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Otolith chemistry indicates the distinct spawning grounds and regional connectivity of *Pagothenia borchgrevinki* between the Antarctic Peninsula and Prydz Bay, Antarctica

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Abstract Samples for this study were collected from Geologists Island and Prydz Bay in different seasons. Otolith sections were analyzed for elemental composition in the nucleus, juvenile, and edge areas. Elements including Mg, Sr, P, K, Fe, and Zn, normalized to calcium (C_{Me}/C_{Ca}), were selected for analysis. To explore population structure, we studied factors influencing population dynamics during life stage, and regional distribution characteristics. For identified individual origins and explored the distribution and migration between regions and migration from hatching to adulthood provide a basis. So as to understand the distribution and migration pattern of *Pagothenia borchgrevinki* across various life history stages. Results indicated a consistent *P. borchgrevinki* population spawning across various regions of Southern Ocean, with eggs distributed at the bottom. Coastal slope topography changes and water compensation facilitated egg transportation from the bottom to under sea ice during hatching to juvenile stages. Long-distance migration was facilitated by the Antarctic Circumpolar Current and regional currents during development to adulthood. Multiple spawning grounds and ocean currents contributed to diverse distribution environments during the hatching period. Differences in individual development were important factors during the juvenile period, while ocean currents and autonomous behaviors influenced regional transportation patterns in the post development stages. Therefore, the research holds that differences in distribution environment and behavior during each period led to distinct factors influencing C_{Me}/C_{Ca} variations.

Keywords **otolith chemistry, period characteristics, *Pagothenia borchgrevinki*, life history connectivity, Antarctic Peninsula, Prydz Bay**

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1 Introduction

Pagothenia borchgrevinki is widely distributed in Antarctic Surface Water (AASW) (DeWitt, 1972) and has evolved into the most significant cryopelagic species near the undersurface of the sea ice through buoyancy evolution (Eastman and DeVries, 1981, 1982). *P. borchgrevinki*, as an active cryopelagic species, depends on its unique oxygen transportation, which differs significantly from that of other benthic fish. As an important constituent of the high-productivity ice fauna in the polar ecosystem, it is vertically separated from other Nototheniidae species by feeding. During the Southern Hemisphere winter, *P. borchgrevinki* mainly feeds on *Euphausia crystallorophias* and mesozooplankton. In addition, *P. borchgrevinki* serves as a prey for higher predators, including Antarctic toothfish (*Dissostichus mawsoni*) and Weddell seals (Eastman and DeVries, 1985). In the polar cryogenic ecosystem, the food chain consists of the ice algae, *Paralabidocera antarctica*, *P. borchgrevinki*, Antarctic toothfish, and Weddell seal, making *P. borchgrevinki* an important connective species with significant ecological meaning.

Fish otoliths record the complete life history period of an individual from birth to capture (Edmonds et al., 1991). Research on fish otoliths has focused on: (1) population identification (Campana and Thorrold, 2001); (2) analysis of individual origin (Rohtla et al., 2014; Zeigler and Whitledge 2010, 2011); (3) reconstruction of life history (Catalán et al., 2018; Phelps et al., 2012; Zeigler and Whitledge, 2011). The marine environment is considered the dominant factor affecting element deposition in otoliths (Brown and Severin, 2009). Moreover, the deposition characteristics of different periods in the otolith can distinguish life history periods. The origin and transport pathway during the life history period can be inferred and traced by combining elements deposited in the otolith with environmental characteristics (Limburg et al., 2003). Environmental heterogeneity caused by migration in each period is reflected in the characteristics of elements deposited in otoliths.

In the present study, we analyzed elements deposited in the nucleus, juvenile, and edge areas of *P. borchgrevinki* otolith from different regions in the Southern Ocean. Samples were grouped based on region and season, and elemental differences were examined between groups. (1) Analysis of elements in the nucleus of individuals from different regions and seasons aimed to identify potential multiple populations of *P. borchgrevinki* and test environmental heterogeneity during spawning and hatching periods. (2) Element analysis was conducted in the juvenile and pre-capture periods to explore environmental characteristics for individuals during these stages. (3) Based on the elements measured in otoliths, traceability analysis of elements in each period from the 4 groups was performed to investigate origin differences between groups. The results of the traceability analysis indicated the direction of migration in each period. Combined with physiological activity and distribution as indicated by the element causing differences between groups, this information was used to infer effective transport pathways between actual and predicted regions.

2 Materials and methods

2.1 Fish sampling

During the 38th and 39th Chinese Antarctic Research Expeditions, 62 *P. borchgrevinki* were fishing collected from the waters of Geologists Island and Prydz Bay. The fish collected from Geologists Island were sampled from a location designated as GW-01, which included two seasons. Additional sampling locations in Prydz Bay were labeled as ZS-01 and ZS-02 (Figure 1).

Following collection from all three sampling locations, on-site measurements were conducted (Table 1). After finished the measurements, the fish were freeze-stored at −20 ℃ and transported to the Polar Research Institute of China via the research vessels *Xuelong* and *Xuelong 2*.

2.2 Otolith element analysis

The left sagittal otolith from each individual was extracted in biology laboratory. It was then cleaned with Milli-Q water and dried before storage. Otoliths were rinsed with the Milli-Q water to remove any contamination on the surface of otolith, followed by secondary cleaning with 20% hydrogen peroxide, and rinsed again in Milli-Q water. Every otolith was then mounted on a new slide by using crystal bond to grind from the anterior end using 2000 and 4000 grit waterproof sandpapers until the transverse section of the nucleus was obtained. And the section was then polished with 1 μm alumina powder until nucleus and rings could be observed clearly (Figures 2, S1 and S2) after rinsing with the Milli-Q water.

Element concentrations in the otoliths of *P. borchgrevinki* were measured using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). The elements ^{24}Mg, ^{88}Sr, ^{31}P, ^{39}K, ^{57}Fe, ^{66}Zn, and ^{42}Ca were selected, and their ratios to calcium (C_{Me}/C_{Ca}) were calculated for otolith chemistry analysis. Elements sampling positions were located in the nucleus, juvenile, and edge areas of the otolith on the section of nucleus exposure (Figure 2). These positions were used to analyze element concentrations during the hatching, juvenile, and pre-capture periods of the life history.

The laser denudation sampling method was adopted the single point denudation with 90 s in total time, including 20 s blank background acquisition, followed by a 50 s data acquisition for otolith elemental concentrations and concluded with 20 s washout to clean the sample injection system after denudation. Ultra-pure helium was used as carrier gas during the process of denudation. An Analytik

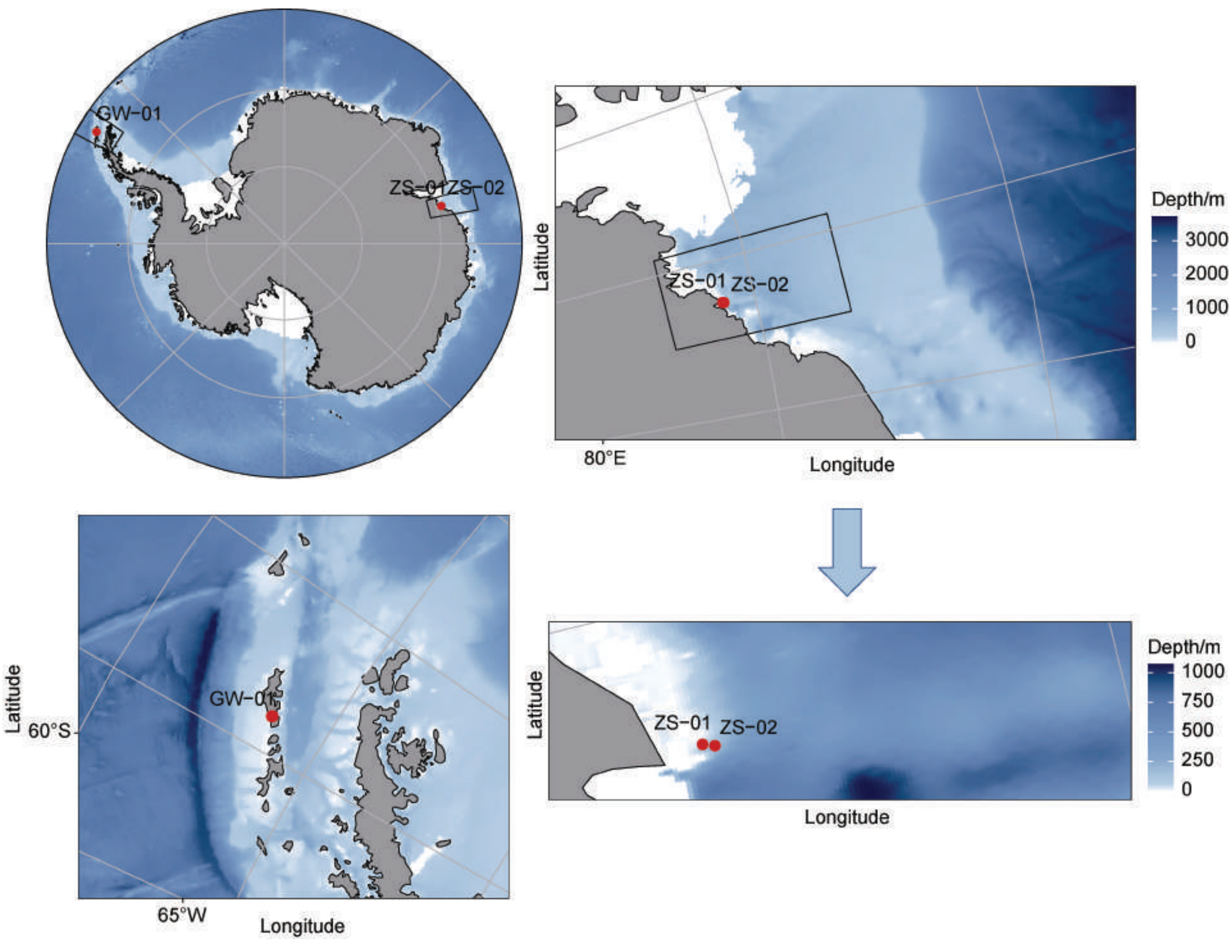

Figure 1 Map of sampling positions for *Pagothenia borchgrevinki*.

Table 1 Sampling data of *P. borchgrevinki* during the 38th and 39th Chinese Antarctic Research Expeditions conducted in the Geologists Island and Prydz Bay

Date	Area	Group	Longitude	Latitude	Total Length/cm	Body Weight/g	Sample Size
Sep. 2021	GW-01	code 01	62°13′47.08″S	58°55′33.00″W	15.00±2.30	27.52±11.44	5
Mar. 2021	GW-01	code 02	62°13′47.08″S	58°55′33.00″W	14.20±1.17	28.45±5.74	5
Jan. 2023	ZS-01	code 03	76°21′26.50″S	69°22′25.74″E	15.73±2.89	41.33±21.82	30
Jan. 2023	ZS-02	code 04	76°21′45.12″S	69°22′10.38″E	20.34±3.75	86.51±43.95	22

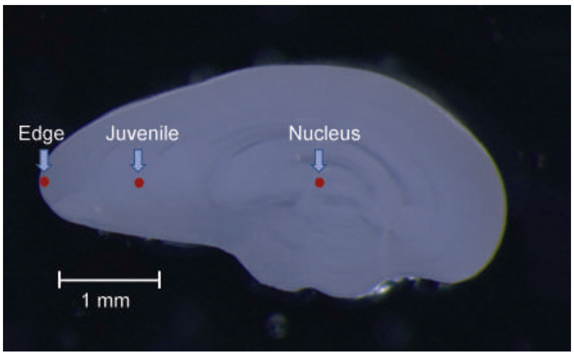

Figure 2 Elements sampling positions on the otolith section.

Jena PlasmaQuant MS ICP-MS instrument coupled with the RESOLution 193 nm excimer laser ablation system was used to acquire ion-signal intensities by using a laser beam of 30 μm diameter, 6 Hz of frequency and 5 J·cm^{-2} of power (Ashford et al., 2012; Jones and Chen, 2003). A set of reference materials, including NIST 610, NIST 612, BHVO-2G, BCR-2G, and BHIR-1G, was analyzed after every 10 denudation points to quantitatively calculated the element concentrations (Liu et al., 2008; Pearce et al., 1997). ICPMSDataCal (version 9.5) was used for offline data processing, including selection and integration of sample signals and blank background, correction for instrument sensitivity drift, and calculation of element concentrations (Liu et al., 2008).

2.3 Statistical analysis

Multivariate outliers of the ratio of element with calcium data from nucleus, juvenile and edge of *P. borchgrevinki* otoliths were identified by plotting the squared Mahalanobis distances (Di^2) of the residuals against the corresponding quantiles (Q-Q plot) of the χ^2 distribution (Khattree and Naik, 2018). Based on Q-Q plots Di^2, correlation coefficients with Pearson method showed significant multicollinearity, variance-covariance matrices were not equal, and the Shapiro-Wilk test (Royston, 1982) results for the nucleus, juvenile and edge data did not conform to multivariate normality.

Univariate power transformation (Ashford et al., 2007, 2012) was applied to data, including C_{Mg}/C_{Ca}, C_P/C_{Ca}, and C_{Zn}/C_{Ca} of the nucleus; C_{Mg}/C_{Ca}, C_P/C_{Ca}, and C_{Zn}/C_{Ca} of the juvenile; and C_{Sr}/C_{Ca}, C_{Fe}/C_{Ca}, and C_{Zn}/C_{Ca} of the edge, in order to stabilized the variances. The transformed data conformed to multivariate normality with equal variance-covariance matrices. Specific transformations selected were as follows: for the nucleus data, $y^{-0.8}$ for C_{Mg}/C_{Ca} (P=0.321), $y^{-0.9}$ for C_P/C_{Ca} (P=0.399), and $y^{0.2}$ for C_{Zn}/C_{Ca} (P=0.706); for the juvenile data, $y^{-0.8}$ for C_{Mg}/C_{Ca} (P=0.186), $y^{-1.2}$ for C_P/C_{Ca} (P=0.195), and $y^{0.4}$ for C_{Zn}/C_{Ca} (P =0.643); for the edge data, $y^{-3.8}$ for C_{Sr}/C_{Ca} (P=0.261), $y^{0.5}$ for C_{Fe}/C_{Ca} (P=0.808) and $y^{0.1}$ for C_{Zn}/C_{Ca} (P=0.138). No transformations were required for C_{Sr}/C_{Ca} (P=0.082), C_K/C_{Ca} (P=0.787), C_{Fe}/C_{Ca} (P=0.363) of nucleus; for C_{Sr}/C_{Ca} (P=0.072), C_K/C_{Ca} (P=0.919), C_{Fe}/C_{Ca} (P=0.193) of juvenile; and for C_K/C_{Ca} (P=0.592) of the edge. After transformations, multicollinearity based on Pearson method was removed ($|r|$<0.9); variance-covariance matrices were equal; the Levene's test showed homogeneity of variance; and the results of Shapiro-Wilk test of transformation data from nucleus, juvenile and edge conformed to multivariate normality. In contrast, C_{Mg}/C_{Ca} and C_P/C_{Ca} of the edge area could not be transformed to a normal distribution (P <0.001).

Multivariate analysis of variance (MANOVA) was used to test the element data. To examine the influence of individual variation, analysis of covariance (ANCOVA) was used with total length as a covariate. No significant interaction indicated total length had no significant influence among different groups; in contrast, total length needed as a covariance add into the analysis among groups with significant interaction. In this case, the C_{Me}/C_{Ca} ratios (including C_{Sr}/C_{Ca}, C_P/C_{Ca}, C_K/C_{Ca}, C_{Fe}/C_{Ca}, and C_{Zn}/C_{Ca} from the nucleus area; C_{Mg}/C_{Ca}, C_{Sr}/C_{Ca}, C_P/C_{Ca}, C_K/C_{Ca}, C_{Fe}/C_{Ca}, and C_{Zn}/C_{Ca} from the juvenile area; and C_{Sr}/C_{Ca}, C_K/C_{Ca}, C_{Fe}/C_{Ca}, and C_{Zn}/C_{Ca} from the edge area) without significant interaction with body length, were used for MANOVA. As we were interested in the population and environmental heterogeneity of each group, we used multiple comparisons among groups after MANOVA. For C_{Me}/C_{Ca} ratios with significant interactions with the body length, namely C_{Mg}/C_{Ca} in the nucleus and C_{Mg}/C_{Ca} and C_P/C_{Ca} in the edge area, standard ANCOVA was applied to the nucleus data, while nonparametric ANCOVA was used for the edge data. All data results were analyzed, and tables and figures were generated using R software (version 4.3.1).

MANOVA and ANCOVA were used for test: (1) nucleus data for population heterogeneity, which could indicate different populations; (2) juvenile data for environmental heterogeneity to explore the environmental deviation of individual transport processes during the juvenile period; and (3) edge data for environmental heterogeneity of the pre-capture environment with individuals captured from the waters around Geologists Island and Prydz Bay.

3 Results

3.1 Distribution of concentrations for elements

The concentrations of ^{24}Mg, ^{88}Sr, ^{31}P, ^{39}K, ^{57}Fe, and ^{66}Zn were selected, and the ratios of these elements to calcium were calculated for each group and sampling position (Figures 3 and S3).

Table 2 displays the specific elements ratios at each sampling position that were influenced by total length. Among these, only C_{Mg}/C_{Ca} (F=4.784, P=0.005) from the nucleus and both C_{Mg}/C_{Ca} (F=14.14, P<0.001) and C_P/C_{Ca} (F=10.535, P<0.001) from the edge area showed significant interactions among groups with total length.

3.2 Differences of otolith element in groups

Population examination of individuals among groups was conducted using otolith nucleus elements, revealing significant differences according to MANOVA (Pillai's trace; F=4.216, P<0.0001). Similarly, significant differences were observed in otolith juvenile elements, indicating variations in transported environmental deviation among groups (MANOVA; Pillai's trace; F=4.614, P<0.0001). Furthermore, significant differences in pre-capture environmental heterogeneity were identified through edge elements using MANOVA (Pillai's trace; F=6.401, P<0.0001).

In the nucleus, post hoc tests following the MANOVA were conducted for all selected elements except for C_{Mg}/C_{Ca}. C_{Sr}/C_{Ca} (F=5.19, P=0.159), C_{Fe}/C_{Ca} (F=3.30, P=0.348), and C_{Zn}/C_{Ca} (F=5.88, P=0.118) did not show significant differences between groups, while C_K/C_{Ca} (F=22.8, P<0.0001) and C_P/C_{Ca} (F=13.6, P=0.003) exhibited significant differences. In addition, ANCOVA results for C_{Mg}/C_{Ca} , considering the significant interaction in total length among groups (F=4.78, P=0.005), showed significant differences (Table 3). In the juvenile, post hoc tests revealed significant differences for C_{Mg}/C_{Ca} (F=18.7, P<0.001), C_P/C_{Ca} (F=18.6, P<0.001), C_K/C_{Ca} (F=26.6, P<0.0001) and C_{Zn}/C_{Ca} (F=7.25, P=0.064), and no significant difference were detected for C_{Sr}/C_{Ca} (F=2.88, P=0.41) and C_{Fe}/C_{Ca} (F=1.22, P=0.749). Notably, least significant difference (P<0.0001) and Tukey's post hoc tests yielded different results for C_{Zn}/C_{Ca} (Table 3). In edge,

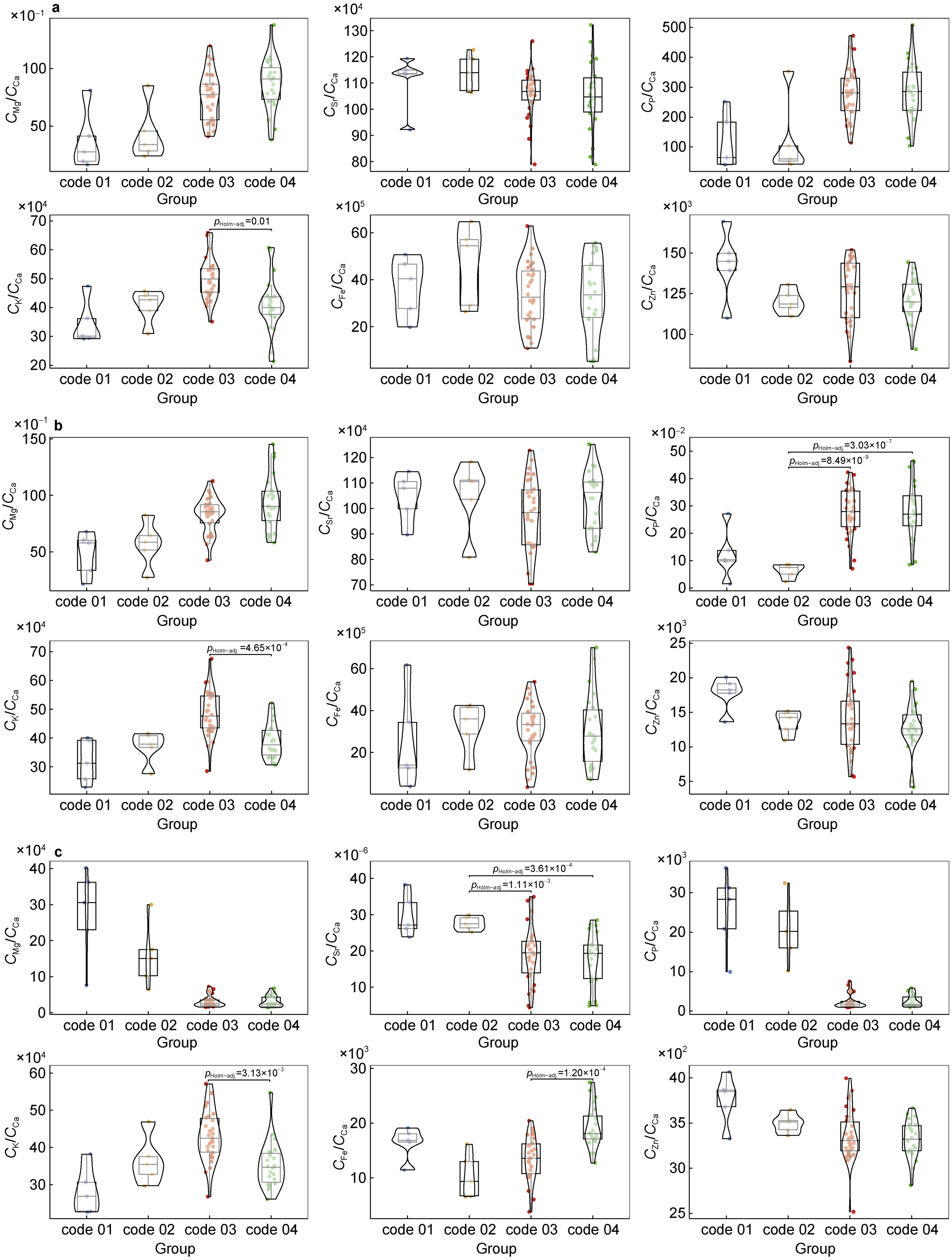

Figure 3 The C_{Mg}/C_{Ca} ratio from otolith nucleus, juvenile, and edge of *P. borchgrevinki*. **a**, nucleus; **b**, juvenile; **c**, edge.

Table 2 Significant interactions with total length among groups

Sampling position	Interactions of group:length	C_{Me}/C_{Ca}					
		C_{Mg}/C_{Ca}	C_{Sr}/C_{Ca}	C_P/C_{Ca}	C_K/C_{Ca}	C_{Fe}/C_{Ca}	C_{Zn}/C_{Ca}
Nucleus	*F*	4.784	0.278	2.610	0.772	0.551	2.082
	P-value	0.005*	0.841	0.061	0.515	0.650	0.113
Juvenile	*F*	2.033	0.810	0.432	0.108	0.359	0.902
	P-value	0.120	0.494	0.731	0.955	0.783	0.446
Edge	*F*	14.140	0.121	10.535	0.106	1.733	1.045
	P-value	<0.001*	0.947	<0.001*	0.956	0.171	0.380

Note: * indicate significant interaction.

Table 3 Multiple pairwise comparisons among each group for C_{Me}/C_{Ca}

Sampling position	C_{Me}/C_{Ca}	Group 1	Group 2	*P*-value	Statistical significance
Nucleus	C_K/C_{Ca}	code 01	code 03	0.026	*
	C_K/C_{Ca}	code 03	code 04	0.002	**
	C_P/C_{Ca}	code 01	code 04	0.046	*
	C_{Mg}/C_{Ca}	code 01	code 03	0.005	**
	C_{Mg}/C_{Ca}	code 01	code 04	0.003	**
	C_{Mg}/C_{Ca}	code 02	code 03	0.037	*
	C_{Mg}/C_{Ca}	code 02	code 04	0.019	*
Juvenile	C_K/C_{Ca}	code 01	code 03	0.020	*
	C_K/C_{Ca}	code 02	code 03	0.021	*
	C_K/C_{Ca}	code 03	code 04	<0.0001	****
	C_{Mg}/C_{Ca}	code 01	code 03	0.048	*
	C_{Mg}/C_{Ca}	code 01	code 04	0.011	*
	C_{Mg}/C_{Ca}	code 02	code 04	0.036	*
	C_P/C_{Ca}	code 02	code 03	<0.0001	****
	C_P/C_{Ca}	code 02	code 04	<0.0001	****
	C_{Zn}/C_{Ca}	code 01	code 04	0.022	*
Edge	C_{Fe}/C_{Ca}	code 02	code 04	0.020	*
	C_{Fe}/C_{Ca}	code 03	code 04	<0.0001	****
	C_K/C_{Ca}	code 01	code 03	0.014	*
	C_K/C_{Ca}	code 03	code 04	<0.001	***
	C_{Sr}/C_{Ca}	code 01	code 03	0.042	*
	C_{Sr}/C_{Ca}	code 01	code 04	0.021	*
	C_{Sr}/C_{Ca}	code 02	code 03	<0.001	***
	C_{Sr}/C_{Ca}	code 02	code 04	<0.0001	****
	C_{Mg}/C_{Ca}	code 01	code 02	<0.001	***
	C_{Mg}/C_{Ca}	code 01	code 03	<0.0001	****
	C_{Mg}/C_{Ca}	code 01	code 04	<0.0001	****
	C_{Mg}/C_{Ca}	code 02	code 03	<0.0001	****
	C_{Mg}/C_{Ca}	code 02	code 04	<0.0001	****
	C_P/C_{Ca}	code 01	code 03	<0.0001	****
	C_P/C_{Ca}	code 01	code 04	<0.0001	****
	C_P/C_{Ca}	code 02	code 03	<0.0001	****
	C_P/C_{Ca}	code 02	code 04	<0.0001	****

Notes: * means P<0.05, ** means P <0.01, *** means P <0.001, and **** means P<0.0001 the MANOVA results showed significant differences among groups with C_{Sr}/C_{Ca} (F=14.7, P=0.002), C_{Fe}/C_{Ca} (F=24.8, P<0.0001), C_{Zn}/C_{Ca} (F=10.0, P=0.019), and C_{K}/C_{Ca} (F=22.8, P<0.0001). Moreover, nonparametric ANCOVA showed significant differences in C_{Mg}/C_{Ca} (P=0.002) and C_{P}/C_{Ca} (P=0.002).

3.3 Identification analysis

To investigate the origins of individuals in each life history period, element types and concentrations collected from different otolith areas were used for tracing their sources through decision tree analysis (Table 4). Among the groups examined, code 01 and code 02 showed 100% external sources in nucleus period. The major source of code 01 and code 02 in nucleus period was identified as code 04, with 80% of the individuals appearing to originate from this group. Conversely, majority of the individuals in code 03 and code 04 (80% and 82%, respectively) were internally sourced within their respective groups, indicating that these groups served as their own primary sources (Table 4, Figure 4a).

Upon reaching the juvenile period, the traceability of sources based on otolith elements from juvenile zones became more apparent. The results indicated that all individuals from code 01 and code 02 showed external sources originating from code 04. The traceability analysis of code 03 and code 04 exhibited similarities to the nucleus period, albeit with specific differences. The number of individuals internally sourced within code 03 increased, accounting for 87%, while in code 04, the proportion decreased to 73%. Notably, no individuals were traced to originate from code 01 and code 02 across all groups (Table 4, Figure 4b).

Table 4 Identification of the origin for *P. borchgrevinki* individuals based on C_{Me}/C_{Ca}

Sampling position	Predicted	Actual			
		code 01	code 02	code 03	code 04
Nucleus	code 01	0	0	0	0
	code 02	0	0	0	0
	code 03	1	1	24	4
	code 04	4	4	6	18
Juvenile	code 01	0	0	0	0
	code 02	0	0	0	0
	code 03	0	0	26	6
	code 04	5	5	4	16
Edge	code 01	4	0	0	3
	code 02	1	5	1	0
	code 03	0	0	28	7
	code 04	0	0	1	12

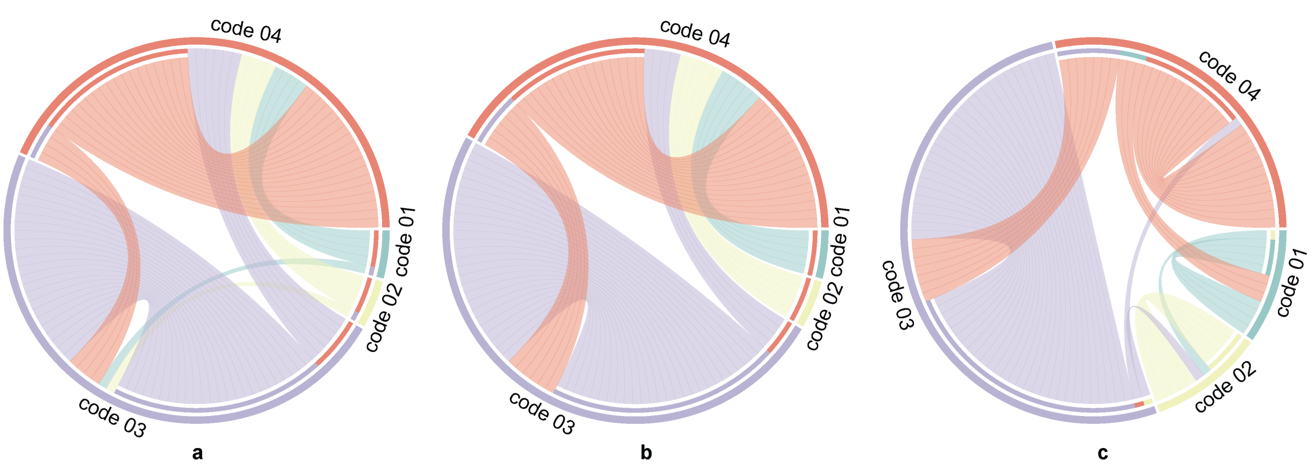

Figure 4 Hypothetical individual transportation between groups. **a**, nucleus; **b**, juvenile; **c**, edge.

Significant differences were detected between the first two previous periods and the edge period, particularly in the sources traced from code 01 and code 02. Individuals in code 01 and code 02 were predominantly internally sourced within their own groups, except for one individual from code 01 that originated from code 02. The results of traceability analysis for code 03 were further emphasized compared to the juvenile period, with the proportion of individuals sourced internally rising to 93%. However, these results were in stark contrast with those obtained for code 04, with more individuals sourced externally, resulting in a drop to 55% from within their own group (Table 4, Figure 4c).

4 Discussion

4.1 Population heterogeneity

Combining the results of Tables 3–4 and Figure 4a could indicate consistency in the spawning grounds or hatching grounds of individuals captured in the same region during different seasons, thereby suggesting consistent population structures between code 01 and code 02. In addition, results demonstrate consistent spawning and hatching periods and environments in adjacent regions.

As C_{Mg}/C_{Ca} is considered a direct reflection of physiological activities (Ashford et al., 2005; Martin and Thorrold, 2005), its significant differences between codes 01, 02 and codes 03, 04 indicate divergent physiological states during spawning and hatching periods. Given that C_{Mg}/C_{Ca} can distinguish Antarctic water masses (Ashford et al., 2010), the observed differences in early physiological activities are likely more attributed to environmental variations. Therefore, C_{Mg}/C_{Ca} differences during this period are likely due to variations in the environment during spawning and hatching periods, suggesting multiple spawning or hatching grounds and environmental heterogeneity between codes 01, 02 and codes 03, 04. Significant differences in C_K/C_{Ca} were also observed between codes 01, 04 and code 03. The differences are likely induced by variations in K concentration in physiological activitiesand environmental characteristics (Zumholz, 2005). Furthermore, differences between code 01 and code 04 were focused on C_P/C_{Ca}. P is influenced by metabolism (Ikeda et al., 1999), and metabolic rate is closely related to environmental temperature (Clarke and Johnston, 1999). Metabolic rate is also related to oxygen demand, which affects physiological activities including behavior, musculation, growth, and reproduction. While the speed of oxygen supply depends on temperature (Robinson and Davison, 2008), metabolic rate reflects temperature changes to some extent (Lowe and Davison, 2006). Therefore, due to differences in physiological activities and distribution environments between codes 01 and 04, metabolism varies correspondingly. Overall these findings suggest that individuals from the same or adjacent captured regions across different seasons originate from the same population, while individuals transported to different regions show significant differences, indicating population or physiological heterogeneity.

Discriminant analysis indicates that the populations from code 01 and code 02 are consistent with those of code 03 and code 04. Combined the significant different factors, which showed that C_K/C_{Ca} and C_{Mg}/C_{Ca} in the nucleus are the dominant factors, it is considered that the population of *P. borchgrevinki* in the four groups is consistent. However, differences in spawning times during the reproductive period, or eggs being carried to different environments after individual spawning, result in differences in physiological activities during spawning and hatching periods.

4.2 Life history heterogeneity

In this study, the juvenile and edge zones were selected to represent the juvenile and pre-captured periods of *P. borchgrevinki*, respectively. The differences between juvenile and edge periods (Table 3) can be attributed to physiological, behavioral and environmental differences. For individuals identified as having the same origin but existing in different groups, the juvenile period may be distributed in the same or similar environment. Due to distinguished from other individuals of the same origin due to ontogenetic differences. The absence of significant differences between code 01 and code 02 in the juvenile, spawning and hatching periods indicates consistency in physiological activities, and the distributed environment from the spawning period to the juvenile period. In contrast, the presence of differences only in C_K/C_{Ca} between code 03 and code 04 suggests feeding differences between groups may be the contributing factor. The identification results of the juvenile period are similar to those of the nucleus (Table 4, Figure 4b). The C_P/C_{Ca}, C_{Mg}/C_{Ca}, C_K/C_{Ca}, and C_{Zn}/C_{Ca} ratios were the dominant factors contributing to differences among groups, in particular reflecting individual growth and development differences (Fernald, 1985; Hairston et al., 1982; Zumholz, 2005).

Because the captured regions differed, the different thermohaline properties of water masses led to differences in the physical and chemical characteristics of water masses distributed in the two regions (Smith et al., 1984; Thompson et al., 2009). Due to the increased distance of captured regions in the edge period, the differences between elements and different groups increased compared to the juvenile period. Near Geologists Island, the AASW in summer is characterized by high temperature and low salinity, and the lower layer is residual Winter Water (WW) with low temperature and low salinity. The temperature differences in the vertical direction disappear in winter, with the unified water column extending to the depth of the water layer is about <250 m (Whitworth et al., 1998). According to thermohaline characteristics, Circumpolar Deep Water (CDW) lies below the AASW is the with a high temperature and high salinity. In Prydz Bay, the surface water is also controlled by seasonal AASW, with a depth of 20–50 m (Smith et al., 1984), underlain by CDW. However, there is no evidence that CDW can extend southward to the continental shelf. When CDW extends southward, it interacts with the Shelf Water (SW), which results in dramatic changes in the characteristics to its properties including decreased temperature and salinity, thus forming modified Circumpolar Deep Water (Whitworh et al., 1998). The SW in Prydz Bay consists primarily of Low Salinity Shelf Water with a depth of approximately 50 m (Carmack, 1977), which is characterized by low temperature and low salinity. According to previous research, *P. borchgrevinki* is not only found in costal AASW (Eastman and DeVries, 1985) but also in water near the sea bottom (Williams, 1988). The distribution range of *P. borchgrevinki* is from surface water (Eastman and DeVries, 1985; Gutt, 2002) to depth exceeding 500 m (Ekau, 1990; Iwami and Abe, 1981). Therefore, combined with the distribution depth range of *P. borchgrevinki*, regional differences indicate that due to the differences in water mass characteristics in Geologist Island and Prydz Bay (Smith et al., 1984; Thompson et al., 2009), the individuals distributed in regions were affected by the environment on physiological activities and metabolism.

Moreover, since individuals collected from code 01 and code 02 were captured in the same region during different seasons (winter and summer), respectively (Table 1). Therefore, differences in the distributed environment caused by different seasons manifested in the physiological activities, specifically reflected in C_{Mg}/C_{Ca} levels. This, combined with their distribution in the AASW (DeWitt, 1972), which is divided into Summer Surface Water (SSW) characterized by high temperature, low salinity and unstable thermohaline properties (Foldvik, 1985), and WW formed from cold water retained during the winter. The discrimination results of the edge area (Table 4, Figure 5c) indicate strong regional characteristics. Temperature is considered an important factor affecting behavior and physiological activities (Franklin et al., 2007; Lowe and Davison, 2006; Seebacher et al., 2005), affected not only by the SSW and WW in this region but also by temperature changes due to depth variations. Among the winter individuals from code 01, those identified as coming from summer may be due to differences in vertical distribution. Therefore, the results from different seasons in the same region suggest the possibility of vertical migration.

Differences between code 03 and code 04 were observed in C_{Fe}/C_{Ca} and C_K/C_{Ca}. Because the body length of code 03 is 15.73 cm ± 2.89 cm and that of code 04 is 20.34 cm ± 3.75 cm (Table 1), there is a large difference in body size between them, leading to differences in prey selection, capture, and habitat. Through field observations (Foster et al., 1987) and laboratory studies (Pankhurst and Montgomery, 1989), it has been found that the feeding behavior of *P. borchgrevinki* is dominated by vision under conditions of sufficient light (Pankhurst and Montgomery, 1990). Although this species is distributed under sea ice with low light, it can significantly improve visual function (Foster et al., 1987) through individual development, especially in body size, thus affecting prey (Hairston et al., 1982) and habitat (Boehlert, 1978; Pankhurst, 1987) selection. The discriminant results showed that code 03 has strong regionality, whereas code 04 does not. In terms of body length, code 03 was obviously smaller than code 04 (Table 1). It is inferred that *P. borchgrevinki* tends to migrate to other regions after reaching a certain body length range, while adults stay in a relatively fixed region for a period of time after maturity. The presence of individuals in the capture region that were identified as originating from other regions in the discrimination results indicates that there may be a transport pathway between the capture region and the discrimination region, allowing individuals to move between regions. According to the discriminant results for the four groups, the factors causing differences between groups were C_P/C_{Ca}, C_{Mg}/C_{Ca}, and C_{Fe}/C_{Ca}, which were influenced by the distributed environment, physiological activities, and metabolism. It can be inferred that individuals were transported to different regions during the pre-capture period, while individuals in the same or adjacent regions exhibit different behaviors depending on body length.

4.3 Transport pathway by circulations in Southern Ocean

The results of discriminant analysis on origin showed the distribution and migration of individuals across each period of their life history between groups. The environment of the captured region is not consistent with the region indicated by the otolith edge deposition elements. The rapid migration to the captured region allows the elements deposited in the otolith to remain indicative of the previous environment.

The spawning of *P. borchgrevinki* occurs once a year during June and July (Clarke, 1988). Spawning females have been found in McMurdo Sound and South Georgia Island (North and White, 1987), suggesting that the spawning grounds of *P. borchgrevinki* may be distributed in the Ross Sea and Weddell Sea. Although the spawning grounds differ, the population structure remains consistent due to the samilar otolith nucleus elemental characteristics. Eggs are typically distributed at the sea bottom and take 3–5 months to hatch (North and White, 1987), and the juvenile individuals after hatching are mostly distributed under sea ice. In addition, both nucleus and juvenile periods were consistent in the discrimination results, suggesting that eggs undergo vertical migration from the bottom to under sea ice in the same region due to the ontogenetic phenomenon of hatching. The vertical movement is usually driven by changes in the topography of the coastal slope and compensatory flow from surface water. When individuals develop from juveniles to adults and reach a certain body length, migration between different regions begins to occur. Due to the considerable distance between regions during this period, although *P. borchgrevinki* exhibits active swimming behavior, it still relies on the circulations and currents in the Southern Ocean for long-distance movement. The east–west circulations are mainly dependent on the Antarctic Circumpolar Current

(ACC) in the north (Ryan et al., 2000), and Antarctic Slope Current (ASC) and coastal currents in the Amundsen Sea and Bellingshausen Seas (Jacobs, 1991) in the south. *P. borchgrevinki* is a pelagic species; juveniles do not appear in the pelagic ocean (Hoshiai et al., 1989), but adults are distributed in both coastal and pelagic waters (Gutt, 2002), facilitating north–south transport between coastal and pelagic waters driven by ocean currents south of the ACC, including the Weddell Gyres (Orsi et al., 1993) and Ross Gyres (Paolo et al., 2015; Rignot et al., 2013). The distribution depth of *P. borchgrevinki* can be up to 646 m (Ekau, 1990), and cyclonic circulation not only exists on the ocean surface but can also penetrate deep into the ocean to transport individuals distributed below the surface. Based on the combination of these three transport modes, it is possible to achieve circumpolar distribution and connectivity between different regions.

5 Conclusion

In this study, combining difference and traceability analyses of each life history stage revealed that the *P. borchgrevinki* populations captured in the same or adjacent regions in different seasons were consistent. However, the hatching and larval stages of individuals in different regions were differently influenced by the external environment and internal physiological activities. Individual growth up to the juvenile stage was mainly influenced by ontogenetic differences, while growth through the pre-capture stage was primarily affected by differences in the physical and chemical properties of the environment and their physiological adaptations to it.

Results of traceability analysis with the data concerning the lifestyle of *P. borchgrevinki*, it was revealed that this species spawns during winter each year in the Southern Hemisphere, and the same population is distributed in multiple spawning grounds around the Antarctica. During the hatching and larval stages, the eggs move vertically from the bottom to the surface water under sea ice due to individual ontogeny. After reaching a certain body length, individuals begin to move east and west across different regions carried by the ACC, ASC, and local ocean currents. Finally, upon reaching the adult stage, individuals move north and south between coastal and pelagic regions through the Weddell Gyre and Ross Gyre.

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