



# Biological parameters of the High-Antarctic icefish, *Cryodraco antarcticus* (Channichthyidae) from the South Shetland Islands

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## Abstract

Despite their wide distribution around the Antarctic continent, the life strategies of the long-fingered icefish *Cryodraco antarcticus* have been rarely investigated and are not well understood. The aim of this paper was to provide more insights on the demographic characteristics of the population living off the South Shetland Islands, focusing attention on key biological traits such as age and growth and the reproductive cycle. Individual age and reproductive status were assessed through the microstructural analyses of sagittal otoliths and histological analysis of gonads, respectively. The sex-balanced sampled population consisted of juvenile and adult fishes covering a wide size range. Both sexes had positive allometric growth, although males exhibited smaller maximum size and lower body condition than females. Fish longevity was comparable between sexes, being 16 and 18 years in males and females, respectively. Applying the von Bertalanffy growth model to length-at-age estimates, males consistently reached lower maximum asymptotic size at a faster rate than females. Based on the gametogenic process, the spawning period was inferred to occur from late summer to early autumn. As commonly found in icefishes, females devoted a great investment to reproduction as gonadosomatic index, egg size, and fecundity. A single female (62 cm TL) spawned about 7730 eggs as large as 3–4 mm. Considering also the results of previous studies conducted in other areas, this species is characterized by a long-lasting pelagic juvenile phase and adults share similar life strategies across the range of their spatial distribution, suggesting the possibility of a single panmictic circum-Antarctic population.

**Keywords** Channichthyid · Population structure · Age · Reproduction

## Introduction

Icefishes (family Channichthyidae) are unique among vertebrates, expressing no oxygen-binding pigments in their blood cells. To compensate for the lack of haemoglobin, channichthyids evolved a suite of physiological adaptations, including a low metabolic rate, increased blood volume and cardiac output, cutaneous uptake of oxygen, increased blood flow with low viscosity, enlarged capillaries, large heart, and increased skin vascularity (Kock 2005). The family Channichthyidae consists of 11 genera and 15 primarily demersal species, which are endemic to the Southern Ocean, except for one species (*Champscephalus esox*), which occurs in the southern Patagonian shelf, in Magellan Strait and in the Beagle Channel (Iwami and Kock 1990). Some icefishes were abundant enough to be exploited by commercial fisheries in the 1970s and 1980s, as the main target species (*Champscephalus gunnari*, *Chaenodraco wilsoni*) or bycatch (*Chaenocephalus aceratus*, *Pseudochaenichthys georgianus* and *Chionodraco rastrispinosus*) (Kock 1992).

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Among channichthyids, the genus *Cryodraco* is currently composed of two species. The long fingered icefish *Cryodraco antarcticus* was initially described by Dollo (1900), from an individual collected during the Belgian Antarctic Expedition in the Bellingshausen Sea. A second species, *Cryodraco pappenheimi* (Regan 1913), previously described as *Pagetodes antarcticus* (Pappenheim 1912), was later considered a junior synonym of *Cryodraco antarcticus* (Norman 1938; Iwami and Kock 1990). *Cryodraco atkinsoni* Regan, 1914, which has long been regarded as a junior synonym of *Cryodraco antarcticus* (Waite 1916; Norman 1938), has been recently recognized as a valid species based on morphological and meristic characters (La Mesa et al. 2002) and genetic analyses (Dornburg et al. 2016). Several phenotypic features differ between the two species, including the presence of a rostral spine on the snout, blotching patterns and fin ray counts. In addition, *C. antarcticus* is widespread all around the Antarctic Continent, while *C. atkinsoni* is largely confined to the East Antarctic Zoogeographic Province (La Mesa et al. 2002).

Despite their wide distribution, information on the main biological aspects of *C. antarcticus* are still very limited (as reviewed in Kock and Jones 2002 and references therein). Around the South Shetland and South Orkney Islands, which represent the northernmost areas of their geographical distribution, *C. antarcticus* is regularly caught over a wide depth range (300–800 m), with average biomass densities of 230 and 100 kg/nm<sup>2</sup>, respectively. Interestingly, the individuals caught around the South Orkney Islands are primarily juveniles, whereas the population collected off the South Shetland Islands consist of juvenile and adult fishes in equal numbers (Kock and Jones 2002). Spawning occurs over a short period, lasting from about mid-March to the end of April. At spawning, mature females produce large eggs (4.2–4.4 mm), attaining a gonado-somatic index (GSI) of 20–28%. Potential and relative fecundities fall within the range observed in other species of channichthyids, being approximately between 5,000–25,000 eggs/female and 7–20 eggs/g, respectively (Kock and Jones 2002).

After an egg incubation period lasting 4 months, larvae of *C. antarcticus* likely hatch in late winter. Off the South Shetland Islands, larvae and postlarvae are commonly found in pelagic waters in spring and summer, completing transformation to the juvenile stage in early autumn (Kellermann 1990). Early juveniles from 8–10 to 20–22 cm standard length (SL), corresponding to 1–2 year old fish, are rarely caught by bottom trawls, as they are still pelagic and rely on a diet of krill, mysids and fish larvae. From a size of 30–35 cm onwards, *C. antarcticus* become progressively more sedentary, being often found close to the bottom waiting for fish prey or occasionally in midwater layers feeding on krill (Takahashi and Iwami 1997).

The aim of the present study was to characterize the life strategies of *C. antarcticus* on the shelves of the South Shetland Islands, focusing attention on age structure and growth rate estimation through the analysis of sagittal otoliths microstructure. Demographic characteristics of the population in terms of fish size and weight, condition, sex ratio and reproductive status through the histological analyses of gonads are provided from samples collected during several bottom trawl surveys spanning a decade, from 2002 to 2012.

## Materials and methods

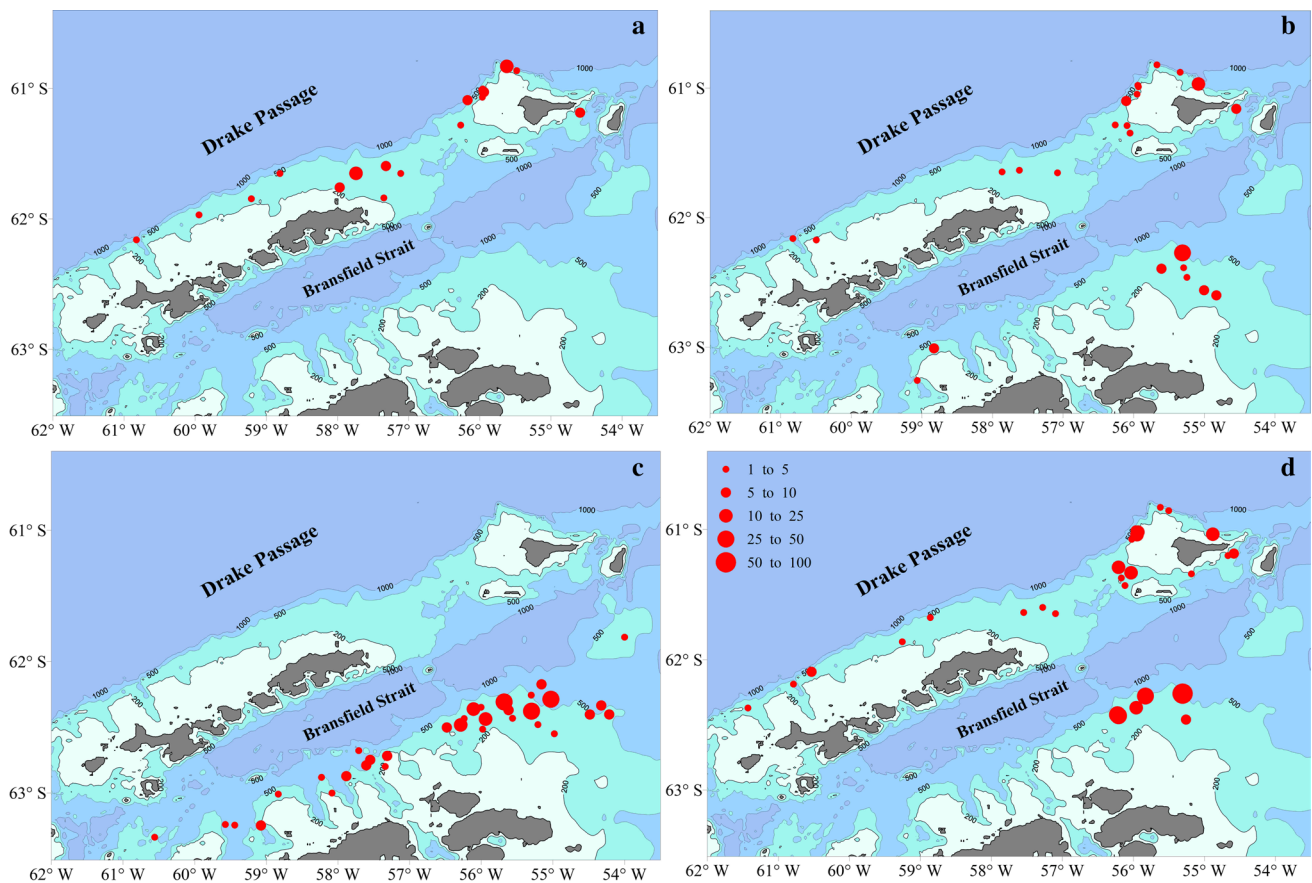
### Field activities

Adult specimens of *C. antarcticus* were collected during several bottom trawl surveys carried out off the South Shetland Islands aboard the RV *Polarstern* (ANT-XIX/3, January–February 2002; ANT-XXIII/8, December 2006–January 2007; ANT-XXVIII/4, March–April 2012) and the RV *Yuzhmorgeologiya* (US AMLR Program, February–March 2006) (Fig. 1). The sampling strategy was the same in all cruises, following a random, depth-stratified survey design with strata defined as 50–100 m, 100–200 m, 200–300 m, 300–400 m and 400–500 m. An additional depth stratum (700–800 m) was surveyed during the AMLR cruise. The fishing gear included a 140' commercially sized two-panel bottom trawl, with mouth opening of 2.5–3.2 m height and 16–18 m width, and a four-panel bottom trawl (in Feb–Mar, 2006) with a mouth opening of 8–10 m height and 16–19 m width. Trawling was conducted during daylight hours, with a nominal haul time of 30 min. Further details on sampling activities are reported in previous studies (Kock et al. 2003, 2008, 2012; Jones et al. 2006).

Juveniles of *C. antarcticus* were collected during a survey of the pelagic fish community off the South Shetlands aboard the RV *Moana Wave* (US AMLR cruise 2011, February–March 2011). Two different gears were employed for sampling, a multiple opening/closing Tucker Trawl with a 4 m<sup>2</sup> mouth opening equipped with three nets of different mesh size (505 µm–5 mm) and a 1.8 m Isaac Kidd midwater trawl (IKMT) with a single net of 505 µm. Further details on sampling strategy are reported in Jones et al. (2014).

### Laboratory activities

After each haul, fish samples were initially sorted to species. Following a standard protocol, individual fish were measured to the nearest cm below (TL), weighed as total weight (TW, g) and sexed. Sexual maturity was assessed by macroscopic analysis of gonads according to a five-point scale (Kock and Kellermann 1991) as follows: (1) immature, (2) resting or developing, (3) developed, (4) gravid or ripe, (5)



**Fig. 1** Map of the study area off the South Shetland Islands, showing the positive sampling stations for *Cryodraco antarcticus* surveyed during the cruises ANT-XIX/3 (a), ANT-XXIII/8 (b), U.S. AMLR

(c) and ANT-XXVIII/4 (d). Dots of different size indicate the number of specimens caught

spent. During the most recent survey (2012), gonads were individually removed from the abdominal cavity, weighed (GW, 0.1 g) and stored in Dietrich solution (900 ml distilled water, 450 ml 95% ethanol, 150 ml 40% formaldehyde, 30 ml acetic acid) for histological analyses. Following a standard protocol, gonads were dehydrated and embedded in paraplast. From each gonad sample, transverse serial thin sections (7  $\mu$ m) were mounted on slides and stained with Harrys' haematoxylin and eosin (Pearse 1985). Tissue sections were observed under a light microscope (Leica DM4000B) using different magnifications, to study gonad maturation. Based on their histological appearance, gonads of both sexes were classified into five phases (Brown-Peterson et al. 2011), as follows: (1) immature, (2) developing, (3) spawning capable, (4) regressing and (5) regenerating. In females close to complete gonad maturation, half the ovary was stored in 10% formaldehyde for fecundity estimation.

A subsample of specimens was randomly selected during each survey (except for the ANT-XIX/3 *Polarstern* cruise) for ageing purposes. Sagittal otoliths were removed, cleaned from adhering tissue and stored dry in labelled vials. As the

dense calcareous matrix in whole otoliths prevented direct age estimation, they were burned at 350 °C and embedded in resin (Crystalbond 509, Aremo products Inc.) on glass slides. Otoliths were then ground with abrasive paper to obtain transverse sections until reaching the core area and polished with 0.05  $\mu$ m alumina powder. Otolith sections were viewed under reflected light with a stereomicroscope (Leica M205C). The inner structure consisted of an alternate pattern of wide opaque zones (light rings) and narrow translucent zones (dark rings) forming an annulus, which was presumed to be laid down annually as in most notothenioids (e.g., Everson 1980). Each otolith was read twice a week apart, and the mean value was taken as final age estimate.

Juveniles of *C. antarcticus* were also measured to the nearest mm below (SL). Sagittal otoliths were removed with fine needles under a stereomicroscope and mounted on glass slides in resin (Petrox 154, Burnham Petrographics LLC) medial side down. Otoliths were slightly ground and polished to reveal the microincrements. Microincrement counts were taken from the primordium to the otolith margin and vice versa, assuming they were laid down with daily

periodicity (e.g., Kellermann et al. 2002). As mentioned previously for adults, the mean value of the two readings was also taken as individual age estimate for juveniles.

## Data analysis

A series of statistical tests were applied to infer some demographic characteristics of the sampled population. Length-frequency distributions of sexes were compared using the Kolmogorov–Smirnov two-sample test. Departure from the 1:1 sex ratio was tested using a  $\chi^2$  goodness-of-fit test. An exponential model, in the form  $TW = aTL^b$ , was fitted to describe body growth as a function of fish size in both sexes. Isometric growth departure (i.e.,  $b \neq 3$ ) was assessed by a  $t$ -test applied to the equation  $t = (b - 3) SE^{-1}$ , where  $SE$  is the standard error of  $b$ . Finally, the allometric indices ( $b$ ) calculated for each sex were compared by applying a  $F$ -test (Sokal and Rohlf 1995). The condition factor ( $K$ ) was calculated using the following relationship,  $K = 10^3 (TW/TL^b)$ , where  $b$  is 3 or  $\neq 3$  in case of isometric or allometric growth, respectively (Bolger and Connolly 1989).

To assess the reproductive investment of individuals, the gonadosomatic index (GSI) was calculated as the proportion of gonad to somatic weight. In advanced females, total fecundity ( $F_{tot}$ ) was estimated by applying the gravimetric method (Murua et al. 2003). Density of vitellogenic oocytes (number of oocytes per gram of ovarian tissue) was assessed in a weighed subsample and multiplied by the total gonad weight. Relative fecundity ( $F_{rel}$ ) was derived from the total fecundity as number of oocytes per gram of total body weight (Witthames et al. 2009). For each sex, a logistic model was fitted to the proportion of sexually mature specimens (i.e., those in macroscopic gonad stages 2–5) per

size class, aiming to estimate the fish size at which 50% of population attains sexual maturity ( $TL_{50}$ ).

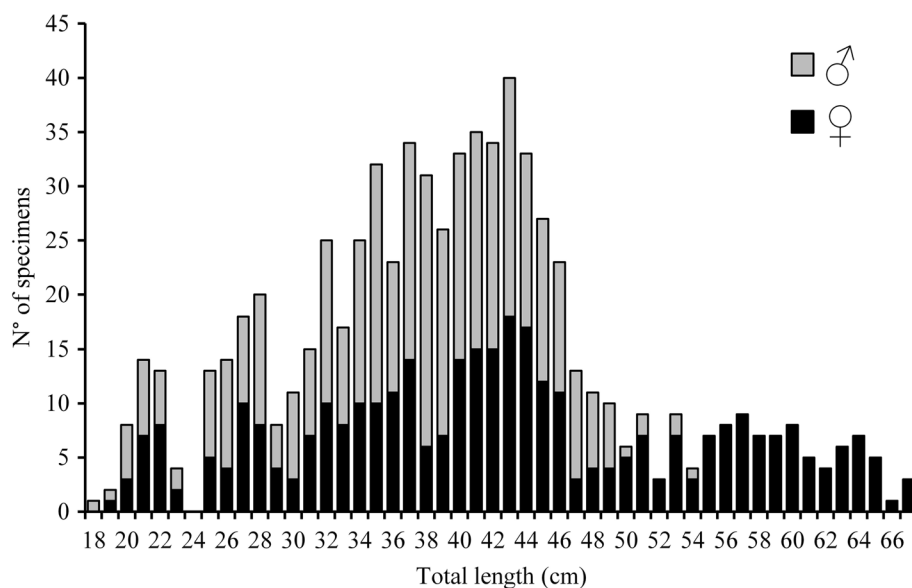
The precision of otolith readings was assessed by calculating the average percentage error (APE) and the mean coefficient of variation ( $CV_{mean}$ ) (Beamish and Fournier 1981; Chang 1982). The von Bertalanffy growth model, as  $L_t = L_{\infty} (1 - e^{-K(t-t_0)})$ , where  $L_t$  is the average length at age  $t$ ,  $L_{\infty}$  is the asymptotic average length,  $K$  is the so-called Brody growth rate coefficient and  $t_0$  is the age when the average length is zero, was fitted to the estimated age-length data pairs. The von Bertalanffy growth parameters, estimated for each sex by least squares methods, were compared using a likelihood ratio test (Kimura 1980). The growth performance index ( $\Phi' = 2 \log L_{\infty} + \log K$ ) was calculated to compare this species with other notothenioids. Estimates of expected length-at-age, derived from the von Bertalanffy growth curve, were calculated for each sex, and compared using a  $t$ -test for paired comparisons. All statistical analyses were performed using the PAST software (Hammer et al. 2001).

## Results

### Demographic characteristics of sampled population

The sampled adult population of *C. antarcticus* collected during surveys consisted of 353 females, ranging from 19 to 66.5 cm TL and from 14 to 2472 g TW, and 368 males ranging from 17.5 to 53.5 cm TL and from 14 to 1,081 g TW. The sex ratio did not differ significantly from 1:1 (goodness-of-fit test,  $\chi^2 = 0.31$ ,  $df = 1$ ,  $p > 0.5$ ). The length-frequency distributions of sexes were different from each other (Fig. 2), females being significantly larger than males (Kolmogorov–Smirnov test,  $D = 0.27$ ,  $p < 0.01$ ).

**Fig. 2** Length–frequency distribution of *Cryodraco antarcticus* collected during all surveys



Overall, four juvenile specimens from 87 to 107 mm SL were collected during the pelagic survey.

The length–weight relationships were fitted with an exponential model for each sex separately (Fig. 3, Table 1). The allometric indices ( $b$ ) were not significantly different between sexes ( $F$ -test,  $F = 1.45$ ,  $df = 1, 717$ ,  $p > 0.1$ ), indicating in both a positive allometric growth ( $t$ -test,  $t = 35.55$ ,  $df = 351$ ,  $p < 0.01$  for females;  $t = 28.59$ ,  $df = 366$ ,  $p < 0.01$  for males). The condition factor ranged between 0.09 and 0.26 in both sexes and was not related to fish size (Fig. 4). Comparing the mean condition factors calculated for the same size classes (cm) in both sexes, males showed consistently lower values than females across the whole size range ( $t$ -test for paired comparisons,  $t = 9.27$ ,  $df = 32$ ,  $p < 0.01$ ).

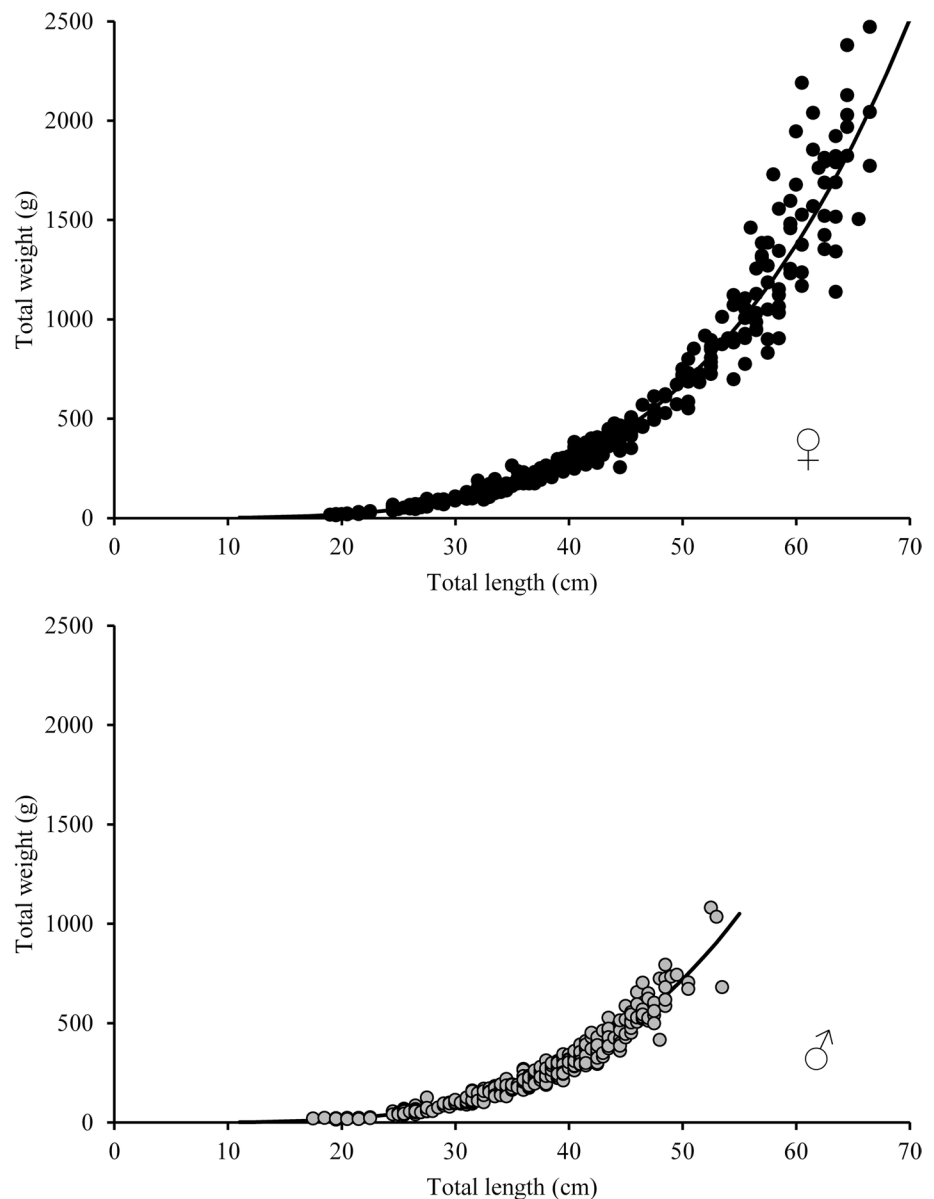
**Table 1** Length–weight relationship parameters estimated for *Cryodraco antarcticus* collected off the South Shetland Islands

Parameters	Males	Females
$a$	0.0001405	0.0001604
$b$	3.94	3.89
SE ( $b$ )	0.033	0.025
$n$	368	353
$r^2$	0.97	0.98

### Reproductive traits

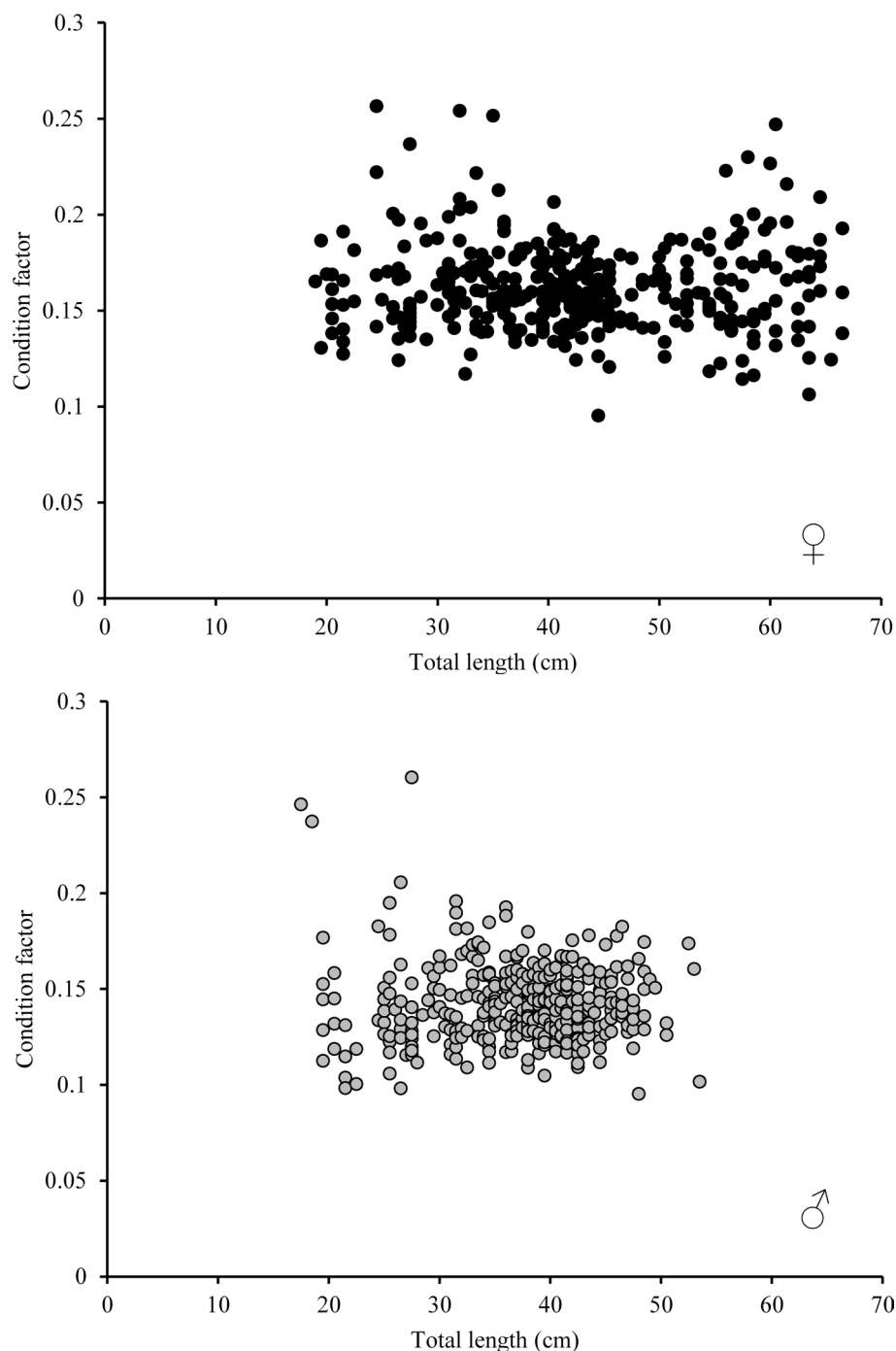
Fish size at sexual maturity was estimated separately for each sex, as females clearly attained larger size than males. Based

**Fig. 3** Length–weight relationship of *Cryodraco antarcticus* collected during all surveys





**Fig. 4** Condition factor in relation to fish size of *Cryodraco antarcticus* collected during all surveys off the South Shetland Islands

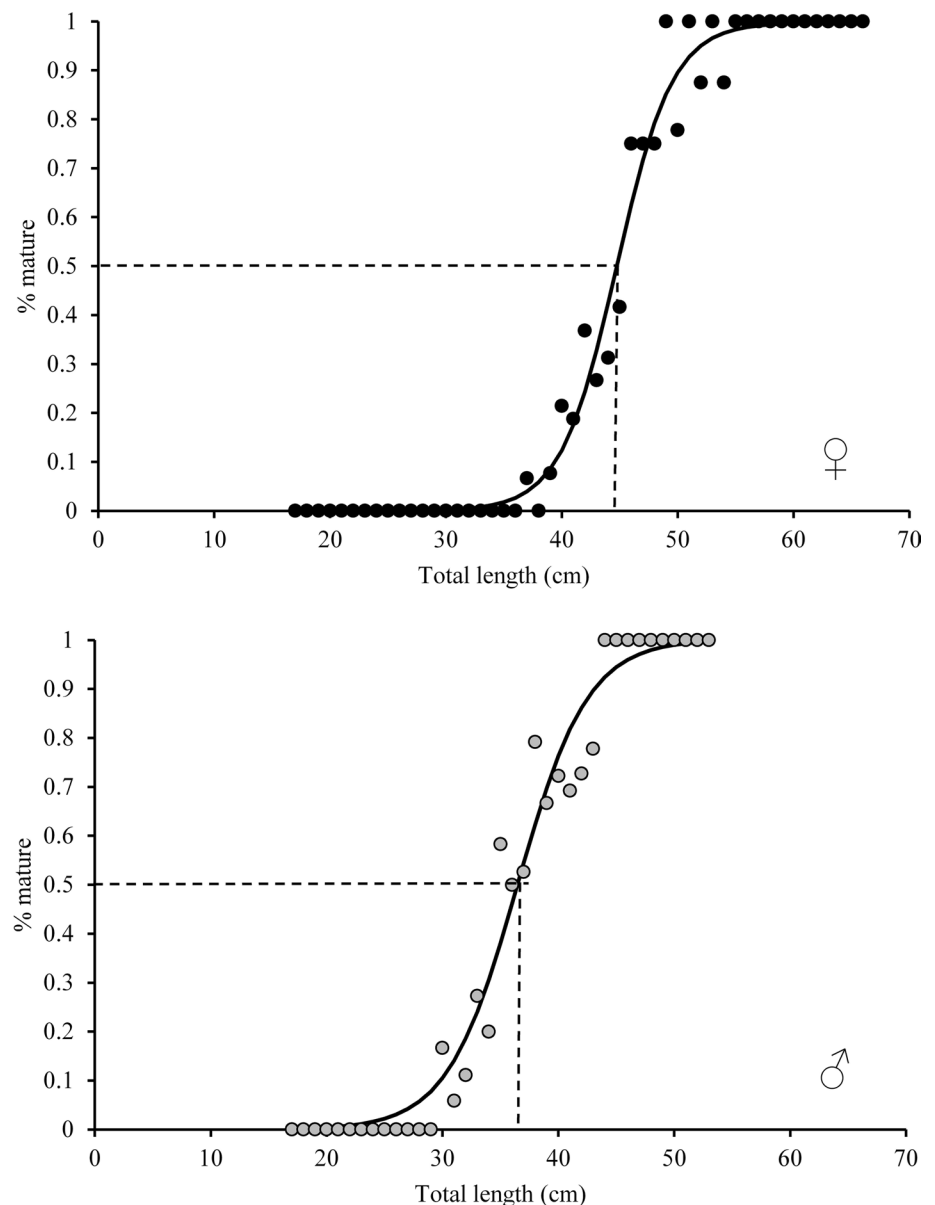


on the logistic model fitted to the proportion of sexually mature specimens, the fish size at which 50% of population attained sexual maturity ( $TL_{50}$ ) was 44.7 and 36.5 cm TL for females and males, respectively (Fig. 5). As a measure of reproductive investment, the gonadosomatic index was calculated within each histological phase of gonad maturity (Fig. 6). Parental contribution to reproduction in terms of GSI was consistently higher in females (0.4–17.2%) than in males (0.1–2.8%) in any stage of maturity. Total fecundity ( $F_{tot}$ ) and relative fecundity ( $F_{rel}$ ) estimated from a single

spawning-capable female (62 cm TL) were 7730 eggs and 5.4 eggs/g, respectively. The ovarian follicles in this specimen consisted of two well-separated groups of oocytes of different size, with vitellogenic oocytes ranging between 2.9–3.9 mm (Fig. 7).

Based on the histological analyses of gonads, females were assigned to four different phases of maturity (Fig. 8). Immature females (7 specimens), which were individuals that never spawned, had small ovaries with a thin ovarian wall, consisting of oogonia and primary growth (PG)

**Fig. 5** Logistic model fitted to the proportion of mature specimens of *Cryodraco antarcticus*, showing size at sexual maturity ( $TL_{50}$ ) estimated for each sex (dotted lines)

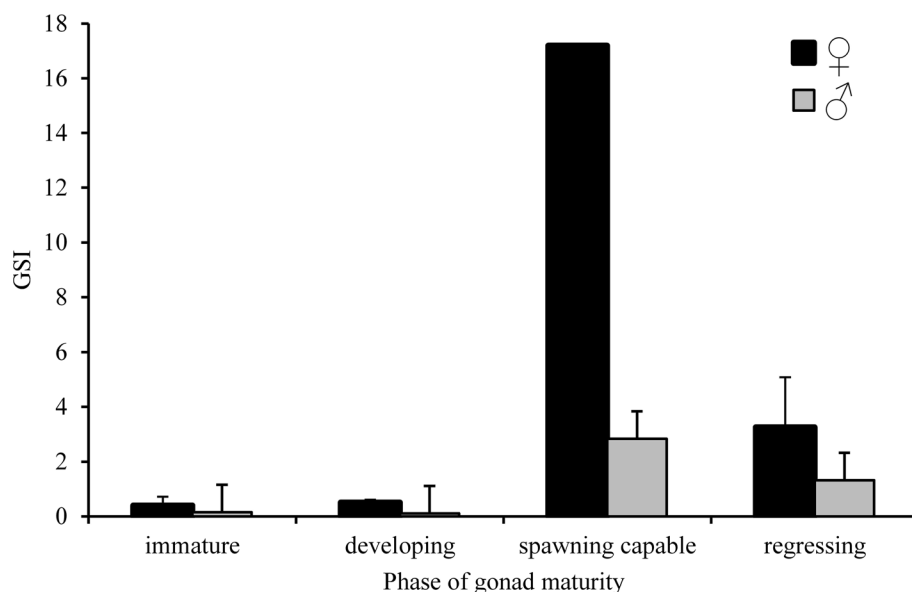


oocytes at chromatin nucleolar and perinucleolar stages tightly arranged from each other (Fig. 8a). Developing females (8 specimens) presented enlarged ovaries composed primarily of cortical alveolar (CA) and a few PG oocytes (Fig. 8b). CA oocytes were characterized by large nuclei with small peripheral nucleoli and granular cytoplasm filled with chromophobic vesicles (cortical alveoli) and surrounded by thick zona radiata (Zr) (Fig. 8c). A single spawning-capable female had ovaries with a thick ovarian wall, consisting of sparsely distributed PG and CA oocytes and many late vitellogenic oocytes (Vtg) with coalescent yolk vesicles and germinal vesicle breakdown (Fig. 8d). Regressing females (11 specimens) had flaccid ovaries with a very thick ovarian wall, large postovulatory follicles (POF) at various stages of degeneration, and some atretic oocytes

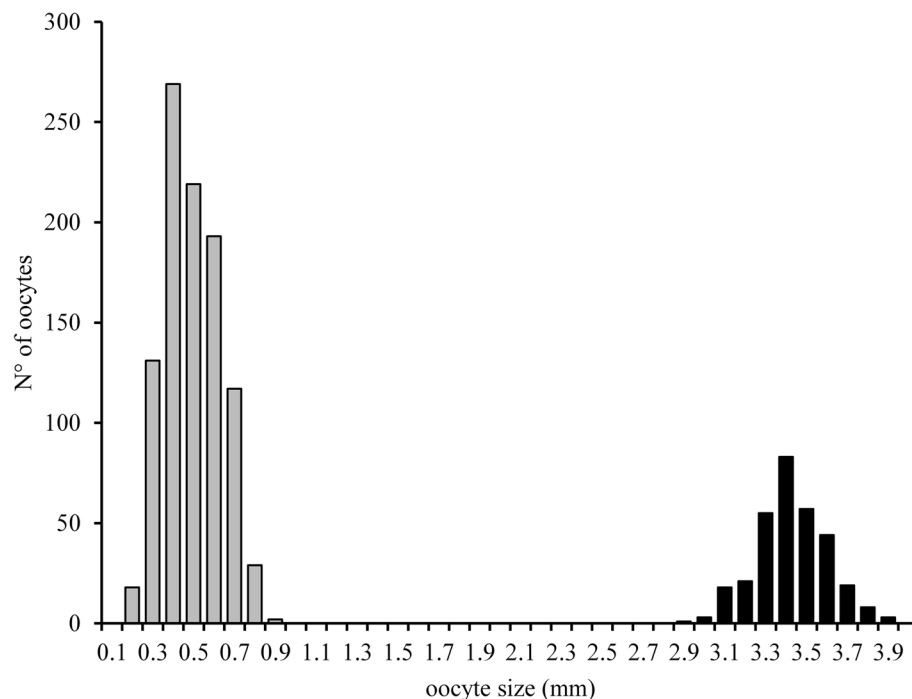
(Atr) (Fig. 8e). A few scattered CA oocytes were also found in regressing females, perhaps represented the reserve for the next spawning (Fig. 8f).

Four different phases were observed in the gonad development of males. Immature males (11 specimens) had small, thread-like testes (Fig. 9a), consisting of interstitial connective tissue and lobules filled exclusively by spermatogonia (Sg) without any evident lobule lumen (Fig. 9b). Only two developing males with enlarged testes were sampled; these were characterized by lobules containing Sg along most of the gonads and a few spermatocytes (Sc) close to the duct (Fig. 9c). Spawning-capable males (5 specimens) had large and firm testes in active spermatogenesis, some of them at an early stage with

**Fig. 6** Mean gonadosomatic index (GSI) calculated for each histological phase of gonad maturity of *Cryodraco antarcticus*. Bars indicate the standard deviations



**Fig. 7** Size-frequency distribution of oocytes in the ovaries of a spawning-capable female of *Cryodraco antarcticus* (62 cm TL), showing the size gap between previtellogenic (grey bars) and vitellogenic oocytes (black bars)



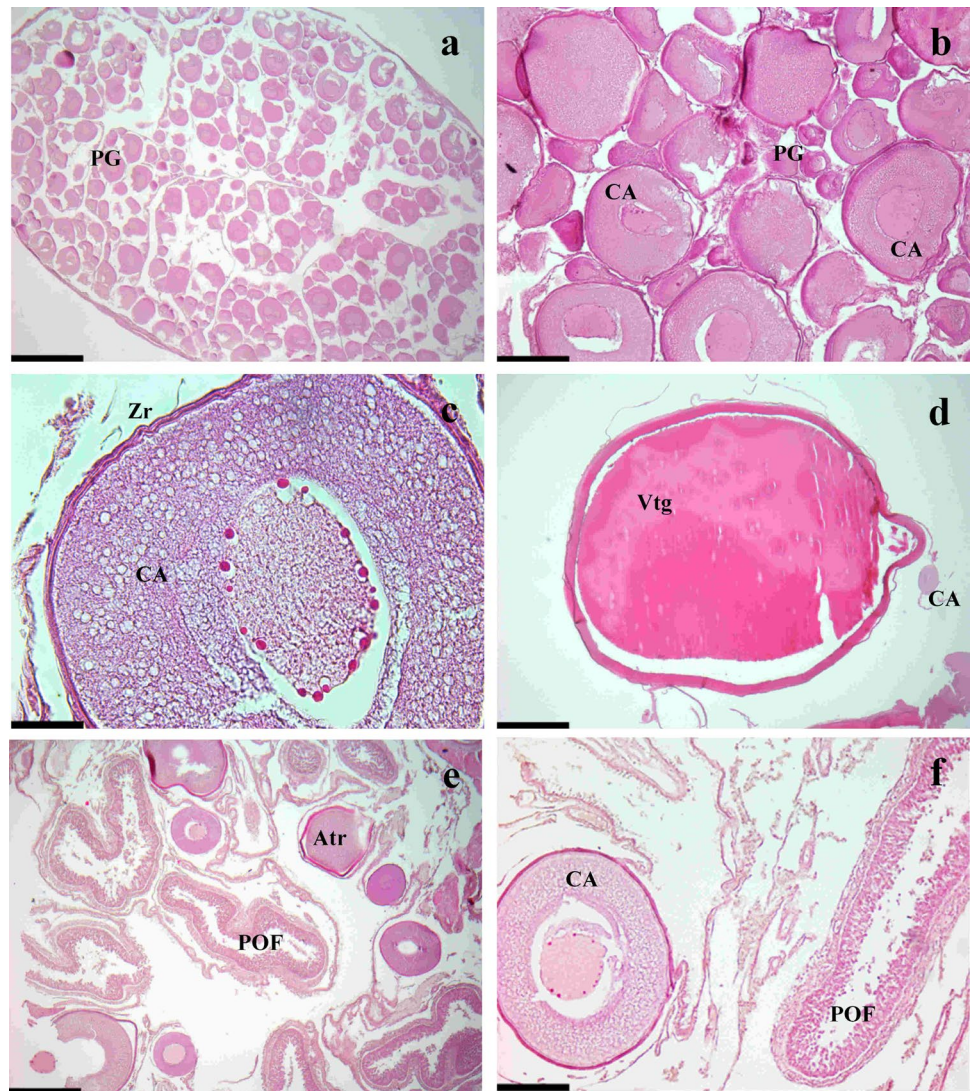
lobules containing peripheral Sg, Sc, spermatids (St) and spermatozoa (Sz) (Fig. 9d), other spawning-capable males were advanced with Sz completely filling the lumen of lobules and the ducts (Fig. 9e). In regressing males (5 specimens) testes were flaccid, being characterized by depleted stores of Sz in the ducts and in the lumen of lobules, as well as by proliferation of cysts of spermatogonia at the periphery (Fig. 9f). The regenerating phase of gonad development was not recorded for either sex.

### Age and growth

For ageing purposes, the adult fish subsample consisted of 128 females ranging from 19 to 66 cm TL and 137 males ranging from 19 to 50 cm TL. All specimens were successfully aged and indices of age precision were both relatively low ( $CV_{\text{mean}} = 3.2\%$ ,  $APE = 2.3\%$ ), indicating good consistency between otolith readings. Age-length data pairs were fitted by the von Bertalanffy growth curves for each sex separately (Fig. 10). Age estimates in adult



**Fig. 8** Gonadal histological sections of *Cryodraco antarcticus* females at different phases of development. **a** Immature; **b, c** developing; **d** spawning-capable; **e, f** regressing. *PG* primary growth, *CA* cortical alveoli, *Vtg* vitellogenic oocyte, *POF* post-ovulatory follicles, *Atr* atresia, *Zr* zona radiata. Scale bars: 50  $\mu$ m (**c**); 200  $\mu$ m (**b, f**); 500  $\mu$ m (**a, e, d**)



specimens ranged from 2 to 18 years for females and from 2 to 16 years for males. Age estimates of juveniles, which ranged from 196 to 226 days, were used to enhance the fitted von Bertalanffy curve at younger ages. By matching age estimates with date of capture, hatching time of juveniles were back-calculated; hatching occurred between late July to early August.

As expected, taking into account the sexual dimorphism in size, the von Bertalanffy growth parameters estimated for males and females differed (Table 2). Applying the likelihood ratio test, the single parameters  $L_{\infty}$  and  $K$  and all parameters pooled together were significantly different between sexes, as males attained lower maximum asymptotic size at faster rate than females (Table 3). Nevertheless, comparing the mean length-at-age derived by the von Bertalanffy growth curve over the estimated age range, the annual increment of body size was lower in males than in females, ranging from 0.4 to 5.3 cm and from 1.3 to 5.0 cm,

respectively ( $t$ -test for paired comparisons,  $t = 5.22$ ,  $df = 17$ ,  $p < 0.01$ ).

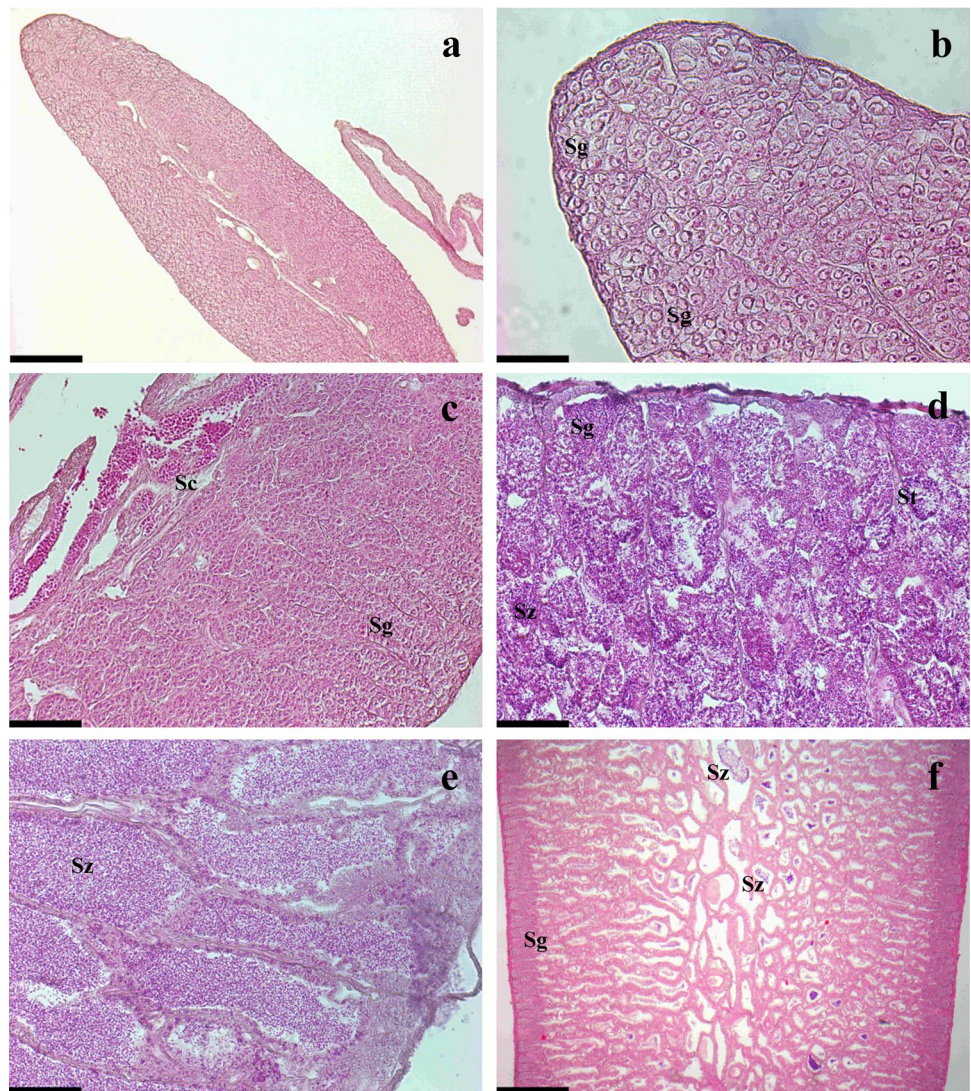
## Discussion

Present results on the *C. antarcticus* population living around the South Shetland Islands largely complement those reported in a previous study conducted between 1996 and 2001 summer seasons (Kock and Jones 2002). In particular, we reported further insight on demographic structure and reproductive characteristics of this species through histological analyses of gonads, and completely new data on age structure and growth rates.

The sampled population of *C. antarcticus* was widely distributed on the continental shelf all around the South Shetland Islands and north of the Antarctic Peninsula, preferentially between 200 and 500 m depth, but also in waters as



**Fig. 9** Gonadal histological sections of *Cryodraco antarcticus* males at different phases of development. **a, b** Immature; **c** developing; **d, e** spawning-capable; **f** regressing. Sg primary spermatogonia, Sc spermatocyte, St spermatid, Sz spermatozoa. Scale bars: 50  $\mu$ m (**b**); 100  $\mu$ m (**c–e**); 200  $\mu$ m (**a**); 500  $\mu$ m (**f**)



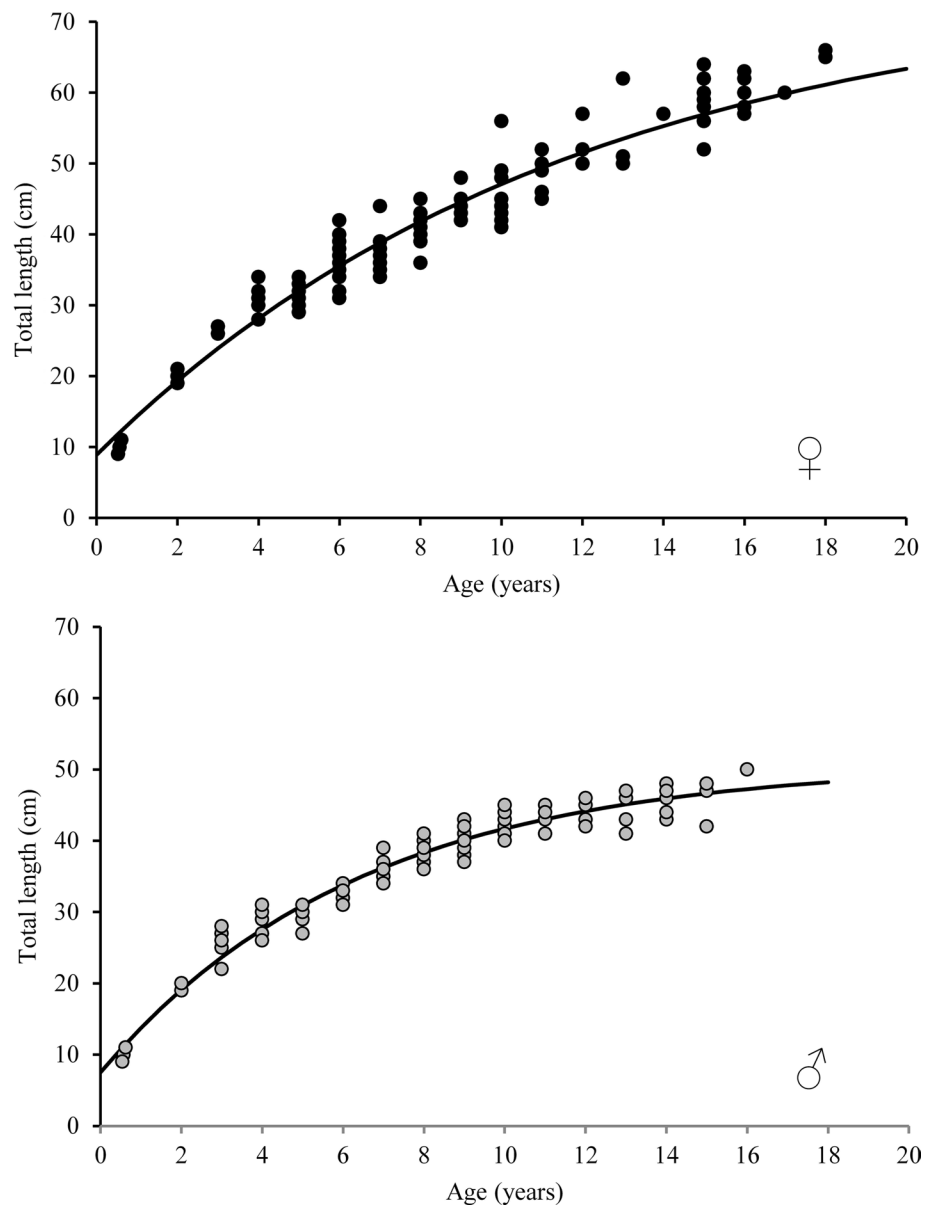
deep as 750 m. Adults were caught by bottom trawls in close proximity of the seafloor, whereas juveniles were collected in the upper layers of the water column between 150 and 300 m depth. The underlying habitat shift is consistent with a change in feeding habits during ontogeny, as juveniles feed primarily on krill and mysids whereas adults feed mainly on demersal fishes (Jones et al. 2006; Kock et al. 2013). When adult, *C. antarcticus* switch to a benthic mode of life and adopt a sit and wait feeding strategy, having often been observed perching on the substrate using their long pelvic fins (e.g., La Mesa et al. 2019).

The length-frequency distribution of fish samples represented the whole size range of the species, slightly increasing the maximum size previously reported (i.e., 65 cm TL) (Eastman 2019). The number of specimens caught were equally distributed between sexes, with a noticeable sexual size dimorphism. The smaller sizes of males can be related to reduced sperm competition associated with some degree

of parental care (Parker 1992), as observed in another icefish phylogenetically close to *C. antarcticus* (i.e., *C. aceratus*) (Kock and Jones 2002). Positive allometry characterized the length–weight relationships in both sexes of *C. antarcticus*, as commonly found in several species of channichthyids (e.g., Kock et al. 2000; Artigues et al. 2003). The condition factor was significantly lower in males than in females over the whole size range investigated, as it was inversely related to the allometric index which was slightly higher in males.

The reproductive traits of *C. antarcticus* closely resembled those reported elsewhere for other channichthyids (Kock and Kellermann 1991). Histologic analyses of gonads confirmed that this species is a total spawner, as females release eggs in a single batch during each breeding season. The gametogenic process in maturing females complied with the group-synchronous development type, in which two groups of oocytes can be distinguished: a fairly synchronous group of larger oocytes to be spawned

**Fig. 10** Length-at-age data pairs fitted by the von Bertalanffy growth curves estimated for *Cryodraco antarcticus*, assuming an annual deposition of light and dark rings



during the current breeding season, and a more heterogeneous group of smaller oocytes (consisting of PG and CA oocytes) to be spawned in future breeding seasons (Murua et al. 2003). The maternal contribution of the single female estimated in this study, in terms of total and relative fecundity, fell within the range reported previously from the same area (5653–24,445 eggs/female and 4.9–10.2 eggs/g,

$n = 14$ ) (Kock and Jones 2002) or from the Weddell Sea (3500–10,000 eggs/female and 7.1–7.4 eggs/g,  $n = 3$ ) (Ekau 1991; Duhamel et al. 1993). Egg size and GSI of the single spawning female were both slightly less than those previously reported in this species (i.e., 4.2–4.4 mm and 23–28%, Kock and Jones 2002), probably because it had gonads with eggs in late vitellogenesis just before hydration, a process that greatly increase egg size and, consequently, GSI (Brown-Peterson et al. 2011). Consistent with previous studies, off the South Shetland Islands *C. antarcticus* spawn in late summer or early autumn, as in April we found many specimens of both sexes in regressing or postspawning conditions. At the same time, a greater number of males were still capable of spawning, indicating that they likely mature the gametes and remain

**Table 2** The von Bertalanffy growth parameters estimated for *Cryodraco antarcticus* collected off the South Shetland Islands

Parameters	Males	Females
$L_{\infty}$	50.8	75.4
$K$	0.15	0.08
$t_0$	−1.02	−1.46
$\Phi'$	2.60	2.68

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

Parameter	Females			Males			RSS	$\chi^2$	df	p
	$L_{\infty}$	k	$t_0$	$L_{\infty}$	k	$t_0$				
Hypothesis independent	75.4	0.08	−1.46	50.8	0.15	−1.02	1857			
$H_0: L_{\infty} = k; = t_0$	72.5	0.07	−1.95	72.5	0.07	−1.95	3579	180.9	3	**
$H_0: L_{\infty}$	72.2	0.09	−1.28	72.2	0.06	−3.11	2183	44.5	1	**
$H_0: k$	72.1	0.09	−1.19	60.4	0.09	−2.26	2012	22.1	1	**
$H_0: t_0$	74.5	0.08	−1.31	52.1	0.14	−1.31	1870	1.8	1	ns

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

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

\*\*Significant at  $\alpha=0.01$

in spawning condition for a longer period than females, as reported for *Chionodraco hamatus* (La Mesa et al. 2003).

Otoliths have generally been considered the most suitable structures for ageing notothenioid fishes because they contain a complete record of growth during the entire life cycle (e.g., Kock and Everson 1998). The growth patterns of alternating opaque and translucent zones revealed in otolith sections of *C. antarcticus* were very similar to those observed in other channichthyids, in which the annual deposition has been validated by indirect methods (La Mesa and Vacchi 2001). In addition, the good consistency between repeated otolith readings (i.e., high precision) confirmed the reliability of the ageing protocol adopted. The estimated life span was similar between sexes, although the body-growth pattern differed considerably between them. As a result of the marked sexual size dimorphism, males of *C. antarcticus* attained a shorter maximum size at a faster rate than females. Nevertheless, the overall growth performance was similar between sexes, and comparable to other channichthyids sharing the same geographic area, such as *C. aceratus* and *C. rastrispinosus* (La Mesa et al. 2004; La Mesa and Ashford 2008).

Age determination of juveniles *C. antarcticus* enabled us to shed more light into early life history-strategies as well. Starting from the back-calculation from age estimates, and assuming daily increments, larval hatching takes place in winter, confirming previous hypothesis based on catches of early larvae in the spring within shelf and slope waters of Bransfield Strait and Elephant Island (Kellermann 1990). At the end of summer or early autumn (February–March), juveniles are roughly 7 months old and attain a size of 9–11 cm SL, in agreement with the temporal progression of larval size reported in literature (Kellermann 1986, 1989). At this stage of development, juveniles are pelagic and are frequently associated with the Antarctic krill swarms (Slosarczyk 1986; Wei et al. 2017). It is still unclear whether juveniles remain pelagic in the following winter, but the lack of juveniles smaller than 18–20 cm in benthic trawl catches would indicate that they

likely stay in the water column for a much longer period. Such a long-lasting pelagic phase of early life stages of this species would potentially promote high connectivity through dispersal at a large continental scale, accounting for virtually no genetic structure between populations encompassing the Ross Sea and the southern Scotia Arc (Dornburg et al. 2016). Consistently, adults exhibited similar life strategies across their range of their distribution, suggesting the possibility of a single panmictic population around the Antarctic continent.

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## Compliance with ethical standards

**Conflict of interest** The authors declare to have no conflict of interest and that all applicable institutional, national or international guidelines for the use and care of animals were strictly followed in the present study.

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