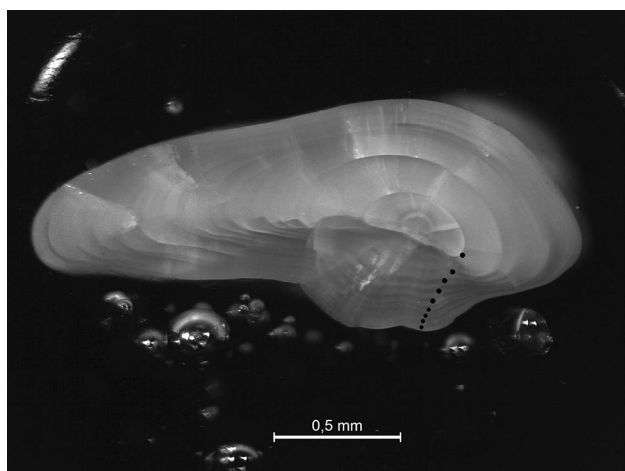


Fig. 11 Transverse otolith section from a 9-year-old specimen (female, 22 cm TL) of *Gerlachea australis*, showing the annulation pattern (black dots)

Age structure and growth

All available fish samples were successfully aged. Indices of age precision were both relatively low ($CV = 3.1\%$; $APE = 2.2\%$), indicating a good consistency between repeated readings (Campana 2001). The von Bertalanffy growth curves were fitted to age–length data for each sex and the whole population (Fig. 10). To improve the fit, two six-month-old juvenile fishes collected in February in the

Weddell Sea were added to adult samples, assuming that they hatched approximately in late winter or spring (Kellermann 1990). The age range was similar between sexes, with a maximum age estimate of 14 years in females (Fig. 11). The von Bertalanffy growth parameters (L_∞ , k , t_0) and the growth performance index (Φ') are set out in Table 2. Based on a likelihood ratio test, the growth curves estimated for males and females differed significantly from each other when comparing all parameters pooled together, or the asymptotic length (L_∞) (Table 3). Consistently, the fish length-at-age derived from the von Bertalanffy growth model differed between sexes (t test for paired comparison, $t = 4.66$, $df = 14$, $p < 0.01$), with an annual growth over the estimated age range between 0.1 and 5.4 cm and 0.3–5.1 cm in males and females, respectively (Table 4).

Discussion

Previous investigations on demersal fish fauna of the Weddell Sea were carried out along the eastern shelf between 70 and 78°S, from Atka Bay to Gould Bay (e.g. Schwarzbach 1988, Ekau 1990). Cold deep waters characterizing the Filchner Depression hosted a different fish fauna compared to the eastern and southern shelves of the Weddell Sea, being dominated by the bathydraconids *G. australis* and *Akarotaxis nudiceps*, whereas notothenioids were rare. Previous catches of *G. australis* consisted of individuals ranging from 13 to 24 cm SL collected within a wide depth

Table 2 The von Bertalanffy growth parameters (L_∞ , k , t_0) estimated for *Gerlachea australis* collected in the Weddell Sea

Parameter	Females		Males		Population	
	Value	CI	Value	CI	Value	CI
L_∞	27.75	1.01	22.53	0.58	25.47	0.60
k	0.21	0.02	0.29	0.03	0.24	0.02
t_0	− 0.20		− 0.18		− 0.19	
Φ'	2.21		2.17		2.19	

Φ' growth performance index, CI 5% confidence interval

Table 3 Likelihood ratio test comparing the von Bertalanffy growth parameters estimates for both sexes of *Gerlachea australis*

Parameter	Females			Males			RSS	χ^2	df	p
	L_{∞}	k	t_0	L_{∞}	k	t_0				
Hypothesis										
Independent	27.75	0.21	− 0.20	22.53	0.29	− 0.18	116.93			
$H_0\colon L_{\infty}; = k; = t_0$	25.76	0.23	− 0.24	25.76	0.23	− 0.24	224.74	43.12	3	**
$H_0\colon L_{\infty}$	25.90	0.27	− 0.05	25.90	0.18	− 0.72	139.42	11.61	1	**
$H_0\colon k$	26.62	0.25	− 0.08	23.35	0.25	− 0.37	120.82	2.16	1	ns
$H_0\colon t_0$	27.74	0.22	− 0.19	22.54	0.29	− 0.19	116.92	0.002	1	ns

Statistics are based on four null hypotheses, assuming that each parameter or all of them do not differ between sexes

RSS residual sum of squares, df degrees of freedom, ns not significant

** Significant at $\alpha = 0.01$

Table 4 Fish length-at-age derived from the von Bertalanffy growth model for both sexes of *Gerlachea australis*

Age class (years)	Females		Males	
	Total length (cm)	Annual growth (cm)	Total length (cm)	Annual growth (cm)
0	1.2		1.2	
1	6.3	5.1	6.6	5.4
2	10.5	4.1	10.6	4.0
3	13.8	3.3	13.6	3.0
4	16.5	2.7	15.9	2.2
5	18.7	2.2	17.6	1.7
6	20.4	1.8	18.8	1.3
7	21.9	1.4	19.7	0.9
8	23.0	1.1	20.5	0.7
9	23.9	0.9	21.0	0.5
10	24.7	0.7	21.4	0.4
11	25.3	0.6	21.7	0.3
12	25.7	0.5	21.9	0.2
13	26.1	0.4	22.0	0.2
14	26.4	0.3	22.2	0.1

range (430–840 m) by Schwarzbach (1988), closely resembling size composition and sampling depth of our samples.

Although sampling activities were restricted to the austral summer, present data enable us to assess the reproductive strategies of *G. australis*. The bimodal size–frequency distributions of oocytes and the lack of post-ovulatory follicles in the histological sections of ovaries of pre-spawning females support the hypothesis of a determinate fecundity pattern. This further supports the contention that eggs are individually released within a single spawning event during the reproductive cycle (i.e. total spawner). Nevertheless, the presence of simultaneous spawning capable and regressing individuals indicates a low degree of synchronization among individual spawning periods,

suggesting an extended spawning season at the population level.

Considering the different developmental stages of oocytes found in regressing ovaries, the presence of cortical alveolar oocytes as part of the smallest cohort for the next breeding season is consistent with prolonged gametogenesis in Antarctic fish. Compared to the GSI at spawning reported for other notothenioids (Kock and Kellermann 1991), the GSI calculated for *G. australis* was relatively low, especially for females. This was likely due to the lack of actively spawning females undergoing final oocyte hydration in our samples, a process which determines a remarkable increase of egg size (doubled in our case, namely from 1.7 to 3.2 mm) and consequently of GSI before ovulation.

Our results indicated that spawning of *G. australis* in the Weddell Sea takes place in summer, lasting from late December to late February, in agreement with a previous study from the same area (Van der Molen and Matallanas 2003). Based on larval appearance and length–frequency distribution through time, hatching is likely to occur in late winter (Hubold 1990, Kellermann 1990). The incubation period of eggs therefore would last approximately 5–6 months, consistent with the relatively large egg size and low water temperature in the Filchner Depression. A single estimate of total and relative fecundity evaluated in a previous study (Duhamel et al. 1993) falls within the range estimated in the present study, and are comparable to other bathydraconids of similar size inhabiting the High-Antarctic Zone, such as *Racovitzia glacialis* and *Bathydraco marri* (Kock 1992). Comparing the length at first spawning and the maximum asymptotic size derived from the von Bertalanffy growth model, *G. australis* spawn for the first time at approximately 80% of their maximum size, which is at the upper end of values recorded in notothenioids (Kock and Kellermann 1991).

Sexual dimorphism in size was found in *G. australis*, with females significantly larger than males. Both sexes exhibited positive allometric growth, as commonly found

in notothenioid fishes from the Weddell Sea (Artigues et al. 2003). Fish ageing using sagittal otoliths has proven to be a reliable method in this species, as indicated by the low values of indices of precision (Campana 2001). Compared with other notothenioid families inhabiting the High-Antarctic Zone (La Mesa and Vacchi 2001), *G. australis* grew somewhat more rapidly at a moderate size and showed a moderate longevity, reaching a maximum estimated age of about 14 years. Consistent with the observed sexual dimorphism in size, the estimated growth curves differed significantly between sexes, as females reached a higher asymptotic length than males at comparable growth rates. As a result, growth performance was higher in females than in males.

The comparison of the index of growth performance calculated for the whole population of *G. australis* with those reported for other bathydraconids distributed in the Seasonal Pack-ice and in the Ice-free Zones, such as *Parachaenichthys charcoti* and *P. georgianus*, revealed an inverse latitudinal trend, being 2.33 and 2.53, respectively (La Mesa et al. 2012). This was consistent with the water temperature gradient experienced by these species in the relevant areas of distribution, increasing from the Weddell Sea (*G. australis*) to the southern Scotia Arc (*P. charcoti*) to South Georgia (*P. georgianus*).

In conclusion, the Antarctic dragonfish *G. australis* exhibit most of the life history traits commonly described for high-Antarctic notothenioids, such as long gametogenesis, large eggs associated with low fecundity, long egg incubation period, relatively rapid body growth until reaching a delayed sexual maturity, moderate longevity and maximum size, as well as low growth performance.

Acknowledgments We wish to thank all of the crew members and personnel aboard the R/V *Polarstern* on the PS 82 and PS 96 cruises, for their valuable support during field samplings activities and special thanks to all the fish teams involved in fish sorting aboard the vessel. We are particularly grateful to Christopher D. Jones for editing the early draft of the manuscript, as well as three anonymous reviewers for their useful comments. This work was financially supported by the Programma Nazionale di Ricerche in Antartide (PNRA).

Funding Funding was provided by Progetto di Ricerca 2013/C1.07.

References

- Artigues B, Morales-Nin B, Balguerías E (2003) Fish length-weight relationships in the Weddell Sea and Bransfield Strait. *Polar Biol* 26:463–467
- Balushkin AV, Voskoboinikova OS (1995) Systematics and phylogeny of antarctic dragonfishes (Bathydraconidae, Notothenioidei, Perciformes). *J Ichthyol* 35:89–104
- Beamish RJ, Fournier DA (1981) A method of comparing the precision of a set of age determinations. *Can J Fish Aquat Sci* 38:982–983
- Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK (2011) A standardized terminology for describing reproductive development in fishes. *Mar Coast Fish* 3:52–70
- Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J Fish Biol* 59:197–242
- Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. *Can J Fish Aquat Sci* 39:1208–1210
- Duhamel G, Kock K-H, Balguerías E, Hureau J-C (1993) Reproduction in fish of the Weddell Sea. *Polar Biol* 13:193–200
- Eastman JT (1993) Antarctic fish biology: evolution in a unique environment. Academic Press, San Diego
- Eastman JT, Eakin RR (2000) An updated species list for notothenioid fish (Perciformes; Notothenioidei), with comments on Antarctic species. *Arch Fish Mar Res* 48:11–20
- Ekau W (1990) Demersal fish fauna of the Weddell Sea, Antarctica. *Antarct Sci* 2:129–137
- Ekau W, Gutt J (1991) Notothenioid fishes from the Weddell Sea and their habitat, observed by underwater photography and television. *Proc NIPR Symp Polar Biol* 4:36–49
- Gon O (1990) Bathydraconidae. In: Gon O, Heemstra PC (eds) Fishes of the southern ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp 364–380
- Grier HJ, Linton JR, Leatherland JF, De Vlaming VL (1980) Structural evidence for two different testicular types in teleost fishes. *Am J Anat* 159:331–345
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontol Electron* 4:1–9
- Hubold G (1990) Seasonal patterns of ichthyoplankton distribution and abundance in the southern Weddell Sea. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer, Berlin, pp 149–158
- Hubold G, Ekau W (1990) Feeding patterns of post-larval and juvenile notothenioids in the southern Weddell Sea (Antarctica). *Polar Biol* 10:255–260
- Kellermann A (1990) Catalogue of early life stages of Antarctic notothenioid fish. *Ber Polarforsch* 67:45–136
- Khun KL, Near TJ, Detrich HW III, Eastman JT (2011) Biology of the Antarctic dragonfish *Vomeridens infuscipinnis* (Notothenioidei: Bathydraconidae). *Antarct Sci* 23:18–26
- Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. *Fish Bull* 77:765–776
- Knust R, Schröder M (2014) The expedition PS82 of the research vessel *Polarstern* to the southern Weddell Sea in 2013/2014. *Ber Polar- Meeresforsch* 680:1–155
- Kock K-H (1989) Reproduction in fish around Elephant Island. *Arch FischWiss* 39:171–210
- Kock K-H (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge
- Kock K-H, Kellermann A (1991) Reproduction in Antarctic notothenioid fish. *Antarct Sci* 3:125–150
- Kock K-H, Schneppenheim R, Siegel V (1984) A contribution to the fish fauna of the Weddell Sea. *Arch FischWiss* 34:103–120
- La Mesa M, Vacchi M (2001) Review: age and growth of high Antarctic notothenioid fish. *Antarctic Sci* 13:227–235
- La Mesa M, Catalano B, Kock K-H, Jones CD (2012) Age and growth of the Antarctic dragonfish *Parachaenichthys charcoti* (Pisces, Bathydraconidae) from the southern Scotia Arc. *Polar Biol* 35:1545–1553
- Murua H, Kraus G, Saborido-Rey F, Witthames PR, Thorsen A, Junquera S (2003) Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *J Northwest Atl Fish Sci* 33:33–54
- Pauly D, Munro JL (1984) Once more on the comparison of growth in fish and invertebrates. *Fishbyte* 2:21

- Pearse AGE (1985) Histochemistry. Theoretical and applied analytical technology. Churchill Livingstone, Edinburgh
- Schröder M (2016) The expedition PS96 of the research vessel Polarstern to the southern Weddell Sea in 2015/2016. Ber Polar- Meeresforsch 700:1–142
- Schwarzbach W (1988) The demersal fish fauna of the eastern and southern Weddell Sea: geographical distribution, feeding of fishes and their trophic position in the food web. Ber Polarforsch 54:1–93
- Sokal RR, Rohlf FJ (1995) Biometry. The principle and practice of statistics in biological research. Freeman, San Francisco
- Van der Molen S, Matallanas J (2003) Oocyte development and maturity classification of *Gerlachea australis* from the Weddell Sea, Antarctica. Polar Biol 26:653–658
- Wallace RA, Selman K (1981) Cellular and dynamic aspects of oocyte growth in teleosts. Am Zool 21:325–343
- White MG (1991) Age determination in Antarctic fish. In: Di Prisco G, Maresca B, Tota B (eds) Biology of Antarctic fish. Springer, Berlin, pp 87–100
- Witthames PR, Thorsen A, Murua H, Saborido-Rey F, Greenwood LN, Dominguez R, Korta M, Kjesbu OS (2009) Advances in methods for determining fecundity: application of the new methods to some marine fishes. Fish Bull 107:148–164