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# Early life history traits and geographical distribution of *Parachaenichthys charcoti*

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**Abstract:** The geographical distribution of the two species of the genus *Parachaenichthys* is allopatric and restricted to the inner shelves of South Georgia–South Sandwich Islands (*P. georgianus*) and South Orkney Islands–South Shetland Islands (*P. charcoti*). To evaluate the consistency between the geographical patterns of adult distribution and early life history traits of *P. charcoti*, sagittal otoliths were used to estimate growth rate and pelagic duration in larvae and juveniles of this species collected in the Bransfield Strait in winter and summer, respectively. Individual age was determined through microincrement counts, assuming they were daily increments. The Gompertz model was fitted to age–length estimates, providing a mean growth rate of 0.22 mm $day^{-1}$ estimated for 28–204-day-old individuals. Larval hatching was spread over a relatively wide period, lasting from July throughout September. The pelagic larval duration of *P. charcoti* was about six months based on ageing data of larvae and juveniles, as reported for *P. georgianus* from South Georgia. The strong dependence of larvae on the inshore habitat may hamper their dispersal at large spatial scale limiting the connectivity among distant populations, providing clues to interpret the present geographical distribution of the two species.

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**Key words:** age and growth, Antarctic Peninsula, bathydraconid, juveniles, larvae, zoogeography

## Introduction

The area off the Antarctic Peninsula, including the Bransfield Strait and adjacent waters, hosts a diverse Antarctic larval fish assemblage (Loeb *et al.* 1993). The bottom topography and dominant water circulation pathways within the Bransfield Strait give rise to a large clockwise gyre, promoting larval retention and limiting dispersal by currents (Loeb *et al.* 1993). However, the confluence in the Bransfield Strait of water masses of different origins, such as the Weddell and Bellingshausen seas (e.g. Huneke *et al.* 2016), contributes to enrich the larval fish assemblage with species spawning elsewhere. Species composition and relative abundance of fish larval stages in this area show extreme seasonal and interannual variability, possibly linked to several biotic and abiotic factors (Kellermann 1989, Morales-Nin *et al.* 1995). Differences associated with variabilities in the reproductive effort of adults, egg and larval survival, and environmental conditions affecting dispersal, as well as the use of different sampling gear or locations, strongly determine the understanding of temporal changes of larval fish assemblages (Loeb *et al.* 1993).

The larval fish assemblage within the zone of seasonal pack ice cover off the Antarctic Peninsula is dominated by notothenioids (e.g. Kellermann 1986), a benthic group of fishes that has progressively radiated into several ice-associated or water column habitats (Eastman 1993). The early life stages of many notothenioids are pelagic, spending 1–2 years in the water column before they become predominantly demersal (Kock 1992). Hence, larval dispersal can be one of the most important mechanisms for promoting connectivity among different populations of circum-Antarctic notothenioids, which are often confined to coastal shelf areas during their adult stages (Damerau *et al.* 2014). Dispersal is greatly influenced by growth rate and pelagic larval duration, which is one of the main factors determining the structure of marine populations (Shanks 2009). However, physical mechanisms allowing retention, such as local gyres, or shelf-break frontal systems limiting offshore transport of larvae should promote genetic heterogeneity among distant populations, fostering speciation (White 1998). The role of larval dispersal in population structure and, on a longer timescale, to biogeography of notothenioids is still debated (Damerau *et al.* 2012).

During pelagic sampling efforts in the Antarctic Peninsula area, the Antarctic dragonfish *Parachaenichthys charcoti* (Vaillant) was the most frequently encountered bathydraconid species of the larval fish community (Kellermann 1989), as it is collected all year round except in winter (Morales-Nin *et al.* 1995). Unlike most

bathydraconids with a circum-Antarctic distribution, *P. charcoti* is confined to the southern Scotia Arc, including the South Orkney Islands, the South Shetland Islands and the tip of the Antarctic Peninsula (Gon 1990). The sister species within the genus, *P. georgianus* (Fischer), has an allopatric distribution and is endemic to the shelves of South Georgia and the South Sandwich Islands (Gon 1990). Adult specimens of both species prefer inshore waters down to 90 m depth, and are predominantly encountered in fjords (Burchett 1983). Both species produce relatively large demersal eggs, which are spawned in late summer (*P. charcoti*) or autumn (*P. georgianus*) in shallow waters (Burchett *et al.* 1983, Barrera-Oro & Lagger 2010). Nesting behaviour in *P. charcoti* has been recently described in the inner part of Potter Cove (South Shetland Islands) at 30 m depth (Barrera-Oro & Lagger 2010). All of these data suggest a limited gene flow between adult populations of *Parachaenichthys* inhabiting islands separated by deep oceanic waters, such as those forming the southern Scotia Arc.

However, the contribution of the early life history counterparts in determining the current population structure and zoogeography within the genus *Parachaenichthys* remains unclear, as larval traits of these species are still poorly understood. To address this, the sagittal otolith microstructure from larvae and juvenile *P. charcoti* collected off the Antarctic Peninsula during summer and winter were analysed. Microincrement patterns were used to determine hatch dates, yolk absorption time and growth rates in the field, as well as to estimate pelagic larval duration for this species. Comparing the present data with those from *P. georgianus* reported in literature, we attempted to assess the consistency between geographical patterns of distribution and early life history traits of the two species of *Parachaenichthys*.

## Materials and methods

### *Field activities*

Early juveniles of *P. charcoti* were collected during a summer survey carried out in the Bransfield Strait from Brabant to Joinville islands and the shelf north of Elephant Island. As part of the US Antarctic Marine Living Resources (AMLR) programme, the cruise was conducted in February/March 2011 aboard the RV *Moana Wave* using two different mid-water net systems for comparative purposes. A total of 70 stations were sampled using a 1.8 m Isaac Kidd mid-water trawl (IKMT) with a mesh size of 505 µm towed at 0–170 m depth, and a 4 $m^2$ multiple opening and closing Tucker trawl equipped with three nets (mesh size between 505 µm and 5 mm) towed at 0–170 m, 170–300 m and 300–600 m depth strata (Jones *et al.* 2014).

Early larvae of *P. charcoti* were sampled during two winter surveys carried out in the same area. The two AMLR cruises were conducted in August/September 2013 and 2014 aboard the RV *Nathaniel B. Palmer*, exclusively using the IKMT. Overall, 85 stations set at 40–600 m depth and 117 stations set at 60–220 m depth were sampled during the 2013 and 2014 surveys, respectively.

### *Sample sorting and processing*

The early life stages of *P. charcoti* were sorted and identified according to Kellermann (1990). The stage of development was assigned to each specimen according to Koubbi *et al.* (1990). Larvae and juveniles were measured from the tip of the snout to the end of caudal peduncle (standard length, SL) to the nearest mm below and stored in ethanol for further analyses. From larval samples, the amount of yolk was calculated by measuring major and minor axes of the yolk sac from images acquired by digitized computer video system (Leica Application Suite 4.3.0; Leica Microsystems, Wetzlar, Germany) composed of a CCD camera (Leica IC80HD) connected to a stereomicroscope (Leica M205C). Assuming the shape of yolk sac to be similar to a prolate spheroid, the volume was calculated applying the formula:

$$V = 4/3\pi a^2 b, \quad (1)$$

where a and b were half minor and major axes, respectively. The yolk sac at hatching was assumed to be roughly a spheroid of 3 mm diameter.

Sagittal otoliths were removed from all specimens under a stereomicroscope using fine needles and mounted on glass slides. They were embedded medial side down in Petropoxy 154 resin (Burnham Petrographics LLC, Rathdrum, ID, USA) and left to be cured in an oven at 80°C for *c.* 12 h. For juveniles, it was necessary to grind otoliths after embedding to get to the core using metallographic grinding paper discs and to polish with 0.05 µm alumina powder.

### *Ageing procedure*

Otolith microstructure was analysed using a light microscope (Leica DM4000B) connected by a digital camera (Leica DFC295) to a computer equipped with a digital video system. Microincrement counts were made from the primordium to the otolith margin at 630x magnification, recording along the count path microincrement width and the presence of checks. Each otolith was read twice and the mean value was calculated unless counts differed by >10% from each other. In these cases otoliths were discarded. Individual age in days was estimated by counting all microincrements, assuming that they were laid down from hatching

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with daily periodicity as in many other notothenioids (e.g. Kellermann *et al.* 2002).

### *Data analyses*

The index of average percent error (APE) (Beamish & Fournier 1981) and the mean coefficient of variation ($cv_{mean}$) (Chang 1982) were calculated to assess the precision (or reproducibility) between matched pairs of age readings. Generally, APE and $cv_{mean}$ values not exceeding 7% and 5%, respectively, provide good ageing precision (Campana 2001). Age estimates and bias plots were generated to measure systematic differences between readings. Monthly hatch date distribution was obtained considering individual age estimate and date of capture for all specimens successfully aged.

Based on the Akaike Information Criterion (AIC), early growth of *P. charcoti* was best described by the Gompertz model, which is usually suitable for modelling growth of larvae and juveniles of fishes (Campana & Jones 1992). The model fitted to the age–length data pairs was:

$$SL = L_\infty \exp(-k \exp(-Gt)), \quad (2)$$

where $L_\infty$ is the asymptotic length, k is a dimensionless parameter, G is the instantaneous growth rate at the inflexion point of the curve and t is the age of fish. The absolute daily growth rate at age was calculated starting from the equation above, as follows:

$$g_t = GL_t(\ln L_\infty - \ln L_t), \quad (3)$$

where $g_t$ is the absolute growth rate at age t, G is the instantaneous growth rate, $L_\infty$ and $L_t$ are the fish length at the asymptote and at age t, respectively (Campana & Jones 1992).

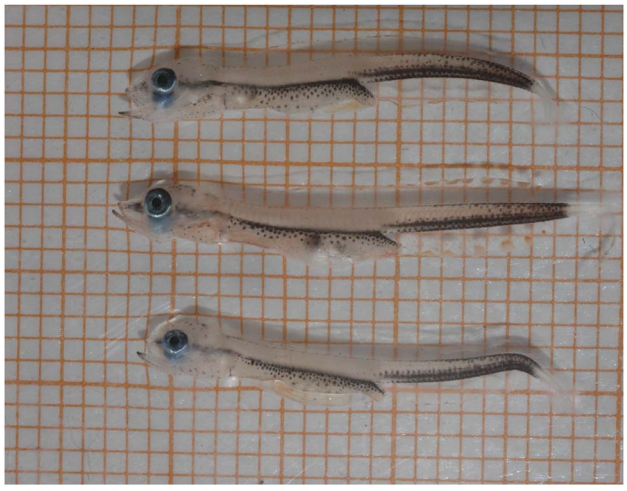

**Fig. 1.** Yolk sac larvae of *P. charcoti* collected in the Bransfield Strait during the winter, showing the overall pigmentation pattern.

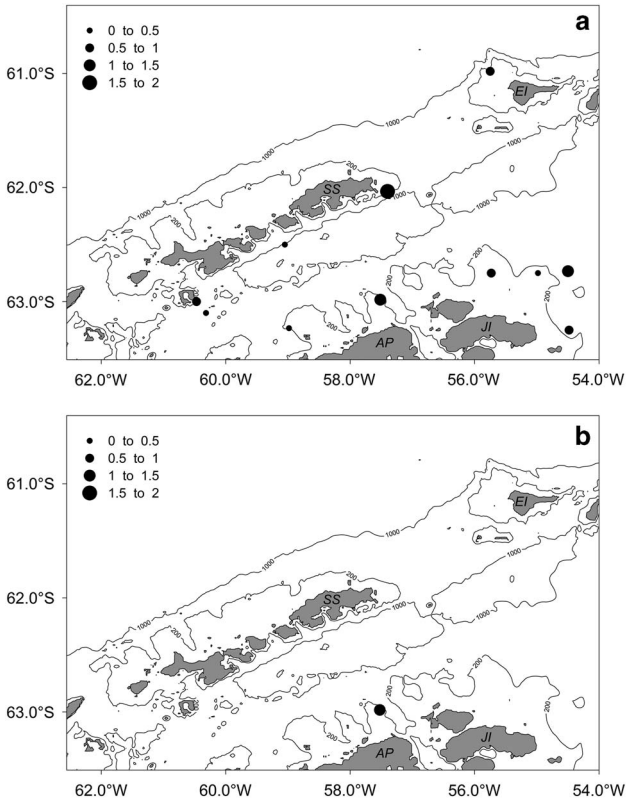


**Fig. 2.** Spatial distribution of catches of early life stages of *P. charcoti* in the study area: **a.** larvae and **b.** juveniles. Dots indicate the relative abundance as individuals per 1000 $m^3$ of filtered seawater. AP = Antarctic Peninsula, EI = Elephant Island, JI = Joinville Island, SS = South Shetland Islands.

Yolk sac resorption rate in larval specimens was assessed by fitting individual age estimate and yolk sac volume to an exponential model of decay in the form:

$$V_t = V_0 \exp(rt), \quad (4)$$

where $V_t$ is the volume of yolk sac at age t, $V_0$ is the volume of yolk sac at hatching, r is the resorption rate and t is the age of larva. All 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.

## Results

### *Composition, abundance and spatial distribution of fish samples*

Overall, 24 larvae of *P. charcoti* ranging from 15–23 mm SL and four juveniles ranging from 47–56 mm SL were collected in winter and summer, respectively. Sixteen larvae were at stage 1 (yolk sac) and eight were at stage 2 (preflexion) of development. All juveniles were at stage 4 (fin rays formed). The pigmentation patterns of larvae closely

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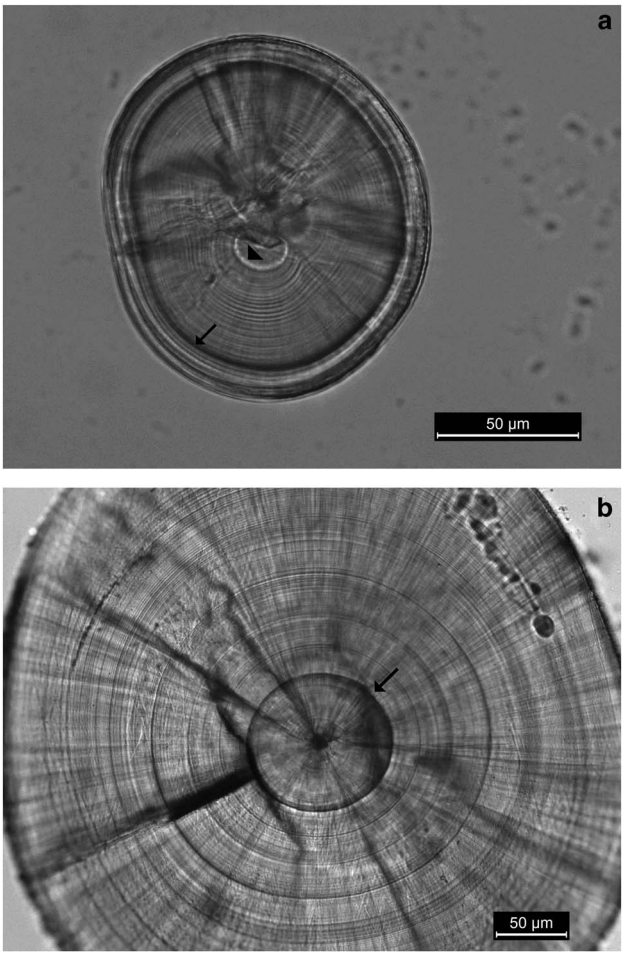


**Fig. 3.** Light micrographs of sagittal otolith of early life stages of *P. charcoti*. **a.** Larva 35 days after hatching, showing multiple primordia delimited by the hatching check (arrow head) and the first feeding check (arrow) close to the margin. **b.** Juvenile showing the microincrement patterns beyond the first feeding check (arrow).

resemble those reported previously for larger individuals collected in the Antarctic Peninsula Region between late October and early December, consisting of a dorsal row and a ventral band of melanophores in the postanal section, as well as a dorsal and lateral pigment on the abdomen (Fig. 1).

Larvae were sampled almost exclusively in the Bransfield Strait, along the inner shelf of the South Shetland Islands and Joinville Island at depths < 200 m (Fig. 2a). The relative larval abundance ranged between 0.28 and 1.53 individuals per 1000 $m^3$ of filtered seawater (mean ± standard error: 0.75 ± 0.13). Juveniles were only collected by the Tucker trawl from a single station located off the Antarctic Peninsula at 0–110 m depth (Fig. 2b).

### *Microstructure of sagittal otoliths*

Sagittal otoliths of larvae and juveniles of *P. charcoti* have a discoid shape, with a maximum diameter of 104–155 µm and 480–580 µm, respectively (Fig. 3). Otoliths grow from single or multiple primordia, surrounded by a pronounced check assumed to be laid down at hatching. After hatching, thin and evenly spaced microincrements (width range 1–1.5 µm) are deposited and encircled by another evident check located at 25–35 microincrements from the primordium (Fig. 3). This check is probably linked to the onset of exogenous feeding (feeding check) rather than to yolk sac resorption, as it was evident in individuals with and without the yolk sac. Beyond the feeding check, microincrements become progressively wider (up to 1.6 µm) towards the otolith margin.

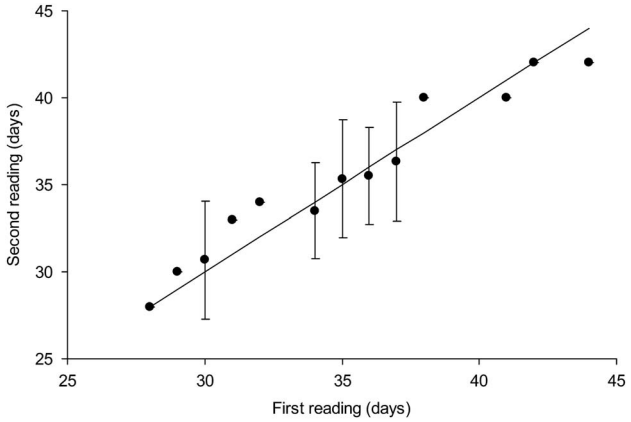


**Fig. 4.** Bias plot applied to age readings carried out on *P. charcoti* larvae. Bars represent 95% confidence intervals.

### *Estimating age and growth rate*

All individuals of *P. charcoti* were successfully aged, showing a clear alternating pattern of growth rings formed by a discontinuous zone (D-zone) and an increment zone (L-zone) which appeared dark and light

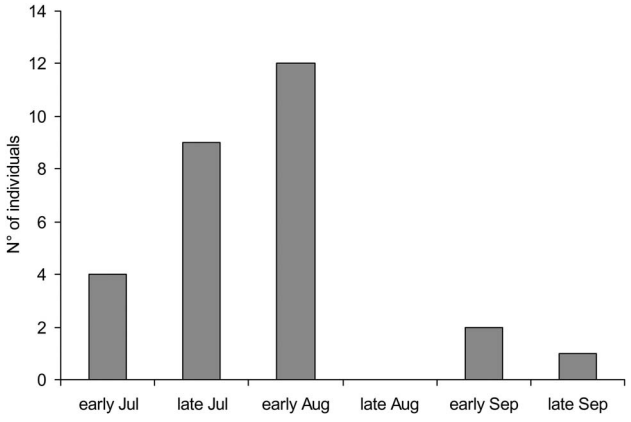


**Fig. 5.** Hatch date distribution back-calculated by age estimates and sampling dates of early life stages of *P. charcoti*. 'Early' and 'late' represent the first and second half of the month, respectively.

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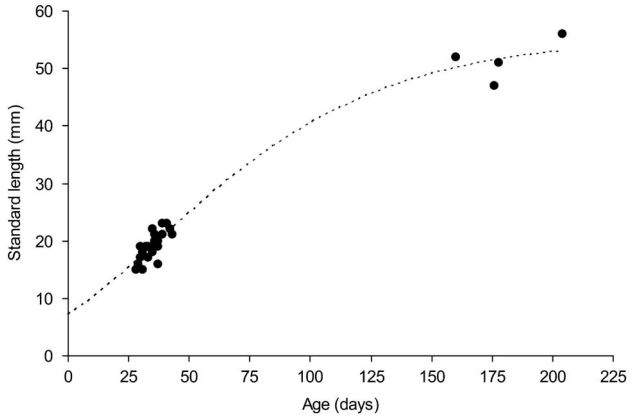


**Fig. 6.** Gompertz growth curve fitted to age–length data pairs estimated for early life stages of *P. charcoti*.

under transmitted light. Based on microincrement counts, age estimates ranged between 28–43 days for larvae and 160–204 days for juveniles. As measures of ageing precision, APE and $cv_{mean}$ were relatively low (2.9% and 2.0%, respectively), indicating good consistency between readings. Difference between readings and bias plots showed no systematic error or bias across the estimated age range (Fig. 4). Matching individual age estimate and date of capture, hatch date distribution was spread over a relatively wide period, lasting from July to September (Fig. 5).

The Gompertz model was fitted to age–length data pairs of larvae and juveniles (Fig. 6), providing the following relationship:

$$SL = 55.494 \exp(-2.053 \exp(-0.019\, t)), \quad (5)$$

where SL is the standard length (mm) and t is the age (days). Applying the model, the larval size at hatching (i.e. SL at age $t = 0$) was *c.* 7.1 mm and the absolute daily growth rate ($g_t$) was 0.05–0.38 mm $day^{-1}$ (mean ± standard error: 0.22 ± 0.008).

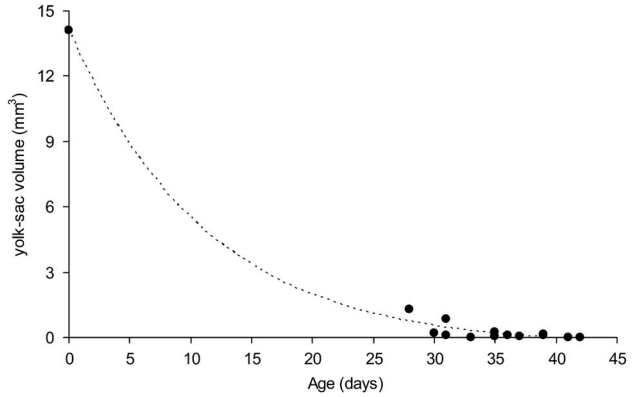


**Fig. 7.** Exponential curve fitted to yolk sac resorption rate calculated for *P. charcoti* larvae.

*Yolk sac resorption rate*

Yolk resorption rate was assessed by plotting yolk sac volume against individual age of larvae with yolk remains (Fig. 7). The exponential model fitted to these data was:

$$V_t = 14.572 \exp(0.0897\, t), \quad (6)$$

where $V_t$ is the volume at age t ($mm^3$) and t the age (days). The resorption rate in larvae older than 30 days was relatively low and fairly constant, consistent with the onset of exogenous feeding before completing yolk resorption observed in most individuals.

## Discussion

The demersal fish community inhabiting the continental shelves of the South Shetland Islands and South Orkney Islands consists of several species of notothenioids, of which *P. charcoti* is a minor component (e.g. Kock *et al.* 2000, Jones *et al.* 2009). During bottom trawl surveys, catches of this species are made up almost exclusively of juvenile or sub-adult individuals collected within the 200 m depth isobath (La Mesa *et al.* 2012). Large adults are generally caught in small coves or fjords where they spawn in summer (Barrera-Oro & Lagger 2010), as reported for *P. georgianus* from South Georgia (Burchett *et al.* 1983). Based on field observation of nesting behaviour of *P. charcoti* (Barrera-Oro & Lagger 2010) and hatch date distribution estimated by microincrement counts of larvae, the time spent by parents guarding eggs until hatching is extremely long, lasting at least four months. The apparent spatial segregation of spawners in inshore waters and the limited bathymetric distribution of the entire population may have contributed to determine the allopatric distribution patterns of the two species within the genus *Parachaenichthys*. Based on genetic data, a similar distribution pattern has been reported in *Lepidonotothen nudifrons* (Lönnberg), which includes two morphologically identical but genetically distinct species along the Scotia Arc (Dornburg *et al.* 2016).

Nevertheless, as spatial connectivity among different populations of notothenioids is mainly promoted by passive larval dispersal (e.g. Damerau *et al.* 2014), early life history traits can play a key role in determining the geographical patterns of distribution at the species level. In turn, dispersal is influenced by the spawning location of adults and larval behaviour. Based on a modelling approach for notothenioid fishes, larvae hatching in inshore waters are more likely to be retained on the shelf than those hatching on the outer shelf, which are more vulnerable to advection by currents (Young *et al.* 2012). Considering the spatial distribution of early larvae of *P. charcoti* off the Antarctic Peninsula, they are almost exclusively confined to the Bransfield Strait on the inner

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shelves of Joinville Island and the South Shetland Islands (Kellermann 1989, Morales-Nin *et al*. 1995, present data). This area is characterized by a large cyclonic basin-scale circulation with several minor eddies, assisting in larval retention and the possibility of a long residence time in a food-rich environment (Zhou *et al*. 2002). Similarly, at South Georgia, *P. georgianus* spawn in the deep fjord of Cumberland East Bay, where early larvae are found from June onwards (Burchett *et al*. 1983, North & Murray 1992). The high density and species diversity of early life stages of notothenioids within Cumberland Bay provides evidence of the importance of the fjord as a nursery and spawning area of the demersal fish community of the South Georgia shelf through mechanisms of larval retention (Belchier & Lawson 2013).

Based on microincrement counts made on sagittal otoliths, the mean growth rate estimated for early life stages of *P. charcoti* from the Antarctic Peninsula is within the range reported for other notothenioids (North 1991), although faster than for *P. georgianus* derived from modal progression of larval size through time (North 1998, Belchier & Lawson 2013). Early growth differences between the two species could be due to the different methodological approaches, taking into account that mean growth rates derived from field data of larval size through time may be underestimated in species with protracted spawning, multiple cohorts and advection of larvae from neighbouring areas. Larval hatching of both species of *Parachaenichthys* is spread over a relatively long period throughout the winter. To be able to cope with low food availability during winter, newly hatched larvae exhibit large yolk reserves, which are totally consumed within 6–8 weeks of hatching (North 1991, present data). However, in cases of food availability, both species start to feed before full yolk sac resorption (North & Ward 1989, present data).

Compared to other notothenioids (North 1991), the pelagic larval duration of *P. charcoti* is relatively short, lasting about six months. From hatching in winter, larvae take advantage of favourable food conditions during the following spring and summer, developing to the early juvenile stage of 45–50 mm in January/February (Kellermann 1989, present data). At South Georgia, the pelagic larval duration of *P. georgianus* is very similar to its southern congener, lasting from June to January, when juveniles attain a size of 55 mm (Efremenko 1983). From March onwards, juveniles of both species probably recruit to suitable inner shelf nursery grounds, as they are no longer sampled in pelagic waters until the following winter. Consequently, the short pelagic phase during the early ontogeny would restrict the passive transport of larvae driven by the local currents, limiting the larval dispersal between distant populations.

In conclusion, early life history traits and ecological characteristics of adults are consistent with the current allopatric geographical distributions of *P. charcoti* and *P. georgianus*, which include the South Shetland Islands–South Orkney Islands and South Georgia–South Sandwich Islands, respectively. Abiotic factors, such as fine-scale circulation patterns that promote retention for larval stages, and biological factors, such as short pelagic larval duration and spatial distribution of adults restricted to inshore waters, may have contributed to limit the gene flow between neighbouring populations producing, on an evolutionary timescale, the vicariant speciation within the genus *Parachaenichthys*.

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## Author contribution

MLM conceived the study and wrote the paper. ER and CDJ conducted the field activities providing fish samples and contributed significantly to the interpretation of data and manuscript editing before submission.

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