Research Article

Gross morphology of the cephalic sensory canal pores in Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898 from southern Chile (Perciformes: Nototheniidae)

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ABSTRACT. This study describes the cephalic sensory canal pores of the Patagonian toothfish's juvenile and adult specimens (*Dissostichus eleginoides*) from southern Chile. Specimens exhibited four supraorbital, eight infraorbital, and five mandibular pores, followed by six preoperculars, one coronal pore, one supratemporal pore, and four temporal pores. Juveniles exhibited circular pores in the mandibular, infraorbital, and preopercular region. The first two supraorbital pores are circular, the third is rectangular, and the fourth triangular. The coronal pore is circular with a bifurcation; the supratemporal pore is rectangular. In adults, the first mandibular canal pore is circular, and the last four are elongated. The preopercular canal pores are elongated. The two first supraorbital canal pores are circular, unlike the third and fourth, which are rectangular. The coronal pore is rectangular without bifurcation, and the supratemporal pore has a T-shape. The jaw of juveniles does not present all mandibular canal pores; in the infraorbital region, the first five pores extend as a thin canaliculus, while the adjacent pores appear as longer canaliculi in adults. The differences could be related to changes in spatial distribution during larval, juvenile, and adult stages. Adult cephalic sensory canal pores may have an important role in detecting vibratory waves allowing them to capture their prey and perceive potential predators. Our results provide information regarding the cephalic sensory canal pores of the Patagonian toothfish that may stimulate future studies of this species' mechanosensory system.

Keywords: *Dissostichus eleginoides*; Patagonian toothfish; Nototheniidae; head pores; lateral line; mechanosensory system; southern Chile

INTRODUCTION

The Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898 is an abysso-benthic species whose bathymetric distribution fluctuates between 80 and 2500 m in depth (Collins *et al*., 2010; Cáceres *et al.*, 2016) with broad circumpolar biogeography, spreading to the southeastern Pacific (Arana *et al*., 1994; Murillo *et al*., 2008; Collins *et al*., 2010; Aramayo, 2016), and Occidental and southwestern Atlantic (Miller, 1993; Nelson *et al*., 2016).

Collins *et al.* (2010) suggested that species distribution is conditioned by age, and adult and juvenile populations appear to be separated. Aramayo (2016) indicates that this species' ontogenetic cycle stimulates vertical migrations within its habitat during the early stages of growth, its behaviour is mainly pela-gic, and during adulthood, it becomes a deep-sea fish. Other studies indicate that this species can be distributed by size relative to depth, where smaller fish are found in shallower waters (Aramayo, 2016; Céspedes *et al*., 2016). Variation of the water column's abiotic parameters at different depths suggests that *D. eleginoides* may exhibit a mechanosensory system that allows them to survive even in low light conditions. In general, Antarctic fishes, and especially Antarctic notothenioids, present sensory adaptations to the low light levels that are observed during winter or summer ice conditions; sharing some sensory characteristics with fishes from similar habitats, such as eyes designed to increase visibility and improve non-visual sensory systems, chemosensory systems, and the lateral line mechanosensory system (Pankhurst & Montgomery, 1989; Montgomery *et al*., 1994, 1997; Jansen, 1996;

Macdonald & Montgomery, 2005; Pointer *et al.*, 2005; Eastmann & Lanoo, 2011; Ferrando *et al.*, 2019).

The mechanosensory system is formed by a series of pores and canals present on the surface of both the head and lateral line of the trunk (Macdonald & Montgomery, 2005; Webb, 2014) and is related to prey detection and predators, feeding, swimming, rheotaxis, schooling formation, intraspecific communication, and wave source location (Engelmann *et al.*, 2002; Kasumyan, 2003; Mogdans *et al.*, 2003, 2004; Chao *et al.*, 2017; Spiler *et al.*, 2017; Marranzino & Webb, 2018). Between each pore, there is a set of cells that are sensitive to vibration called neuromasts, which can be of two types: superficial neuromasts distributed on the surface of the body and whose cupulae are bathed by water, and a second type, called canal neuromasts, located inside the bony canals, which have pores that communicate with the outer environment (Kasumyan, 2003; Barbin & Humphrey, 2009; Webb, 2014; Butler & Maruska, 2016; Herzog *et al.*, 2017). The canal neuromasts receive information through these pores, which are captured by the cupula then transmitted to the stereocilia, being the kinocilium the one that transmits the information afferent neurons to be processed in the brain (Mogdans *et al.*, 2003; Webb, 2014; Chao *et al.*, 2017).

In notothenioid fishes, the mechanosensory system is characterized by the presence of large cephalic pores (Balushkin, 2000; MacDonald & Montgomery, 2005; Cziko & Cheng, 2006), which are in contact with broad and semi-membranous canals such as those in the Channichthyidae family (Iwami *et al.*, 1999). The cephalic canal pore has diverse morphological specializations suggesting that this sensory style is important in Nototheniidae (Balushkin, 2000; MacDonald & Montgomery, 2005). However, these structures have scarcely been studied. Consequently, there are only general descriptions in the literature, such as; Balushkin (2000) described four different patterns of pore distribution in some genera of the Pleuragrammatinae subfamily, as *Gvozdarus*, *Aethotaxis*, *Pleuragramma*, and *Dissostichus*. Iwami *et al.* (1999) described the pores of some species of the family Channichthyidae. Jansen (1996) described the position of the pores in some species of the Nototheniidae family.

Considering all the previously reported antecedents, it appears that Patagonian toothfish *D. eleginoides* change their vertical distribution either during their juvenile or adult phase. Since information regarding the morphological characteristics of the cephalic sensory canal pores of this species is scarce, we consider it necessary to perform a comparative analysis of pore patterns in juvenile and adult specimens. Likewise, analyse if there are any differences in shape, quantity,

and arrangement of cephalic sensory canal pores between both development stages that would allow the pattern to be associated with the bathymetric distribution of the specimens.

MATERIALS AND METHODS

The cephalic sensory canal pores were studied in four specimens of *Dissostichus eleginoides*, two of them juveniles of 195 and 243 mm in total length (TL); 65 and 81 mm head length (HL); and two adults of 600 and 610 mm in TL; 130 and 140 mm HL, provided by fishermen located in southern Chile (15 miles from the city of Valdivia, 39°48'30"S, 73°14'30"W).

The study consisted of determining the quantity, shape, and distribution of the cephalic sensory canal pores present on the epidermis in all studied specimens. Observations were done under a stereomicroscope Olympus SZ51; specimens were photographed with a Canon PowerShot Elph135 digital camera. The pores were listed sequentially from left to right.

The infraorbital region was divided into three sectors to describe the location of the infraorbital sensory canal pores: an anterior sector with pores located in the first anterior third of the infraorbital zone in front of the orbit; a middle sector with pores located on the second third of the infraorbital zone below the orbit; and a posterior sector, those pores located in the last third of the infraorbital zone behind the orbit.

The experiment was performed under the guidelines for using laboratory animals established by the Comisión Nacional de Ciencia y Tecnología de Chile (CONICYT) and the Universidad Austral de Chile, code of ethical protocol 261/2016. This article does not contain any studies with human participants performed by any of the authors.

RESULTS

The cephalic sensory canal pores in *Dissostichus eleginoides* are characterized by oval and varying shape according to their location in juveniles and elongated shape in adults.

Cephalic sensory canal pores in juveniles

The cephalic sensory canal pores, in juvenile specimens, are in seven different areas on the head. Differences were recorded among these specimens in the position and shape of the mandibular pores.

In the 195 mm specimen, the first two mandibular pores (mp 1, 2) were scarcely observed while the pores mp 3, 4, and 5 are notorious, circular, and widely separated from each other; the fourth pore (mp 4) is

located in the second third of the mandible. Meanwhile, the fifth pore (mp 5) is located in the last third (Fig. 1a).

In the 243 mm specimen, the first two pores (mp 1-2) are very inconspicuous, while the remaining three pores (mp 3-5) are quite notorious and elongated (Fig. 1b). The mp 4 is located below the mandibular commissure; the fifth pore (mp 5) is found near the first preopercular pore (pop 1).

In the preopercular region, there are six pores (pop 1-6); three of them (pop 1-3) are located in the horizontal shaft; the first two pores (pop 1-2) are circular, and the third pore (pop 3) is elongated. The next three pores (pop 4-6) are elongated in shape; the fourth pore (pop 4) is at the flexion point of the preoperculum, and another two pores (pop 5-6) emerge along the vertical shaft of this bone (Fig. 1c).

There are eight pores in the infraorbital region (iop 1-8); all of them are circular, arranged in three sectors: the anterior, middle, and posterior. In both specimens, in the first five pores (iop 1-5), the canaliculi are separate one from the other (Figs. 1d-e) while the canaliculi of iop 6 and iop 7 (Can 1-2) are very close together (Figs. 1f-g). Some differences were found in the position of the fourth pore (iop 4) among the juvenile specimens. In 195 mm specimen, the first three pores (iop 1-3) are located in the anterior sector while in four following pores (iop 4-7) are located in the middle sector. The eighth pore (iop 8) sits in the posterior sector; it is circular and has no canaliculus (Fig. 1d). In the 243 mm specimen, the first four pores (iop 1-4) are located in the anterior sector while the three following pores (iop 5-7) are in the middle sector. The eighth pore (iop 8) sits in the posterior sector, is circular, and has no canaliculus (Fig. 1e).

At the supraorbital region, four pores (sop 1-4) are observed, the first and second (sop 1-2) are circular and are located in the upper medial side of the anterior nasal opening. The third pore (sop 3) is rectangular while the fourth pore (sop 4) is triangular; both are located along the frontal bone, medial about the orbit (Fig. 1h).

In the middle region of the head, the coronal commissure (CC) has an oval-shaped coronal pore (cp), which exhibits a bifurcation forming two "wing-shape" located distally to the central point of the pore. The supratemporal pore (stp) is rectangular and is in the supratemporal commissure (STC), behind the interorbital pore (Fig. 1h). There are four oval temporal pores (tp 1-4) (Fig. 1i).

Cephalic sensory canal pores in adults

In adults, the sensory canal pores are located in seven different areas of the head; in the mandibular region, five mandibular pores (mp) were observed, which begin near the symphysis (mp 1), one of them is circular (mp 1), and the last four (mp 2-5) are elongated (Fig. 2a). In the preopercular region, there are six elongated pores; three of them (pop 1-3) are located in the horizontal shaft of the preoperculum, the fourth pore (pop 4) is at the flexion point of this bone, and another two pores (pop 5-6) emerge along the vertical shaft of this bone (Fig. 2b).

In the infraorbital region, eight pores are difficult to visualize; they are arranged in three different sectors: the anterior, middle, and posterior. The first five pores (iop 1-5) are located in the anterior sector and their canaliculi are thin and separated from each other (Figs. 2c-d). The middle sector exhibits the two following pores (iop 6-7) whose canaliculi are quite notorious and separated from each other (Figs. 2e-f). The first canaliculus (Can 1) is located just below the middle of the eye, while the second (Can 2) is located just before reaching the orbit's posterior edge. The eighth pore (iop 8) sits in the posterior sector and has no canaliculus (Figs. 2c-d).

At the supraorbital region, four pores (sop 1-4) are observed, the first and second pores (sop 1-2) are circular and are located in the upper medial side of the anterior nasal opening, while the next two pores (sop 3-4) are rectangular and they are located along the frontal bone, medial about the orbit (Fig. 2g).

In the head's middle region, the coronal commissure (CC) has a coronal pore (cp) and is rectangular with no bifurcation (Fig. 2g). Behind the CC, the supratemporal commissure (STC) has a pore with a T shape (Fig. 2g).

In the temporal region, there are four temporal pores (tp 1-4); all of them are rectangular with rounded edges (Fig. 2h).

DISCUSSION

The cephalic canal pores of the Antarctic fish play an important role in detecting prey since they inhabit areas where low levels of light last long periods during the polar winter (Montgomery *et al.*, 1988; Eastman & Lanoo, 2008). These structures make the first contact with the surrounding environment and then transmit the vibrations to neuromasts (Kasumyan, 2003; Barbin & Humphrey, 2009; Webb, 2014; Herzog *et al.*, 2017; Marranzino & Webb, 2018). Thereby specimens receive hydrodynamic signals from potential prey organisms and detect predators' presence (Janssen, 1996; Montgomery *et al*., 1997; Butler & Maruska, 2016; Chao *et al*., 2017; Spiler *et al*., 2017).

The scarce literature on the pores of the cephalic sensory canal of *Dissostichus eleginoides* does not allow comparisons with our results. However, illustra-
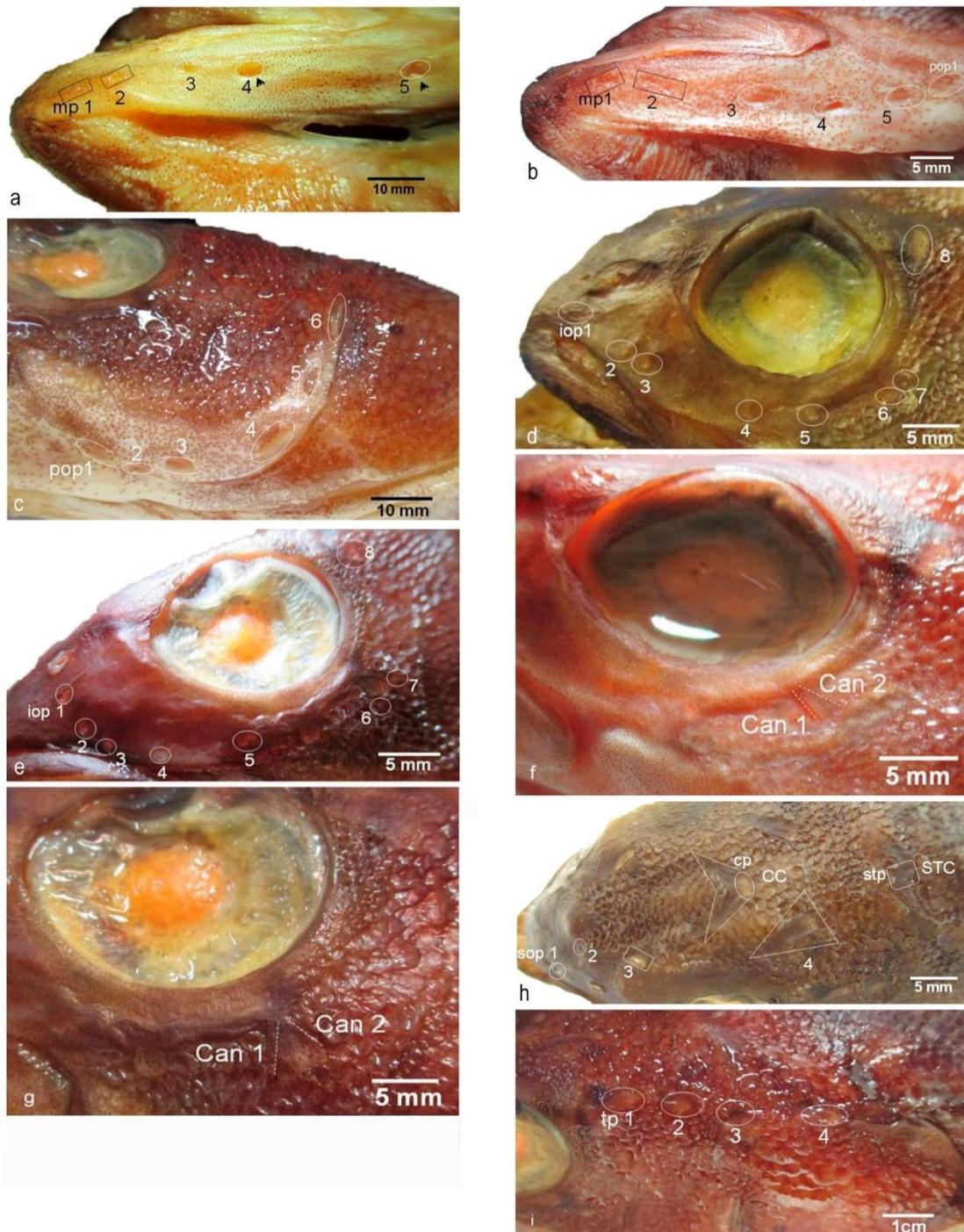
Figure 1. Distribution of cephalic sensory canal pores in juvenile specimens of *Dissostichus eleginoides*. a) Ventral view, mandibular sensory canal pores (mp) distribution in juvenile specimens TL 195 mm. The black rectangles show the first two pores (mp 1-2). Black arrows indicate the separated mp 4-5; b) ventral view, specimen total length (TL) of 243 mm, the black rectangles indicate the first two pores (mp 1-2). First preopercular pore (pop 1); c) lateral view, preopercular sensory canal pores (pop) distribution; d) lateral view, infraorbital sensory canal pores distribution in specimen TL 195 mm and e) specimen of TL 243 mm; f) lateral view, stages of differentiation for canaliculi 1 and 2 (Can 1, Can 2) between juvenile specimen TL 195 mm and g) specimen TL 243 mm; h) dorsal view, supraorbital pores (sop), coronal pore (cp), coronal commissure (CC), supratemporal pore (stp) and supratemporal commissure (STC) in juvenile sample TL 243 mm. The dotted line indicates the cp bifurcation; i) lateral view, temporal sensory canal pores (tp) distribution juvenile sample TL 243 mm.
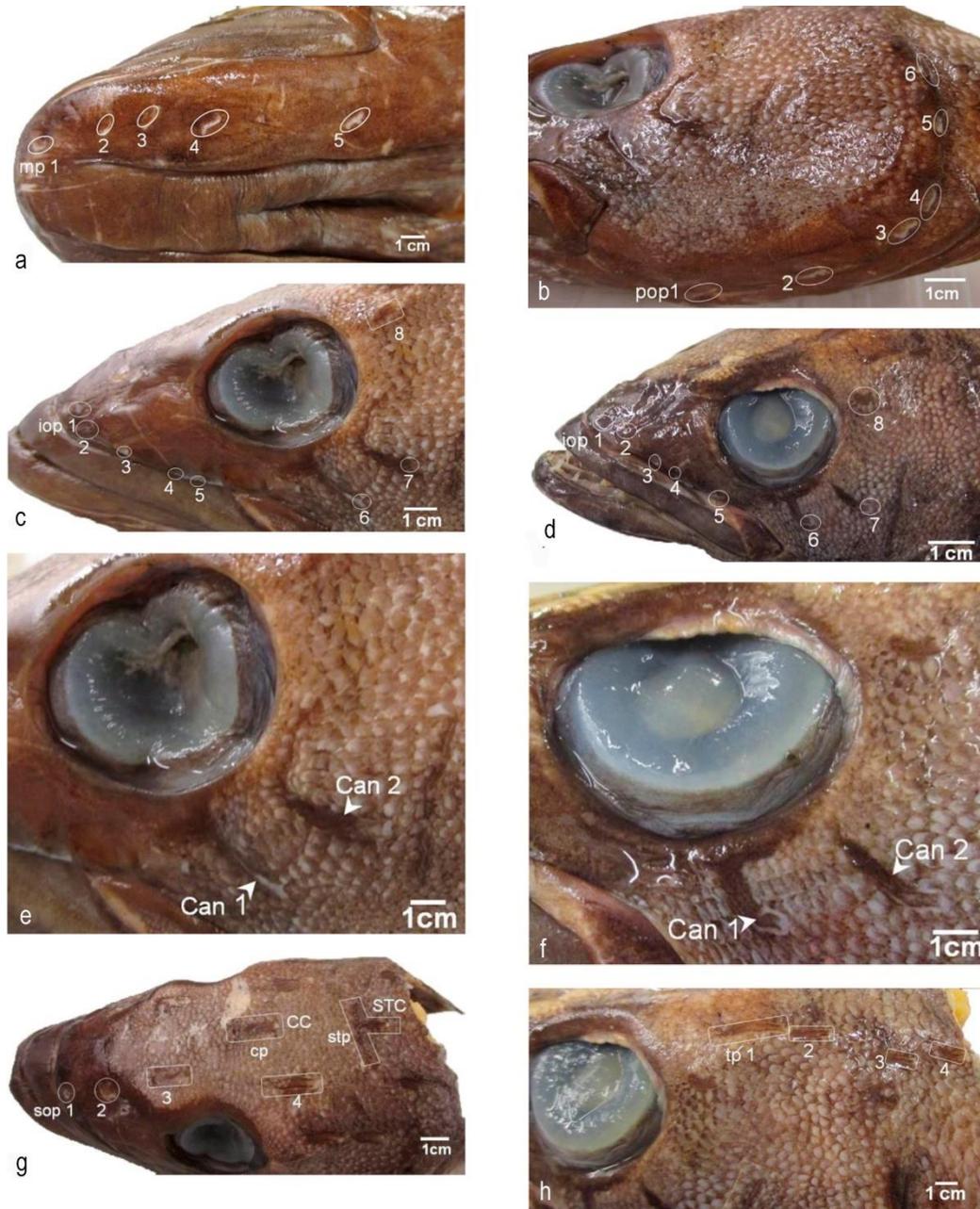
Figure 2. Cephalic sensory canal pore distribution in adult specimens of *Dissostichus eleginoides*. a) Ventral view, mandibular sensory canal pores (mp) distribution in specimens 600 mm total length (TL); b) lateral view, preopercular sensory canal pores (pop) distribution in specimen 600 mm TL; c) lateral view, infraorbital sensory canal pores (iop) distribution in specimen 600 mm TL and d) specimen 610 mm TL; e) lateral view, stages of differentiation for canaliculi 1 and 2 (Can 1, Can 2) in specimen TL 600 mm and f) specimen TL 610 mm; g) dorsal view, supraorbital pores (sop), coronal pore (cp), coronal commissure (CC), supratemporal pore (stp) and supratemporal commissure in sample TL 600 mm; h) lateral view, temporal sensory canal pores (tp) distribution in adult sample TL 600 mm.

tions by Baluskin (2000), reporting the distribution and pore number in adult specimens of the genus *Dissostichus* allow us to conclude a pattern similar to that described in this study.

The results reported in this study show morphological differences between the mandibular pores of juvenile and adult specimens of *D. eleginoides*. It is possible to assume that these variations are associated to the size of the fish and the eventual change of habitat

that they experience as they grow in size; consequently, the juveniles that regularly inhabit a pelagic or semi-pelagic environment move towards a demersal environment when they are adults (Belchier & Collins, 2008; Collins *et al*., 2010; Aramayo, 2016). This habitat change allows the early cephalic pore system to develop as the individual grows, reaching its maximum expression in adults, where wide, elongated, and membranous pores are observed in the upper part of the head while they appear elongated and circular in the preoperculum, jaw, and around the eye.

The presence of two commissures on the head in *D. eleginoides*, a coronal and a supratemporal, were also described in several other Notothenioidei species (Balushkin, 2000; Balushkin & Prut'ko, 2006; Shandikov & Eakin, 2013). These commissures allow sensory canals to connect on opposite sides of the body (Iwami *et al*., 1999; Balushkin, 2000). The change in habitat suggests that the mandibular pore system is not as important in juveniles as the role of vision during the fish's growth stage. Belchier & Collins (2008) indicated that larvae of *D. eleginoides* of South Georgia hatch in spring or summer when the luminosity is greater. Consequently, during this pelagic phase, but also during both early-juvenile and juvenile phases, the visual system would be predominant and characterized by the presence of a retina with a large number of cones and a small number of rods, while certain brain areas related to the mechanosensory system, such as *eminentia granularis* and *corpus cerebralis*, would be in the formation stage. In contrast, in adult specimens, the mandibular pores become highly important for detecting prey and vision, which would have a complementary role.

During the pelagic phase, juveniles are active carnivores, and their diet is based mainly on fish and small amounts of krill (Belchier & Collins, 2008); for this reason, preopercular pores could play an important role in the detection of prey as described by Montgomery *et al.* (1988) in the Antarctic pelagic species *Pagothenia borchgrevinki*. These authors determined that in the presence of vibrations (that could be emitted by an organism when swimming), there is a response between pores 2 and 3 of the horizontal shaft of the preoperculum, where a neuromast is located in connection with the afferent neuron of the lateral line (Montgomery & Macdonald, 1987; Montgomery *et al*., 1988). The change in habitat previously described for this species occurs between autumn and winter just when there is less light intensity associated with a reduction in water temperature; by this time, the juveniles proceed to migrate vertically to greater depths where they complete their development and become adults (Belchier & Collins, 2008). In this phase of

development, along with changing their diet, the retina of the eyes presents a large number of rods and a lower amount of cones and exhibiting a highly developed *eminentia granularis* and *corpus cerebralis.* The increase in the number of sensory vision cells is a complement to the mechanosensory system that facilitates adult survival in a low-luminosity environment (Eastmann & Lanno, 2011).

The canaliculi of the infraorbital region correspond to an extension of the infraorbital canal; morphologically, its anterior part is shorter than the middle zone (Iwami *et al*., 1999), and its function is to act as a filter against hydrodynamic disturbances when the fish swims or is in turbid/fast waters (Janssen, 1996; Eastman & Lanoo, 2007). In *D. eleginoides*, there are morphological differences between the infraorbital canaliculi of juveniles and adults, being more developed in adults. These membranous secondary canals present in juveniles and adults are also found in other notothenioid fish, such as juveniles and adults of *Eleginops maclovinus*, a non-Antarctic and bentho-pelagic notothenioid (Eastman & Lanoo, 2008; Sáez *et al*., 2019) as well as in *Bovichthus diacanthus* and various fish taxa (Janssen, 1996; Eastman & Lanoo, 2007).

The sensory canal pores located in the dorsal part of the head and the temporal region of *D. eleginoides* are lengthened along with the changes related to the growth of the fish's head and body from the juvenile to the adult stage. During the adult stage, individuals are submitted to greater water pressure onto the body and head. Therefore, semi-membranous pores must resist this pressure (Windsor & McHenry, 2009; Ristroph *et al*., 2015).

The results reported in this study reveal the morphological changes experienced by the individual in their passage from a juvenile to adult are related to the habitat change experienced by juveniles of this species. From a functional point of view in adult fishes, the cephalic pores would have an important role in catching vibratory waves, allowing them to capture food and facilitating their survival by detecting potential predators but also facilitating their adaptation to an environment with less visibility as well as allowing its feeding and survival in an environment of low temperatures and scarce luminosity.

Although results here establish an important morphological record since this characteristic has not been previously studied in this species, several more studies are required to obtain significant knowledge of the morphology and histology of cephalic sensory canal pores and their connections neuromasts. Also, histological studies that describe the retinal organization from juvenile and adult stages of Patagonian toothfish *D. eleginoides* are required.

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