First Insights Into the Growth and Population Structure of *Cottoperca trigloides* (Perciformes, Bovichtidae) From the Southwestern Atlantic Ocean

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The aim of this work was to describe the growth of *Cottoperca trigloides*, a notothenioid species with a non-Antarctic distribution, and to test the existence of different nursery areas and fish stocks through changes in the otolith elemental composition. Fish were collected during spring 2009 over the Patagonia continental shelf, including the Marine Protected Area Namuncurá/Burdwood Bank, in the southwestern Atlantic Ocean. The age and growth analyses were performed by counting marks in *sagittae*, assuming an annual periodicity of their deposition, and identified 8-year classes (0+ to 7+). Given the size range of the fish, length-at-age data were fitted to the Gompertz growth model $TL_t = 55.45 [\exp ((\exp (-0.32 (t - 1.89)))$, explaining more than 95% of the growth pattern. Moreover, the chemical composition of otolith core and edge areas was analyzed by laser ablation inductively coupled plasma mass spectrometry. The canonical analysis of principal coordinates successfully allocated 72.92% of the fish for the core and 91.67% for the edge area of the otolith, in three groups corresponding to “northern Patagonia shelf,” “southern Patagonia shelf,” and “Marine Protected Area Namuncurá/Burdwood Bank” areas, suggesting a high segregation among them over the Patagonian shelf. Thus, otolith elemental composition has proven to be an efficient approach to identify different nursery areas and stocks for the species. The present results provide new information on the growth and the population structure of *C. trigloides*, from a geographical area where information on this issue is still scarce, constituting an essential tool to develop conservation principles for the species.

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INTRODUCTION

*Cottoperca trigloides* (Forster, 1801) is the unique species of the family Bovichtiidae (Balushkin, 2000; Eastman and Eakin1, version December 30, 2019), the members of which are atypical notothenioids in having a largely non-Antarctic distribution (Eastman, 1993). This species has been reported from 41° to 54°S over the southeastern Pacific and the southwestern Atlantic Oceans (the Patagonian region of Chile and Argentina), including the Strait of Magellan, the Beagle Channel, the Burwood Bank, the Staten Island, and the Malvinas/Falklands Islands (Lloris and Rucabado, 1991; Fernández et al., 2009). Although its bathymetric distribution was indicated between 10 and 270 m depth (Lloris and Rucabado, 1991), Laptikhovsky and Arkhipkin (2003) also pointed out that *C. trigloides* is commonly found between 150 and 400 m, in the outer shelf and slope around the Malvinas/Falklands Islands. According to the fishery statistics of these islands, the incidental catch of the species was 48.4 tons during 2018 (Falkland Islands Government [FIG], 2019). Despite its abundance and its quite remarkable bycatch during finfish and squid trawl fishing, data on its life history and population structure of fish (Walther and Limburg, 2012; Tanner et al., 2016; Avigliano et al., 2018a). There are different mechanisms for the incorporation of trace elements in otoliths, such as calcium substitution, in which some divalent ions are incorporated in the substitution to calcium (Ca2+) into the otolith carbonatic matrix, and random trapping of free ions (Thomas and Swearer, 2019). For the elements that substitute for Ca, there may be some proportion with its environmental availability, while for the elements that do not replace Ca, the relationships with the environment are less clear (Thomas et al., 2017; Thomas and Swearer, 2019).

By tracking changes in elemental concentrations over time in an individual fish or among fish captured from different locations, it is often possible to deduce much about their environmental history, such as the previous habitat uses, stock compositions, and nursery locations (Thresher, 1999; Brazner et al., 2004; Avigliano et al., 2018b; Soeth et al., 2019). In recent years, otolith chemical composition has been applied to the study of small pelagic (Ma et al., 2014; Carvalho et al., 2017) and demersal (Volpedo and Fernández Cirelli, 2006; Albuquerque et al., 2012; Avigliano et al., 2017a) fish in the southwestern Atlantic Ocean. Moreover, this technique resolved the population structure of some notothenioid species, such as the Patagonian toothfish *Dissostichus eleginoides* (Smitt, 1898) (Ashford et al., 2005, 2006), and the Scotia Sea icefish *Chaenocephalus aceratus* (Lönnberg, 1906) (Ashford et al., 2010) successfully. Previously, Radtke and Targett (1984) and Radtke et al. (1993) also employed otolith chemical analyses to characterize the environmental life history of two Antarctic fish, *Notothenia larseni* (Lönnberg, 1905) and *Pleuragramma antarcticum* (Boulenger, 1902).

In line with previous studies, we aimed to describe the growth of an extra-Antarctic notothenioid species, *C. trigloides*, and to test the existence of different nursery areas and fish stocks, corresponding to the “northern Patagonia shelf,” “southern Patagonia shelf,” and “Marine Protected Area (MPA) Namuncurá/Burdwood Bank” areas along the southwestern Atlantic Ocean, by using otolith chemistry. The present results represent the first data on the growth and the population structure of *C. trigloides*, from a geographical area where information on the subject is still scarce, constituting an essential tool to develop conservation strategies to the species.

MATERIALS AND METHODS

Ethics Statement

*Cottoperca trigloides* is not protected under wildlife conservation laws (local legislations, International Union for Conservation of Nature [IUCN], or Convention on International Trade in Endangered Species [CITES]). Individuals employed in this

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1https://people.ohio.edu/eastman/
study were captured within the framework of the Pampa Azul interministerial initiative, promoted by the Ministerio de Ciencia, Tecnología e Innovación Productiva. As the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) does not possess formal Committees regarding the fish welfare and sampling protocols, fish handling during sampling was performed following guidelines of the ethical committee of the Universities Federation for Animal Welfare (UFAW) Handbook on the Care and Management of Laboratory Animals³.

**Fish Sampling and Processing**

Fish were collected during November–December 2009 from the Oceanographic Vessel Puerto Deseado of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina) over the Patagonia continental shelf (PS) in the southwestern Atlantic Ocean (41°16′–55°03′S and 57°22′–68°15′W), including the Burdwood Bank (55°S, 59°W) (Figure 1). This latter area is a shallow seamount located in the northeastern portion of the Drake Passage. It has been recently declared a marine sanctuary, since it constitutes a highly productive ecosystem and an important migration destination for a wide variety of seabirds and marine mammals (Namuncurá Marine Protected Area; Schetjer et al., 2016).

Along the “northern Patagonia shelf” (NPS), “southern Patagonia shelf” (SPS), and “MPA Namuncurá/Burdwood Bank” (BB) areas, which were defined according to the circulation patterns observed over the PS, *C. trigloides* individuals were collected at 11 sampling stations employing a demersal bottom trawl pilot net (6 m total length, 25 mm mesh on the wings and 10 mm in the cod end, 0.6 m vertical opening and 1.8 m horizontal aperture). Hauls were performed during the day and night, with a target time of 15 min and a tow speed between 2 and 3.7 knots. Individuals captured in station nos. 1, 2, 3, 7, and 8 were assigned to the NPS group, individuals from station nos. 12, 13, 15, 16, and 18 composed the SPS group, and those from station 17 were included in the BB group. The sampling stations with no *C. trigloides* captures (4, 5, 6, 10, 14, 19, 20) were not included in the analyses. Fish were counted and identified following Gon and Heemstra (1990) and specific taxonomic articles. Individual *C. trigloides* were measured to total length (TL, ±0.1 mm) and sexed when possible, since gonads of some individuals were indistinguishable. The sagittae were extracted, cleaned mechanically with distilled water, and stored dry.

Moreover, a Seabird SBE 21 thermosalinograph was used to measure the sea surface temperature and salinity and an echo-sounder Monhaz was used to measure depth.

**Age and Growth Analysis**

The right otoliths of 141 *C. trigloides* individuals (84–510 mm TL) were embedded in crystal polyester resin and cut transversely through the core using a low-speed, diamond blade IsoMet™ LS saw. The number, width, and radius of each mark and otolith radius (OR) were recorded, along the longest axis of the transverse section, under an Olympus SZH10 stereomicroscope (10×) and an image analysis system (Otoli 32). The average percent error (APE, Beamish and Fournier, 1981) and the coefficient of variation (CV, Chang, 1982; Campana, 2001) were used to determine the precision level of age interpretations.

Because it was not possible to validate the periodicity of growth mark deposition in otoliths for *C. trigloides*, an annual periodicity was assumed according to the observations performed in other notothenioid species such as *Eleginops maclovinus* (Cuvier and Valenciennes, 1830) (Brickle et al., 2005; Licandro et al., 2006) and *Patagonotothen ramsayi* (Regan, 1913) (Brickle et al., 2006).

After verifying linearity between OR and TL, the Fraser–Lee procedure (Campana, 1990) was used to back-calculate TL of each fish at past ages according to

\[
TL_i = b + (TL - b) OR^\alpha OR_d
\]

where \(TL_i\) and \(OR_d\) are the fish total length (cm) and otolith radius (µm) at some previous age \(a\), TL and OR are the fish total length (cm) and otolith radius (µm) at capture, and \(b\) is the intercept of the linear regression between OR and TL.

Annual growth rates were calculated as

\[
GR = TL_i - TL_{i-1}
\]

where GR is the individual growth rate (cm year⁻¹), \(TL_i\) is the total length of fish back-calculated at age \(i\), and \(TL_{i-1}\) is the total length of fish back-calculated at age \(i - 1\).

Differences in TL and GR at previous ages were evaluated with one-way repeated measures analysis of variance (RM ANOVA) followed by pairwise multiple comparison procedures (Holm–Sidak test). Sphericity was previously assessed using the Mauchly test. The statistical decisions were based on \(α = 0.05\) (Zar, 1984; Sokal and Rohlf, 2011).

Moreover, TL at first maturity was estimated following Froese and Binohlan (2000), who proposed the following equations:

- **Females:** \(\log TL_m = 0.9469 \log TL_\infty - 0.1162\)
- **Males:** \(\log TL_m = 0.8915 \log TL_\infty - 0.1032\)

where \(TL_m\) is the total length at maturity and \(TL_\infty\) is derived from

\[
TL_\infty = 0.044 + 0.9841 TL_{\text{max}}
\]

where \(TL_{\text{max}}\) is the maximum total length of the species. \(TL_{\text{max}}\) values used (80 cm for males and 60 cm for females) are those reported by Arkhipkin et al. (2015).

According to the size range of *C. trigloides* present in the samples and the low percent of mature individuals (7.2%) resulting from previous equations, the Gompertz function was chosen to model the growth of the species, as it is more appropriate in describing the growth of juvenile fish (Ricker, 1979). Thus, length-at-age data were fitted to the following equation:

\[
TL_t = TL_\infty e^{-k(t-I)}
\]

where \(TL_t\) is the total length at age \(t\), \(TL_\infty\) represents the asymptotic total length, \(k\) is the growth rate, \(t\) is the age, and \(I\) is the age at the inflection point (Gompertz, 1825). Owing to the low number of individuals, no distinctions between sexes

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³http://www.ufaw.org.uk
FIGURE 1 | Study area and sampling stations during November-December 2009 in the southwestern Atlantic Ocean. The solid black line represents the 200 m isobath, circles with a fish represent stations where *C. trigloides* was captured and empty circles represent stations where *C. trigloides* was not captured. Different colors indicate different geographic areas (NPS: northern Patagonia shelf, green; SPS: southern Patagonia shelf, blue; and BB: Burdwood Bank, pink). Stations without colors were not included in elemental analyses. Black arrows represent main currents over the PS according Palma et al. (2008).
or capture areas were made to fit the model. The estimates of the parameters of the model were performed using the program Growth II (Henderson and Seaby, 2006).

**Elemental Analysis**

Because the otolith material is continuously deposited and not reabsorbed (Campana, 1999; Takagi and Takahashi, 1999), the otolith core chemistry, which corresponds to the early stage of life, is a useful spawning or nursery area natural marker. On the other hand, the outer area composition, which represents the last time of life, is often used as a stock indicator (Campana, 2014; Avigliano et al., 2017b; Biolé et al., 2019). Thus, the chemical compositions of the otolith core and edge were analyzed separately to evaluate differences in the stocks and nursery structure of *C. trigloides* between NPS, SPS, and BB areas.

Transverse sections (400 µm) of the left otoliths (*N*<sub>total</sub> = 48, *N*<sub>NPS</sub> = 12, *N*<sub>SPS</sub> = 30, *N*<sub>BB</sub> = 6; 119–475 mm TL) were mounted onto glass slides with cyanoacrylic glue. Otolith surfaces were polished with silicon carbide paper (no. 8000), washed with Milli-Q water (resistivity of 18.2 mOhm cm<sup>−1</sup>), and mounted onto glass slides with cyanoacrylic glue. Otolith and the last (stock indicator, 296±74 mm) otolith core and edge. These areas represent approximately the entire core area (nursery area indicator, 1338±247 µm) and the last (stock indicator, 296 ± 74 µm) complete annuli. A Q-switched pulsed 266 nm Nd:YAG laser (LSX 100, CETAC Technologies Inc., Omaha, NE, United States) was used to analyze *C. trigloides* otoliths. The laser was set up with a scan speed of 20 µm/s, a pulse frequency of 20 Hz, and an energy output of 0.4–0.6 mJ per pulse. This setup resulted in a ∼25 µm crater width. Laser and ICP-MS were linked through a Tellon-coated tube, using argon as carrier gas (0.85 dm<sup>3</sup> min<sup>−1</sup>). The ICP-MS power was set at 1500 W, with an outer and intermediate gas flow of 15 and 1.1 dm<sup>3</sup> min<sup>−1</sup>, respectively. Before the analysis, the ICP-MS was optimized using the Daily Performance tool, with maximum analytic intensities and minimum interferences determined using oxides and double-charged ions. The samples were randomly analyzed to avoid systematic bias through the analytical session. Moreover, Ca was used as an internal standard to correct for the elemental fractionation caused by sensitivity drift, differences in ablation yield, and matrix effect (Jackson, 2008; Lin et al., 2016). Standardization to otolith Ca is used in otolith chemical analyses for reducing intersample variance because it is the major element and is relatively invariant (Campana et al., 1997). Furthermore, the reference material NIST1834 (National Institute of Standards and Technology, Gaithersburg, MD, United States), which was certified for Ba, Ca, Mg, and Sr (NIST, 1990), was measured as external standard 10 times among the 48 samples analyzed. The relative standard deviation (RSD,%) between the NIST1834 measurements was 2.4% for Ba, 4% for Sr, 7% for Mn, and 9.5% for Mg, which indicated acceptable repeatability and low drift throughout the analytical session. The values obtained in both the otoliths and NIST1834 were systematically above the limit of detection (LOD), which was calculated from the gas blank before laser ignition (Geffen et al., 2013) as the mean element:Ca ratio plus 3 standard deviations of the background. LODs were 0.058, 0.096, 0.278, and 0.042 for Ba:Ca, Mg:Ca, Mn:Ca, and Sr:Ca, respectively. Element counts per second (cps) were subtracted from the background level, and element:Ca ratios were then calculated for core and edge transects separately.

Otolith chemical composition was simplified and only the four most informative variables were retained (Ba:Ca, Mg:Ca, Mn:Ca, and Sr:Ca) and were log (∗1000) transformed to balance their influence. The comparisons of these elemental ratios among geographic areas were made with one-way analysis of variance (ANOVA) or Kruskal–Wallis one-way analysis of variance on ranks (Kruskal–Wallis), followed by pairwise multiple comparison procedures (Tukey test or Dunn's test). The assumptions of normality and homoscedasticity were evaluated through Shapiro–Wilks and Levene tests, respectively. All statistical decisions were based on α = 0.05 (Zar, 1984; Sokal and Rohlf, 2011). Moreover, as the growth rate can affect the incorporation of trace elements into the otolith, the effect of size on the elemental ration was tested using Spearman's rank-order correlation (Biolé et al., 2019).

In the following analyses, the existence of different nursery areas and stocks of *C. trigloides* between geographic areas along the southwestern Atlantic Ocean was tested. For each area of the otolith, a Euclidean distance matrix was constructed using the log-transformed elemental ratios. A one-way non-parametric permutational multivariate analysis of variance (PERMANOVA) was performed to determine whether significant differences exist in the chemical composition of fish grouped by geographical areas (NPS, SPS, and BB) for both the otolith core and edge. The responsible elements for the intragroup similarity were assessed through a percentage of similarity analysis (SIMPER). The resemblance matrix was further employed in a canonical analysis of principal coordinates (CAP) to visualize the spatial variability of the otolith chemical composition and to measure the degree of fish allocation success within the geographical groups. All the multivariate analyses were performed using the statistical package PRIMER v7 (Anderson et al., 2008; Clarke et al., 2014).

**RESULTS**

Environmental characteristics regarding depth, salinity, and temperature, of each sampling station over the PS in the southwestern Atlantic Ocean are shown in Table 1. Between 41° and 54°S, salinity values were quite similar and ranged from 32.5 (station 11) to 34.0 (station 17). On the other hand, temperature values were more variable, ranging between 5.43°C (station 17) and 12.50°C (station 4); this variability was associated not only with latitude but also with depth.
Age and Growth Analysis

The age and growth analysis of the species was performed by counting annual marks in sagittae. These otoliths showed complex patterns of growth mark formation, making them difficult to read. However, the simple regression analysis (R^2 = 0.81, p < 0.001) showed an agreement between the two readers. Moreover, the values from both the APE (2.58%) and the CV (3.65%) indicated a good level of precision for readings. The count of annual marks allowed identifying 8-year classes, the CV (3.65%) indicated a good level of precision for readings. Moreover, the values from both the APE (2.58%) and the CV (3.65%) indicated a good level of precision for readings.

The relationship between OR and TL can be expressed as follows, TL = 8.618 + 0.0135 OR (R^2 = 0.807, p < 0.001). Mean back-calculated TL by sex are shown in Table 2. Sizes at previous ages were significantly different only for ages 3 (RM ANOVA, F = 5.179, p = 0.009) and 4 (RM ANOVA, F = 6.711, p = 0.017), with males larger than females and unsexed fish. The GR was individually estimated based on back-calculated TL (Table 3). Mean GR showed significantly larger values for males at previous ages 2 (RM ANOVA, F = 7.238, p = 0.002) and 3 (RM ANOVA, F = 11.063, p = 0.003).

Considering the TL_max values reported for males (50–80 cm) and females (40–60 cm) of C. trigloides (Arkhipkin et al., 2015) and following Froese and Binohlan (2000), the TL_max of males and females of the species was estimated at 40.3 and 38.2 cm, respectively. These values indicated that few mature individuals

TABLE 1 | Location of sampling stations, environmental factors measured, and the number of C. trigloides captured in the southwestern Atlantic Ocean.

| Sampling station | Latitude (S) | Longitude (W) | Depth (m) | Salinity | Temperature (°C) | C. trigloides (n) |
|------------------|-------------|---------------|-----------|----------|-----------------|------------------|
| 1                | 41°16’12”   | 58°16’48”    | 78        | 33.5     | 8.14            | 1                |
| 2                | 41°17’24”   | 57°22’48”    | 123       | 33.6     | 5.70            | 2                |
| 3                | 41°33’36”   | 58°32’24”    | 137       | 33.6     | 6.9             | 6                |
| 4                | 43°25’29”   | 63°45’29”    | 76        | 33.5     | 12.5            | 0                |
| 5                | 44°32’24”   | 63°25’48”    | 83        | 33.6     | 7.25            | 1                |
| 6                | 44°33’00”   | 64°06’00”    | 86        | 33.6     | 7.19            | 1                |
| 7                | 45°08’24”   | 62°11’24”    | 85        | 33.7     | 6.31            | 3                |
| 8                | 46°23’59”   | 64°21’27”    | 113       | 33.1     | 9.64            | 5                |
| 9                | 48°15’41”   | 61°27’08”    | 175       | 33.6     | 7.78            | 0                |
| 10               | 52°27’55”   | 67°03’58”    | 96        | 33.1     | 6.66            | 1                |
| 11               | 52°39’29”   | 68°15’57”    | 71        | 32.5     | 6.97            | 0                |
| 12               | 53°12’38”   | 66°09’52”    | 103       | 33.0     | 7.09            | 21               |
| 13               | 53°25’09”   | 67°41’04”    | 54        | 32.6     | 6.34            | 11               |
| 14               | 53°37’13”   | 67°39’31”    | 46        | 32.6     | 7.56            | 0                |
| 15               | 54°09’08”   | 66°27’35”    | 65        | 32.7     | 6.88            | 24               |
| 16               | 54°12’33”   | 64°22’17”    | 121       | 33.7     | 5.86            | 8                |
| 17               | 54°26’05”   | 61°11’48”    | 97        | 34.0     | 5.43            | 11               |
| 18               | 54°37’57”   | 63°38’23”    | 88        | 33.2     | 6.32            | 33               |
| 19               | 54°54’08”   | 64°19’19”    | 145       | 33.2     | 6.34            | 3                |
| 20               | 55°03’44”   | 65°53’59”    | 125       | 32.9     | 6.74            | 10               |

TABLE 2 | Back-calculated total length (TL, mean ± standard deviation) for past ages of C. trigloides from the southwestern Atlantic Ocean.

| Past ages (years) | Unsexed | Males | Females |
|-------------------|---------|-------|---------|
| 1                 | 8.77 ± 2.92a | 9.35 ± 2.87a | 9.39 ± 3.07a |
| 2                 | 16.52 ± 3.33a | 18.38 ± 3.60a | 17.47 ± 3.29a |
| 3                 | 22.16 ± 3.96a | 25.94 ± 4.06b | 23.50 ± 3.88a |
| 4                 | 32.13 ± 4.88a | 39.10 ± 4.25b | 29.10 ± 4.25b |
| 5                 | 38.11 ± 4.54 |          |         |
| 6                 | 42.77 ± 3.28 |          |         |

Different letters indicate significant differences between sexes.

Elemental Analysis

No significant relationships were detected between the four elemental ratios in the otolith core or edge and fish size (Spearman’s correlation, 0.0343 < r < 0.169; 0.284 < p < 0.816); therefore, it was not necessary to make any correction on the original variables.

Comparisons of element:Ca ratios at the otolith core and edge and fish size were not significant relationships between the four elemental ratios in the otolith core or edge and fish size.
TABLE 3 | Annual growth rates (GR, mean ± standard deviation) for past ages of
C. trigloides from the southwestern Atlantic Ocean.

| Past ages (years) | Unsexed | Males | Females |
|-------------------|---------|-------|---------|
| 1                 | 7.74 ± 2.78<sup>a</sup> | 9.02 ± 2.91<sup>a</sup> | 8.11 ± 3.14<sup>a</sup> |
| 2                 | 4.76 ± 2.40<sup>b</sup> | 7.48 ± 2.15<sup>b</sup> | 5.58 ± 2.13<sup>b</sup> |
| 3                 | 6.35 ± 1.96<sup>b</sup> | 4.54 ± 1.60<sup>b</sup> |         |
| 4                 | 4.47 ± 1.75 |         |         |
| 5                 | 2.73 ± 0.73 |         |         |

Different letters indicate significant differences between sexes.

DISCUSSION

Age and Growth Analysis

The present study describes, for the first time, the age and growth of C. trigloides from the southwestern Atlantic Ocean. Although their sagittae showed a complex pattern of growth mark formation, age estimates were precise enough, suggesting that these otoliths were appropriate structures for the age estimation of the species. According to the available information in the literature related to the growth of different notothenioid species, an annual growth mark deposition was assumed on these otoliths (Brickle et al., 2005, 2006; Licandeo et al., 2006). This fact was due to the absence of the necessary samples to verify the periodicity of mark formation in the present samples, given that the sampling program performed included many stations but in a limited period.

Cottoperca trigloides captured between 41° and 54°S of the southwestern Atlantic Ocean, with sizes ranging from 8.4 to 51.5 cm TL, belonged to 8-year classes, and 92.8% of them were juveniles. In this regard, Lobao-Tello and Hüne (2012) mentioned that C. trigloides less than 55 cm TL are the most frequent individuals in wild populations, in agreement with the size range registered by Vanella et al. (2007) and Fernández et al. (2012, 2018). The lack of older fish in the capture restricted the ages to a narrow range that is functionally linear and makes it difficult to fit a non-linear function, especially those with a horizontal asymptote. In consequence, the Gompertz growth function was fitted, being more appropriate for this type of data. This model described the growth of the species adequately, with an estimated TL∞ (52.85 cm) quite similar to that of the larger fish (51.5 cm) registered in the samples and a large k value (0.33) that reflected the typically fast growth observed in juvenile fish. Moreover, the back-calculation of TL at previous ages revealed some growth differences related to sex. Cottoperca trigloides males attained larger TL than females and exhibited faster growth rates since the age of 2 years. Given that the growth of some nototheniid fish from the sub-Antarctic area has been described through the von Bertalanffy growth model (Brickle et al., 2005, 2006; Licandeo et al., 2006), it was not possible to make interspecific comparisons of the growth performance. Nevertheless, Brickle et al. (2006) reported that P. ramsayi is a relatively slow-growing fish, with a maximum age of 14 years, and that males have lower growth rates and larger TL than females. For the same geographic area, Brickle et al. (2005) described the growth of E. maclovinus and characterized it as a short-lived
FIGURE 3 | Box plots showing the mean (dashed line), the median (solid line) and 25th and 75th percentiles of Ba:Ca, Mg:Ca, Mn:Ca, and Sr:Ca ratios for otolith core and edge areas of *C. trigloides* from the southwestern Atlantic Ocean. Different letters indicate significant differences among geographic areas. BB, Burdwood Bank; NPS, northern Patagonia shelf; SPS, southern Patagonia shelf.
species, attaining a maximum age of 11 years, with an average growth rate of 10.2 cm year\(^{-1}\) for the first 6 years. In the central-southern Chilean coasts, Licandeo et al. (2006) found that the same species reached smaller sizes with a slower growth pattern. According to the maximum ages registered in other notothenioids from the same geographic area and the \(T_{L\ max}\) of \textit{C. trigloides} (∼80 cm) registered by Lobao-Tello and Húme (2012) and Arkhipkin et al. (2015), it is likely that older \textit{C. trigloides} individuals will be found in Patagonian populations. A greater sample, encompassing a larger age range, would allow us to describe the growth of the species by applying the von Bertalanffy growth function and hence to support the intersex differences obtained from the back-calculated sizes. Moreover, the estimated parameters will allow comparison of the growth of notothenioids with different sizes through the growth performance index (Pauly and Munro, 1984). About it, Kock and Everson (1998) and La Mesa and Vacchi (2001) found that the growth performances of sub-Antarctic notothenioid species appear to be higher than those estimated for commercially harvested species from the seasonal pack-ice and the high Antarctic zones.

### Elemental Analysis

In this study, the analysis of the chemical composition in \textit{C. trigloides} otolith edges was an efficient approach to discriminate among NPS, SPS, and BB areas, which suggests the possible existence of different stocks. Also, core analysis revealed marked segregation during the early stages of life for the

### Table 4

**SIMPER analyses for the three groups of \textit{C. trigloides} individuals identifying the most relevant element:Ca ratios responsible for the grouping for the core and edge areas of the otolith.**

| Groups     | Element:Ca ratios | Average value | Contribution% | Cumulative% | Average squared distance |
|------------|-------------------|---------------|---------------|-------------|-------------------------|
| **Otolith core** |                  |               |               |             |                         |
| NPS        | Sr:Ca             | 2.15          | 1.52          | 1.52        | 0.03                    |
|            | Ba:Ca             | 0.36          | 8.00          | 9.52        |                         |
|            | Mg:Ca             | 1.72          | 30.96         | 40.48       |                         |
|            | Mn:Ca             | 0.82          | 59.52         | 100.00      |                         |
| SPS        | Sr:Ca             | 2.18          | 6.07          | 6.07        | 0.04                    |
|            | Mn:Ca             | 0.64          | 24.61         | 30.68       |                         |
|            | Ba:Ca             | 0.41          | 28.86         | 59.53       |                         |
|            | Mg:Ca             | 1.66          | 40.47         | 100.00      |                         |
| BB         | Mg:Ca             | 1.66          | 7.12          | 7.12        | 0.01                    |
|            | Sr:Ca             | 2.16          | 8.80          | 15.93       |                         |
|            | Ba:Ca             | 0.29          | 39.79         | 55.72       |                         |
|            | Mn:Ca             | 0.49          | 44.28         | 100.00      |                         |
| **Otolith edge** |                  |               |               |             |                         |
| NPS        | Sr:Ca             | 2.07          | 10.47         | 10.47       | 0.04                    |
|            | Mn:Ca             | 0.36          | 24.31         | 34.78       |                         |
|            | Mg:Ca             | 1.20          | 31.70         | 66.48       |                         |
|            | Ba:Ca             | 0.35          | 33.52         | 100.00      |                         |
| SPS        | Sr:Ca             | 2.18          | 15.27         | 15.27       | 0.06                    |
|            | Ba:Ca             | 0.29          | 19.74         | 35.01       |                         |
|            | Mn:Ca             | 0.33          | 25.35         | 60.37       |                         |
|            | Mg:Ca             | 1.42          | 39.63         | 100.00      |                         |
| BB         | Sr:Ca             | 2.34          | 1.44          | 1.44        | 0.12                    |
|            | Mn:Ca             | 0.42          | 18.52         | 19.96       |                         |
|            | Mg:Ca             | 1.92          | 28.92         | 48.88       |                         |
|            | Ba:Ca             | 0.63          | 51.12         | 100.00      |                         |

**BB, Burdwood Bank; NPS, northern Patagonia shelf; SPS, southern Patagonia shelf.**

![FIGURE 4 | CAP ordination diagram for \textit{C. trigloides} based on the otolith chemical composition (Ba:Ca, Mg:Ca, Mn:Ca, and Sr:Ca) for the otolith core area. Geographical areas: northern Patagonia shelf (NPS, squares), southern Patagonia shelf (SPS, triangles), and Burdwood Bank (BB, circles).](image-url)
The similarities within these groups, identified throughout the ontogeny of *C. trigloides*, were mainly due to Mn:Ca, Mg:Ca, and Ba:Ca ratios. Factors influencing the incorporation of trace elements into otolith calcium carbonate matrix are element and species specific, and can be related to environmental variables (Elsdon and Gillanders, 2003; Brown and Severin, 2009; Avigliano et al., 2019), genetics (Clarke et al., 2011), physiology (Sturrock et al., 2014, 2015), growth rate, and ontogeny (Walther et al., 2010), among others.

For instance, the otolith Sr:Ca ratio is usually positively correlated with salinity, while otolith Ba:Ca shows the opposite pattern (Martin and Thorrold, 2005; Brown and Severin, 2009; Avigliano et al., 2018b). Thus, these ratios have been used as habitat indicators in environments with salinity gradients, especially in diadromous fish (Albuquerque et al., 2010; Mai et al., 2014; Avigliano et al., 2017b). However, in several marine systems, where the salinity is relatively homogeneous, as observed in this study, otolith Sr:Ca and Ba:Ca can vary with other factors, such as temperature, water composition (mainly Ba), genetics, ontogeny, and diet (Miller, 2009; DiMaria et al., 2010; Walther et al., 2010; Clarke et al., 2011). Specifically, Miller (2009) found a positive relationship between temperature and water concentration on the otolith incorporation of Ba:Ca in juvenile black rockfish *Sebastes melanops* (Girard, 1856) under experimental conditions. Walther et al. (2010) found interactive effects between temperature, ontogeny (stage of the life history), and food quantity with otolith Ba:Ca, and significant interactions between stage and food with Sr:Ca in the coral reef fish *Acanthochromis polyacanthus* (Bleeker, 1855). Moreover, DiMaria et al. (2010) described a negative relationship between Sr:Ca and Ba:Ca with temperature, and no relationship between Mg:Ca and this environmental factor, in the Pacific cod *Gadus macrocephalus* (Tilesius, 1810). For that species, they suggested that the kinetic effects could be more important in the incorporation of Sr and Ba while metabolic effects would have a greater effect on the Mg incorporation. For the pelagic-neritic fish *Menidia menidia* (Linnaeus, 1766), a significant temperature effect on both Sr:Ca and Ba:Ca was reported (Clarke et al., 2011). Nevertheless, it turned out to be complex, not linear, and there was also an interaction with genetics (Clarke et al., 2011).

In addition, the coastal waters are richer in Ba, due to the influence of water and continental sediments (Wolgemuth and Broecker, 1970). Unlike what happens with Sr, the levels of Ba in the ocean are not homogeneous and can vary both horizontally and vertically, especially in the Atlantic Ocean (Wolgemuth and Broecker, 1970). A Ba-enrichment was also reported in deep water, which reflects the uptake of Ba by the particles in the surface water and the subsequent release into deep waters (Wolgemuth and Broecker, 1970).

Concerning Mn:Ca, a relationship with environmental concentration was found in some species (Dorval et al., 2007; Mohan et al., 2012), while in others, it was not (Walther and Thorrold, 2008; Miller, 2009). It has been reported that the concentration of dissolved oxygen is negatively associated with Mn:Ca in marine species such as the Atlantic cod *Gadus morhua* (Linnaeus, 1758), the European flounder *Platichthys flesus* (Linnaeus, 1758), the winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792), and the Atlantic croaker *Micropogonias undulatus* (Linnaeus, 1766) (Mohan et al., 2014). The hypoxic or anoxic environments that are often associated with otolith Mn peaks are typically related to high depths (Limburg et al., 2015). This ratio also seems to be strongly associated with ontogenetic changes because a peak has been found in the otolith core of several marine species such as *Dascyllus marginatus* (Rüppell, 1829) (Ben-Tzvi et al., 2007), *Sicydium punctatum* (Perugia, 1896), and *Sillaginodes punctatus* (Cuvier, 1829) (Rogers et al., 2019).

In the present study, most of the sampling stations were located far from the coast, and only two sites with *C. trigloides* captures (13 and 15) could be associated with fresher sub-Antarctic waters (advected from Chile and entering the PS via Magellan and Le Maire Straits) around Tierra del Fuego Island. Nevertheless, salinity was relatively constant among sampling sites; therefore, the otolith Ba:Ca variation would not seem to be related to the proximity of continental water bodies. On the other hand, the heterogeneity in the bathymetry of the study area (Piola et al., 2018) could affect the concentration or bioavailability of element:Ca ratios (mainly Sr:Ca, Ba:Ca, and Mn:Ca) in water (Wolgemuth and Broecker, 1970; Limburg et al., 2015), and thus on their incorporation into the otolith, which should be particularly studied. Over the PS, the temperature ranged up to 9.97 ºC between sampling stations and was more related to the depth than to latitude. Thus, we cannot rule out the potential effect of depth or some physicochemical parameters (i.e., temperature) on the element:Ca ratios responsible for the grouping.

Oceanographic phenomena could create barriers for fish populations and contribute to segregation, which could be reflected in the composition of otoliths (Cadrin et al., 2013;
Wilson et al., 2018). Thus, we proposed that the circulation pattern in the PS and Burdwood Bank could also explain the multivariate differences found among areas. Numerical simulations suggested that the mean circulation over the PS consists of a broad northeastward flow that intensifies toward the outer shelf, with anticyclonic gyres and relatively weak poleward coastal currents within the Grande Bay and San Jorge Gulf (Palma et al., 2008; Combes and Matano, 2014; Piola et al., 2018). This circulation pattern may be the physical feature involved in maintaining the integrity of NPS and SPS nursery areas and fish stocks. A similar association between the existence of a geographically stable larval retention area for Sprattus fueguensis (Jenyns, 1842) and the anticyclonic current circulation and sinking of shelf waters in southern Patagonia was also indicated by Sánchez et al. (1995). Regarding BB, Matano et al. (2019) suggested that it is an active center for the obduction of deep, fertile waters to the surface layers of the Drake Passage. This phenomenon, which includes upwelling and mixing, is primarily driven by tides and strengthened by winter convection. According to numerical models, the resulting circulation patterns over the BB consists of a broad anticyclonic flow around the bank's rim and anticyclonic vortices on top of the interior seaamounts that increase the retention of fluid parcels. Therefore, it could be contributing to the retention of C. trigloides individuals within the BB area. Moreover, considering that it is species living on or near the bottom, with adult males being territorial (Arkhipkin et al., 2015), low connectivity of individuals among different geographic areas could be expected.

Finally, the objective of this study was not to reveal the factors that influence the incorporation of elements into the C. trigloides otolith; however, this type of information could contribute to revealing the population structure with greater depth. In this sense, it is recommended to evaluate the relationship between different endogenous and exogenous factors in the incorporation of different elements. Moreover, future studies could incorporate other markers such as Li:Ca, Cu:Ca, Rb:Ca, Zn:Ca, and other methods such as genetics or otolith stable isotopes, which could also contribute to a better understanding of the observed differences over the PS.

**CONCLUSION**

This is the first time that the growth of C. trigloides has been described by using the Gompertz model, with males attaining larger sizes at faster growth rates. Moreover, the chemical analyses showed high segregation among the studied groups along the southwestern Atlantic Ocean, suggesting the presence of different stocks and nursery areas. The information obtained regarding the growth and population structure of C. trigloides could provide new information, constituting an essential tool to develop conservation principles for the species.

**DATA AVAILABILITY STATEMENT**

The datasets generated for this study are available on request to the corresponding author.

**ETHICS STATEMENT**

As the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) does not possess formal committees regarding the fish welfare and sampling protocols, fish handling during sampling was performed following guidelines of the Ethical Committee of the UFAW Handbook on the Care and Management of Laboratory Animals (http://www.ufaw.org.uk).

**AUTHOR CONTRIBUTIONS**

ML conceived and wrote the manuscript, with contributions from MB, and read the otoliths. FL and EA analyzed the data with contributions from ML. MR read the otoliths and contributed to age and growth analyses. ID prepared the otoliths for biochemical analyses. CB, FV, and DF participated in the research cruise and collected the fish samples. CA conducted the biochemical analyses. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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