



## Different populations of the Antarctic notothen fish *Trematomus scotti* differ in key life history traits

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### ABSTRACT

Antarctic notothenioid fish form an adaptive radiation that diversified in the Southern Ocean over the past 10 million years. The biology and life history of about a third of notothenioids have been studied, however, most frequently from a single location. Because species distributions can be discontinuous and depend on environmental conditions, local populations might differ substantially both genetically and phenotypically from distant conspecifics. Among notothenioids, the 15 *Trematomus* species diversified to occupy environments ranging from subsurface cryopelagic habitats to the deep sea and many *Trematomus* species likely have circumpolar distributions. Here, we analyzed life history traits of the notothen *Trematomus scotti* from two distinct geographic areas: Andvord Bay, a fjord on the Western Antarctic Peninsula, and the Weddell Sea at the edge of pack ice zones. These two populations inhabit drastically different areas with important differences in environmental conditions driven by latitude, temperature and ice cover, thus enabling the study of the effects of the environment on life history traits. We first found no evidence for substantial genetic heterogeneity based on the mitochondrial marker *mt-co1*. Fish in Andvord Bay, however, grew faster and reached longer sizes than congeners in the Weddell Sea. Furthermore, females in Andvord Bay had higher fecundity but produced smaller eggs compared to females in the Weddell Sea. Thus, these two populations of *T. scotti* displayed distinct life histories likely in response to local environmental conditions. Local life history traits such as these are crucial to consider to evaluate the vulnerability of a species to environmental change.

### 1. Introduction

Antarctic notothenioids, or cryonotothenioids, form a remarkable adaptive radiation of over 100 species (Eastman and Eakin, 2021) that diversified in the Southern Ocean over the past ~10 million years (Bista

et al., 2023). This success was due in part to the innovation of antifreeze glycoproteins that enabled them to inhabit the icy Antarctic waters (Chen et al., 1997). Among cryonotothenioids, the genus *Trematomus*, which includes small to medium-sized fish, further diversified into 15 species that inhabit disparate environments. For example,

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*T. borchgrevinki* inhabits subsurface cryopelagic habitats, and *T. loennbergii* and *T. lepidorhinus* are able to live at depths greater than 1000 m (Eastman, 2017). Many species in the genus may also have circumpolar distributions from the lower latitudes along the southern Scotia Arc to the high latitudes of the seasonal and permanent pack ice zones in the Ross and Weddell Seas (Duhamel et al., 2014; Eastman, 2024).

The biology and life history of about a third of notothenioid fishes have been studied, however, usually from specimens from a single location (See La Mesa and Eastman, 2023). Thus, the study of life histories across populations of the same species living in different habitats is often lacking. Life history traits in polar fishes strongly depend on latitude, depth, and temperature, however (e.g., Kock and Kellermann, 1991; Forster et al., 2020; La Mesa and Eastman, 2023). Furthermore, while many cryonotothenioids have extended to circumpolar distributions, including some *Trematomus* species, we lack information on connectivity between populations for the vast majority of them. The length of the pelagic larval phase and specialization for particular habitats can play important roles in the differentiation of populations, and thus have an effect on the genetic structure of a species (e.g., Van de Putte et al., 2012). Therefore, we do not know if life history traits observed at one limited geographic area can be extrapolated to the entire species range, which may be discontinuous and may vary in environmental conditions such as depth, temperature, trophic network, sea ice coverage, and solar illumination. Among cryonotothenioids, these abiotic factors tend to influence the growth and reproductive strategy of individual species, with high-latitude species generally growing slower, maturing later, and producing fewer but larger eggs compared to lower-latitude species (Kock and Kellermann, 1991; La Mesa et al., 2021; La Mesa and Eastman, 2023). Accounting for disparities in life history strategies and population connectivity across a species' distribution range is, however, crucial to evaluate the vulnerability of a species and its various populations to environmental change and direct anthropogenic pressures to motivate sustainable management and conservation policies (Caccavo et al., 2021; Maschette et al., 2024). Indeed, a population that would be genetically, morphologically, or physiologically different from other populations of the same species could stimulate protection efforts by creating an Antarctic Specially Protected Area (ASP) (Burrows et al., 2023; Hughes et al., 2013), by advocating to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for localized fishing regulations on the krill fishing industry that might capture the larvae of the sensitive or divergent population as by-catch (Brooks et al., 2022; Corso et al., 2024), or by designating the species as an Antarctic Specially Protected Species (Hughes et al., 2024).

In this context, we analyzed the life history traits of the notothen *Trematomus scotti* (Boulenger, 1907) from two distinct geographic areas: from Andvord Bay, a fjord on the Western Antarctic Peninsula (WAP), and from the Filchner Trough in the Weddell Sea at the edge of pack ice zones. These two populations inhabit drastically different areas with important differences in environmental conditions driven by latitude, temperature and ice cover, thus enabling the study of the effects of the environment on life history traits. We hypothesized that these two populations of *T. scotti* have evolved distinct life histories in response to the local environmental conditions that they experience. To test this hypothesis, we first analyzed the population genetic structure of the species from the two study areas to see if they exhibited major genetic differences and then compared important life history traits between the two populations, including age structure, growth patterns, and reproductive biology.

## 2. Methods

### 2.1. Collection of specimens

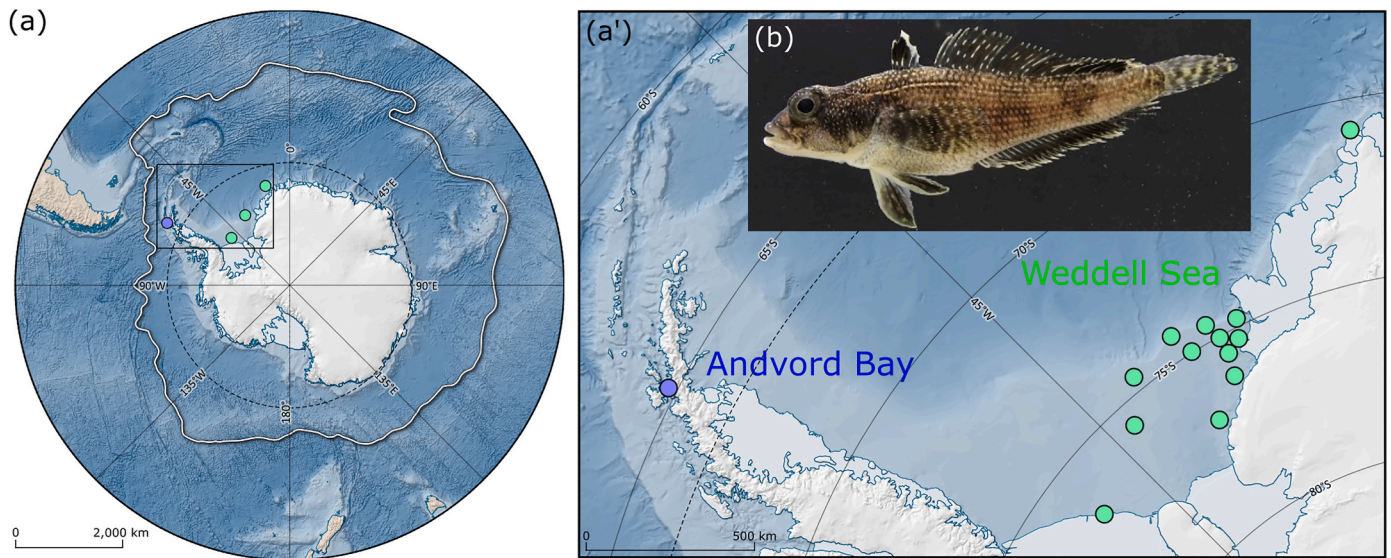
Off the WAP, 66 *Trematomus scotti* specimens (27 females and 39 males) were captured in Andvord Bay (AB) (64°50'S–62°39'W) by

bottom trawl from the ARSV *Laurence M. Gould* (Fig. 1) on the night of May 29th to May 30th, 2018, at a depth of 380–400 m, as previously described (Desvignes et al., 2022). Many specimens captured that night exhibited skin xenomas caused by the unicellular X-cell parasite *Notoxcellia coronata* (Desvignes et al., 2022). Only specimens with no apparent X-cell infection were included in the present study. Water currents in Andvord Bay are typically slow allowing limited water exchange with the outer shelf in the Gerlache and Bransfield Strait where the Antarctic Peninsula Coastal Current (APCC) flows northwards (Moffat and Meredith, 2018; Ziegler et al., 2020b). In Andvord Bay, the greatest water mass exchanges have been associated with episodic katabatic wind events, which have been shown to efficiently flush the upper layer waters, but to have little influence on deep waters in the inner bay where the *T. scotti* specimens were caught (Lundesgaard et al., 2019). These environmental conditions in turn make Andvord Bay a hotspot of benthic biodiversity and biomass (Grange and Smith, 2013) due to substantial organic carbon transfer from the water column to the benthos (Ziegler et al., 2020a). To assess conditions at the time of sampling, we measured bottom temperatures in Andvord Bay using a DST centi-TD Miniature Temperature and Depth Data Logger (Star-Oddi, Garðabær, Iceland) mounted on one of the two otter boards of the fishing net (Desvignes et al., 2022).

A few notothenioid larvae were captured with a 500- $\mu$ m mesh net mounted on a two-by-two meter frame lowered to approximately 75 m and brought back up in Andvord Bay on April 18th, 2014, as previously described (Desvignes et al., 2020). Larvae were immediately euthanized in an MS-222 sea water solution at 250 mg/L, fixed in 1 % paraformaldehyde (PFA) for 1 h, washed in 100 mM Tris pH 7.5, then progressively dehydrated in increasing ethanol solutions, and stored at room temperature in 80 % ethanol until further analysis. Among the notothenioid larvae captured that night, three were subsequently identified as *T. scotti* based on the descriptions and keys in Efremenko (1983) and Kellermann (1990).

In the Weddell Sea (WS), 172 specimens of *T. scotti* (100 females and 72 males) were collected by bottom trawl during two R/V *Polarstern* cruises on the continental shelf of the south-eastern Weddell Sea from January 3rd to February 17th, 2014 (PS82) and from December 24th, 2015, to January 21st, 2016 (PS96). Samples were collected on a total of 18 (PS82) and 9 (PS96) stations located between 70°53'S–11°07'W and 76°42'S–52°04'W (Fig. 1), at depths ranging from 261 to 649 m and from 293 to 623 m, respectively. Due to large variation in the number of fish captured at each site (17 sites yielding five or fewer specimens and 13 sites having specimens of only one or the other sex), it was not possible to study population variability at different sites within the Weddell Sea, thus all specimens were combined into a single broad Weddell Sea population. The sampling area, encompassing mainly the north-eastern flank of the Filchner Trough, is characterized by Warm Deep Water (WDW) up-flowing from the deep Weddell Basin and, further south, by Modified Warm Deep Water (MWDW). Compared to the Ice Shelf Water (ISW), coming from the south under the Filchner Ice Shelf and flowing into the Filchner Trough, the WDW and MWDW are relatively warm and productive with temperature ranging between  $-1$  and  $0.5$  °C (Schroder et al., 2014, 2016).

For each fish from each population, the total weight (TW), standard length (SL), sex, and gonad weight were recorded. We used the standard length because the total length of 12 of 66 specimens from Andvord Bay was unfortunately not reported at dissection and some animals had eroded caudal fins. Because these fish represent almost a fifth of the Andvord Bay samples, which is already lower than in the Weddell Sea given that many fish in Andvord Bay had parasitic xenomas (Desvignes et al., 2022), we thus decided to use the SL for which all specimens had a reported measurement. From each fish, a piece of muscle or fin clip was preserved in 70–95 % ethanol for subsequent molecular analyses, and a fragment of gonad was preserved in Bouin's or Dietrich's fixative for histological analyses. Sagittal otoliths were also removed from the cranial cavity and stored dry in vials for further analysis.

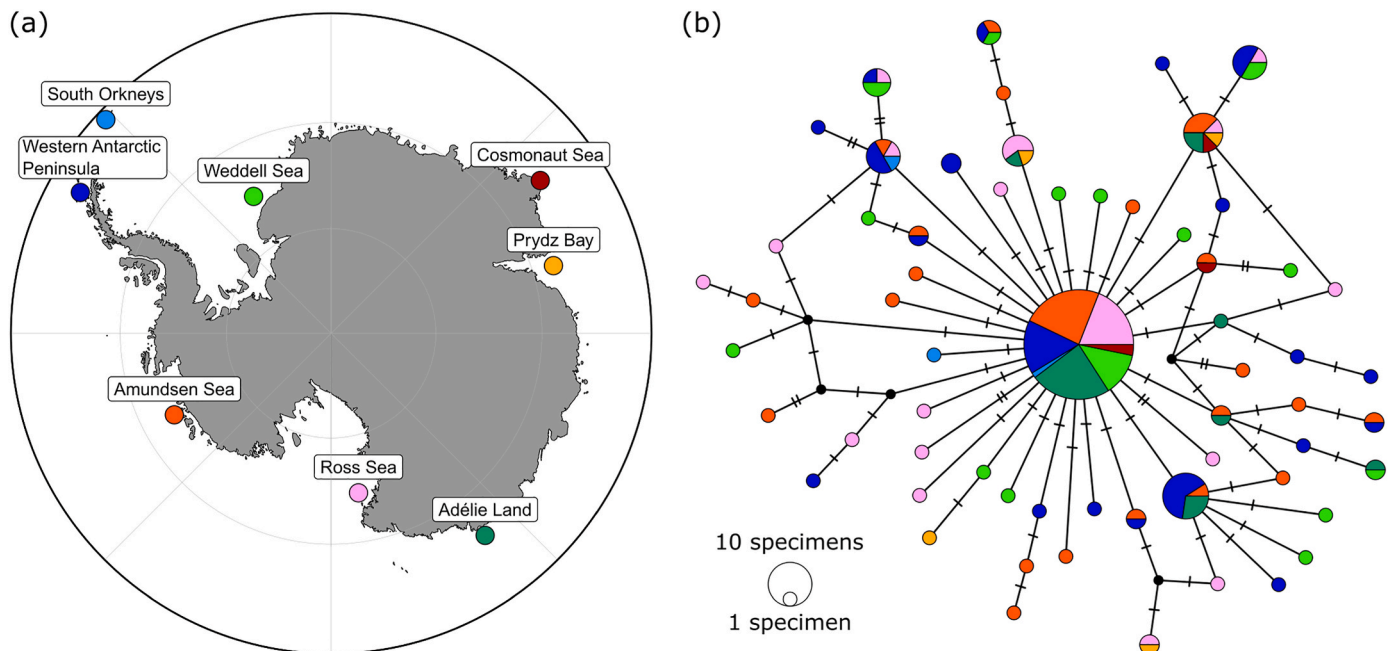


**Fig. 1.** Capture locations of *Trematomus scotti* specimens. (a) In the context of the entire Antarctic continent; (a') focused on the Antarctic Peninsula and the Weddell Sea. (b) A female *Trematomus scotti* specimen from Andvord Bay. The white line in (a) represents the Polar Front, and the dashed line in (a-a') represents the Antarctic Circle. Capture locations in Andvord Bay and the Weddell Sea are represented by blue and green dots, respectively. The maps were generated with Quantarctica v.3.2 (Matsuoka et al., 2021). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

All procedures on the ARSV *Laurence M. Gould* were performed according to protocols approved by the Institutional Animal Care and Use Committees (IACUC) of the University of Oregon (#13-27RRAA). Sample collection during the cruises with R/V *Polarstern* was approved by the competent German authority for Antarctic research, the UBA (Umweltbundesamt), under permits I 3.5-94003-3/308 (PS82) and II 2.8-94003-3/346 (PS96) and all procedures were performed according to and within laws, guidelines and policies of the German and European Animal Welfare legislations.

2.2. Genetic analysis

DNA from 20 specimens from each of the two populations was extracted using Qiagen DNeasy Blood & Tissue Kit following manufacturer's instructions, and the mitochondrial marker *mt-co1* (cytochrome c oxidase I, mitochondrial) was amplified as previously described in Desvignes et al. (2019) and in Ivanova et al. (2007). In brief, 1 µl of DNA extract was combined with 1 µl of forward and reverse primers at 10 µM each, 10 µl of PCR Master Mix, 13 µl of ultra-pure water, and 0.1 µl of Taq polymerase. The resulting mix was subjected to 2 min at 94 °C,



**Fig. 2.** *Trematomus scotti* mitochondrial genetic diversity. (a) The origin of the sequences combined by broad geographic areas is labeled and color-coded on the map. (b) In the haplotype network of the mitochondrial marker *mt-co1* (cytochrome c oxidase I, mitochondrial), sequences generated in this study and recovered from GenBank, each circle represents a haplotype. The size of the circles is proportional to the number of sequences that share that haplotype. Tick marks on the lines connecting the circles represent the number of nucleotide changes between haplotypes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

followed by 36 cycles of 30 s at 94 °C, 30 s at 56 °C, and 60 s at 72 °C, and finished by 5 min at 72 °C until holding at 4 °C. Successful DNA amplifications were verified by running 5 µl of each sample on a 3 % agarose gel. PCR amplicons were Sanger sequenced either in one direction by Eurofins Genomics ([www.eurofinsgenomics.eu](http://www.eurofinsgenomics.eu)) for the Weddell Sea specimens using the primer M13F (Ivanova et al., 2007), or in both directions by Genewiz (Cambridge, MA, USA) for the Andvord Bay specimens using the *mt-co1* primer pair from Desvignes et al. (2019). The two different sequencing strategies produced amplicons of similar size that covered the same region of the *mt-co1* gene. Resulting sequences were assembled and trimmed to a final length of 643 nucleotides using BioEdit v.7.7.1 (Hall, 1999) and verified for accurate species identification by alignment to the NCBI GenBank nucleotide sequence collection. An additional 127 *T. scotti mt-co1* sequences from GenBank and published articles from individuals captured around Antarctica (Fig. 2a) were added to the analysis (Cao et al., 2022; Dettai et al., 2011; Lautredou et al., 2010; Li et al., 2022, 2024; Mabragaña et al., 2016; Rock et al., 2008; Smith et al., 2012). Each sequence was assigned to one of eight broader geographic areas: Western Antarctic Peninsula, Amundsen Sea, Ross Sea, Adélie Land, Prydz Bay, Cosmonaut Sea, Weddell Sea, and South Orkneys. All 167 *mt-co1* sequences were aligned using MAFFT v.7.526 (Katoh et al., 2019). The resulting 652 nucleotide-long alignment was manually inspected for alignment errors before proceeding to downstream analyses.

Descriptive statistics (number of segregating sites  $S$ , number of haplotypes  $h$ , haplotype diversity  $H_d$ , and nucleotide diversity  $\pi$ ) for each geographic region were obtained with DNAsp v.6.12.03 (Rozas et al., 2017). Pairwise  $F_{ST}$  indices of genetic differences between geographic areas and corresponding  $p$ -values were calculated with Arlequin v.3.5.2.2 (Excoffier and Lischer, 2010) based on 10,000 permutations. Multiple testing correction was performed in R using the  $p.adjust$  function and Benjamini-Hochberg procedure, and genetic differences were considered significant at  $p$ -value  $\leq 0.01$ . A haplotype network was built with PopART v.1.7 (Leigh and Bryant, 2015) using the TCS algorithm (Clement et al., 2002) to visually display sequence variability and reveal potential haplogroups reflecting population structure.

### 2.3. Demographic and morphological analyses

The sex ratio in each population was tested for departure from a balanced 1:1 ratio using a Chi-square goodness of fit test.

The size frequency distributions for each sex in each population were compared using a two-sided  $t$ -test after verifying applicability with Levene's and Shapiro-Wilk tests.

The influence of each variable (i.e., SL, sex, and fish origin) and all their interactions on the fish TW was assessed using a stepwise model approach pruning the model at each step from the most non-significant parameter determined by an ANOVA until only significant parameters remained. Length-weight relationships were then calculated separately for each population as  $TW = a SL^b$ , where the TW is in grams and the SL in centimeters. The allometric indices  $b$  were then compared between populations using an  $F$ -test and checked for isometry (i.e.,  $b = 3$ ).

The Fulton's condition factor  $K$  was calculated for each fish in the form of  $K = 100 \times TW/SL^b$  and analyzed separately in each population to verify its independence from SL before comparing the two populations using a non-parametric Welch's  $t$ -test because the equality of variances between populations was not verified.

### 2.4. Age and growth analyses

For each specimen, one randomly selected sagittal otolith was burned to enhance the contrast between growth rings (Christensen, 1964) and then sectioned to reveal the inner pattern. Based on previous studies on ageing nototheniids (e.g., Cali et al., 2017; La Mesa et al., 2018) and to enhance the contrast between growth rings, otoliths were burned for few minutes (depending on the otolith size) in an oven at

350 °C until they reached an amber color. Transverse sections were obtained by grinding otoliths on abrasive papers and polished with alumina powder on a lapping machine to eliminate scratches. Presumed annuli consisting of contiguous opaque and translucent zones were counted using a stereomicroscope. The age was estimated after two blind readings made by a single reader a week apart, assuming one ring per year (North, 1988). Precision of age estimates was assessed by calculating the average percentage error (APE) and the mean coefficient of variation ( $CV_{mean}$ ) between the readings (Beamish and Fournier, 1981; Chang, 1982). The small values of precision indices APE and  $CV_{mean}$  (4.3 % and 4.8 %, respectively) confirmed good consistency between paired readings.

Age-length data pairs were fitted to the von Bertalanffy growth model for each sex in each population. To overcome the lack of the first year age classes in both samples and to obtain a reliable fitting of the starting point of growth curves, we applied the von Bertalanffy growth model to the length-at-age data pairs in the form:  $L = L_{\infty} - (L_{\infty} - L_0) e^{-kt}$ , where  $L$  is the SL (cm),  $L_{\infty}$  is the asymptotic length,  $L_0$  is the hatching size (cm),  $k$  is the Brody growth rate coefficient ( $\text{year}^{-1}$ ), and  $t$  is the age (years) (Cailliet et al., 2006). We assumed a size at hatch of 0.9 cm, as reported in a previous study focusing on larval stages of this species in the Bransfield Strait (La Mesa et al., 2015). The fitting was made by non-linear equations using the least squares method, implemented by the PALEontological Statistics software (PAST, version 4.17) (Hammer et al., 2001). Considering different combinations of growth parameters, alternative models were fitted to the data and compared using the Akaike Information Criterion (AIC) (Akaike, 1974). Growth parameter estimates were compared using likelihood ratio tests (Kimura, 1980). Growth performance was calculated as  $\Phi' = 2 \log L_{\infty} + \log k$ , where the asymptotic length  $L_{\infty}$  (cm) and the Brody growth rate coefficient  $k$  are the von Bertalanffy growth parameters (Pauly and Munro, 1984).

### 2.5. Reproductive analyses

To estimate reproductive investment, the gonadosomatic index, which is the proportion of gonad to TW ( $GSI = \text{gonad weight}/TW \times 100$ ), was calculated for both sexes and both locations, and then compared between locations with a Welch  $t$ -test because of a lack of normality in the data.

From females in advanced stage of oogenesis, oocytes from a subsample of fixed ovaries were separated from the stroma, imaged under a stereomicroscope, and their diameters measured using ImageJ (Schneider et al., 2012) or IMAQ Vision Builder 6 software ([www.ni.com](http://www.ni.com)).

The absolute fecundity, as the number of vitellogenic oocytes per female, and relative fecundity, as the number of vitellogenic oocytes per gram of TW, were estimated for these females by a gravimetric method (Murua and Saborido-Rey, 2003). The effects of SL and fish origin on the absolute and relative fecundities were analyzed using an ANOVA.

For histological analyses, gonads were taken from their fixative solution, washed multiple times in 70 % ethanol, and dehydrated through increasing concentrations of ethanol solution from 70 % to 100 % and put in Histolemon. Each sample was embedded in liquid Paraplast, allowing the tissues to cool and harden to room temperature for 14–16 h before storage in a fridge. Gonad samples were then sectioned in thin slices of 7 µm that were mounted on slides and stained with Harris' hematoxylin and eosin (Pearse, 1985). Stained sections were observed under a Leica DM4000B light microscope at different magnifications to assign the stage of gonad maturity according to Lowerre-Barbieri et al. (2023).

### 2.6. Data availability

Morphometric and genetic data generated and analyzed in this study are all available in a designated repository in the United States Antarctic Program Data Center (USAP-DC Project [p0010221](https://doi.org/10.26007/2151-7613.p0010221)) and deposited in

NCBI GenBank (Acc # [PV090789-PV090828](#)).

### 3. Results

#### 3.1. Population genetic structure

Although the number of *mt-co1* sequences per geographic area varied substantially, thus diminishing the informativeness of the number of segregating sites (*S*) and number of haplotypes (*h*), estimates of haplotype and nucleotide diversity ( $H_d$  and  $\pi$ , respectively) were comparable across geographic areas (Table 1). The *T. scotti* populations tended to share similar trends with high haplotype diversity  $H_d$  and low nucleotide diversity  $\pi$  (Table 1).

Pairwise  $F_{ST}$  estimates of genetic differentiation between populations were highly variable, ranging from 0 to 0.471 (Table 2). The lowest  $F_{ST}$  values were associated with comparisons involving specimens from Prydz Bay (PB) or from the South Orkney Islands (SO), two geographic areas with the fewest sequences, thus decreasing  $F_{ST}$  reliability (Table 2). Similarly,  $F_{ST}$  comparisons involving the four specimens from the Cosmonaut Sea (CS) are likely unreliable due to low specimen number (Table 2). All the other pairwise comparisons were statistically significant, even between neighboring geographic areas such as in the Western Antarctic Peninsula (WAP) vs. Amundsen Sea (AS) or the Ross Sea (RS) vs. Adélie Land (AL) population comparisons (Table 2).

From the haplotype network, no patterns of clusters or groups of specimens stood out (Fig. 2). The network, instead, displays a star-like shape, with one central allele and many rare haplotypes, differing by one or a few substitutions. The most frequent haplotype was shared by all locations except Prydz Bay, from where only four sequences were available, and less frequent alleles were private to one or a few locations (Fig. 2).

#### 3.2. Fish size and sex ratio

Overall, fish from Andvord Bay were significantly longer than fish in the Weddell Sea ( $t = 9.15$ ,  $df = 236$ ,  $p < 0.001$ ) and reached a longer maximum size (Fig. 3a). In Andvord Bay, fish ranged from 9.3 to 17.2 cm SL ( $n = 66$ ; Mean  $\pm$  SD =  $12.4 \pm 1.54$  cm), while they ranged from 6.0 to 14.0 cm SL in the Weddell Sea ( $n = 172$ ; Mean  $\pm$  SD =  $10.3 \pm 1.59$  cm) (Fig. 3a).

The sex ratio in the Weddell Sea deviated from a 1:1 ratio, with significantly more females than males (100 females and 72 males;  $\chi^2 = 4.56$ ,  $df = 1$ ,  $p = 0.03$ ). In contrast, the sex ratio in Andvord Bay was not significantly different from 1:1 (27 females and 39 males;  $\chi^2 = 2.18$ ,  $df = 1$ ,  $p = 0.14$ ), however, only a subset of all specimens captured in Andvord Bay were analyzed. Because the sample size at both locations remains limited, it is, however, not excluded that the Andvord Bay population deviates from a 1:1 ratio as in the Weddell Sea, or that both populations show a balanced sex ratio.

**Table 1**

*Trematomus scotti* population genetics descriptive statistics.

Geographic Area	Number of sequences (N)	Number of segregating sites (S)	Number of haplotypes (h)	Haplotype diversity ( $H_d$ )	Nucleotide diversity ( $\pi$ )
Adélie Land (AL)	24	7	7	0.605	0.160
Amundsen Sea (AS)	38	32	25	0.937	0.426
Western Antarctic Peninsula (WAP)	40	31	23	0.944	0.430
Cosmonaut Sea (CS)	4	2	3	0.833	0.153
Prydz Bay (PB)	4	8	4	1.000	0.613
Ross Sea (RS)	30	30	19	0.908	0.442
South Orkneys (SO)	3	4	3	1.000	0.409
Weddell Sea (WS)	24	27	15	0.891	0.520

#### 3.3. Length-weight relationships

In Andvord Bay, females ranged from 10.7 to 17.2 cm SL and from 25.8 to 89.9 g TW, and males ranged from 9.3 to 14.2 cm SL and from 12.5 to 54.1 g TW (Fig. 3b). In the Weddell Sea, females ranged from 6.0 to 14.0 cm SL and from 2.8 to 45.0 g TW and males ranged from 6.0 to 12.5 cm SL and from 2.8 to 28.0 g TW (Fig. 3b). The length-frequency distributions differed significantly between sexes at both locations with females attaining larger sizes than males (AB:  $t = 3.75$ ,  $df = 64$ ,  $p < 0.001$ ; WS:  $t = 3.47$ ,  $df = 170$ ,  $p < 0.001$ ) (Fig. 3b).

Using a pruning approach to model fish TW by SL, sex, geographic origin, and their interactions, we found that only SL and geographic origin significantly influenced fish TW ( $p < 0.001$  for both SL and fish origin). In contrast, sex did not influence TW ( $F = 0.16$ ;  $df = 1$ ,  $p = 0.69$ ), thus, no sex distinctions were made. Length-weight relationships were summarized with the following equations (Fig. 4a):

$$TW_{AB} = 0.00927 SL^{3.27} \text{ in 66 fish from Andvord Bay.}$$

$$TW_{WS} = 0.00734 SL^{3.30} \text{ in 172 fish from the Weddell Sea.}$$

Somatic growth was allometric in both populations (Fig. 4a) (AB:  $t = 2.88$ ,  $df = 64$ ,  $p = 0.005$ ; WS:  $t = 4.15$ ,  $df = 170$ ,  $p < 0.001$ ). The allometric index  $b$  did not differ between populations ( $F = 0.03$ ,  $df = 1$ ,  $p = 0.85$ ).

The Fulton's condition factor  $K$  was not influenced by the fish SL (AB:  $t = -0.051$ ,  $df = 64$ ,  $p = 0.96$ ; WS:  $t = -0.215$ ,  $df = 170$ ,  $p = 0.83$ ), however, fish from Andvord Bay had a significantly higher Fulton's condition factor  $K$  compared to fish from the Weddell Sea ( $K_{AB} = 0.93$ ,  $K_{WS} = 0.74$ ;  $t = 14.12$ ,  $df = 149.84$ ,  $p < 0.001$ ) (Fig. 4b).

#### 3.4. Age and growth

Assuming one year per annulus in fish otoliths (Fig. 5a), specimens from Andvord Bay ranged from 5 to 24 years old and specimens from the Weddell Sea ranged from 6 to 26 years old. Notably, while in Andvord Bay males and females had comparable age ranges (males: 5–24 years old, females: 6–24 years old), in the Weddell Sea, older individuals tended to be males rather than females (males: 6–26 years old, females: 7–18 years old).

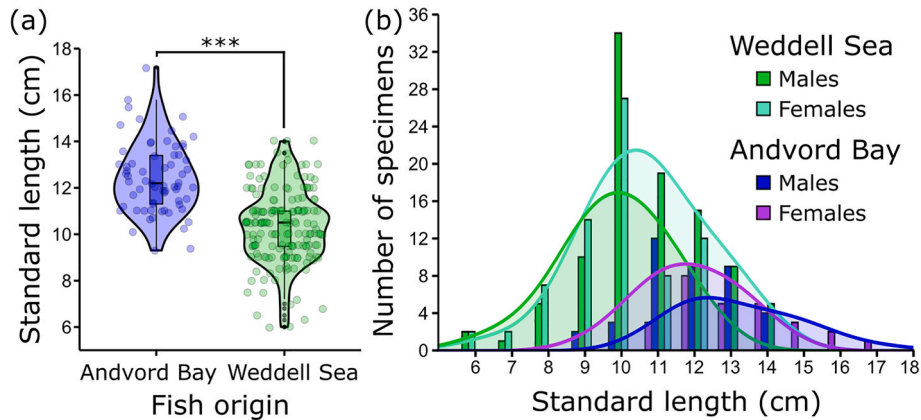
The von Bertalanffy growth model was applied separately for each population and each sex (Fig. 5b). The von Bertalanffy growth parameters, growth performance indexes, and significant differences in model parameters between sexes and populations are summarized in Tables 3–5.

The asymptotic length ( $L_\infty$ ) was significantly greater in females compared to males in Andvord Bay population (Tables 3–4). The overall  $L_\infty$  of fish from Andvord Bay was also significantly greater than that of Weddell Sea fish (Tables 3–4), consistent with the longer *T. scotti* maximum length observed in Andvord Bay compared to the Weddell Sea. The Brody growth rate coefficient  $k$ , however, did not differ between sexes in either population (Tables 3–4), although it was significantly greater in Andvord Bay compared to the Weddell Sea (Tables 3–4), consistent with fish from Andvord Bay growing faster than fish from the Weddell Sea (Fig. 5b). The growth performance index  $\Phi'$

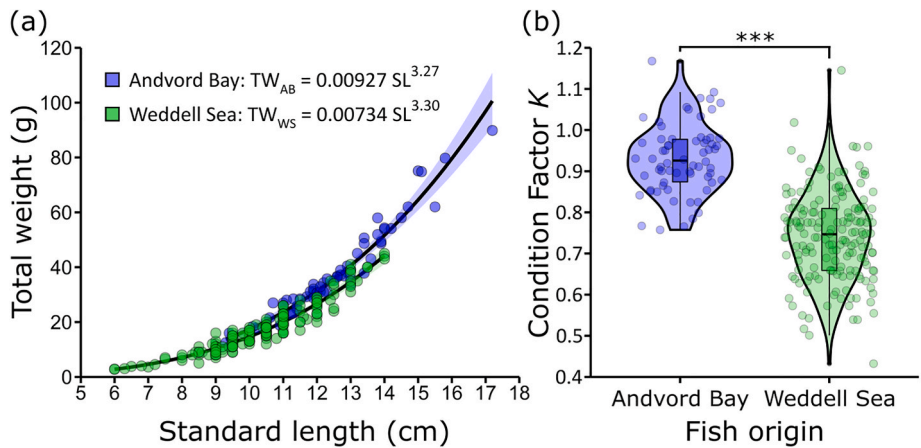
**Table 2**

Pairwise  $F_{ST}$  estimates of genetic differentiation between *Trematomus scotti* populations from eight different geographic areas based on the mitochondrial marker *mt-co1*. Pairwise  $F_{ST}$  estimates are provided below the diagonal and associated  $p$ -values above the diagonal. Negative  $F_{ST}$  were converted to zero. Significant  $F_{ST}$  and  $p$ -values after Benjamini-Hochberg correction are in bold. Geographic areas are shown in Fig. 2.

Geographic Area	N	AL	AS	WAP	CS	PB	RS	SO	WS
Adélie Land (AL)	24	*	< 0.001	< 0.001	0.167	0.217	< 0.001	0.256	<b>0.010</b>
Amundsen Sea (AS)	38	<b>0.202</b>	*	< 0.001	<b>0.001</b>	0.409	<b>0.007</b>	0.464	< 0.001
Western Antarctic Peninsula (WAP)	40	0.177	<b>0.287</b>	*	0.036	0.069	< 0.001	0.216	< 0.001
Cosmonaut Sea (CS)	4	0.027	<b>0.230</b>	0.198	*	0.030	<b>0.007</b>	0.029	0.075
Prydz Bay (PB)	4	0.007	0.006	0.172	0.259	*	0.640	0.888	0.055
Ross Sea (RS)	30	<b>0.174</b>	<b>0.022</b>	<b>0.250</b>	<b>0.166</b>	0.000	*	0.482	< 0.001
South Orkneys (SO)	3	0.000	0.000	0.141	0.394	0.000	0.000	*	0.083
Weddell Sea (WS)	24	<b>0.139</b>	<b>0.471</b>	<b>0.209</b>	0.243	0.244	<b>0.424</b>	0.213	*



**Fig. 3.** *Trematomus scotti* standard length (SL) distributions in each population. (a) With both sexes combined and (b) separated by sex in Andvord Bay and the Weddell Sea. \*\*\* denotes  $p < 0.001$ .



**Fig. 4.** *Trematomus scotti* Length-Weight relationship and Fulton's condition factor  $K$ . (a) Total weight (TW) to standard length (SL) relationships and associated equations for each population. (b) The Fulton's condition factor  $K$  for each population. \*\*\* denotes  $p < 0.001$ .

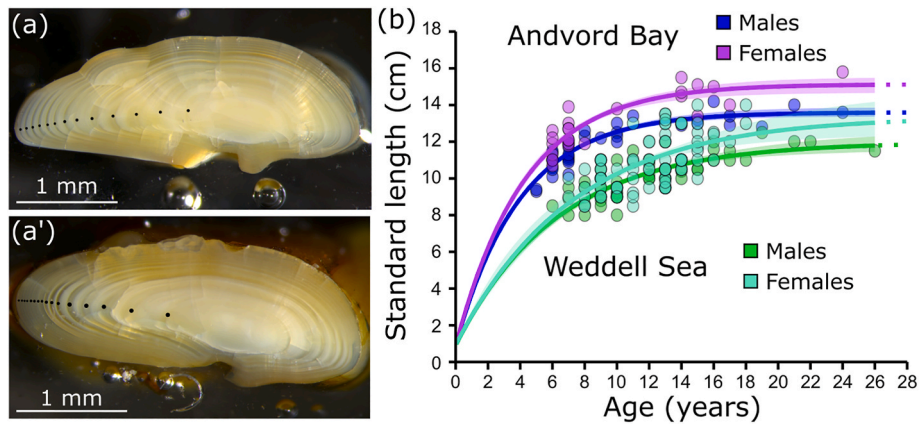
was greater in females than in males in both areas and was greater in fish from Andvord Bay compared to fish from the Weddell Sea (Tables 3–4). Together, the von Bertalanffy growth models without constraints (i.e., those with no common parameters) were the best fitted models in both areas and for both sexes and populations based on Akaike Information Criterion (Table 5).

**3.5. Reproductive characteristics**

As commonly reported in fish, gonadal reproductive investment (i.e., GSI) in females was higher than in males in both populations (Fig. 6a and b). As expected, because fish progress in their reproductive cycle

between February and May, the GSI was also significantly higher in fish from Andvord Bay in May compared to fish from the Weddell Sea in February for both sexes (Fig. 6a and b). The GSI of males ranged from 0.04 to 0.37 % and from 0.14 to 0.73 % in the Weddell Sea and in Andvord Bay, respectively (Fig. 6a,  $t = 7.21$ ,  $df = 45.9$ ,  $p < 0.001$ ). The GSI of females ranged from 0.05 to 4.15 % in January–February in the Weddell Sea and from 7.11 to 11.40 % at the end of May in Andvord Bay (Fig. 6b,  $t = 30.05$ ,  $df = 49.4$ ,  $p < 0.001$ ).

Females at both locations exhibited group-synchronous ovarian development, with two groups of developing oocytes: a group of small previtellogenic oocytes that will mature in a future reproduction season, and a group of larger vitellogenic oocytes that were maturing



**Fig. 5. *Trematomus scotti* age and standard length.** (a) Representative images of a transverse section of a burned sagittal otolith of a 13-year-old female (13.5 cm SL) from the Weddell Sea and (a') of a 16-year-old female (15 cm SL) from Andvord Bay. Inner growth rings are labeled with black dots. (b) The von Bertalanffy growth model was applied separately for each population and each sex.

**Table 3**

The von Bertalanffy growth parameters ( $L_{\infty}$ ,  $k$ ,  $L_0$ ) and growth performance index ( $\Phi'$ ) estimated for both populations and both sexes of *Trematomus scotti* in each investigated area.

Growth parameters	Andvord Bay			Weddell Sea		
	Males (n = 36)	Females (n = 24)	Both sexes (n = 60)	Males (n = 56)	Females (n = 83)	Both sexes (n = 172)
$L_{\infty}$	13.60	15.13	14.23	11.98	13.36	12.69
$k$	0.25	0.23	0.24	0.16	0.14	0.15
$L_0$	0.9	0.9	0.9	0.9	0.9	0.9
$\Phi'$	3.82	3.98	3.89	3.12	3.21	3.18

**Table 4**

Comparisons of the von Bertalanffy growth parameters ( $L_{\infty}$ ,  $k$ ) estimated for *Trematomus scotti* by the likelihood ratio test. Significant differences in models are highlighted in bold.

Area comparison	Andvord Bay		Weddell Sea		Andvord Bay & Weddell Sea	
	between sexes		between sexes		between populations	
$L_{\infty}$	<b>16.89</b>	<b>0.000</b>	3.30	0.069	<b>9.20</b>	<b>0.002</b>
$k$	0.42	0.514	0.50	0.475	<b>17.92</b>	<b>0.000</b>
$L_{\infty}$ & $k$	<b>40.29</b>	<b>0.000</b>	<b>16.97</b>	<b>0.000</b>	<b>191.37</b>	<b>0.000</b>

synchronously and would have been spawned during the upcoming spawning season (Fig. 6c and d). In Andvord Bay, the small previtellogenic oocyte diameter centered around 0.15–0.2 mm, while the larger vitellogenic oocytes centered around 0.85–0.9 mm with the maximum oocyte diameter observed being 1.03 mm (Fig. 6c). In the Weddell Sea, the small previtellogenic oocyte diameter centered around 0.2–0.25 mm, while the larger vitellogenic oocytes centered around 0.8–0.85 mm with the maximum oocyte diameter observed being 1.10 mm (Fig. 6d).

The absolute fecundity, which is independent of the season, was significantly greater in females from Andvord Bay compared to females from the Weddell Sea ( $F = 34.61$ ,  $df = 1$ ,  $p < 0.001$ ) (Fig. 6e). The absolute fecundity of females from the Weddell Sea ranged from 1,312 to 4,961 oocytes per female (Mean  $\pm$  SD = 2,866  $\pm$  1,158 oocytes/female), while it ranged from 3,090 to 8,217 oocytes per female in fish from Andvord Bay (Mean  $\pm$  SD = 5,224  $\pm$  1,620 oocytes/female). In both populations, the absolute fecundity significantly increased with the fish SL (AB:  $t = 9.71$ ,  $df = 16$ ,  $r^2 = 0.85$ ,  $p < 0.001$ ; WS:  $t = 7.83$ ,  $df = 29$ ,  $r^2 = 0.68$ ,  $p < 0.001$ ) (Fig. 6e).

In contrast, relative fecundities were comparable in females from Andvord Bay and from the Weddell Sea ( $F = 2.00$ ,  $df = 1$ ,  $p = 0.16$ ) (Fig. 6f) at 125  $\pm$  20.1 eggs per gram of fish in Andvord Bay and 117  $\pm$  32 eggs per gram in fish from the Weddell Sea. In Andvord Bay, the relative fecundity of females slightly but significantly decreased with length ( $t = -2.61$ ,  $df = 16$ ,  $r^2 = 0.30$ ,  $p = 0.019$ ), while in the Weddell Sea, the relative fecundity of females was not influenced by the fish length ( $t = -0.28$ ,  $df = 29$ ,  $r^2 = 0.002$ ,  $p = 0.78$ ).

Histological analysis of gonads was performed on a subsample representing the entire fish length range sampled and included 24 females and 31 males from Andvord Bay and 25 females and 17 males from the Weddell Sea.

Following the process of follicle maturation, females were assigned to one of three phases: immature, developing, and mature state (Fig. 7). Females captured in the Weddell Sea in January–February were either at the immature or early developing phase and none were in the late developing or mature phases. The smallest females, measuring less than 9 cm SL, were at an immature stage with ovaries containing only primary growth oocytes (PG) (Fig. 7a). Developing females ranged from an early developing phase, with ovaries containing exclusively PG and cortical alveolar oocytes (CA), to a late developing phase with ovaries filled with PG, CA and vitellogenic oocytes (Vtg) at an early stage of development (Fig. 7b). In contrast, females captured in Andvord Bay at the end of May, were all in a mature state and a spawning event imminent phase with ovaries containing mostly late Vtg with coalescent granules of yolk and early germinal vesicle migration, as well as a few PG and CA oocytes (Fig. 7c).

Males captured in the Weddell Sea in January–February, were at the immature, developing, or regenerating phase (Fig. 8). A single immature male, measuring less than 10 cm SL, had testes containing only spermatogonia (Sg) (Fig. 8a). Developing males had testes containing exclusively Sg and spermatocytes (Sc) (Fig. 8b), while regenerating males had testes with Sg, Sc, and signs of past reproduction with occasionally remains of a few scattered spermatozoa (Spz) (Fig. 8c). In contrast, males captured in Andvord Bay at the end of May, were all at a late developing phase with testes containing mostly Sg and Sc (Fig. 8d).

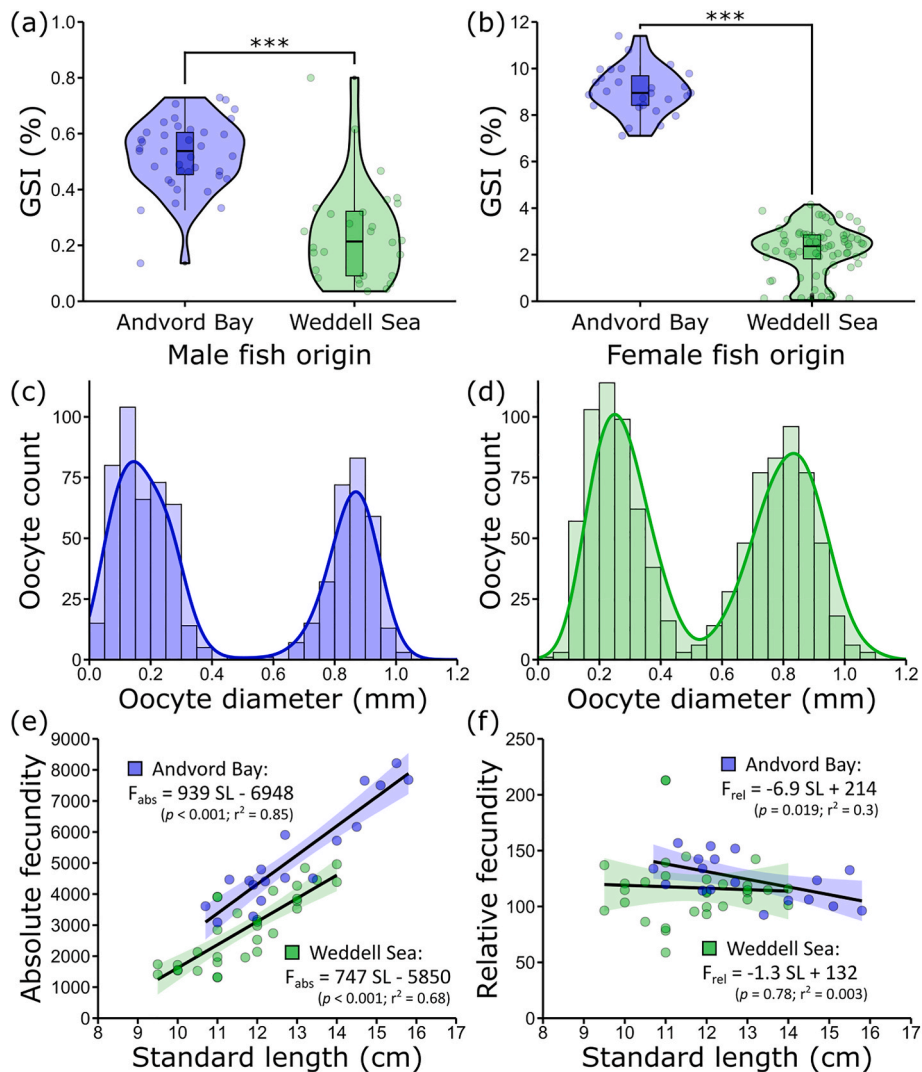
### 3.6. *Trematomus scotti* larvae from Andvord Bay

The three *T. scotti* larvae caught in Andvord Bay on May 18th, 2014, were in post-flexion and measured from 13.9 to 15.4 mm SL (Fig. 9). Based on previous analyses of *T. scotti* larvae collected in the Bransfield Strait (La Mesa et al., 2015), these larvae were possibly around 40–50 days post-hatching, suggesting they may have hatched around mid-February. Given the presumed age of the larvae and the relatively low dispersal of larvae between fjords of the WAP (Ziegler et al., 2020b),

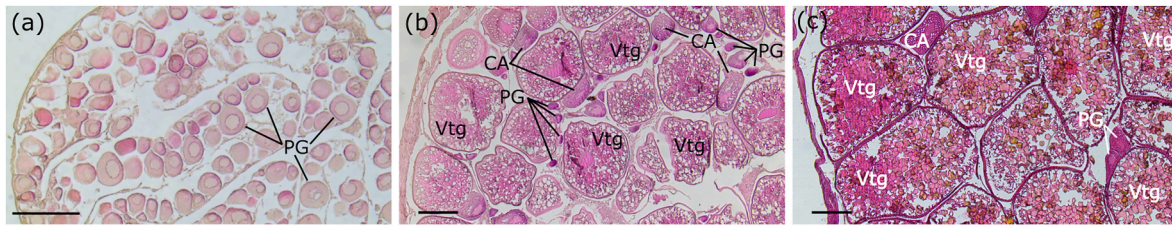
**Table 5**

Fitted von Bertalanffy growth models of *Trematomus scotti* from the two investigated areas compared using Akaike Information Criterion. The lowest AIC is the optimal model (in bold).

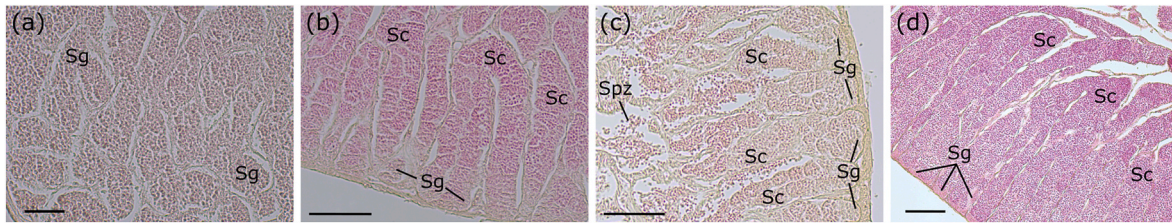
		Females				Akaike Information Criterion		
		Andvord Bay		Weddell Sea		# parameters	AIC	Δ AIC
common parameter	$L_{\infty}$			$L_{\infty}$				
$L_{\infty}$ & $k$		11.82	0.31	11.82	0.31	2	55.37	39.82
$k$		15.94	0.19	12.11	0.19	3	17.25	1.70
$L_{\infty}$		14.74	0.25	14.74	0.10	3	15.56	0.01
<b>none</b>		<b>15.12</b>	<b>0.23</b>	<b>13.35</b>	<b>0.13</b>	4	<b>15.55</b>	<b>0</b>
		Males		Weddell Sea		Akaike Information Criterion		
common parameter	$L_{\infty}$			$L_{\infty}$		# parameters	AIC	Δ AIC
$L_{\infty}$ & $k$		11.37	0.30	11.37	0.30	2	34.82	62.19
$k$		14.11	0.21	11.06	0.21	3	-21.21	6.15
$L_{\infty}$		13.18	0.27	13.18	0.12	3	-23.00	4.36
<b>none</b>		<b>13.60</b>	<b>0.24</b>	<b>11.97</b>	<b>0.15</b>	4	<b>-27.36</b>	<b>0</b>
		Both sexes		Weddell Sea		Akaike Information Criterion		
common parameter	$L_{\infty}$			$L_{\infty}$		# parameters	AIC	Δ AIC
$L_{\infty}$ & $k$		11.68	0.29	11.68	0.29	2	85.21	79.11
$k$		14.89	0.20	11.67	0.20	3	11.88	5.78
$L_{\infty}$		13.82	0.26	13.82	0.11	3	8.09	1.99
<b>none</b>		<b>14.23</b>	<b>0.24</b>	<b>12.68</b>	<b>0.14</b>	4	<b>6.10</b>	<b>0</b>



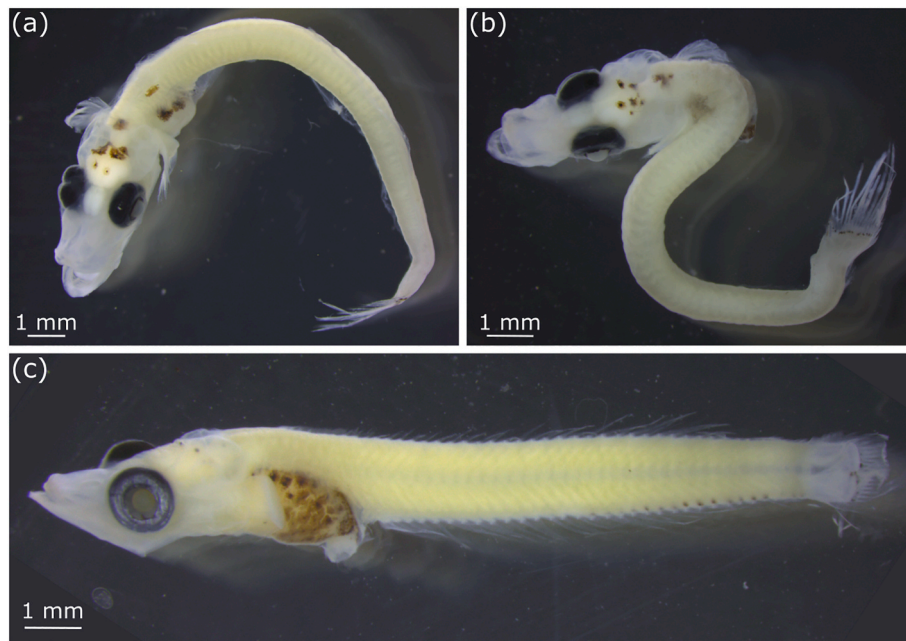
**Fig. 6. *Trematomus scotti* reproductive investment.** Gonadosomatic Index (GSI) in (a) males and (b) females of each population. Oocyte size distributions in maturing females in (c) Andvord Bay and (d) the Weddell Sea. (e) Absolute and (f) relative fecundity to standard length and associated equations in each population. \*\*\* denotes  $p < 0.001$ .



**Fig. 7. *Trematomus scotti* ovary histology.** Representative examples of ovarian development with (a) an immature ovary and (b) a developing ovary from the Weddell Sea, and (c) a spawning-capable ovary from Andvord Bay. Abbreviations: CA: cortical alveolar oocytes; PG: primary growth oocytes; Vtg: vitellogenic oocytes. Scale bars indicate 250  $\mu\text{m}$ .



**Fig. 8. *Trematomus scotti* testis histology.** Representative examples of testicular development with (a) an immature testis, (b) a developing testis, and (c) a regenerating testis from the Weddell Sea, and (d) a developing testis from Andvord Bay. Abbreviations: Sc: spermatocytes; Sg: spermatogonia; Spz: spermatozoa. Scale bars indicate 50  $\mu\text{m}$  in (a) and 100  $\mu\text{m}$  in (b–d).



**Fig. 9.** Three *Trematomus scotti* larvae collected on April 18th, 2014, in Andvord Bay.

it is likely that *T. scotti* reproduces within Andvord Bay and surrounding areas, possibly at the end of winter and early spring, as previously suggested (La Mesa et al., 2015; Shandikov and Faleeva, 1992).

#### 4. Discussion

##### 4.1. Lack of evidence for population genetic structure among populations around the continent

To determine whether life history trait differences between populations can be attributed to environmental differences instead of major genetic differentiation or even cryptic species (Corso et al., 2024; Dornburg et al., 2016), we first evaluated the population genetic

structure of the *T. scotti* species using the mitochondrial marker *mt-co1* from 167 specimens originating from eight broad geographic areas around the Antarctic continent, including 20 specimens from both Andvord Bay and the Weddell Sea that we studied here for morphometry and life history traits.

While the informativeness of the *mt-co1* marker is limited, analysis of its sequence variants did not reveal any clearly individualized populations, thus failing to rule out that *T. scotti* populations are strongly genetically differentiated around the Antarctic continent. Nonetheless, our analyses suggested the presence of genetic differentiation between all studied geographic areas. The haplotype network, however, did not reveal the presence of clusters of sequences. Apart from the locations with too few sequences to be reliable (i.e., Prydz Bay, Cosmonaut Sea,

and South Orkneys with four, four, and three sequences, respectively), the significant differentiation between all other locations is likely due to the presence of many private haplotypes in the different geographic areas rather than a geographic subdivision in the distribution of different haplotypes. Additional specimens and the use of other mitochondrial and nuclear markers or more sensitive genome-wide analyses (e.g., RADseq or low-coverage whole genome sequencing (Lou et al., 2021)) would be necessary to confirm the absence of genetic structure in the species around the continent, or alternatively, reveal the amount of gene flow that may have been occurring between differentiated populations. These preliminary results on *T. scotti* are however in agreement with what was observed in other circum-polar species, including *Pleuragramma antarcticum* (Caccavo et al., 2018), *Akarotaxis nudiceps* (Corso et al., 2024), and *Dissostichus mawsoni* (Ceballos et al., 2021; Maschette et al., 2023).

The star-like shape of the haplotype network, combined with the high haplotype diversity  $H_d$  and low nucleotide diversity  $\pi$ , suggests a recent demographic expansion. This pattern is consistent with what was observed for other Antarctic species (Allcock and Strugnell, 2012; Corso et al., 2024; Díaz et al., 2018; Dornburg et al., 2016; Schiavon et al., 2023; Thatje et al., 2005), for which glaciation oscillations have been shown to have shaped genetic variability by forcing population contractions during glacial expansions and recovery and population growth following glacial retreats. Alternatively, it is also possible that migrations between areas and large-scale egg and larvae dispersal result in low genetic diversity and a panmictic population like is hypothesized for *Dissostichus mawsoni* (Ceballos et al., 2021; Maschette et al., 2023) and for *Pleuragramma antarcticum* (Caccavo et al., 2018), however, given the benthic lifestyle of adult *T. scotti* and therefore its supposed limited dispersal capacity, this alternative appears less likely.

#### 4.2. Lower growth and body condition in the Weddell Sea compared to the Western Antarctic Peninsula

While fish at both locations have comparable age distribution, our morphological analyses revealed that fish from Andvord Bay on the Western Antarctic Peninsula grew heavier and longer than fish from the Weddell Sea and had a greater growth performance index ( $\Phi'$ ). The total weight ranges reported here in Andvord Bay (25.8–89.9 g and 12.5–54.1 g for females and males, respectively) were comparable to those previously reported in the Mawson Sea in East Antarctica, also north of the Antarctic Circle (34–67 g and 27–39 g for females and males, respectively) (Shandikov and Faleeva, 1992). Similarly, maximum specimen sizes in Andvord Bay (17.2 and 14.2 cm SL for females and males, respectively) were similar to those previously reported in the Mawson Sea (17.8 and 17.0 cm total length for females and males, respectively) (Shandikov and Faleeva, 1992). These observations agree with the hypothesis that fish living at higher latitudes have lower growth rates due to colder temperatures (Atkinson, 1994) and that the body size of marine fish species in Antarctica decreases with increasing latitude (Lin and Costello, 2023). Indeed, bottom temperatures measured with loggers attached to the trawls indicated that the bottom temperature in Andvord Bay at the end of May was approximately  $-0.2$  °C (Desvignes et al., 2022) while it was on average  $-1.75$  °C in the Weddell Sea in January and February (Schröder et al., 2016; Schröder and Wisotzki, 2014). Furthermore, fish from Andvord Bay had a greater Fulton's condition factor  $K$ , suggesting that their metabolism may be higher than that of the fish in the Weddell Sea, potentially due to warmer waters. This difference may, however, also be related to a limited sampling at both locations, seasonal variations, and differences in abundance of food resources in Andvord Bay, which is known to be a hotspot of biodiversity with important input of organic matter from the water column to the benthos (Grange and Smith, 2013; Ziegler et al., 2020a).

In addition, aging data revealed that fish from Andvord Bay grew significantly faster than fish from the Weddell Sea (i.e., have a significantly greater Brody growth rate coefficient  $k$  in the von Bertalanffy

equation, Tables 3–4), thus reaching adult size at a younger age (Fig. 5b). As a result, the growth performance index  $\Phi'$  is higher in fish from Andvord Bay than from the Weddell Sea. It is noteworthy that the Brody growth rate coefficient  $k$  and the asymptotic size  $L_\infty$  are generally inversely correlated, meaning that fish that grow faster tend to not grow as long as fish growing slower. However, both parameters are greater for fish from Andvord Bay than for fish from the Weddell Sea in any comparison. From an evolutionary perspective, faster growing fishes reach a large size sooner, which enhances their ability to avoid predators and capture prey, and they may spawn a greater number of eggs because fecundity is positively related to fish size (Fig. 6e) (Metcalf and Monaghan, 2003).

The maximum age observed, however, was comparable between the two populations (24 years in Andvord Bay and 26 years in the Weddell Sea), making it one of the longest life spans known among notothenioids, and the longest-lived *Trematomus* out of the 10 of the 15 species studied to date (La Mesa and Eastman, 2023). While the difference in maximum age between Andvord Bay and the Weddell Sea was small and should be confirmed for each population and in additional populations around the continent given the low number of fish older than 20 years in each population, latitude and temperature may influence longevity in *T. scotti*. This observation would be in agreement with what is usually observed in fish where higher latitude fish tend to live longer as has previously been shown for the Mackerel Icefish *Champscephalus gunnari* and the Antarctic Silverfish *Pleuragramma antarcticum* (La Mesa and Eastman, 2023). It is noteworthy that while females and males in Andvord Bay both reached the observed maximum age, in the Weddell Sea, no females older than 18 years old were found while a 26-year-old male was captured. This observation contrasts with the general trend in notothenioids in which females tend to live longer than males (La Mesa and Eastman, 2023). This result, however, may simply reflect a sampling bias or sample size and would require further sampling in the Weddell Sea and other high latitude areas to be confirmed.

#### 4.3. Differing reproductive strategies between the Weddell Sea and the Western Antarctic Peninsula

Our analysis of *T. scotti* reproductive investment revealed major differences between the Weddell Sea and the Western Antarctic Peninsula, with fish from the Weddell Sea having lower fecundity but producing larger eggs than congeners from Andvord Bay. Indeed, females in Andvord Bay at an advanced spawning-capable stage had vitellogenic oocytes about the same size as oocytes of females from the Weddell Sea that were at a developing stage (0.85–0.9 mm at the end of May in Andvord Bay; 0.80–0.85 mm in January–February in the Weddell Sea). This observation suggests that at spawning, eggs of females from the Weddell Sea would be much larger than spawned eggs from females of Andvord Bay. Thus, female fish from the Weddell Sea produce fewer but larger eggs compared to fish from Andvord Bay, which produce more but smaller eggs. In agreement with data from Andvord Bay, vitellogenic oocytes of spawning-capable females in the Mawson Sea north of the Antarctic Circle ranged from 0.78 to 0.86 mm in diameter in mid-March (Shandikov and Faleeva, 1992). Together, these observations are consistent with a trend previously reported for some other notothenioid species where specimens at higher latitudes produce fewer but larger eggs than fish at lower latitudes (Kock and Kellermann, 1991).

Given the accelerated initial growth of fish in Andvord Bay compared to the Weddell Sea, it is likely that fish from Andvord Bay reached sexual maturity at a younger age than fish from the Weddell Sea. Additional sampling of immature fish is necessary, however, to test this hypothesis because only one immature specimen was analyzed in the present study, thus precluding the analysis of age at maturity. Together, our observations support the prediction that latitude and temperature influence reproductive traits in *T. scotti*.

## 5. Conclusions

The study of *Trematomus scotti* specimens from two distinct geographic areas with differing environmental conditions revealed that fish in each population displayed divergent life history traits, with specimens from the high latitude Weddell Sea characterized by lower growth rate, lower maximum length, lower fecundity, but greater egg size compared to individuals from the lower latitude Andvord Bay area on the Western Antarctic Peninsula. The longevity of specimens appears, however, to be comparable between the two locations. Although the mitochondrial markers we used did not provide evidence for genetic individualization of the two populations, *Trematomus scotti* populations in Andvord Bay and in the Weddell Sea showed clear differences in growth and reproduction parameters, reinforcing the necessity to study species life history and physiology at a more local, population scale and genetics at a broader genomic scale to tease apart the contributions of genetic evolution and phenotypic plasticity in divergent life history traits.

## CRedit authorship contribution statement

**Thomas Desvignes:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alejandro Valdivieso:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation. **Luca Schiavon:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Camilla Sguotti:** Writing – review & editing, Investigation. **Federico Cali:** Writing – review & editing, Investigation. **Emilio Riginella:** Writing – review & editing, Resources, Investigation. **Margaret Streeter:** Writing – review & editing, Investigation. **Jacob Grondin:** Writing – review & editing, Investigation. **Nathalie R. Le François:** Writing – review & editing, Investigation. **Magnus Lucassen:** Writing – review & editing, Resources. **Felix C. Mark:** Writing – review & editing, Resources. **H. William Detrich:** Writing – review & editing, Resources, Funding acquisition. **Chiara Papetti:** Writing – review & editing, Resources, Investigation, Funding acquisition. **John H. Postlethwait:** Writing – review & editing, Resources, Investigation, Funding acquisition, Conceptualization. **Mario La Mesa:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Statements and declarations

The authors declare no competing interests.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

Morphometric and genetic data generated and analyzed in this study are available in a designated repository in the United States Antarctic Program Data Center (p0010221) and deposited in NCBI GenBank.

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