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Reproductive biology in the Antarctic bathydraconid dragonfish *Parachaenichthys charcoti*

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Abstract

Studies on reproduction of the dragonfishes, Bathydraconidae, are scarce, and within this family, the reproductive biology of *Parachaenichthys charcoti* was poorly understood. Herein we present a histologic analysis of *P. charcoti* ovaries together with data on reproductive effort using fish collected with trammel nets in austral summer at Potter Cove, South Shetland Islands (SSI), and compare this information with that reported for the South Georgia congener *Parachaenichthys georgianus*. In gravid females of *P. charcoti*, GSI of 16–31%, mature oocytes of 1.8–3.9 mm and total fecundity (TF) of 9025–18,937 oocytes/individual ($X \pm SD = 12,617 \pm 4019, n = 7$) were recorded. The histology of the ovaries confirmed the common characteristics of the Notothenioidei observed macroscopically, i.e., two distinct batches of oocytes, one in the previtellogenic stage (primary growing or cortical alveoli stages) and the other in vitellogenesis and likely to be released in the current season. A longer incubation period of *P. charcoti* compared with *P. georgianus* is associated to the colder waters at the SSI. Based on our sampling and reproductive effort data, together with the reported nesting behavior for *P. charcoti*, it is assumed that this species spawns in nearshore, sheltered waters in summer, presumably from late December to February. Spawning periods of both congeners differ from those reported for other notothenioids in the same Seasonal Pack-ice Zone, suggesting divergence in some aspects of the life strategies in the genus *Parachaenichthys*. Likewise, although there are no substantial differences between *P. charcoti* and other notothenioids regarding gonadal development, the genus *Parachaenichthys* shows distinct features in its reproductive strategies (e.g., higher TF) compared with other bathydraconid species.

Keywords Notothenioidei · Histology · Fecundity · Parachaenichthys georgianus · South Shetland Islands

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Introduction

The Antarctic notothenioid family Bathydraconidae is composed of 11 genera and 16 species (Eastman and Eakin 2000). The bathydraconid, Parachaenichthys charcoti (Vaillant 1906), Charcot's dragonfish, occurs in the lower Scotia Arc around South Orkney, South Shetland and Elephant Islands and along the west side of the Antarctic Peninsula, from the tip down south to the Bellingshausen Sea, at a depth range of 5-400 m (compiled from Nybelin 1951; Daniels 1982; Gon 1990; Casaux et al. 2003; Matallanas and Olaso 2007). It attains about 55 cm total length and feeds mainly on benthic-demersal organisms, chiefly fish, but also decapods and mysids, and secondarily on the pelagic krill (Targett 1981; Daniels 1982; Kompowski 1992; Casaux et al. 2003). Microincrements (daily rings) and annuli counts in otoliths of early juveniles and juvenile-adults, respectively, indicated an age range of 1–9 years (La Mesa et al. 2012).

Studies on reproduction of the Bathydraconidae are scarce. Although there is some variability, most of the family members show high reproductive effort in females (GSI 10–30%), yolky eggs of 1.4–4.3 mm diameter, and a range of total fecundity considered as low (200–24,000 eggs) (Kock and Kellermann 1991). Histologic descriptions of the gametogenesis are limited to the species *Gerlachea australis* (Van der Molen and Matallanas 2003), *Gymnodraco acuticeps* (Motta et al. 2005), *Akarotaxis nudiceps* and *Bathydraco marri* (La Mesa et al. 2007).

Given this limited background information, it can be seen that the reproductive biology of *P. charcoti* is poorly understood. The spawning period around the South Shetland Island is presumably late austral summer, and there is photographic evidence of nest guarding in the wild (Barrera-Oro and Lagger 2010). Larval hatching takes place in the winter onset of spring, from July to late September (Kellermann 1989; La Mesa et al. 2017). Information on the northern congener Parachaenichthys georgianus (Fischer 1885), endemic to South Georgia and South Sandwich Islands shelves at 5-270 m depth and reaching a maximum size of 60 cm (Gon 1990), is more extensive. Studies of the South Georgia population indicate that benthic eggs of about 4 mm (Permitin 1973; Burchett 1983) are spawned in late austral summer-autumn (North and White 1987), with onset of hatching in mid-August (Efremenko 1983; North 2001) and an absolute fecundity of 15,000-24,000 eggs (Permitin 1973; Burchett 1983). For both bathydraconid species, the histology of the gonads has not been studied.

In this article, we present a histologic analysis of *P. charcoti* ovaries together with data on reproductive effort in terms of GSI, oocyte size distribution at spawning and fecundity using fish collected in austral summer at Potter Cove, King George Island/Isla 25 de Mayo, South Shetland Islands. Our results are compared with those on reproductive traits and strategies reported for the sister species *P. georgianus*.

Materials and methods

Sampling and initial measurements

A total of 19 *P. charcoti* specimens were collected at Potter Cove, King George Island/Isla 25 de Mayo, near Argentine scientific station "Carlini" (formerly known as "Jubany", 62°14'S and 58°40'W) during the austral summer (December to March) from 2008 to 2018. Trammel nets (length 25 m, width 1.5 m, inner mesh 2.5 cm, outer mesh side 12 cm) were set from rubber boats for 16–24 h at rocky macroalgae beds at 20–70 m depth (average, 45 m) in the outer portion of the cove (Fig. 1). For a detailed description of the fishing procedure, as well as of the biotic components and abiotic features of Potter Cove, refer to Casaux et al. (1990). Further data on the fish examined are presented in Table 1.

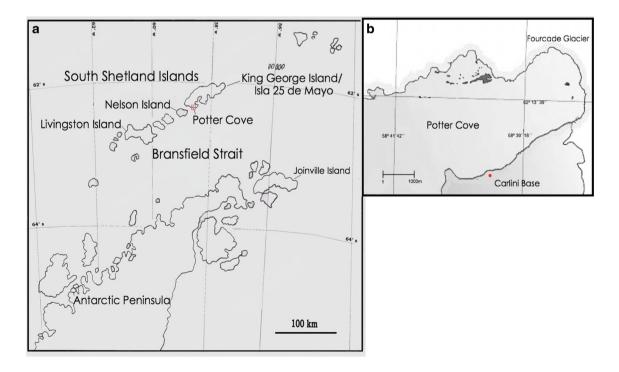


Fig. 1 The South Shetland Islands and Antarctic Peninsula region (a), with enlargement of Potter Cove in King George Island/Isla 25 de Mayo (b), the sampling site for *Parachaenichthys charcoti*

Table 1Details ofParachaenichthys charcotispecimens collected at PotterCove

Specimen	Date	Depth (m)	TL (cm)	SL (cm)	TW (g)	Sex	GSI (%)	Gonad stage
1	21/12/2008	32	47.9	43.3	886.2	Female	23.81	IV
2	12/01/2009	52	46.2	42.1	820.3	Female	21.74	IV
3	19/12/2009	35	43.4	39	576.6	Female	24.12	IV
4	19/01/2010	38	36.6	32.9	233.9	Male	0.11	II
5	01/02/2010	20	48.3	43.8	1170.15	Female	30.89	IV
6	03/02/2010	28	38.7	34.6	366.5	Male	7.70	III
7	16/02/2010	35	42.6	38.9	454.8	Female	1.12	II
8	16/02/2010	35	43.6	39.3	529.2	Female	5.29	V
9	21/11/2010	21	43.2	39	565.7	Male	9.89	III/IV
10	21/12/2011	10	43.5	39.3	784.1	Female	16.35	IV
11	14/01/2013	40	44.2	44	475.6	Female	0.99	II
12	14/02/2013	65	48.9	44.6	787.3	Female	20.59	IV
13	29/01/2014	43	44.6	40.1	624.1	Female	1.83	II
14	24/12/2014	28	51.3	46.4	1090.26	Female	23.41	IV
15	29/12/2014	32	47.4	42.5	916.45	Female	17.99	IV
16	26/01/2016	15	41.7	37.6	427.6	Male	3.72	III
17	25/02/2017	45	38.7	34.8	350.7	Female	0.71	Ι
18	18/01/2018	43	29.2	26.7	98.5	Female	0.51	Ι
19	22/01/2018	50	45.3	41.5	711	Female	26.10	IV

In the laboratory, total length (TL) and standard length (SL) of the fish were measured to the nearest 0.1 cm below, and total weight (TW) in g was recorded. After dissection, the sex and macroscopic gonad stage of maturity were assessed according to the five-point scale of Kock and Kellermann (1991). Gonads were weighed, separated and fixed in 10% buffered formalin for histologic analysis and fecundity estimate. Sex ratios were analyzed with a χ^2 test as the proportion of females compared to an expected balanced ratio. Stomachs were weighed and their content analyzed.

Our sampling was biased toward females; testis samples were not available for histologic analyses.

Reproductive effort

Reproductive effort was elucidated in terms of GSI, fecundity estimations and egg size (Kamler 1992).

As in the specimens, there were no differences in morphology and size between the two ovaries; we used the left for fecundity estimations and the right for histologic analyses. The gonadosomatic index (GSI) was calculated as the percentage of gonad weight to total fish weight. The hepatosomatic index (HSI) was determined in gravid females (stage IV) as the percentage of liver weight to the total fish weight.

Only yolked oocytes from gravid females (stages IV) were used to estimate total fecundity (TF), because in total spawners like *P. charcoti* this oocyte stage corresponds to the only batch that will be released in a single spawning event during the reproductive season (Murua et al. 2003). We used the gravimetric method described by Murua et al. (2003) to estimate the total number of yolked oocytes. Three subsamples from the left ovary of gravid (stages IV) females were dissected and weighed. Oocytes were separated from the surrounding tissue and counted manually under stereomicroscope in a petri dish. The gonad subsamples represented 10% of the gonad total weight. We used the minimum size of the oocytes of the largest cohort (1.8 mm) as the lower limit to infer total fecundity, which was estimated applying the relationship

$$TF = \frac{\left[\sum_{i} \frac{O_i}{W_i}\right]}{n} * W_{\text{ovary}}$$

where O_i is the number of oocytes of subsample *i*, W_i is the weight in g of subsample *i*, *n* is the number of subsamples, and W_{ovary} is the weight of both ovaries. Relative fecundity (F_{rel}) was estimated as the number of oocytes of the current spawning season per gram of TW ($F_{rel} = F_{abs}/TW$). The relationship between total fecundity and fish TW/TL was accomplished by linear regression analysis.

Finally, no differences in oocytes size were found among sections; therefore, we assessed the mean size of mature oocytes by measuring the maximum diameter of 180 oocytes randomly selected from anterior, middle and posterior ovary subsamples.

Histologic analysis

Histologic analysis of ovaries was performed to elucidate the stage of oocyte development to validate the macroscopic features of ovary maturation. One section of the right ovary was removed, dehydrated through increasing concentrations of ethanol and embedded in paraffin, following standardized procedures. Sections 7 μ m thick were cut and mounted on slides and stained with hematoxylin-eosin (H&E) technique. The ovary sections were examined with a Nikon Optiphot-2 microscope, and the histologic staging was based on the stage of oocyte development according to Brown-Peterson et al. (2011).

Results

Fish sample

Overall, we analyzed 15 females between 29.2–51.3 cm TL and 98.5–1170.15 g and 4 males between 36.6–41.7 cm TL and 233.9–565.7 g (sex ratio = 0.79, X^2 = 6.37, df = 1, p = 0.02) (Table 1). The variation between TW and TL for females showed a positive relationship (TW = -1454.68+48.26TL; n = 15; r^2 = 0.76) (Fig. 2).

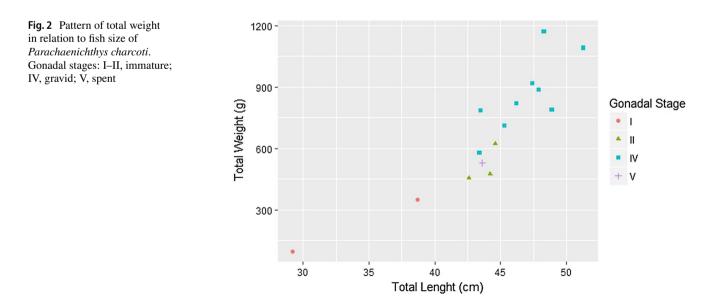
Reproductive effort and macroscopic maturity of gonads

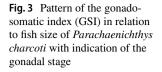
The macroscopic morphology of the gonads showed that five females, between 29.2 and 44.6 cm TL, were immature (stages I–II), with low GSI (0.51–1.82%) (Table 1). Except for one spent female (stage V, GSI 5.29%), the remaining individuals were gravid (stage IV), attaining a GSI between 16.35 and 30.9%. The GSI variation related to fish TL shows a clear gap between gravid and immature-spent females (Fig. 3). Male specimens were either immature (stage II) or developing (stage III) with a GSI between 0.11 and 9.89%. GSI estimations were not biased by the stomach weights because all the stomachs were empty. The values of HSI estimated for gravid females, although limited, constitute the only data available for this index at this stage for *P. charcoti* (Table 1).

Total fecundity was estimated from seven gravid females (stage IV) between 43.4 and 51.3 cm TL (Table 2). The number of yolked oocytes varied from 9025 to 18,937 oocytes/individual ($X \pm SD = 12,617 \pm 4019, n = 7$). Relative fecundity ranged from 11 to 17 yolked oocytes/g $(X \pm SD = 14.6 \pm 2.2, n = 7)$. Total fecundity shows a positive relationship with fish TW and TL (Fig. 4); however, these results should be taken with caution because of the limited number of fish analyzed. The diameter of mature oocytes in gravid females ranged between 1.8 and 3.9 mm, with a mean size of 3.09 mm. As expected, we easily distinguished this mature cohort of larger oocytes from the immature one formed by previtellogenic smaller oocytes, which ranged between 0.3 and 0.7 mm, with a mean of 0.53 mm (Fig. 5). The clear bimodal oocyte diameter distribution is shown in Fig. 6.

Histologic analysis

The histologic analysis of the ovaries collected during the sampling period allowed identification of two maturity gonad stages: females in early developing, with oocytes in cortical alveoli stage (Fig. 7a), and mature females, with yolked oocytes (Fig. 7b). In the last case, two main oocyte batches were seen: the smallest composed of previtellogenic oocytes or in primary growing stage and the largest, corresponding to mature oocytes, characterized by abundant yolk hydrated globules with a thick chorion (Fig. 7c). These





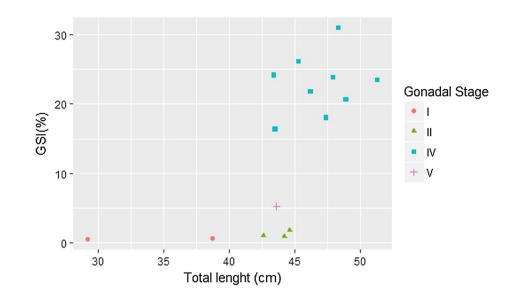


 Table 2
 Comparative information on reproductive effort and spawning time between two dragon fishes of genus Parachaenichthys: P. charcoti from Potter Cove, South Shetland Islands (this study); P. georgianus from South Georgia Islands (literature)

Species	Specimen	HSI	GSI	Fecundity		Oocyte size (mm)		Spawning period	Source
				Absolute (oocytes/ fish)	Relative (oocytes/g)	Range	Mean		
Parachaenichthys charcoti	3	7.41	24.12	9790	17.0	2.7–3.6	3.1 ± 0.2	Late Dec-Feb	This study
	5	4.91	30.89	18,937	16.2	3.1-3.9	3.5 ± 0.2		"
	10	7.23	16.35	11,771	15.0	1.8-3.8	2.9 ± 0.4		"
	12	_	20.59	10,976	13.9	_	_		"
	14	6.80	23.41	17,739	16.3	_	_		"
	15	_	17.99	10,080	11.0	2.7-3.5	3.0 ± 0.2		"
	19	6.00	26.10	9025	12.7	2.8-3.5	3.1 ± 0.1		"
Parachaenichthys georgianus	25 ^a			19,658–23,910			4 ± 0.1	Feb–Apr	Burchett (1983)
	1^{a}			14,090	10.7	2.4-3.4	2.8		Permitin (1973)
								Feb–Apr	North and White (1987)
								Mar–Apr	North (2001)

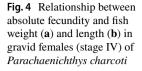
^aNumber of fish examined

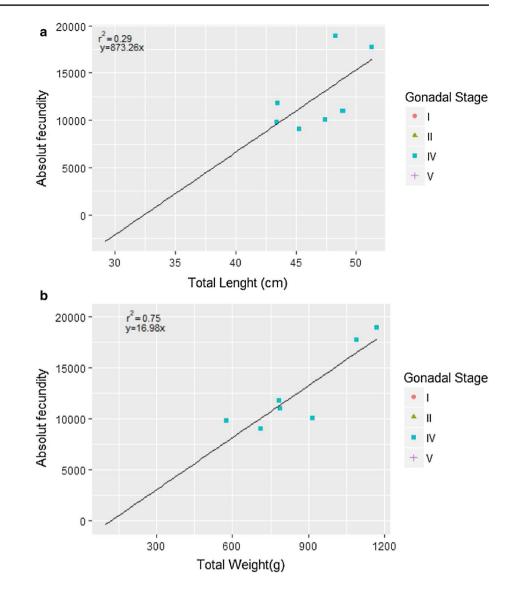
two main batches are the same as described in the oocyte diameter distribution (Fig. 6).

Discussion

Kock and Kellermann (1991) summarized the reproductive biology of the Antarctic notothenioids up to the 1990s. General features of this group include prolonged gametogenesis, one annual spawning event, low fecundity and large oocyte size at the mature stage. Two reproductive strategies are evident with respect to latitudinal distribution. On one hand, the less diverse fauna of the Seasonal Pack-ice Zone and around the islands north of it spawn numerous eggs during autumn and winter and produce small larvae at hatching. On the other hand, the more diverse fauna of the High-Antarctic Zone spawn in spring or summer and exhibit low fecundity and hatch larger larvae. Both of them have larvae with a long pelagic phase. There is also a general trend toward production of fewer but larger eggs in higher latitudes.

In the present study, ovaries of gravid females of *P. charcoti* macroscopically exhibited two different, easily distinguished cohorts of oocytes: a large clutch with the typical orange-reddish vitellogenic oocytes to be spawned in the current spawning event and a second clutch of white cream oocytes in several pre-vitellogenic stages (Fig. 5). This





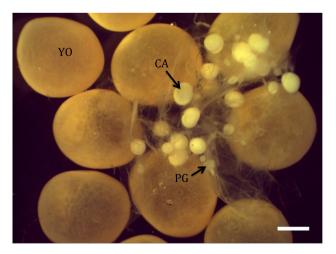
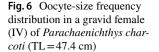
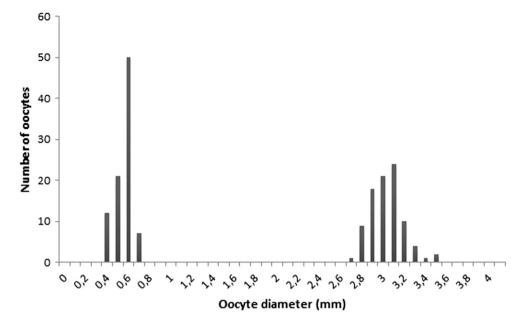


Fig. 5 Ovary of *Parachaenichthys charcoti* gravid female (stage IV) showing different cohorts of oocytes: *PG* primary growth oocytes; *CA* cortical alveoli oocytes; *YO* yolked oocytes; scale bar = 1 mm

oocyte disposition aligns with the Wallace and Selman (1981) classification of a "group synchronous ovary." The two peaks in the oocyte size frequency distribution in *P. charcoti* spawning females support the principle of bimodality shared by most notothenioids (Kock and Kellermann 1991) (Fig. 6). Yolked oocyte diameters at stage IV of gonad development ranged between 2.93 and 3.50 mm and are equivalent to the sizes estimated (3.5–4 mm) in Barrera-Oro and Lagger (2010) from photography of a spawned mass of eggs taken in late February 2008 (Fig. 8), suggesting that the females analyzed in our study were about to spawn. Similar oocyte sizes were reported for the South Georgia congener *P. georgianus*: 2.8 mm (Permitin 1973) and 4.0 mm (Burchett 1983), although the first value was based on the examination of a single gravid female (Table 2).

As far as reproductive effort is concerned, except for four immature (stage I–II) and one spent female (stage V), gravid specimens (stage IV) attained spawning condition





(GSI 16.35–30.9%) in our sampling months, December–February. This is in agreement with the finding of Bellisio (1967), who collected a single female in spawning condition (GSI 25.6%) in January at Half Moon Island, South Shetland Islands. Total fecundity in *P. charcoti* was 9025–18,937 oocytes/female, which is about 40% less oocyte production than in *P. georgianus* (Table 2).

The histologic analysis of the ovaries of *P. charcoti* confirmed the common characteristics of the Suborder Notothenioidei observed macroscopically, i.e., two distinct batches of oocytes, one in the first growing stage and the other in vitellogenesis and likely to be released in the current season (Fig. 7). The histologic description and oocyte diameter distribution are characteristic of total spawners with determinate annual fecundity that releases a single batch of mature oocytes during the spawning season (Murua et al. 2003).

Regarding the common features of low fecundity and relatively large eggs characteristic of notothenioids in general, the associated behavior of nest guarding and parental care within the bathydraconids, seen in P. charcoti, have been also reported for Gymnodraco acuticeps (Evans et al. 2005) and suggested for Akarotaxis nudiceps, based on its very low absolute fecundity (< 300 eggs; La Mesa et al. 2007). In line with the data on egg measurements, GSI and nesting behavior mentioned previously, it can be assumed that *P. charcoti* spawns in summer, presumably from late December to February. Differentially, it has been reported that the spawning months of *P. georgianus* are February–April (Burchett 1983; North and White 1987; North 2001). Therefore, the spawning periods of these sister species differ considerably from those reported for other notothenioids from the Seasonal Pack-Ice Zone fish group (autumn-winter), suggesting divergence in some aspects of the life strategies in the genus *Parachaenichthys*.

Because *P. charcoti* larvae (15–32 mm SL) occur in plankton in the Antarctic Peninsula from August to early December (compiled from Kellermann 1990; La Mesa et al. 2017), and back-calculation estimates of larvae and juvenile's ages suggest that hatching occurs from July to late September, the egg incubation period is probably extended (La Mesa et al. 2012, 2017). Regarding *P. georgianus*, hatching at South Georgia starts in mid-August (see Introduction). Hence, considering the data available on the spawning-hatching times of both congeners, the entire incubation period in *P. charcoti* is longer than in *P. georgianus*.

It is known that fish species from different geographical areas hatch earlier at lower latitudes, which is linked to a decrease of water temperature toward the poles. In line with this premise, different populations of the same species inhabiting South Georgia and the Antarctic Peninsula hatch about 2 months earlier at South Georgia (Kock and Kellermann 1991). Examples include the nototheniids Notothenia coriiceps, Gobionotothen gibberifrons and Lepidonotothen larseni and the channichthyids Champsocephalus gunnari, Chaenocephalus aceratus. Egg size at spawning is also thought to be related to the extension of the incubation period. As previously mentioned, egg size does not differ between the two species of Parachaenichthys. Therefore, the less seasonally variable and colder, by nearly 2 °C in winter, waters at the South Shetland Islands may be a cause of the delay in hatching of *P. charcoti* compared with the hatching time of *P. georgianus* at South Georgia.

Larval development in *P. charcoti* continues until the end of the first austral summer (Kellermann 1990; La Mesa et al. 2017), while similarly for *P. georgianus*, the end of the larval

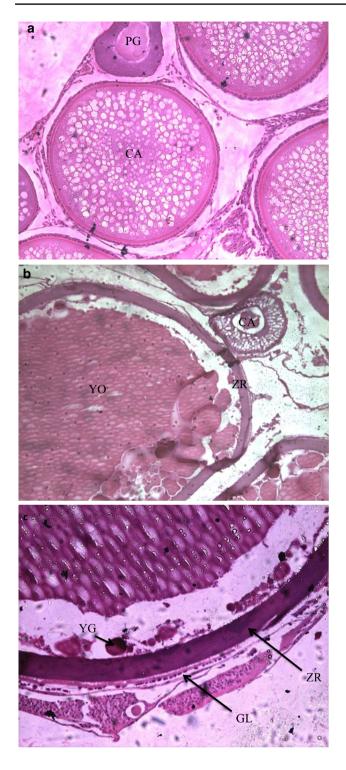


Fig. 7 Histologic sections of *Parachaenichthys charcoti* ovaries at different maturity stages: early developing (**a**), with oocytes in primary growth (PG) and with cortical alveoli (CA); gravid (**b** and **c**), with yolked oocytes (YO) and cortical alveoli stage (CA). *YG* yolk globules; *ZR* zona radiata; *GL* granulosa layer

stage has been reported to be in January–February (North 2001). Thus, compared with other notothenioids (North 1991), the pelagic larval phase in *Parachaenichthys* is only about 6 months (La Mesa et al. 2017).

From January to March, P. charcoti early juveniles (45-58 mm SL) have been caught in shelf and slope waters of the Antarctic Peninsula (Kellermann 1989; La Mesa et al. 2012) and several times within krill swarms (Slosarczyk and Rembiszewski 1982; Acuña et al. 1992). Their pelagic period persists until fall (Kellermann 1990). After a juvenile-adult period of development in deeper offshore waters, it is likely that pre-spawning P. charcoti migrate to shallow inshore waters during summer to spawn, where they cannot be caught by bottom trawl surveys (>100 m) (La Mesa et al. 2012). Our depth sampling data and results on reproductive effort, together with the reported evidence on parental care (Barrera-Oro and Lagger 2010), support the belief that this species spawns at inshore sheltered localities such as Potter Cove. Furthermore, the aforementioned estimate of the hatching period of P. charcoti based on back counting of otolith microincrements (assumed as daily rings) in larvae suggests that the nest guarding behavior may last at least 4 months (La Mesa et al. 2017). The short pelagic larval phase of Parachaenichthys spp. that restricts larval dispersal by currents, together with the apparent prolonged use of inner shallow sites as nursery grounds, may have facilitated speciation and be linked to the allopatric distribution of the sister species P. charcoti and P. georgianus (see La Mesa et al. 2017). A short larval period may be adaptively advantageous to these species given that they are benthic, have heavy skeletons (Eastman et al. 2014) and are among the least buoyant notothenioids with a percentage buoyancy of 5.7% on a 0-6% scale with 6% being the least buoyant (Eastman and Sidell 2002).

With reference to the data presented in Table 2, is the total fecundity of the genus Parachaenichthys within the Bathydraconidae actually low? Excluding this genus, total fecundity values in the family are 200-8500 oocytes/female (compiled from Ekau 1991; Kock and Kellermann 1991; Kompowski 1992; Duhamel et al. 1993; Van der Molen and Matallanas 2003; La Mesa et al. 2007; Kuhn et al. 2011). Furthermore, an estimate of mean total fecundity for only Parachaenichthys spp. indicates 15,300 oocytes/female, which is about 7.5-fold greater than in other family members, even other species from the Seasonal Pack-ice Zone and its northern islands (SPIZ). For example, for Psilodraco breviceps at South Georgia, the estimated maximum fecundity is only 1340 oocytes/female (Permitin 1973). For Vomeridens infuscipinnis at Lavoisier Island (66.25–278S, 66.55–588W), Biscoe Islands, which is an intermediate zone between the SPIZ and the High Antarctic on the west side of the Antarctic Peninsula, TF ranged between 1576 and 2296 oocytes/female (Kuhn et al. 2011). The difference is

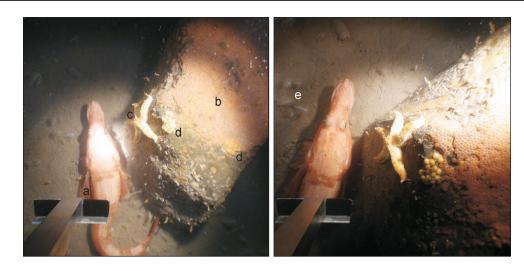


Fig.8 Nest guarding behavior of *Parachaenichthys charcoti* documented at Potter Cove. Photographs reproduced from Barrera-Oro and Lagger (2010). a Adult fish showing an S-shaped defense posture. b Mass of dragonfish eggs adhered to a rock. c The seastar

Diplasterias brucei d Two patches of eggs of the gastropod Neobuccinum eatoni adhered to the same rock. e The sea pen Malacobelemnon daytoni

even more evident compared with dragonfishes of the High-Antarctic Zone, e.g., *Akarotaxis nudiceps, Gerlachea australis, Racovitzia glacialis* and *Bathydraco marri* (200–2200 oocytes/female), where this group is more diverse and abundant. In turn, the relative fecundity in the genus *Parachaenichthys* (range 11–17 oocytes/g) is markedly lower than in other bathydraconids (range 16.2–46.6 oocytes/g), but this index strongly depends on fish size variation, in this case, within the family. Both *P. charcoti* and *P. georgianus* (mean TL: 53.1 cm) are on average about three times larger than the other dragonfishes (mean TL: 18.4 cm).

Independent of regional variation in water temperature, the South Georgia ecosystem is known as unique within Antarctica, with waters characterized by high biomass at every trophic level and also by high rates of growth and transfer between trophic levels (Atkinson et al. 2001). In spite of the high productivity of this region compared with the South Shetland Islands, the two *Parachaenichthys* species share similar diets and a benthopelagic although more benthic habitat (Kompowski 1992; compiled in Barrera-Oro 2002) and have similar growth rates and equivalent longevity (Kompowski and Rojas 1994; La Mesa et al. 2012).

In summary, this study provides macroscopic and histologic evidence that deepens our current understanding aspects and strategies of the reproductive biology of *P. charcoti*. Although there are no substantial differences between *P. charcoti* and other notothenioids regarding gonadal development, the genus *Parachaenichthys* shows distinct features in its reproductive strategies compared with other bathydraconid species. It should be noted that some of these reproductive differences may be attributable to the phylogenetic position given that in recent molecular phylogenetic analyses of notothenioids the Bathydraconidae is paraphyletic and a member of a clade with *Cygnodraco* and *Gerlachea*, while the genera *Gymnodraco* and *Psilodraco* are more closely related to channichthyids than to other bathydraconids (Near et al. 2012). Finally, in addition to information obtained from offshore surveys, our study highlights the utility of ecologic work based on nearshore sampling and its contribution to a more comprehensive understanding of the life cycles of Antarctic notothenioids.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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