Natasha Travenisk Hoff

Wake of Death:

Using historical and contemporaneous data to evaluate the
Isopisthus parvipinnis (Sciaenidae) population structure at
the Southwest Atlantic Ocean (23° - 26.9°S)

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Ph.D. Thesis presented to the Graduate
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Ao meu porto seguro perto mesmo longe... < * >>>< <3

Mostrando que a arte de ensinar vai muito além dos livros!

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A vocês, o meu mais sincero muito obrigado!

”Metade de mim

Agora é assim

De um lado a poesia, o verbo, a saudade

Do outro a luta, a força e a coragem pra chegar no fim

E o fim é belo incerto... Depende de como você vê

O novo, o credo, a fé que você deposita em você e só”

Fernando Anitelli

O Teatro Mágico - O Anjo Mais Velho

Preface

This thesis resulted from my research undertaken at the Oceanographic Institute of the University of São Paulo, Brazil (IO-USP), in partnership with the Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), with financial support of the National Council of Scientific and Technologic Development (CNPQ, 163116/2015-6) and the Coordination for the Improvement of High-Level Education Personnel (CAPES, PDSE nº47/2017, Process 88881.189862/2018-01). The research was conducted under the supervision of the professor Dr. J.F. Dias (IO-USP) and professor Dr. A.T. Correia (CIIMAR), representing an original work with the PhD student as the first author of all manuscript. All co-authors have contributed significantly to the work, participating in drafting and revising critically the intellectual content of each manuscript. Thus, part of the information contained in this PhD thesis has been presented in international and national events, published in peer-viewed international journal and scientific communication media, as follow:

- Hoff N.T., Dias J.F., Zani-Teixeira, M.L., Correia, A.T. (2019). Body morphology as a tool to infer about the population structure of bigtooth corvina (*Isopisthus parvipinnis*) in the SE Brazilian coast. Front. Mar. Sci. Conference Abstract: XX Iberian Symposium on Marine Biology Studies (SIEBM XX). Poster. <https://doi.org/10.3389/conf.fmars.2019.08.00172>
- Hoff N.T., Dias J.F., Zani-Teixeira, M.L., Correia, A.T. (2019). Bigtooth corvine, *Isopisthus parvipinnis*, population structure in Southeast Brazilian coast inferred from otolith shape analysis. Front. Mar. Sci. Conference Abstract: XVI European Congress of Ichthyology. Poster. <https://doi.org/10.3389/conf.fmars.2019.07.00161>
- Hoff N.T., Dias J.F., Zani-Teixeira, M.L., Correia, A.T. (2019). Otolith chemistry as a tool to infer about the population structure of the bigtooth corvina (*Isopisthus parvipinnis*) in the Southeast Brazilian coast. Front. Mar. Sci. Conference Abstract: XVI European Congress of Ichthyology. Poster. <https://doi.org/>

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- Hoff, N.T. Wake of Death: Using historical and contemporaneous data to evaluate the *Isopisthus parvipinnis* (Sciaenidae) population structure at the Southwest Atlantic Ocean (23° - 26.9°S). 1º Encontro da Pós-Graduação da Universidade de São Paulo, 2020. Video. <https://www.youtube.com/watch?v=Q1zaqprxQe0>

It is worth highlighting the importance of biological collections in assessing temporal and spatial variations in fishes population structure as they preserve and make data and structures available, and this can generate meaningful information for fisheries management and environmental assessment.

Resumo

A presente tese buscou responder três questões sobre a estrutura populacional de *Isopisthus parvipinnis* ao longo da área sul de sua distribuição no Oceano Atlântico Sudoeste (23°S – 26,9°S): - se existem unidades populacionais fenotípicas distintas da espécie; - se há manutenção espacial e temporal da estrutura populacional; - e se marcadores naturais como a forma do corpo, morfometria do otólito e composição química do otólito são capazes de identificar estas diferenças fenotípicas. Os indivíduos de *I. parvipinnis* (entre 66 - 139 mm de comprimento) foram coletados em setembro e novembro de 1975 (projeto Fauna Nectônica - FAUNEC) e entre setembro de 2018 e maio de 2019, por capturas comerciais e científicas. A análise da morfometria corporal foi aplicada apenas aos dados contemporâneos, enquanto os índices de forma (SIs), os descritores elípticos de Fourier (EFDs) e a análise da composição de elementos químicos dos otólitos após dissolução total foram aplicados aos dois períodos. Técnicas estatísticas uni- e multivariadas detectaram variações em todos os marcadores naturais, tanto em relação às localidades (São Paulo: norte - NSP, centro - CSP, e sul – SSP; Paraná – PR; Santa Catarina - SC) quanto aos períodos de coleta. Todas as distâncias morfométricas corporais mostraram-se significativas, enquanto os EFDs responderam melhor às variações espaciais e temporais que os SIs. Ao menos sete razões elementares mostraram diferenças significativas entre as localidades nos dois períodos. Os resultados sugerem mudanças na estrutura populacional de *I. parvipinnis*, de uma ou duas unidades populacionais em 1975 para, ao menos, quatro unidades populacionais em 2018/2019 (NSP, CSP, SSP/PR, SC), a depender do método utilizado, respondendo às diferentes características oceanográficas da área de estudo, dos padrões de alimentação, influências antropogênicas, poluição e mudanças climáticas. Além disso, observou-se uma melhora na reclassificação dos indivíduos para seu local de origem em: 79% pela morfometria corporal, de 42 para 81% pela morfometria do otólito e de 58 para 80% pela composição química do otólito para os dois períodos de amostragem (1975, 2018/2019).

Palavras-chaves: Sciaenidae, rede de treliça, otólitos, índices de forma, descritores elípticos de Fourier, microquímica, unidades populacionais.

Abstract

This thesis aimed to answer three questions about the population structure of *Isopisthus parvipinnis* along the southern area of its distribution in the Southwest Atlantic Ocean (23°S - 26.9°S): - if there are phenotypic population units of the species; - whether there is spatial and temporal maintenance of the population structure; - and whether natural markers such as body morphometry, otolith morphometry-shape and chemical composition of otolith can identify these phenotypic differences. The individuals of *I. parvipinnis* (between 66 - 139 mm in total length) were collected in September and November 1975 (Nectonic Fauna Project - FAUNEC) and between September 2018 and May 2019, by commercial and scientific fishing. The morphometric body analysis was applied only to contemporary data, while the form indexes (SIs), the Fourier elliptic descriptors (EFDs) and the analysis of the chemical composition of the post-total dissolution otoliths were applied to both periods. The statistical analysis detected variations for all natural tags, concerning the locations (São Paulo: north - NSP, center - CSP, and south - SSP; Paraná - PR; Santa Catarina - SC) and the collection periods. All body morphometric distances presented significant differences among locations, while EFDs responded better to spatial and temporal variations than SIs. At least eight elementary ratios showed significant differences between the localities in both periods. The results suggest changes in the population structure of *I. parvipinnis* from one or two population units in 1975 to at least four population units in 2018/2019 (NSP, CSP, SSP / PR, SC), depending on the adopted method, as a response to the different oceanographic characteristics of the study area, feeding patterns, anthropogenic influences, pollution, and climate change. Besides, there was an improvement in the reclassification of individuals to their place of origin: 79% by body morphometry, from 42 to 81% by otolith morphometry and from 58 to 80% by otolith chemical composition for both periods (1975, 2018/2019).

Keywords: Sciaenidae, Truss network, otoliths, shape indices, elliptical Fourier descriptors, microchemistry, population units.

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1 Introduction

1.1 Natural tags in fisheries management

Fisheries management consists of an “integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with enforcement as necessary, of regulations or rules which govern fisheries activities in order to ensure the continued productivity of the resources and the accomplishment of other fisheries objectives”, according to Cochrane and Garcia (2009). Among many possibilities approaching biological, economic and social aspects, fisheries management aims to ensure the continued productivity of target species as well as minimize fishing impacts on bycatch (non-target), associated and dependent species and on the environment (Cochrane and Garcia, 2009).

Understanding fish populations structure in space and time, and the consequent discrimination of different population units of target and non-target species are important prerequisites for fisheries management (Begg and Waldman, 1999; Cadrin et al., 2014). Population structure can have significant consequences, including the mediation of species in a response to fishing pressure and environmental changes and playing a key role in species persistence (Kerr et al., 2017). Thus, stock identification, a multidisciplinary field comprising genetics, mark-recapture techniques, biometrics, and chemical analyses of tissues and hard parts (Cadrin and Friedland, 1999), emerges as a meaningful science for fisheries management. From both theoretical, regarding the faunal diversification, and practical, in estimating stocks size, points of view, it is of fundamental importance to determine if each species is homogeneous in all its distribution area, or if there is geographical differentiation (Vazzoler, 1971). Variations in characters may occur only due to the environmental influence (individual, phenotypic variations), or geographical differentiation based on genetics may also occurs, culminating in reproductive isolation, thus constituting each group in a reproductively isolated population (Vazzoler, 1971), given rise to different population units which may respond differently to exploitation and rebuilding, and must be managed separately to optimize their yield (Galli and Norbis, 2013).

Despite its importance, it's necessary to define what is a population unit. Through decades, the concept of population unit (term adopted in this work), also called stock, unit stock or management unit - most of them not differing greatly -, has been discussed (Templeman, 1983; Coyle, 1998; Begg and Waldman, 1999). A population unit was defined by Marr (1957) as a self-sustaining population. For some other authors (Templeman, 1979; IHssen et al., 1981; Milton and Shaklee, 1987; Ferguson et al., 2011), the term stock originally referred to one or more group of fish (breeding populations) available for exploitation in a given area and time period. As arbitrary groups, stocks are large enough to be essentially self-reproducing and with individuals having similar life history characteristics (Hilborn and Walters (1992) *apud* Begg and Waldman (1999)), comprising a series of sub-populations (Ferguson et al., 2011). These stocks, that should be considered independent from each other for management purposes, are usually separate out during spawning and mix outside the spawning season (Bone and Moore, 2008).

Complementary, Saila and Jones (1983) stated the term unit stock as "subareas of the total species range can have a characteristic single population or a set of sub-populations or groups. Either the characteristic population or the subgroups may be recognized as unit stocks in the biological sense and as preferred units for management. The taxonomic status of the unit stock is unclear. In some cases, the unit stock may be the species, in others it may be a taxonomic race within a species, and in others it may conform to no accepted taxonomic classification. However, distinct unit stocks have been perceived and labeled as such for many species. Unit stocks have been recognized and labeled as such based on physical characteristics since the turn of the century." In addition to physical characteristics, biological (as growth, spawning, age at maturity) and biochemical data would also offer bases for stocks distinction (Brown et al., 1987).

Coyle (1998) distinguished stock concept in: genetic, when reproductively isolated units genetically different; phenotypic or environmental, when fish groups present different adaptations to their respective environment but genetic differences are not enough; and fishery and harvest, referring to group of fish exploited by a specific method or in a specific area.

According to Pita et al. (2016), those concepts are more elusive, depending on the discipline dealing with its definition, which may lead to fishery resources over-exploitation or sub-exploitation. Still, these authors also suggest that a successful rapprochement would allow better fisheries structuring and resources exploitation.

Fish phenotypic plasticity, a chameleon-like feature of fishes, according to Lindsey (1981), supports their adaptability to natural or anthropogenic induced environmental change by modification in their physiology and behavior, which may not be related to genetic changes, leading to changes in their reproduction, morphology or survival that mitigate the effects of environmental variation. Thus, the detection of those population differences cannot usually be taken as evidence of genetic differentiation (Swain and Foote, 1999; Turan, 1999).

Natural tags, as body meristic and morphometric characters, parasites, otoliths shape, and chemical and isotopic composition, have been commonly used in fisheries biology, providing evidences for stock discreteness (Templeman, 1983; Turan, 1999; Bone and Moore, 2008). The use of natural tags has an advantage over artificial marking methods since they do not demand handling the organisms, and every organism contains a tag, meaning that information is available from all captured specimens (Gillanders, 2009). Using different approaches and integrating their results offers an increasing in the ability to identify fish population structure and in the likelihood of a correct identification of the population units (Cadrin and Secor, 2009).

Population units identification has usually and successfully been addressed on the analysis of natural tags, as body shape, e.g. Vazzoler (1971); Paiva Filho and Cergole (1988); Spach and Yamaguti (1989a,b); Murta (2000); O'Reilly and Horn (2004); Turan (2004); Sabadin et al. (2010); Galli and Norbis (2013); Pérez-Quñonez et al. (2018); otolith shape, e.g. Spach and Yamaguti (1989c); Tuset et al. (2003); Pothin et al. (2006); Stransky et al. (2008); Vasconcelos et al. (2018); Adelir-Alves et al. (2019); Moreira et al. (2019); Soeth et al. (2019); or otolith elemental composition, e.g. Campana et al. (2000); Ferguson et al. (2011); Correia et al. (2012); Avigliano et al. (2014); Correia et al. (2014); Daros et al. (2016b); Avigliano et al. (2017); Fortunato et al. (2017); Adelir-Alves et al.

(2019). It is possible that the results obtained from the analyses of more than one of these approaches together could differ once each variable respond differently due to environmental and/or genetic causes, providing a better understand of populations dynamics (Pérez-Quñonez et al., 2018). Therefore, complimentary analyses are relevant and more informative (Begg and Waldman, 1999).

1.1.1 Otoliths

In all gnatostomated vertebrates, the inner ear has an important role not only in auditive system, responsible by sound perception, but also vestibular, detecting linear and angular acceleration, maintaining the equilibrium of the organisms in the aquatic environment (Wright et al., 2002; Volpedo and Vaz-dos Santos, 2015). In actinopterygians, inner ear is made of three pairs of semicircular channels in the cranium, with endolymph and a mineralized structure in each one. These structures are called otoliths (Fig. 1) and to each symmetric pair is given a name: *sagitta*, *lapillus* and *asteriscus*. The *sagittae* are the larger ones in most species, easier to extract, and they are also the most used in growth and ageing studies (Wright et al., 2002; Rossi-Wongtschowski, 2015; Volpedo and Vaz-dos Santos, 2015; Rossi-Wongtschowski et al., 2016).

Otoliths are carbonate concretions made of calcium carbonate (CaCO_3 – 95%, mainly in the aragonite mineral form), organic matter (3 – 5%) and trace or vestigial elements (Campana, 1999). Their growth occurs by the regular addition of concentric layers of CaCO_3 under a protein (otolin) base, beginning in a nucleus established during embryonic development. Biomineralization process makes them structurally different compared to other chemical precipitates (Friedrich, 2009; Hüsey et al., 2020). The compositional and seasonal fluctuations of the layers of daily deposition result in areas with distinct optical properties, products of physical and chemical changes of water properties, diet (food preferences and assimilation), reproductive activity, growth, or any physiological processes that require energy (Campana, 2005b; Elsdon et al., 2008; Rossi-Wongtschowski et al., 2016).

Chemical elements intake for otoliths formation occurs through water and food,

Figure 1: Otoliths' position within the inner ear of Teleost fish: a dorsal view of the vestibular apparatus in a typical Teleost species (a); and otoliths within the labyrinth systems of typical Teleost and Cyprinoid fishes. Ast = asteriscus; Lag = lagena; Lap = lapillus; Sac = sacculus; Sag = sagitta; Utr = utricle. From Wright et al. (2002)

at the water/food-blood and endolymph-blood interfaces. These elements may be in the crystal of aragonite, on the crystal or in the proteins (Friedrich, 2009). The varied mechanisms that occur since the entrance of the elements in the organisms until their deposition in the otolith are not fully clear. For example, Friedrich (2009) reported that the input of Ca, Na, sulfates and phosphates is regulated by active transport; Cu, Zn and Fe are important for fish health and found in proteins, entering the fish body through the gills or food; trace elements depend on their relative ionic concentration in the environment and vary from species to species; Mg and Ba are the ones with the lowest rate of entry into the body by water; Sr can be captured from both water and food.

Otoliths are said to be species-specific, presenting distinct characteristics, such as shape, size and microstructure (Fig. 2). Differences in the otolith shape usually reflect fish phylogeny and development, varying intra- and interspecifically. The variation patterns in otoliths shape have been used in the phenotypic identification of fish stocks or populations/subpopulations (Wright et al., 2002; Rodríguez Mendoza, 2006).

Otoliths are metabolically inert, which means that they do not undergo mineral resorption and have their chemical composition unchanged over time, recording all information and growing throughout the fish lifetime. For this reason, they are important for the understanding of the history of life of the actinopterygians and their populations, useful, for example, in sclerochronology, fish stocks, migration, physiology, or population dynamic studies (Green et al., 2009; Avigliano and Volpedo, 2016; Tzadik et al., 2017). Furthermore, they are not degraded even after individual's death, even in external environments, as in *sambaquis* or sediments, aiding in paleoenvironmental studies; or inside the stomach of their predators, assisting in studies on diet or trophic chains (Wright et al., 2002).

One of the greatest challenges faced by decision-makers about fisheries management is related to the kind of information that would best describe the historical and current situation of the respective stocks to ensure fisheries sustainability. In this context, the collection, preparation and interpretation of otolith data provide relevant information that has historically been incorporated into fisheries management in different regions of

Figure 2: Example of different otoliths' shape and structures. From Rossi-Wongtschowski et al. (2016)

the world (Green et al., 2009).

Marine fish usually present high genetic flow due to their long larval phase duration, large effective population and the lack of physical barriers to their dispersion, which hamper the use of conventional molecular biology tools (Bradbury et al., 2008; Correia et al., 2012). Thus, otoliths have proven to be valuable in assessing fish population structure, movement patterns and habitat connectivity in systems with high genetic flow in water masses heterogeneity in a spatial scale (Higgins et al., 2013; Correia et al., 2014; Daros et al., 2016b; Moreira et al., 2019).

1.1.2 Body morphology

A variety of body shapes are created as a result of a variability on ontogenetic features, such as growth, maturation, and development, which can also suffer the interactive effects of environment, selection, and genetics, producing morphometric differences within a species (Fig. 3) (Swain and Foote, 1999; Cadrin, 2000). For more than a century, geographic variation in body shape has been used to discriminate phenotypic population units, a basic requirement for fisheries science and management (Cadrin and Friedland, 1999; Swain and Foote, 1999; Turan, 2004).

Meristic characters are countable morphological structures that have been historically used as an important basis for distinguishing fish population units (Begg and Waldman, 1999). Providing discrete data, which facilitate statistical analysis, these characters - generally related to the counting of vertebrae, fin rays, scales, or gill rakers - are controlled by environmental and genetic factors, remaining stable throughout life once they are settled early in fish's ontogeny, in embryos or larvae (Winans, 1987; Begg and Waldman, 1999; Turan, 2004). Therefore, environmental influences are restricted to a brief time in larval development (Begg and Waldman, 1999; Turan, 2004).

Also influenced by genetic and environmental factors, body morphometric characters, as length, depth, and width of fish, are continuous characters which describe aspects of body shape (Winans, 1987; Turan, 2004). Unlike meristic characters, morphometric ones present ontogenetic changes related to allometric growth and may be labile

Figure 3: Interaction of environment, heredity, and selection on morphometric variability (Cadrin, 2000)

Figure 4: Truss network used for *Isopisthus parvipinnis* body morphometric analysis with 13 selected landmarks on the fish left side (adapted from Figueiredo and Menezes, 1980)

to environmental influences throughout life (Swain and Foote, 1999). Conventionally focused in the head and caudal regions of the fish body, this analysis started to be questioned in the 1980s by some authors (Winans, 1987). Some of them were Strauss and Bookstein (1982) who proposed the use of a “truss network”, used until the present and adapted for this work (Fig. 4). It is important to consider that morphometric analysis must consider a correction for size differences among specimens (Begg and Waldman, 1999).

For decades, the study of fish body shape has been proven as a useful tool for population units discrimination so much for the use of only meristic characters (Spach and Yamaguti, 1989a), morphometric characters based on distances (Spach and Yamaguti, 1989b) or “truss network” (Sabadin et al., 2010; Sheehan et al., 2005; Silva, 2003; Valentin et al., 2008); or the combination of morphometry (“truss network”) and genetics (Santos et al., 2006), body and otoliths morphometry (Pérez-Quñonez et al., 2018), or, finally, meristic and morphometric characters (Galli and Norbis, 2013; Murta, 2000; O’Reilly and Horn, 2004; Paiva Filho and Cergole, 1988; Turan, 2004; Turan et al., 2006; Vazzoler, 1971; Yamaguti, 1979). In the last case, only Turan et al. (2006) and Turan (2004) worked with a “truss network” instead of isolated distances. Moreover, advances in image processing techniques, allowing us to obtain two- or three-dimensional, and

even volumetric data, and analytical tools have made the quantification of shape more efficient and facilitated the morphometric methods progress and diversification (Cadrin and Friedland, 1999; Cadrin, 2000; Mitteroecker and Gunz, 2009).

1.2 *Isopisthus parvipinnis* (Cuvier, 1830)

Fish from Sciaenidae family are commonly found in the shallow waters of the continental shelf under sandy or muddy bottoms. Sciaenid fish constitute one of the most important demersal fishery resources in the coastal zone of the Brazilian SE coastal zone, being representative in biomass, number, frequency of occurrence, and presenting high diversity of species (Giannini and Paiva Filho, 1990; Branco and Verani, 2006; Branco et al., 2015; Imoto et al., 2016; Spier et al., 2018; Rotundo et al., 2019), generally related to the occurrence and fishery of penaeid shrimp due to similar requirements of the abiotic factors that will influence their distribution and from their prey, such as depth and type of substrate (Schmidt and Dias, 2012; Branco et al., 2015).

Isopisthus parvipinnis (Cuvier, 1830) (Fig. 5), commonly known as bigtooth corvina or, in Portuguese, *tortinha* or *pescadinha*, is an euryhaline sciaenid fish (Andrade-Tubino et al., 2008) widely distributed in the shallow waters of the continental shelf, under 50 m (Menezes and Figueiredo, 1980), from Costa Rica to Southern Brazil, until Santa Catarina State (Fig. 6, Socorro and Miranda (2015)). Together with other sciaenid fish, such as *Paralichthys brasiliensis* (banded croaker), *Micropogonias furnieri* (whitemouth croaker), and *Larimus breviceps* (shorthead drum), *I. parvipinnis* was associated with the warmer waters in Ubatuba region, in the North of São Paulo state (Soares, 1989; Rocha and Rossi-Wongtschowski, 1998). Despite its importance at the food web of marine and estuarine ecosystems, as food for piscivorous fishes, marine birds and cetaceans (Santos et al., 2002; Soares et al., 2008; Miotto et al., 2017), the species is described as seasonal in shallow and intermediate depths in the continental shelf of São Sebastião (São Paulo, Brazil), moving into shallower waters upon SACW outcrops conditions (Rossi-Wongtschowski and Paes, 1993).

Isopisthus parvipinnis is a demerso-pelagic carnivorous species with a restricted

Figure 5: *Isopisthus parvipinnis* (Cuvier, 1830) specimen collected in Ubatuba city (São Paulo, Brazil) in November of 2018. Photo by Maria de Lourdes Zani-Teixeira

Figure 6: Currently known distribution of *Isopisthus parvipinnis* in the Western Atlantic, from Costa Rica to Southern Brazil (Froese and Pauly, 2019)

food range, consisting primarily of teleosts and decapods, varying between the different occurrence regions. In Brazilian waters, Decapoda Dendobranchiata was the most frequent prey in Ilhéus, Bahia state - BA (Romero et al., 2008), and São Sebastião, São Paulo state - SP (Soares et al., 2008); while in the Guaratuba bay, in Paraná state - PR (Chaves et al., 1998), and in Corumbau Extractive Marine Reserve - BA (Santos et al., 2016), it was fish. Changes in food preferences can also be observed, such as in the Santos bay (SP), where decapods were described by Soares (1989) as the main preys in the 1970s, and fish, in the 2000s, by (Muto et al., 2014).

Specimens of *I. parvipinnis* can reach approximately 250 mm of total length (Menezes and Figueiredo, 1980), reaching first gonadal maturation about 159 mm (Romero et al., 2008). Chaves et al. (1998) described that the reproduction of this species occurs during spring and summer either in the Guaratuba bay (PR) mangrove or in the open sea. For the same seasons, Romero et al. (2008) suggested a movement of adult individuals to the mangrove areas in Ilhéus (BA), and Souza and Chaves (2007) described intense reproductive activity in Paraná and Santa Catarina state (SC).

Isopisthus parvipinnis otoliths were described by Rossi-Wongtchowski et al. (2014) as presenting an oblong shape and a plane-convex profile, with no rostrum or antirostrum. Its sulcus acusticus occurs in the median position and horizontal orientation (Fig. 7).

Isopisthus parvipinnis is pointed out as one of the main species in number of fish caught in coastal fisheries in Brazil, primarily in South and Southeastern regions, where many fluctuations in its catches have been observed since the 1970s, from 0.5 to 189 ton per year and state (IBAMA, 2009; MPA, 2011; PMAP-IP, 2018). In Figure 8, historical catches of *I. parvipinnis* show a decrease in catches but an increase in added value per kilogram in the last decade. Together with three other sciaenid fishes (*Stellifer rastrifer*, *S. brasiliensis*, and *Paralonchurus brasiliensis*), they represented more than 50% of the bycatch from shrimp fisheries along the coast of SP (Coelho et al., 1986; Paiva Filho and Schmiegelow, 1986) and PR (Santos et al., 2006; Sedrez et al., 2013), reaching 82% in SC (Branco and Verani, 2006). *I. parvipinnis* has some economic importance (Spier et al.,

Plate 28. The illustrations (above) and photographs (below) of *Isopisthus parvipinnis* otoliths from fish with total lengths: A. 85 mm (PI.AF.L3.33) and B. 170 mm (PI.AF.L2.1). The medial face is shown in A1 and B1; the lateral face in A2 and B2; and the ventral profile in A3 and B3 (Illustrator: Silvia de Almeida Gonsales; Photos: Cesar Santificetur).

Figure 7: The three pairs of otoliths of *Isopisthus parvipinnis* (Sciaenidae), from Rossi-Wongtchowski et al. (2014).

Figure 8: *Isopisthus parvipinnis* catches (kg/year) and estimated value collected (US\$/kg) for 20 years in São Paulo state, Brazil (PMAP-SP, 2018)

2018), and, depending on its size, this species can be sold as mixture with other species or individually, or discard (Graça Lopes et al., 2002; Freire and Pauly, 2015).

The discarding of bycatch species represents both an economic loss, because of the potential commercial value of some species which are not exploited due to their small size, and an environmental loss, because of their key role in the community structure (Branco et al., 2015). Regarding the conservation of bycatch resources, Romero et al. (2008) highlighted the importance of protecting *I. parvipinnis* and other bycatch species growth areas through a decrease in trawling time, the use of net escape devices, changes in the fishing period, but mainly through the implementation of a fishery policy to minimize the magnitude of the bycatch problem.

2 Oceanographic features of the South Brazil Bight

The South Brazil Bight (SBB), our study area (Fig. 9), is located on the Southeast coast of the Brazilian continental shelf between 23.387°S and 29.341°S , from São Paulo to Santa Catarina states. Bound by two Capes, Cabo Frio (23°S) and Cabo de Santa Marta ($28^{\circ}40'\text{S}$), the SBB presents a crescent shape, being narrowest nearby the Cabo Frio (50 km) and Cabo de Santa Marta (70 km) and widest in its central part (230 km), with isobaths paralleling the coastline and the shelf-break at 150 – 180 m depth (Castro and Miranda, 1998; Castro, 2014).

The continental topography is characterized by the Serra do Mar mountain range and narrow coastal plains bordered landward by a high plateau (1000 m, approximately). Drainage systems therefore run mainly inland, nourishing the Paraná/La Plata-Uruguay rivers basin to the southwest of the study area, and, to a much lesser extent, the Paraíba river basin to the north (Gyllencreutz et al., 2010). Minor fluvial systems, as observed in the Paranaguá and Cananéia-Iguape estuarine systems, run directly from the adjacent lands towards the sea, implying that the sedimentary input from adjacent lands is limited and that modern sedimentation probably is confined to allochthonous sources (Mahiques et al., 2004; Gyllencreutz et al., 2010).

Water masses in the SBB are a result of mixing between the Tropical Water (TW), superficial, warm and salty (0 – 200 m, $T > 20^{\circ}\text{C}$, $S > 36.4$), the South Atlantic Central Water (SACW), a cold water below the TW ($T < 20^{\circ}\text{C}$, $S < 36.4$, 200 – 500 m), and the Coastal Water (CW), a mixture of saline basin water and land runoff ($T > 20^{\circ}\text{C}$, $S < 35$) characterized by high silicate, and nitrate and phosphate depending on continental influence (Miranda, 1985; Castro, 1996; Castro and Miranda, 1998). The first two water masses are transported by the Brazil Current (Fig. 10), a boundary current off the SBB, which originates south of 10°S , as a south branch of the South Equatorial Current, flowing southward until the Subtropical Convergence ($33 - 38^{\circ}\text{S}$), where occurs the confluence with the Malvinas Current. Thus, BC has its origin and development off Brazilian coast, consisting in the most important ocean feature in the west edge of the South Atlantic Ocean (Castro et al., 2006). Driving the hydrodynamic system in the

Figure 9: Map of the study area, located in the Brazilian South Bight, from São Paulo to Santa Catarina states (23.387°S to 29.341°S)

SBB together with BC, the Brazilian Coastal Current (BCC) flows northward in the inner shelf from the Brazil-Malvinas confluence region to almost Rio de Janeiro's latitude, 23°S (Campos et al., 1996; Souza and Robinson, 2004; Gyllencreutz et al., 2010), carrying sediments from the Río de la Plata (Mahiques et al., 2008) in the low-salinity and low-temperatures Plata Plume Water (Möller Jr et al., 2008). This hydrographic structure results in oligotrophic conditions and regenerative production in the SBB between Cabo de São Tomé (Rio de Janeiro state) and Chuí (Rio Grande do Sul state), even nearshore and out of the influence of upwelling conditions or continental runoff (Lutz et al., 2018).

An important oceanographic phenomenon, with significant impact on marine ecosystems and regional climate in consequence, is observed in the SBB extremes – the upwelling, which is a mechanism for carrying cold and nutrient-rich waters into the euphotic zone due to persistent upwelling-favorable winds observed throughout the year north of Rio de Janeiro (RJ) and during spring and summer south of the Ilha de Santa Catarina (Mazzini and Barth, 2013). In addition, its high intensity in the RJ waters, SACW outcrops in the north of São Paulo (SP) continental shelf is also registered (Pires-Vanin and Matsuura, 1993; Castro et al., 2008; Mazzini and Barth, 2013; Castro, 2014).

Figure 10: Currents system observed in the South Brazilian Bight, adapted from Gyllencreutz et al. (2010)

This process generates a stratification in the water column, and alters the water chemical properties, as dissolved oxygen, nitrate and phosphate, resulting in an increase in phytoplankton primary production, that support a higher biomass of herbivore zooplankton, and, consequently, offers better conditions for fish and benthic larvae survival (Pires-Vanin and Matsuura, 1993; Castro et al., 2008). Cyclonic meanderings (eddy) of the Brazil Current between 70 and 100 m mainly on the northern and southern limits of the SBB also brings SACW to surface layers, inputting nutrients in the photic zone, and may account for primary production (Paes and Moraes, 2007).

Figures 11 and 12 present summer and winter data of temperature and salinity compiled from historical data by (Castro and Miranda, 1998). Most of superficial temperature remains about 25 and 27°C during summer in the SBB, except in the Northern part, when an influence of the persistent upwelling near Cabo Frio was detected (near-bottom temperatures are also usually lower than 18°C), and higher salinities were observed in the outer shelf ($S > 36.0$), as an influence of TW, while lower salinities were observed in the inner shelf, especially in the SBB central part. During winter, surface temperatures are more homogeneous ($20 < T < 23^{\circ}\text{C}$) in Central and Northern portions of the SBB, while the penetration of cold and relatively fresh water ($T < 18^{\circ}\text{C}$, $S \approx 34.0$) in South is apparent. No significant seasonal variations were observed in near-bottom salinities.

As a result of this complex hydrodynamics evolving oceanic dynamics, shelf circulation and allochthonous input from fluvial sediments, a heterogeneity of sediments was observed northward of São Sebastião Island (Fig. 13), region indicated as a boundary between two main sedimentary zones, based on different inorganic and organic fractions of sediments. Southward from this island, the bulk organic matter characteristics, indicating high productivity zones, resulted from the interactions between the BCC, the meanders of the BC as well as the shelf morphology (Mahiques et al., 2004).

Biological patterns are also influenced by the hydrodynamics processes in SBB. Fish spawning strategies are said to be highly related to water masses dynamics, especially with the SACW outcrops, affecting larvae mortality and, consequently, recruitment (Katsuragawa et al., 2006). Therefore, three main ichthyoplanktonic associations, as well

Figure 11: Means fields calculated from historical hydrographic data for superficial (left) and near-bottom (right) temperature in summer (top) and winter (bottom), adapted from Castro and Miranda (1998)

Figure 12: Means fields calculated from historical hydrographic data for superficial (left) and near-bottom (right) salinity in summer (top) and winter (bottom), adapted from Castro and Miranda (1998)

Figure 13: Distribution of the mean diameter (ϕ) in the surface sediments collected between 22°S and 29°S from Mahiques et al. (2004)

as a transitional association between the first two, were identified: one coastal assemblage, including Sciaenidae, Gerreidae and Mugilidae larvae, many of them that occur in low-salinity and estuarine waters; one neritic assemblage, which involves families and species of wide distribution, such as *Engraulis anchoita* and *Trichiurus lepturus*; and an oceanic one, characterized mainly by mesopelagic fishes (Itagaki, 1999; Katsuragawa et al., 2006).

According to Rotundo et al. (2019), the SBB is the region with the highest abundance of Brazilian fishery resources. From Cabo Frio (RJ) to Torres (RS), the same authors registered 245 species of demersal fishes in fishery fleet landings of São Paulo State between 2005 and 2012, including target and non-target (bycatch) species, whereas 50 of them were classified as constants (17 occurring in all sample period, such as *Dactylopterus volitans*, *Prionotus punctatus*, *Orthopristis ruber*, and *Cynoscion jamaicensis*). Sciaenidae presented the highest species richness followed by Paralichthyidae, Serranidae, Engraulidae, and Carangidae.

Our study area is also inserted in the Biogeographic Province of Argentina, a faunistic transition zone from Cabo Frio until the Península Valdéz (Argentina), where occurs a group of endemic species, as well as a set of tropical and temperate species, geographically limited by this province (Figueiredo, 1981). Studies carried out in the Paranaguá estuarine system and in the Laje de Santos Marine State Park (Luiz Jr. et al., 2008; Passos et al., 2012) evidenced the importance of province of Argentina in the marine and estuarine diversity of Southern Brazil ichthyofauna (Rotundo et al., 2019).

3 Thesis hypotheses

This work aims to test three hypotheses:

- *Isopisthus parvipinnis* presents different phenotypic population units in the Southwest Atlantic Ocean;
- Population of *Isopisthus parvipinnis* kept its temporal and spatial structure from 1975 to 2018/2019;
- Natural tags are capable of distinguishing phenotypic population units of *Isopisthus parvipinnis*.

3.1 Goals

The main purpose of this work was to investigate the population structure of *Isopisthus parvipinnis* in the Southwestern Atlantic Ocean from São Paulo to Santa Catarina states, Brazil. To achieve this main goal, three secondary objectives were established:

- Assess the population structure using body morphology, otolith shape analysis and otolith chemical signatures;
- Verify the long-term temporal stability of the population structure from historical and contemporaneous samples (1975 and 2018/2019) through otoliths chemical elemental signatures and shape;
- Evaluate which tool best describe the phenotypic variations of the *Isopisthus parvipinnis* population units.

4 Population structure of the bigtooth corvina *Isopisthus parvipinnis* from the Southwest Atlantic Ocean as determined by whole-body morphology

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Abstract

Geometric morphometrics analysis provides evidence from the adaptive character of fish to the aquatic environment resulting from an evolutionary process. Thus, phenotypic variations among individuals are primarily due to heritability of genetic factors modulated by the surrounding environment. Analysis of body morphometry can provide important information on fish population structure, an essential prerequisite for conservation requirements and sustainable fisheries management. The “bigtooth corvina”, *Isopisthus parvipinnis*, is an euryhaline sciaenid fish widely distributed in the shallow and warm waters from the western Atlantic Ocean. It is often caught as bycatch of shrimp fisheries in Brazil. Although there is some basic ecological information about the species, knowledge about the stock structure is, at present, very limited. This work aims to investigate if the different environments of the South-Southeastern Brazilian coastal waters (São Paulo, Paraná, and Santa Catarina states) could affect the body shape of *I. parvipinnis*, allowing to define different population units through phenotypic geometric morphometrics. Juvenile fish, ranging between 66 and 139 mm of total length, were captured from September 2018 to May 2019 by research vessels and artisanal fleets using an otter trawl. Fish were photographed with 13 anatomical landmarks, and truss network analyses were performed using tpsUtil and tpsDig softwares. Data were analyzed through uni and multivariate statistical tests. Results showed significant differences among locations for all morphometric distances individually. Moreover, reclassification matrix presented a relatively high overall rate (79%). The hereby data suggest that *I. parvipinnis* in the study area is not a single and homogeneous stock, supporting the existence of a metapopulation structure. However, it is highly recommended to use complementary information, namely other natural tags, to corroborate these findings.

Keywords: Sciaenidae, natural tags, geometric morphometrics, fish stock(s)

4.1 Introduction

Understanding the fish population structure in space and time is an important prerequisite for fisheries management (Begg and Waldman, 1999; Cadrin et al., 2014), in order to ensure the sustainability of target species, as well as to minimize fishing impacts on bycatch (non-target), associated and dependent species, and on the environment (Begg and Waldman, 1999; Cochrane and Garcia, 2009; Kerr et al., 2017). Moreover, the accurate knowledge about the population structure of a fish species allows us to understand the response of a species to fishing pressure and environmental changes, which plays a key role in species persistence (Kerr et al., 2017). The accurate identification of fish population units is a multidisciplinary field comprising genetics, mark-recapture techniques, biometrics and chemical analyses of tissues and hard parts (IHssen et al., 1981; Begg and Waldman, 1999; Cadrin et al., 2014). Natural tags, such as morphometric and meristic characters, parasitic fauna, shape and chemical signatures of otoliths, besides other tools, have been commonly used in fisheries biology, providing evidences for stock discreteness (Coyle, 1998; Cadrin et al., 2014; ICES, 2016).

The identification of different fish population units through geometric morphometrics is a common practice in ichthyology (Murta, 2000; Turan et al., 2006; Pérez-Quñonez et al., 2018), namely because of the great phenotypic plasticity exhibited by the fish shape (Robinson and Wilson, 1996; Turan, 1999; Turan et al., 2006). The fish geometric morphometrics (e.g., length, depth, and width) are continuous characters which describe aspects of the external body shape and are influenced by genetic and environmental factors (Turan, 2004; Winans, 1987). Moreover, fish shape presents ontogenetic changes related to allometric growth and may be labile to environmental influences throughout life, unlike meristic characters (Swain and Foote, 1999). There is a growing interest in using landmark-based truss measurements for stock discrimination purposes, since they are dependent on the environmental conditions, impose no restrictions on the variation or location direction of shape changes and has proven to be highly effective in capturing information about an organism shape (Strauss and Bookstein, 1982; Mojekwu and Anumudu, 2015; Rawat et al., 2017).

The Sciaenidae is one of the most common fish families in the coastal and estuarine waters from the Southwestern Atlantic Ocean. From the 286 registered species, 54 of them occur in the Brazilian waters (Froese, R. and Pauly, D., 2018). This family represents an important resource for the demersal fisheries, as target or bycatch species (Sedrez et al., 2013; Imoto et al., 2016; Rotundo et al., 2019). The bigtooth corvina, *Isopisthus parvipinnis* (Cuvier 1830), is an euryhaline sciaenid fish widely distributed at the Atlantic Ocean, from Costa Rica to Southern Brazil (Andrade-Tubino et al., 2009; Socorro and Miranda, 2015). It occurs in marine coastal waters up to 50 m (Menezes and Figueiredo, 1980), but it is also found in estuarine waters under 15 m (Lowe-McConnell, 1966), usually associated with sandy and muddy bottoms, where it feeds on benthic invertebrates and small fish (Romero et al., 2008; Soares, 1989). In the South Brazilian Bight, between Santos (São Paulo state) and Paranaguá (Paraná State), the spawning occurs during the spring season, namely in an area between the Santos Bay and Cananéia (Soares, 1983). It is pointed out as one of the main species from the Sciaenidae family caught as bycatch of the shrimp trawl fisheries in the South-Southeastern Brazilian coastal waters

Therefore, this work aimed to investigate the spatial morphological variability of *I. parvipinnis* in Southwestern Atlantic Ocean among São Paulo, Paraná and Santa Catarina Brazilian states, using a truss network analysis, producing relevant information about its population structure.

4.2 Material and Methods

4.2.1 Fish sampling and image acquisition

Fish were captured by otter trawl between September 2018 and May 2019 by artisanal fishing and research vessels, in the shallow waters of the continental shelf along the Brazilian South-Southeastern coast, encompassing São Paulo (with three sites: North — NSP, Center — CSP, and South — SSP), Paraná — PR, and Santa Catarina — SC (Fig. 14). Samples were preserved on ice and transported to the laboratory for processing. Fish were identified to the species level (*I. parvipinnis*) using existent identification guides (Menezes and Figueiredo, 1980). Each specimen was measured for standard length (SL,

1 mm) and weighted (W, 0.01 g).

Figure 14: Sampling locations (stars) of *Isopisthus parvipinnis* individuals collected from September 2018 to May 2019 in the SW Atlantic Ocean, between São Paulo and Santa Catarina States (Brazil). Legend: North of São Paulo — NSP, Center of São Paulo — CSP, South of São Paulo — SSP, Paraná — PR, and Santa Catarina — SC

4.2.2 Body morphometric analysis

The size range of individuals selected for body shape analysis was restricted to between 66 and 139 mm of SL (Table 1), to include only juvenile fish (size at first maturity < 159 mm: Romero et al. (2008)) and to minimize the ontogenic effects on phenotypic body variation (Cadrin, 2000). A photograph from the left side of each fish with the 13 anatomical landmarks was taken from a fixed distance with a high-quality digital camera (Fig. 15) (Erguden et al., 2009). A truss network system standard protocol (Strauss and Bookstein, 1982) was used for body morphometric analysis, determining 27 distances among the 13 anatomical landmarks along the body contour (Table 2). Landmarks were processed using tpsUtil — Version 1.76 (Rohlf, F.J., 2008) and tpsDig — Version 1.40 (Rohlf, F.J., 2004) softwares.

Table 1: Sampling locations and their respectively acronyms, period of capture, sample size (n), and standard length (SL: mean $\pm$ standard deviation) of *Isopisthus parvipinnis*

Location	City	Acronym	Date	n	SL (mm)
São Paulo	Ubatuba	NSP	November 2018	30	96 $\pm$ 9
	Peruíbe	CSP	November 2018	30	118 $\pm$ 4
	Cananéia	SSP	October 2018	30	96 $\pm$ 7
Paraná	Paranaguá	PR	September 2018	30	95 $\pm$ 11
Santa Catarina	Navegantes	SC	May 2019	30	62 $\pm$ 8

North of São Paulo — NSP, Center of São Paulo — CSP, South of São Paulo — SSP,
Paraná — PR, and Santa Catarina — SC

Figure 15: Truss network used for *Isopisthus parvipinnis* body geometric morphometrics analysis with 13 selected landmarks on the fish left side

Table 2: Anatomical landmarks defined along the body contour of *Isopisthus parvipinnis* and morphometric distances used for the geometric morphometrics analysis. *Source:* Adapted from Erguden et al. (2009)

Body landmarks		
Number	Location	
1	Anterior tip of snout at upper jaw	
2	Most posterior aspect of neurocranium	
3	Origin of dorsal fin	
4	Insertion of dorsal fin	
5	Origin of second dorsal fin	
6	Insertion of second dorsal fin	
7	Anterior attachment of dorsal membrane from caudal fin	
8	Posterior end of vertebrae column	
9	Anterior attachment of ventral membrane from caudal fin	
10	Insertion of anal fin	
11	Origin of anal fin	
12	Insertion of pelvic fin	
13	Posterior most point of maxillary	
Morphometric distances		
Distances	Landmarks	Description
D1	1 to 2	Head length
D2	1 to 12	Distance between the anterior tip of snout and pelvic fin
D3	1 to 13	Maxilla length
D4	2 to 3	Distance from most posterior aspect of neurocranium to 1st dorsal fin
D5	2 to 11	Anterior diagonal of body height
D6	2 to 12	Posterior height of head
D7	2 to 13	Anterior height of head
D8	3 to 4	Length of 1st dorsal fin
D9	3 to 11	Distance between origin of 1st dorsal fin and origin of anal fin
D10	3 to 12	Anterior body height
D11	3 to 10	Diagonal between origin of 1st dorsal fin and insertion of anal fin
D12	4 to 5	Distance between 1st and 2nd dorsal fins
D13	4 to 10	Distance between insertion of 1st dorsal fin and insertion of anal fin
D14	4 to 11	Posterior body height
D15	5 to 6	Length of 2nd dorsal fin
D16	5 to 10	Anterior diagonal height of posterior body
D17	6 to 7	Distance between 2nd dorsal fin and caudal fin
D18	6 to 9	Anterior diagonal of caudal peduncle
D19	6 to 10	Anterior caudal peduncle height
D20	7 to 8	Distance between dorsal insertion of caudal fin and posterior end of vertebrae column
D21	7 to 9	Posterior caudal peduncle height
D22	7 to 10	Posterior diagonal of caudal peduncle
D23	8 to 9	Distance between ventral insertion of caudal fin and posterior end of vertebrae column
D24	9 to 10	Distance between anal fin and caudal fin
D25	10 to 11	Length of anal fin
D26	11 to 12	Distance between pelvic fin and anal fin
D27	12 to 13	Distance from maxilla to pelvic fin

4.2.3 Statistical analyses

Data were checked for normality (Shapiro–Wilk’s test) and variance homogeneity (Brown–Forsythe’s test). Since parametric premises were satisfied, Analyses of Covariance (ANCOVAs) were used to test the relationship between the twenty-seven morphometric distances (D1 to D27) and the standard length (SL: distance from landmarks 1 to 8). Location was treated as a fixed factor and SL as the covariate. Once all distances presented significant results for ANCOVA ($p < 0.05$), variation outcomes from allometric growth were eliminated using the following transformation (Reist, 1985): $D = \log(M) - \beta * [\log(SL) - \log(MSL)]$, where M is the original morphometric measurement, D is the transformed morphometric measurement, β is the slope of the regression of $\log(M)$ on $\log(SL)$, SL is the standard length of fish, MSL is the overall mean of standard length for all fish from all samples for each variable. Thereafter, significant differences among locations were tested by the One-Way Analysis of Variance (ANOVA) for each morphometric distance, followed by a Tukey post-hoc test, if significant ($p < 0.05$). Morphometric distances were also tested with a linear discriminant function analysis (LDFA). Reclassification accuracies of the discriminant functions for each location were evaluated through the percentage of correctly re-classified individuals using a jack-knifed cross-validation. To perform these statistics, standard procedures were applied (Zar, 2010) using Past 3.26 (Hammer et al., 2001). Multimorphometric distances comparisons among locations were conducted using a permutational multivariate analysis of variance (PERMANOVA) based on the Euclidean distance measure using Monte-Carlo simulations (9999 random permutations), followed by permutational pairwise comparisons (pseudo-t statistic) among all pairs of levels, if needed ($p < 0.05$). A canonical analysis of principal coordinates (CAP) based on Euclidian distances was also performed to detect body morphometric differences among locations. PERMANOVA and CAP were run using PRIMER 7 + PERMANOVA (Anderson et al., 2008). Pearson correlations ($r > 0.50$) of the original variables with canonical axis patterns were also recorded. A statistical level of significance (α) of 0.05 was used. Data is presented as mean $\pm$ standard deviation.

4.3 Results

Significant differences were recorded for body morphology among locations (ANOVA, followed by Tukey post-hoc tests, $p < 0.05$) for all 27 morphometric distances (Table 3). One-third of all measurements (D3, D5, D9, D11, D13, D17, D18, D22, and D24) presented significant results in distinguishing SC and CSP, which recorded the lowest and highest mean values, respectively, from other locations. While D3 refers to the mouth size, D17, D18, D22, and D24 are related to the fish posterior region. D21, posterior caudal peduncle height, also presented a significant difference between SC and NSP/CSP/SSP/PR. D15 and D26, related to the length of the second dorsal fin and to the distance between the pelvic and anal fins, respectively, were able to detect significant differences among CSP, SSP, NSP/PR, and SC. When analyzed together, the morphometric distances also presented significant differences among the sampling locations (PERMANOVA, $p < 0.05$, Table 4). Moreover, all pairwise tests revealed significant differences between locations (Pseudo-t test, $p < 0.05$, Table 4).

Jackknife reclassification accuracy showed a moderate to high overall rate of 79% (Table 5). Samples from SC showed the best reclassification success (87%), while NSP exhibited the lowest reclassification (67%). LDFA presented a well-distinguished group for SC, but some overlap exists between samples from São Paulo state (NSP, CSP, and SSP), and from NSP and PR (Fig. 16). Axis 1 explained 70% of total variation and Axis 2, 16%. Likewise, CAP showed CSP, SSP, PR, and SC as well-distinguished groups between themselves, but NSP showed some overlapping with PR and SSP (Fig. 17). Group separation was primarily driven by D4, D5, D8, D9, D11, D13, D15, D16, D18, and D25 (Pearson > 0.90) on CAP Axis 1 ($\delta_1 = 0.88$), while CAP Axis 2 ($\delta_1 = 0.61$) was driven mainly by D12 (Pearson = -0.62).

Table 3: Body morphometric distances (mean $\pm$ SD) calculated for *Isopisthus parvipinnis* sampled from São Paulo to Santa Catarina states (Brazil) between September 2018 and May 2019. Same letters mean no significant differences between locations (Tukey's *post-hoc* test, $p > 0.05$) in each body morphometric distance that presented significant results in ANOVA. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

Distance	NSP	CSP	SSP	PR	SC
D1	2.143 $\pm$ 0.262 ^{a,b}	2.358 $\pm$ 0.161 ^a	2.051 $\pm$ 0.188 ^b	2.275 $\pm$ 0.277 ^a	1.522 $\pm$ 0.201 ^c
D2	2.877 $\pm$ 0.301 ^a	3.470 $\pm$ 0.160 ^b	3.054 $\pm$ 0.227 ^c	3.010 $\pm$ 0.355 ^{a,c}	1.905 $\pm$ 0.281 ^d
D3	1.143 $\pm$ 0.163 ^a	1.347 $\pm$ 0.123 ^b	1.124 $\pm$ 0.148 ^a	1.172 $\pm$ 0.149 ^a	0.703 $\pm$ 0.173 ^c
D4	1.394 $\pm$ 0.184 ^{a,b}	1.821 $\pm$ 0.174 ^c	1.484 $\pm$ 0.169 ^a	1.332 $\pm$ 0.186 ^b	0.863 $\pm$ 0.160 ^d
D5	4.102 $\pm$ 0.493 ^a	5.326 $\pm$ 0.301 ^b	4.162 $\pm$ 0.401 ^a	4.091 $\pm$ 0.538 ^a	2.484 $\pm$ 0.397 ^c
D6	0.738 $\pm$ 0.187 ^a	1.115 $\pm$ 0.169 ^b	1.006 $\pm$ 0.161 ^b	0.740 $\pm$ 0.162 ^a	0.388 $\pm$ 0.186 ^c
D7	1.008 $\pm$ 0.226 ^{a,b}	1.019 $\pm$ 0.195 ^{a,b}	0.937 $\pm$ 0.205 ^{b,c}	1.109 $\pm$ 0.188 ^a	0.825 $\pm$ 0.152 ^c
D8	1.291 $\pm$ 0.165 ^{a,b}	1.731 $\pm$ 0.172 ^c	1.410 $\pm$ 0.157 ^a	1.246 $\pm$ 0.220 ^b	0.825 $\pm$ 0.162 ^d
D9	2.709 $\pm$ 0.345 ^a	3.505 $\pm$ 0.213 ^b	2.679 $\pm$ 0.272 ^a	2.759 $\pm$ 0.391 ^a	1.622 $\pm$ 0.273 ^c
D10	0.670 $\pm$ 0.198 ^a	0.720 $\pm$ 0.191 ^a	0.497 $\pm$ 0.155 ^b	0.606 $\pm$ 0.108 ^a	0.487 $\pm$ 0.110 ^b
D11	4.421 $\pm$ 0.440 ^a	5.620 $\pm$ 0.210 ^b	4.452 $\pm$ 0.378 ^a	4.332 $\pm$ 0.508 ^a	2.724 $\pm$ 0.393 ^c
D12	0.824 $\pm$ 0.189 ^a	1.044 $\pm$ 0.180 ^b	0.652 $\pm$ 0.111 ^c	0.936 $\pm$ 0.167 ^b	0.509 $\pm$ 0.096 ^d
D13	3.130 $\pm$ 0.362 ^a	3.890 $\pm$ 0.221 ^b	3.043 $\pm$ 0.283 ^a	3.087 $\pm$ 0.358 ^a	1.899 $\pm$ 0.276 ^c
D14	1.419 $\pm$ 0.298 ^{a,b}	1.776 $\pm$ 0.219 ^c	1.272 $\pm$ 0.205 ^b	1.515 $\pm$ 0.259 ^{a,c}	0.798 $\pm$ 0.182 ^d
D15	2.042 $\pm$ 0.046 ^a	2.644 $\pm$ 0.023 ^b	2.207 $\pm$ 0.037 ^c	2.002 $\pm$ 0.048 ^a	1.263 $\pm$ 0.038 ^d
D16	2.307 $\pm$ 0.246 ^a	2.846 $\pm$ 0.141 ^b	2.392 $\pm$ 0.208 ^a	2.151 $\pm$ 0.257 ^c	1.390 $\pm$ 0.224 ^d
D17	1.574 $\pm$ 0.195 ^a	1.792 $\pm$ 0.140 ^b	1.476 $\pm$ 0.138 ^a	1.550 $\pm$ 0.154 ^a	1.017 $\pm$ 0.136 ^c
D18	1.588 $\pm$ 0.197 ^a	1.784 $\pm$ 0.126 ^b	1.486 $\pm$ 0.124 ^a	1.522 $\pm$ 0.157 ^a	0.976 $\pm$ 0.140 ^c
D19	0.274 $\pm$ 0.128 ^a	0.216 $\pm$ 0.076 ^{a,b}	0.202 $\pm$ 0.076 ^{a,b}	0.190 $\pm$ 0.093 ^{b,c}	0.145 $\pm$ 0.064 ^c
D20	0.312 $\pm$ 0.085 ^a	0.391 $\pm$ 0.089 ^b	0.279 $\pm$ 0.079 ^a	0.180 $\pm$ 0.062 ^c	0.156 $\pm$ 0.046 ^c
D21	0.096 $\pm$ 0.024 ^a	0.101 $\pm$ 0.046 ^a	0.093 $\pm$ 0.026 ^a	0.090 $\pm$ 0.025 ^a	0.076 $\pm$ 0.038 ^b
D22	1.312 $\pm$ 0.166 ^a	1.593 $\pm$ 0.144 ^b	1.294 $\pm$ 0.129 ^a	1.403 $\pm$ 0.199 ^a	0.891 $\pm$ 0.133 ^c
D23	0.300 $\pm$ 0.099 ^a	0.400 $\pm$ 0.103 ^b	0.270 $\pm$ 0.066 ^a	0.209 $\pm$ 0.055 ^c	0.196 $\pm$ 0.051 ^c
D24	1.322 $\pm$ 0.170 ^a	1.581 $\pm$ 0.128 ^b	1.300 $\pm$ 0.111 ^a	1.372 $\pm$ 0.189 ^a	0.848 $\pm$ 0.128 ^c
D25	1.714 $\pm$ 0.149 ^a	2.117 $\pm$ 0.115 ^b	1.776 $\pm$ 0.157 ^a	1.575 $\pm$ 0.156 ^c	1.103 $\pm$ 0.152 ^d
D26	3.369 $\pm$ 0.450 ^a	4.215 $\pm$ 0.277 ^b	3.160 $\pm$ 0.340 ^c	3.356 $\pm$ 0.445 ^a	2.102 $\pm$ 0.294 ^d
D27	1.735 $\pm$ 0.190 ^a	2.124 $\pm$ 0.162 ^b	1.931 $\pm$ 0.193 ^{b,c}	1.839 $\pm$ 0.233 ^{a,c}	1.203 $\pm$ 0.142 ^d

Table 4: Main and pairwise PERMANOVA comparisons for the 27 body morphometric distances among the five sampling locations of *Isopisthus parvipinnis*

Main PERMANOVA						Pairwise PERMANOVA		
Source	df	SS	MS	Pseudo-F	p(MC)	Groups	t	p(MC)
Location	4	30.40	7.60	44.56	0.0001	NSP – SSP	2.619	0.0001
Residual	145	24.73	0.17			NSP – CSP	4.236	0.0001
Total	149	55.14				NSP – PR	3.147	0.0001
						NSP – SC	7.528	0.0001
						CSP – SSP	5.006	0.0001
						CSP – PR	6.167	0.0001
						CSP – SC	11.548	0.0001
						SSP – PR	3.729	0.0001
						SSP – SC	7.977	0.0001
						PR – SC	7.049	0.0001

North of São Paulo — NSP, Center of São Paulo — CSP, South of São Paulo — SSP, Paraná — PR, and Santa Catarina — SC.

Table 5: Jackknifed cross-validation reclassification matrix of the linear discriminant function analysis for the body morphometric distances calculated for *Isopisthus parvipinnis* specimens sampled from São Paulo to Santa Catarina states (Brazil) between September 2018 and May 2019

Original location	Predicted location					% correct
	NSP	CSP	SSP	PR	SC	
NSP	20	1	3	6	0	67
CSP	1	25	2	2	0	83
SSP	5	2	23	0	0	77
PR	5	0	1	24	0	80
SC	0	0	1	3	26	87
	Total					79

North of São Paulo — NSP, Center of São Paulo — CSP, South of São Paulo — SSP, Paraná — PR, and Santa Catarina — SC.

Figure 16: Canonical variable plot (LDFA) displaying spatial differences for the body morphometric distances calculated for *Isopisthus parvipinnis* collected in the five sampling locations of the SW Atlantic in 2018/2019. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC. Ellipses represent 95% confidence intervals around the data, and data points represent individual fish

Figure 17: Canonical analysis of principal coordinates (CAP) plots for the body morphometric distances calculated for *Isopisthus parvipinnis* collected in the five sampling locations of the SW Atlantic in 2018/2019. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

4.4 Discussion

Landmark-based truss network analysis has been used worldwide for decades as a successful tool for fish stock population discrimination, alone (Silva, 2003; Sheehan et al., 2005; Valentin et al., 2008), or combined with genetics (Santos et al., 2006; Sabadin et al., 2010; Kaouèche et al., 2013), otolith morphometry (Pérez-Quñonez et al., 2018; Vasconcelos et al., 2018), and with meristic and morphometric characters (Turan, 2004; Turan et al., 2006; Galli and Norbis, 2013). Moreover, the advances in the image and analytical processing techniques have made the quantification of shape quicker and more efficient (Cadrin and Friedland, 1999; Cadrin, 2000). The analysis of morphometric characteristics in fish, whose expression is influenced simultaneously by genetic and physiological factors driven by environmental factors, such as water temperature, salinity, depth and substrate type, provides valuable information on phenotypic population units (Begg and Waldman, 1999; Cadrin, 2000, 2005).

Some studies addressing the geographic differentiation of different Sciaenid species (e.g. *Micropogonias furnieri*, *Macrodon ancylodon*, *Nebris microps* and *Cynoscion jamaicensis*) were conducted during the 1970s and 1980s on the Brazilian SE-S coast (Vazzoler, 1971; Yamaguti, 1979; Paiva Filho and Cergole, 1988; Spach and Yamaguti, 1989b). Those previous studies were mainly based on fish meristic (e.g. number of traces of the first branchial arch, soft rays of the dorsal fin, and the number of rays of the anal fin) and morphometric (e.g. total and standard length, head length, orbit diameter, interorbital distance, body and caudal peduncle height) characteristics. Moreover, those works showed that the observed morphological or meristic changes are species-specific and result from regional environmental characteristics through natural or anthropogenic induced changes.

I. parvipinnis body morphometric analysis revealed significant differences among all sampling locations, namely between SC and CSP. LDFA and CAP plots were similar, showing some overlap between groups, mainly between samples from NSP and PR and among all groups of São Paulo. Thus, a moderate to high reallocation success (overall of 79%) of individuals to the original regions was observed. Although presenting some

visual overlapping, NSP and PR are geographically far from each other. Despite this geographic distance (190 km), the lack of morphometric differentiation among the distinct geographical locations suggests that individuals from these locations may inhabit similar environments, as previously suggested for another sciaenid, *M. ancylodon*, for which population structure was assessed through genetics and morphometric differentiation (Santos et al., 2006).

CSP and SC locations, which exhibited the larger and smaller individuals, respectively, also presented the highest (23 from 27 distances) and lowest (26 from 27 distances) morphometric distances. Despite the fact that these values have been corrected for the fish allometric growth, it is possible that some morphological changes can be due to fish size sampling asymmetries. In fact, an isometric growth of the morphometric characteristics (head and pectoral fin length; pre-dorsal, pre-pectoral, pre-ventral, and preanal distances) of *M. furnieri* in the Guanabara Bay (Rio de Janeiro, Brazil) was already reported (Andrade-Tubino et al., 2009). However, the observed findings could have other explanations, such as the hydrographic regional features, the different diets along the coast, and the response to anthropogenic pressures; or is probably a response to an interaction among all these factors (Landaeta et al., 2019).

The study area is characterized by coastal waters under estuarine influence and/or by surface currents and upwelling processes (Cerdeira and Castro, 2014). SSP and PR are influenced by two interconnected estuarine systems: Cananéia-Iguape and Paranaguá Estuarine Complex, respectively. The Cananéia-Iguape system receives a significant contribution of the freshwater runoff from the Ribeira de Iguape River (300 to more than 1200 m³/s), in addition to the input of anthropogenic metallic contamination (Mahiques et al., 2009, 2013). On the other hand, the Paranaguá Estuarine Complex contributes with a freshwater input close to 200 m³/s (Lana et al., 2001), and in spite of being considered as one of the least impacted coastal systems in Southeastern Brazil, sediments levels of organic compounds were low, but significant amounts of cytotoxic compounds and endocrine disrupters were found (Rizzi et al., 2017). Thus, these two areas are characterized by similar hydrographical influences and pollution profiles. The CSP has the largest con-

tinental shelf and coastal water events dominate. In contrast to previous locations, both SC and NSP sampling points are located in narrow portions of the continental shelf. For this reason, both locations are exposed to seasonal intrusions of the South Atlantic Central Water (SACW), a cold and salty water mass transported by the Brazil Current along the Brazilian continental slope (Mazzini and Barth, 2013; Castro, 2014). Furthermore, SC is also under the influence of another oceanographic process, the Brazilian Coastal Current, which flows northward bringing waters of low salinity and temperature resulting of a mixture from the Río de La Plata discharge, in the frontier between Argentina and Uruguai, and waters from the Brazil-Malvinas Confluence (Campos et al., 2008). Another plausible explanation for the observed regional body variations is the feeding habits and strategies of *I. parvipinnis* (Palmeira and Monteiro-Neto, 2010; Kaouèche et al., 2013; Farré et al., 2016). Diet variations for *I. parvipinnis* were observed in different Brazilian coastal regions. In Ilhéus and Corumbau regions (Bahia state), as well as in São Sebastião (São Paulo state, close to the NSP sampling location), decapods are the main prey (Romero et al., 2008; Santos et al., 2016; Soares et al., 2008). However, in Guaratuba bay (Paraná state, south of the PR sampling location) fish was described as the main prey (Chaves et al., 1998). Moreover, food preferences can also change over time, as observed in the Santos Bay (central coast of São Paulo state), where decapods were described as the main prey in the 1970s (Soares, 1989), and fish, in the 2000s (Muto et al., 2014). It was recently demonstrated for the tiger tooth croaker *Otolithes ruber*, that the availability and type of prey, which are conditioned by the oceanographic conditions, and the interspecific competition, can influence the fish body shape, mainly in head region, since fish may prefer feeding on the most frequently encountered prey rather than actively seeking for a particular prey (Chhandaprajnadarsini et al., 2019). It is also known that phenotypic characters can be related to a strong selection pressure and individual fitness, which may result in a rapid genetic divergence in fish morphology before the accumulation of neutral genetic differences between the groups (Swain and Foote, 1999). For this reason, a last possible explanation for the present results could be an adaption mechanism of the *I. parvipinnis* population to anthropogenic influences affecting our study area, such as

fishing pressure (Begossi et al., 2017), and even pollution (Mahiques et al., 2009, 2013). This is reinforced by a reduction tendency of catches observed between 1998 and 2018, and reported by the Fishery Institute of São Paulo state (PMAP-IP, 2018). Moreover, the study area includes intense port activity in the Santos (CSP), Paranaguá (PR) and Itajaí (SC) harbors, which implies waste discharge, oil pollution and dredging activities (Castro et al., 2012), besides a high degree of urbanization, resulting in the discharge of untreated and illegal domestic waste to the water bodies (Medeiros et al., 2017).

bycatch species from other major fisheries since they also have ecosystem importance, besides their commercial value.

Credit authorship contribution statement

Natasha Travenisk Hoff: Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft. June Ferraz Dias: Conceptualization, Investigation, Supervision. Maria de Lourdes Zani-Teixeira: Investigation. Marcelo Soeth: Investigation. Alberto Teodorico Correia: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing - review & editing.

Declaration of competing interest

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

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5 Spatio-temporal evaluation of the population structure of the bigtooth corvina *Isopisthus parvipinnis* from South-west Atlantic Ocean using otolith shape signatures

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Abstract

Isopisthus parvipinnis, commonly known as “bigtooth corvina”, is a marine estuarine-dependent fish captured in the southeast and south Brazilian coast as bycatch of the shrimp fishery. This work used the sagittae morphology as a tool to primarily study the population structure of *I. parvipinnis* between São Paulo and Santa Catarina states (23°S to 26.9°S) in Brazil. Secondly, it intended to verify the existence of morphological alterations over time, by comparing otoliths of fish captured in 1975 and 2018/2019. Otolith shape analyses were performed in individuals ranging from 66 to 139 mm of total length, obtained from historical (1975) and present catches (2018/2019) in the shallow coastal areas off North of São Paulo (NSP), Centre of São Paulo (CSP), South of São Paulo (SSP), Paraná (PR) and Santa Catarina (SC). Otoliths were analyzed using shape indices (SIs), elliptical Fourier descriptors (EFDs) and both tools combined. Morphological variations among locations and between years were tested using uni and multivariate statistics. Data showed regional differences in the otolith shape analysis over the years. Samples from 1975 presented an overall low reclassification rate (43%), with a high overlap of individuals among locations, suggesting the existence of a single group. Differently, samples from 2018/2019 discriminated four distinct spatial units with a good overall reclassification (74%): group 1 - NSP; group 2 - CSP; group 3 - SSP + PR; and group 4 - SC. The hereby data suggests regional changes at long term in the population dynamics of *I. parvipinnis*, from a single panmictic population in the past to a metapopulation structure in the present days, with consequences for the rational and sustainable management of the fishery. However, once it was the first evaluation of the population structure of *I. parvipinnis*, it is highly recommended to use complimentary phenotypic and/or genetic approaches to corroborate the hereby observed findings.

Keywords: Sciaenidae, *sagittae*, otolith shape indices, elliptical Fourier descriptors, population units

5.1 Introduction

Understanding fish population structure of target and non-target species in space and time is an important prerequisite for fisheries management (Begg and Waldman, 1999; Cadrin et al., 2014). Solid scientific data about the population dynamics of a fish species allow us to understand its response to fishing pressure and environmental changes, which plays a key role in species resilience (Kerr et al., 2017). Thus, stock identification emerges as a meaningful multidisciplinary field for fisheries management, comprising several complementary approaches such as genetics, mark-recapture techniques, biometrics and chemical analyses of tissues and hard parts (Cadrin and Friedland, 1999). The mechanism of fish population differentiation and habitat connectivity within the marine environment is complex, and evolves the habitat requirements through fish life cycle, the fish behavior (e.g. natal homing, spawning and life history strategies), and the oceanographic and environmental features, which can act at the initial stages of life, promoting eggs and larvae retention or dispersal, and as an important selective pressure for population structure maintenance (Kerr et al., 2017). This gives rise to different population units which may respond differently to exploitation and must be managed separately (Galli and Norbis, 2013).

The otolith shape has been successfully used in providing information on habitat connectivity, movement patterns and population structure of fish (Ferreira et al., 2019; Moreira et al., 2019; Soeth et al., 2019). Otoliths are metabolically inert calcium carbonate structures within the inner ear of teleost fish whose function is related to sound perception and equilibrium maintenance (Popper et al., 2005). Those structures grow daily by the accretion of aragonite concentric layers during the fish somatic development, allowing the use of its sclerochronological properties for ichthyological purposes (Rossi-Wongtchowski et al., 2014). Otolith shape is known to be unaffected by short-term changes in fish condition, is species-specific and is primarily driven by genetics and environmental factors (Campana and Casselman, 1993; Begg and Brown, 2000; Zhao et al., 2017). This makes otolith's morphology a successfully tool for detecting distinct fish population units which may need to be managed regionally (Moreira et al., 2019). More-

over, the use of both otolith shape indices and elliptical Fourier analysis has proven to be useful in distinguishing phenotypic units of different fish species (Begg and Brown, 2000; Ferguson et al., 2011; Ferreira et al., 2019).

Isopisthus parvipinnis (Cuvier, 1830), commonly known as “big-tooth corvina” (in Portuguese: *tortinha* or *pescadinha*), is a common coastal sciaenid of the southwestern Atlantic (Andrade-Tubino et al., 2008). It is widely distributed in the shallow waters of the continental shelf, under 50 m (Menezes and Figueiredo, 1980), from Costa Rica to Southern Brazil, until Santa Catarina State (Socorro and Miranda, 2015). Soares (1983) described the life cycle, feeding habitats and bionomy of the species in the Brazilian southeast, between Cabo Frio (23°S) and Torres (29°21’S). Latter, Romero et al. (2008) studied the fish water column distribution, diet, and some reproductive aspects in the Brazilian northeast (Ilhéus, Bahia). It is a species that lives in the water column, namely in regions of sandy or muddy bottoms, where young and adult fish feed mainly on crustaceans and fish, respectively (Romero et al., 2008; Soares, 1989). Spawning occurs during spring and summer (Chaves et al., 1998; Giannini and Paiva Filho, 1994; Romero et al., 2008). However, knowledge about its population structure is, at present, inexistent.

Isopisthus parvipinnis, together with three other sciaenids species (e.g. *Stellifer rastrifer*, *S. brasiliensis*, and *Paralichthys brasiliensis*), represents more than 50% of the bycatch from shrimp fisheries along the coast of São Paulo and Paraná states (Coelho et al., 1986; Paiva Filho and Schmiegelow, 1986; Sedrez et al., 2013). *Isopisthus parvipinnis* catches, namely in Southeastern and South regions of Brazil, recorded fluctuations since the 1970s, ranging from 0.5 to 189 ton per year and state (IBAMA, 2009; PMAP-IP, 2018). Recently, a decline in fish landings was reported in São Paulo State (PMAP-IP, 2018). *Isopisthus parvipinnis* is a species with commercial value (Spier et al., 2018), but depending on its size, it can be sold as mixture, with other species, or individually (Graça Lopes et al., 2002). Although it has a low commercial value (R\$2.50 or US\$0.61, at the Companhia de Entrepostos e Armazéns Gerais de São Paulo - CEAGESP), the knowledge about this species is relevant due to its importance for the marine and estuarine ecosystems, as food for piscivorous fishes, marine birds and cetaceans (Santos et al.,

2002; Soares et al., 2008; Miotto et al., 2017) and as shrimp fishery bycatch (Freire and Pauly, 2015). The co-occurrence of sciaenids and penaeid shrimp in the coastal marine catches is due to similar abiotic requirements, such as water depth and type of substrate, that will influence their distribution (Schmidt and Dias, 2012).

In view of the ecological importance of the species in food webs and its volume in the shrimp fisheries, the aim of this work was to investigate the use of otolith shape analyses to elucidate the population structure of *I. parvipinnis* in the area between São Paulo and Santa Catarina Brazilian states (23°S to 26.9°S) in Southwestern Atlantic Ocean. Moreover, this structure will be compared through samples collected 43 years apart (1975 and 2018/2019) to verify the long-term temporal stability of otolith shape and the subsequent formation of different phenotypic groups.

5.2 Material and Methods

5.2.1 Fish sampling

Juvenile individuals (total length < 159 mm: age at first maturity according to Romero et al. (2008)) were obtained from commercial catches and field works in the shallow areas of the Brazilian Southeast and South coast, among North of São Paulo (NSP), Centre of São Paulo (CSP), South of São Paulo (SSP), Paraná (PR) and Santa Catarina (SC) States (Figure 18).

Fish were captured using an otter trawl between September and November of 1975, during the project Nectonic Fauna (FAUNEC) from the Oceanographic Institute of the University of São Paulo, and between September of 2018 and May of 2019 by local fishermen. The size range of individuals selected for otolith shape analyses was restricted to the most similar total length range (TL: 66-139 mm) (Table 6) to minimize the ontogenic effects on phenotypic variation (Campana et al., 2000; Moreira et al., 2019).

Historical (1975) and contemporaneous (2018/2019) samples were processed similarly, as described below. Samples were frozen and transported to the laboratory where they were identified to the species level using morphological and meristic diagnostic characters (Travassos and Paiva, 1957; Menezes and Figueiredo, 1980). Each speci-

Figure 18: Sampling locations of *Isopisthus parvipinnis* individuals collected in 1975 (yellow squares) and 2018/2019 (red stars) in the SW Atlantic Ocean from 23°S to 26.9°S, between São Paulo and Santa Catarina States (Brazil)

Table 6: Sampling locations and codes, period of capture, sample size (n), total length (TL, mm) and otolith length (OL, mm) of *Isopisthus parvipinnis* used in this study

Area	Location	Code	Period	n	TL (mm)	OL (mm)
São Paulo	Ubatuba	NSP	Sep./Nov. 1975	30	109±12	5.34±0.55
	Peruíbe	CSP	Sep./Nov. 1975	30	108±14	5.47±0.66
	Cananéia	SSP	Sep./Nov. 1975	30	109±14	5.50±0.68
Paraná	Paranaguá	PR	Sep./Nov. 1975	30	109±14	5.60±0.73
Santa Catarina	Navegantes	SC	Sep./Nov. 1975	30	111±14	5.52±0.72
São Paulo	Ubatuba	NSP	Nov. 2018	30	110±11	5.62±0.50
	Peruíbe	CSP	Nov. 2018	30	134±5	6.71±0.26
	Cananéia	SSP	Oct. 2018	30	113±7	5.72±0.34
Paraná	Paranaguá	PR	Sep. 2018	30	112±11	5.71±0.53
Santa Catarina	Navegantes	SC	May 2019	30	76±10	3.98±0.52

TL and OL are presented as mean ± standard deviation.

Abbreviations: CSP, Center of São Paulo; NSP, North of São Paulo; SSP, South of São Paulo; PR, Paraná; SC, Santa Catarina.

men was measured for total length (TL, 1 mm), weighted (0.01 g), and sagittal otoliths were removed from sacculi, washed with distilled water and stored dry in plastic packages (Soares, 1983).

5.2.2 Image acquisition

Right otoliths were placed with the outer face down, showing the sulcal groove up, and with the rostrum pointing upwards. Orthogonal two-dimensional digital images of otoliths were captured using a modular stereomicroscope with motorized zoom (ZEISS SteREO Discovery.V12) at 8x magnification. High contrast digital images were obtained with the Axion Vision 4.8 software using reflected light against a dark background, producing a bright two-dimensional photograph (Figure 19a1 and b1).

Figure 19: *Isopisthus parvipinnis* inner face of the right sagitta showing the original photograph (a1 and b1), the B&W binary image (a2 and b2) and the otolith averaged outline shape (a3 and b3) from individuals collected in 1975 and 2018/2019, respectively. a and b are otolith images from CSP individuals with 108 and 132 mm of TL, respectively. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

5.2.3 Otolith shape analysis

After image BW binarization (Figure 2a2 and b2), each otolith was described using shape indices (SIs) and elliptical Fourier descriptors (EFDs). To obtain the SIs, morphometric measurements (in mm) from area (A), perimeter (P), length (OL), and width (OW) were made from each otolith using the ImageJ v. 1.51q software (Rasband, W., 2017). Thereafter, these variables were used to calculate five SIs: form factor (FF), roundness (RO), circularity (CI), rectangularity (RE) and ellipticity (EL) (Table 7; Tuset et al. (2003)).

Table 7: Otolith shape indices calculated from the morphometric measurements [A: area (mm²), P: perimeter (mm), OL: length (mm) and OW: width (mm)] according to Tuset et al. (2003)

Shape indices	Formula
Form-factor (FF)	$\frac{4\pi A}{P^2}$
Roundness (RO)	$\frac{4A}{\pi OL^2}$
Circularity (CI)	$\frac{P^2}{A}$
Rectangularity (RE)	$\frac{A}{OL*OW}$
Ellipticity (EL)	$\frac{OL-OW}{OL+OW}$

SHAPE v.1.3 software (Iwata and Ukai, 2002) was used to extract the otolith shape contour and to determine the number of EFDs that best describe the otolith outline (Ferguson et al., 2011). The elliptical Fourier harmonics for each otolith were normalized to the first harmonic with SHAPE software and invariant to otolith size (Kuhl and Giar-dina, 1982; Iwata and Ukai, 2002; Pothin et al., 2006). The first three coefficients (a1, b1, and c1) were constant for all outlines. The first 7 harmonics reached 99% of the mean cumulative power for both periods (excluding coefficients b7, c7 and d7). Twenty-two EFDs [i.e. $(7 \times 4) - 3 - 3 = 22$] summarized the otolith shape for each location and year.

5.2.4 Data analysis

The relationship between SIs and fish size (expressed as OL) was tested with analysis of covariance (ANCOVA), using otolith length as a covariate. To avoid body size and allometric effects that occur during otolith growth (Ferreira et al., 2019; Moreira et al., 2019; Soeth et al., 2019), SIs were length-detrended by subtraction of the common within-group linear slope when ANCOVA results were significant (Campana et al., 2000).

Data was checked for normality (Shapiro-Wilk's test) and homoscedasticity (Levene's test). Statistical differences regarding locations for SIs and EFDs were tested individually within each year using One-Way Analysis of Variance (ANOVA), followed by a Tukey *post-hoc* test, if significant ($p < .05$). Thereafter individuals were grouped by a canonical analysis of principal coordinates (CAP), that provided a visualization of the spatial differences between locations. The reclassification accuracy for each location was obtained by a leave-one-out cross-validation. Pearson's correlations ($r > .50$) between the variables and the canonical axes patterns were shown in CAP graphics. Multivariate comparisons among locations and between years were conducted using a permutational multivariate analysis of variance (PERMANOVA). The matrices of dissimilarity were based on the Euclidean distance and p-values were generated using Monte-Carlo simulations (9999 random permutations) (Ferreira et al., 2019; Moreira et al., 2019; Soeth et al., 2019). The average EFDs reconstruction of the otolith shapes of each location and year was also used for visual evaluation of the main differences in otolith contours (Libungan and Pálsson, 2015; Soeth et al., 2019).

All statistical analyses were performed using Minitab 18 and PRIMER 6+ PERMANOVA software, with a statistical level of significance (α) of 0.05. Results are presented as mean $\pm$ standard deviation.

5.3 Results

Otoliths shape contour presented a few visual regional differences mainly in the 2018/2019 reconstructions from EFDs averages (Figure 19a3 and b3). FF, CI, and RE were the SIs that presented significant differences among regions in 1975, as well as the

EFDs b2, c2, b3, d3, and b5 (Table 8, ANOVAs, $p < .05$). In the period of 2018/2019, all SIs presented significant results, whereas FF, RO, CI and EL showed differences between SC samples and the others; and RE differentiated SSP and PR from the other locations (Table 9, ANOVAs, $p < .05$). All EFDs showed significant differences among locations (Table 9, ANOVAs, $p < .05$), with exception of a4. The PERMANOVA analysis detected significant differences between years and among locations for SIs, EFDs and for SIs and EFDs together, as well as a significant effect of the interaction between the years and locations for both analyses (Table 10).

Concerning the year of 1975, multivariate pairwise analysis for the SIs and the combination of SIs and EFDs showed that NSP was significantly different from CSP and PR, and SC from CSP and PR (Table 10, SIs and SIs + EFDs, PERMANOVA, $p < .05$). No differences were however observed concerning the EFDs (Table 10, EFDs, PERMANOVA, $p > .05$), except for NSP and PR. For 2018/2019, SIs and the combination of the shape descriptors (SIs and EFDs) presented the same response again, showing that SC was statistically different from all other locations (Table 10, SIs and SIs + EFDs, PERMANOVAs, $p < .05$). For the EFDs, all comparisons were considered significant, except between SSP and PR (Table 10, EFDs, PERMANOVA, $p < .05$).

The CAP for the year 1975, using only SIs, presented a high overlap among all samples (Figure 20, SIs) with a low overall reclassification success of 31% (Table 11, SIs). Samples from PR were the most rightly reallocated to the original location (53%), compared to SSP that recorded the lower reclassification success (7%). In Figure 20 (SIs), vector overlays indicated that samples distribution was primarily driven by FF (Pearson, $r = .85$) and CI (Pearson, $r = -.85$) on CAP Axis 1 ($\delta^2 = 0.36$), while CAP Axis 2 ($\delta^2 = 0.32$) was basically influenced by RE (Pearson, $r = -.99$). The reallocation of samples using EFDs recorded an overall reclassification success to 35% (Table 11, EFDs) and CAP presented some degree of separation between NSP/CSP from the other locations (Figure 20, EFDs). The combination of both shape indicators, slightly improved the overall reclassification success to 42% (Table 11, SIs and EFDs), and CAP result were similar to EFDs alone, with an increase in SC distinction (Figure 20, SIs and EFDs). In

this last case, vector overlays indicated that samples distribution was primarily driven by FF (Pearson, $r = .47$), CI (Pearson, $r = -.46$) and b2 (Pearson, $r = -.54$) on CAP Axis 1 ($\delta 1 = 0.36$), while CAP Axis 2 ($\delta 1 = 0.32$) was influenced by RE (Pearson, $r = -.54$) and c2 (Pearson, $r = -0.56$).

Regarding the period 2018/2019, and only using the SIs, samples presented high overlap in the CAP plot (Figure 20, SIs), resulting in a low overall reclassification success of 49% (Table 11, SIs). Higher values of correct reclassification were however reached for NSP (63%) and SC (90%) locations. Vector overlays of all four indexes were plotted in Figure 20. SIs indicated that samples distribution was primarily driven by FF (Pearson, $r = -.66$), RO (Pearson, $r = .61$), CI (Pearson, $r = .65$) and EL (Pearson, $r = -.65$) on CAP Axis 1; while on CAP Axis 2 separation was driven by RE (Pearson, $r = -0.71$). By using EFDs the overall reclassification reached however 74% (Table 11, EFDs) and in CAP four groups could be somewhat discriminated: NSP, CSP, SSP/PR and SC (Figure 20, EFDs). Vector overlays indicated that group separation was primarily driven by d1, d2, b3, d3, b5, c5, and a6 on CAP Axis 1, with Pearson correlation higher than 0.70, a2 (Pearson, $r = -.59$), a3 (Pearson, $r = -.67$), b4 (Pearson, $r = -.51$), d4 (Pearson, $r = -.56$), and a6 (Pearson, $r = .69$) on the same axis; and by c3, d5 (Pearson, $r = -.56$ for both) and a7 (Pearson, $r = .52$) on CAP Axis 2. Finally, the combination of both shape indicators had an additional meaningful improvement in the overall reclassification for 81% (Table 11, SIs and EFDs), standing out the high reclassification of CSP (90%) and SC (93%). CAP was graphically similar to the EFDs alone, but with an increase in CSP and SC separation was evident (Figure 20, SIs and EFDs). Only PR samples presented a high overlap with NSP and SSP samples. This group separation was primarily driven by four SIs (FF, RO, CI, EL, $r = .50$) and 11 Fourier coefficients (d1, a2, d2, a3, b3, d3, d3, b4, d4, b5, c5, and a6 on CAP Axis 1 ($\delta 1 = 0.93$), and by c3 (Pearson, $r = -.49$), d5 (Pearson, $r = -.58$) and a7 (Pearson, $r = .57$) on CAP Axis 2 ($\delta 1 = 0.80$).

Table 8: Otolith shape indices and elliptical Fourier descriptors from *Isopisthus parvipinnis* collected in SE-S Brazil between São Paulo and Santa Catarina in 1975

	1975				
	NSP	CSP	SSP	PR	SC
FF	$0.878 \pm 0.010^{a,b}$	0.884 ± 0.010^a	$0.880 \pm 0.010^{a,b}$	0.884 ± 0.009^a	0.876 ± 0.010^b
RO	0.834 ± 0.014^a	0.832 ± 0.011^a	0.836 ± 0.016^a	0.835 ± 0.014^a	0.836 ± 0.014^a
CI	$13.914 \pm 0.224^{a,b}$	13.795 ± 0.221^b	$13.871 \pm 0.221^{a,b}$	13.796 ± 0.189^b	13.976 ± 0.236^a
RE	0.774 ± 0.010^b	0.773 ± 0.009^b	$0.778 \pm 0.009^{a,b}$	0.781 ± 0.010^a	$0.779 \pm 0.008^{a,b}$
EL	0.062 ± 0.011^a	0.063 ± 0.007^a	0.063 ± 0.012^a	0.066 ± 0.013^a	0.064 ± 0.011^a
d1	0.691 ± 0.024^a	0.696 ± 0.024^a	0.688 ± 0.030^a	0.682 ± 0.024^a	0.685 ± 0.032^a
a2	0.005 ± 0.005^a	0.005 ± 0.005^a	0.004 ± 0.004^a	0.005 ± 0.005^a	0.003 ± 0.005^a
b2	$-0.033 \pm 0.006^{a,b}$	$-0.032 \pm 0.005^{a,b}$	$-0.034 \pm 0.005^{a,b}$	-0.035 ± 0.004^b	-0.030 ± 0.005^a
c2	-0.070 ± 0.007^b	-0.070 ± 0.005^b	$-0.066 \pm 0.007^{a,b}$	$-0.065 \pm 0.008^{a,b}$	-0.064 ± 0.008^a
d2	-0.004 ± 0.007^a	-0.006 ± 0.006^a	-0.004 ± 0.007^a	-0.007 ± 0.008^a	-0.003 ± 0.007^a
a3	0.043 ± 0.005^a	0.044 ± 0.004^a	0.043 ± 0.005^a	0.042 ± 0.004^a	0.045 ± 0.004^a
b3	$-0.006 \pm 0.003^{a,b}$	$-0.006 \pm 0.003^{a,b}$	$-0.005 \pm 0.003^{a,b}$	-0.006 ± 0.002^b	-0.004 ± 0.003^a
c3	-0.013 ± 0.004^a	-0.012 ± 0.004^a	-0.012 ± 0.004^a	-0.011 ± 0.004^a	-0.010 ± 0.004^a
d3	0.049 ± 0.004^b	0.049 ± 0.005^b	$0.051 \pm 0.005^{a,b}$	0.053 ± 0.005^a	$0.050 \pm 0.006^{a,b}$
a4	0.003 ± 0.003^a	0.003 ± 0.003^a	0.003 ± 0.003^a	0.002 ± 0.003^a	0.003 ± 0.003^a
b4	-0.016 ± 0.003^a	-0.017 ± 0.003^a	-0.016 ± 0.002^a	-0.015 ± 0.002^a	-0.015 ± 0.003^a
c4	0.023 ± 0.003^a	0.022 ± 0.003^a	0.021 ± 0.004^a	0.022 ± 0.003^a	0.021 ± 0.004^a
d4	-0.004 ± 0.004^a	-0.004 ± 0.004^a	-0.006 ± 0.004^a	-0.005 ± 0.005^a	-0.004 ± 0.005^a
a5	-0.003 ± 0.003^a	-0.003 ± 0.003^a	-0.003 ± 0.003^a	-0.004 ± 0.002^a	-0.003 ± 0.002^a
b5	$-0.013 \pm 0.003^{a,b}$	-0.012 ± 0.003^b	$-0.012 \pm 0.003^{a,b}$	$-0.012 \pm 0.003^{a,b}$	-0.010 ± 0.003^a
c5	-0.011 ± 0.005^a	-0.011 ± 0.005^a	-0.012 ± 0.004^a	-0.011 ± 0.005^a	-0.010 ± 0.005^a
d5	0.021 ± 0.003^a	0.022 ± 0.003^a	0.022 ± 0.004^a	0.023 ± 0.003^a	0.023 ± 0.003^a
a6	0.000 ± 0.002^a	0.000 ± 0.003^a	0.000 ± 0.002^a	-0.001 ± 0.003^a	0.000 ± 0.003^a
b6	0.003 ± 0.002^a	0.002 ± 0.002^a	0.002 ± 0.002^a	0.003 ± 0.001^a	0.002 ± 0.002^a
c6	0.007 ± 0.003^a	0.007 ± 0.002^a	0.007 ± 0.003^a	0.006 ± 0.002^a	0.006 ± 0.002^a
d6	0.007 ± 0.002^a	0.008 ± 0.002^a	0.007 ± 0.002^a	0.007 ± 0.002^a	0.007 ± 0.002^a
a7	-0.009 ± 0.002^a	-0.009 ± 0.002^a	-0.009 ± 0.002^a	-0.009 ± 0.001^a	-0.010 ± 0.002^a

Same letters mean no significant differences between locations [One-Way ANOVA, followed by Tukey's *post-hoc* test if needed ($p < 0.05$). Data are represented as mean $\pm$ standard deviation.

Abbreviations: CI, circularity; CSP, Center of São Paulo; EL, ellipticity; FF, form-factor; NSP, North of São Paulo; PR, Paraná; RE, rectangularity; RO, roundness; SC, Santa Catarina. SSP, South of São Paulo.

Table 9: Otolith shape indices and elliptical Fourier descriptors from *Isopisthus parvipinnis* collected in SE-S Brazil between São Paulo and Santa Catarina in 2018/2019

	2018/2019				
	NSP	CSP	SSP	PR	SC
FF	0.873 $\pm$ 0.007 ^a	0.872 $\pm$ 0.014 ^a	0.872 $\pm$ 0.010 ^a	0.873 $\pm$ 0.010 ^a	0.857 $\pm$ 0.013 ^b
RO	0.809 $\pm$ 0.014 ^b	0.812 $\pm$ 0.015 ^b	0.813 $\pm$ 0.019 ^b	0.817 $\pm$ 0.015 ^b	0.833 $\pm$ 0.019 ^a
CI	14.081 $\pm$ 0.160 ^b	14.120 $\pm$ 0.319 ^b	14.118 $\pm$ 0.213 ^b	14.083 $\pm$ 0.213 ^b	14.448 $\pm$ 0.284 ^a
RE	0.760 $\pm$ 0.008 ^b	0.762 $\pm$ 0.009 ^b	0.764 $\pm$ 0.010 ^{a,b}	0.770 $\pm$ 0.010 ^a	0.762 $\pm$ 0.009 ^b
EL	0.080 $\pm$ 0.011 ^a	0.080 $\pm$ 0.010 ^a	0.079 $\pm$ 0.015 ^a	0.080 $\pm$ 0.013 ^a	0.063 $\pm$ 0.012 ^b
d1	0.660 $\pm$ 0.015 ^b	0.694 $\pm$ 0.021 ^c	0.686 $\pm$ 0.019 ^b	0.686 $\pm$ 0.022 ^b	0.757 $\pm$ 0.023 ^a
a2	0.008 $\pm$ 0.003 ^b	0.004 $\pm$ 0.004 ^a	0.005 $\pm$ 0.005 ^{a,b}	0.006 $\pm$ 0.004 ^{a,b}	-0.001 $\pm$ 0.007 ^c
b2	-0.030 $\pm$ 0.007 ^{a,b}	-0.032 $\pm$ 0.005 ^a	-0.037 $\pm$ 0.004 ^c	-0.035 $\pm$ 0.006 ^{b,c}	-0.033 $\pm$ 0.006 ^{a,b,c}
c2	-0.068 $\pm$ 0.007 ^{a,b,c}	-0.064 $\pm$ 0.007 ^c	-0.066 $\pm$ 0.007 ^{b,c}	-0.061 $\pm$ 0.008 ^{a,b}	-0.061 $\pm$ 0.007 ^a
d2	-0.008 $\pm$ 0.006 ^b	-0.007 $\pm$ 0.005 ^b	-0.008 $\pm$ 0.005 ^b	-0.005 $\pm$ 0.006 ^b	0.011 $\pm$ 0.008 ^a
a3	0.045 $\pm$ 0.004 ^{a,b}	0.043 $\pm$ 0.003 ^a	0.040 $\pm$ 0.004 ^b	0.042 $\pm$ 0.004 ^b	0.035 $\pm$ 0.005 ^c
b3	-0.007 $\pm$ 0.003 ^{c,d}	-0.006 $\pm$ 0.002 ^d	-0.004 $\pm$ 0.002 ^b	-0.004 $\pm$ 0.003 ^{b,c}	0.002 $\pm$ 0.004 ^a
c3	-0.013 $\pm$ 0.005 ^b	-0.013 $\pm$ 0.003 ^b	-0.008 $\pm$ 0.003 ^a	-0.007 $\pm$ 0.005 ^a	-0.008 $\pm$ 0.004 ^a
d3	0.055 $\pm$ 0.004 ^b	0.050 $\pm$ 0.003 ^a	0.052 $\pm$ 0.004 ^b	0.052 $\pm$ 0.004 ^{a,b}	0.040 $\pm$ 0.004 ^c
a4	0.003 $\pm$ 0.003 ^a	0.004 $\pm$ 0.003 ^a	0.003 $\pm$ 0.003 ^a	0.004 $\pm$ 0.003 ^a	0.005 $\pm$ 0.003 ^a
b4	-0.015 $\pm$ 0.003 ^a	-0.015 $\pm$ 0.002 ^a	-0.014 $\pm$ 0.003 ^a	-0.015 $\pm$ 0.003 ^a	-0.019 $\pm$ 0.003 ^b
c4	0.021 $\pm$ 0.004 ^a	0.022 $\pm$ 0.004 ^{a,b}	0.020 $\pm$ 0.004 ^{a,b}	0.020 $\pm$ 0.004 ^{a,b}	0.019 $\pm$ 0.006 ^b
d4	-0.003 $\pm$ 0.003 ^a	-0.004 $\pm$ 0.004 ^a	-0.004 $\pm$ 0.004 ^a	-0.005 $\pm$ 0.004 ^a	-0.009 $\pm$ 0.004 ^b
a5	-0.003 $\pm$ 0.003 ^{a,b}	-0.004 $\pm$ 0.003 ^a	-0.005 $\pm$ 0.002 ^b	-0.005 $\pm$ 0.003 ^b	-0.005 $\pm$ 0.003 ^b
b5	-0.014 $\pm$ 0.002 ^c	-0.013 $\pm$ 0.002 ^c	-0.011 $\pm$ 0.002 ^b	-0.010 $\pm$ 0.002 ^b	-0.005 $\pm$ 0.004 ^a
c5	-0.016 $\pm$ 0.003 ^b	-0.011 $\pm$ 0.004 ^c	-0.014 $\pm$ 0.003 ^c	-0.011 $\pm$ 0.004 ^b	-0.003 $\pm$ 0.005 ^a
d5	0.021 $\pm$ 0.003 ^{b,c}	0.022 $\pm$ 0.003 ^{c,d}	0.026 $\pm$ 0.003 ^a	0.024 $\pm$ 0.003 ^b	0.019 $\pm$ 0.003 ^d
a6	-0.002 $\pm$ 0.002 ^c	-0.001 $\pm$ 0.003 ^d	0.000 $\pm$ 0.002 ^{b,c}	0.001 $\pm$ 0.002 ^b	0.004 $\pm$ 0.002 ^a
b6	0.003 $\pm$ 0.002 ^a	0.004 $\pm$ 0.001 ^a	0.003 $\pm$ 0.002 ^a	0.002 $\pm$ 0.002 ^a	0.000 $\pm$ 0.004 ^b
c6	0.005 $\pm$ 0.003 ^b	0.006 $\pm$ 0.002 ^b	0.007 $\pm$ 0.003 ^{a,b}	0.006 $\pm$ 0.002 ^b	0.008 $\pm$ 0.003 ^a
d6	0.007 $\pm$ 0.002 ^a	0.008 $\pm$ 0.002 ^{a,b}	0.006 $\pm$ 0.002 ^{b,c}	0.005 $\pm$ 0.002 ^c	0.006 $\pm$ 0.003 ^{b,c}
a7	-0.009 $\pm$ 0.002 ^{a,b}	-0.010 $\pm$ 0.002 ^a	-0.012 $\pm$ 0.001 ^c	-0.011 $\pm$ 0.002 ^{b,c}	-0.009 $\pm$ 0.002 ^a

Same letters mean no significant differences between locations [One-Way ANOVA, followed by Tukey's *post-hoc* test if needed ($p < 0.05$). Data are represented as mean $\pm$ standard deviation.

Abbreviations: CI, circularity; CSP, Center of São Paulo; EL, ellipticity; FF, form-factor; NSP, North of São Paulo; PR, Paraná; RE, rectangularity; RO, roundness; SC, Santa Catarina. SSP, South of São Paulo.

Table 10: Overall and pairwise PERMANOVA comparisons among the five sampling locations of *Isopisthus parvipinnis* regarding the otolith shape indices (SIs), the elliptic Fourier descriptors (EFDs), and both tools (SIs + EFDs), for fish collected in 1975 and 2018/2019

SIs		Main PERMANOVA					Pairwise PERMANOVA				
<i>Source</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo-F</i>	<i>p (MC)</i>		NSP	CSP	SSP	PR	SC
Location	4	2.928	0.732	13.456	0.0001	NSP		0.0443	0.4561	0.0293	0.2970
Years	1	6.792	6.792	124.84	0.0001	CSP	0.5541		0.1959	0.8833	0.0029
Interaction	4	0.774	0.193	3.554	0.0067	SSP	0.4411	0.9918		0.1600	0.0793
Residual	290	15.778	0.054			PR	0.8123	0.5889	0.5094		0.0021
Total	299	26.272				SC	0.0001	0.0002	0.0001	0.0001	
2018/2019											
EFDs		Main PERMANOVA					Pairwise PERMANOVA				
<i>Source</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo-F</i>	<i>p (MC)</i>		NSP	CSP	SSP	PR	SC
Location	4	0.091	0.023	25.487	0.0001	NSP		0.5094	0.2216	0.0178	0.0996
Years	1	0.007	0.007	7.490	0.0017	CSP	0.0001		0.5431	0.0900	0.2365
Interaction	4	0.099	0.025	27.829	0.0001	SSP	0.0129	0.0001		0.4108	0.5531
Residual	290	0.258	8.9E-04			PR	0.0289	0.0001	0.2239		0.3628
Total	299	0.456				SC	0.0001	0.0001	0.0001	0.0001	
2018/2019											
SIs+EFDs		Main PERMANOVA					Pairwise PERMANOVA				
<i>Source</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo-F</i>	<i>p (MC)</i>		NSP	CSP	SSP	PR	SC
Location	4	3.020	0.755	13.652	0.0001	NSP		0.0436	0.4599	0.0306	0.2978
Years	1	6.799	6.799	122.95	0.0001	CSP	0.4251		0.1760	0.8317	0.0032
Interaction	4	0.873	0.218	3.947	0.0032	SSP	0.4141	0.6896		0.1566	0.0800
Residual	290	16.038	0.055			PR	0.7485	0.4941	0.5079		0.0016
Total	299	26.731				SC	0.0001	0.0001	0.0001	0.0001	
2018/2019											

Note: Significant differences ($p < .05$) were marked in bold values.

Table 11: Leave-one-out cross-validation reclassification matrix of the CAP analysis using the otolith shape (otolith shape indices - SIs, elliptical Fourier descriptors - EFDs and both - SIs + EFDs) from *Isopisthus parvipinnis* for all sampling locations in the year 1975 and 2018/2019

1975							
	Original location	Predicted location					% correct
		NSP	CSP	SSP	PR	SC	
SIs	NSP	4	9	2	6	9	13
	CSP	5	13	1	7	4	43
	SSP	5	5	2	10	8	7
	PR	3	7	1	16	3	53
	SC	6	4	1	7	12	40
	Total						31
EFDs	NSP	11	9	4	0	6	37
	CSP	12	11	3	2	2	37
	SSP	1	5	12	7	5	40
	PR	1	2	9	11	7	37
	SC	6	3	5	8	8	27
	Total						35
SIs + EFDs	NSP	8	9	2	5	6	27
	CSP	7	13	3	4	3	43
	SSP	3	6	6	11	4	20
	PR	1	5	3	18	3	60
	SC	2	2	4	4	18	60
	Total						42
2018/2019							
	Original location	Predicted location					% correct
		NSP	CSP	SSP	PR	SC	
SIs	NSP	19	3	3	4	1	63
	CSP	7	14	0	8	1	47
	SSP	14	1	3	8	4	10
	PR	5	2	8	11	4	37
	SC	0	0	2	1	27	90
	Total						49
EFDs	NSP	22	3	1	4	0	73
	CSP	2	24	0	4	0	80
	SSP	0	1	23	6	0	77
	PR	0	6	5	19	0	63
	SC	2	0	0	0	28	93
	Total						74
SIs + EFDs	NSP	21	3	0	6	0	70
	CSP	0	27	0	3	0	90
	SSP	0	1	26	3	0	87
	PR	1	5	5	19	0	63
	SC	1	0	0	1	28	93
	Total						81

Abbreviations: CSP, Center of São Paulo; NSP, North of São Paulo; PR, Paraná; SC, Santa Catarina; SSP, South of São Paulo.

Figure 20: Canonical analysis of principal coordinates (CAP) plots for the otolith shape indices (SIs), elliptic Fourier descriptors (EFDs) and using both tools (SIs and EFDs) from *Isopisthus parvipinnis* collected in the five sampling locations of the SW Atlantic in the years 1975 and 2018/2019. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

5.4 Discussion

The hereby data showed significant morphological variations of *I. parvipinnis* sagittae among locations and between years. Both SIs and EFDs showed to be useful for discriminating fish from different locations. The SIs were useful in discriminating individuals from the North and Center of São Paulo to the southernmost locations in 1975, and individuals from SC from the other locations in 2018/2019. On average RO and RE recorded higher values in 1975, but lower EL and CI values compared to 2018/2019 samples. This data reinforces the existence of rounder otoliths in the past and a more elliptical shape in contemporaneous otoliths. In overall, the present data showed similar values of RE, but lower values of CI compared to those reported previously for *I. parvipinnis* individuals ranging between 83 and 170 mm, and collected in various oceanographic surveys on the Brazilian continental shelf between 22° and 34°S (Rossi-Wongtchowski et al., 2014). On the other hand, EFDs were responsible for detecting significant differences among all sampling locations, namely in 2018/2019. Furthermore, the present study showed that the combined use of SIs and EFDs can improve the discrimination power, as

observed in previous studies (Galley et al., 2006; Jónsdóttir et al., 2006; Moreira et al., 2019). However, a greater number of variables (e.g. SIs + EFDs) does not necessarily imply in a better insight into the variation of the overall otolith shape, once EFDs itself could provide a better scenario about the otolith phenotypic variation in *I. parvipinnis* population structure. Re-classification of fish to the original locations was smaller for 1975 compared to 2018/2019 (42% vs 81%, respectively). Data from 1975 showed a high overlap of fish, with no clear distinction between groups. Data from 2018/2019 were well reallocated to the original sampling locations and allowed a clear separation into four groups: NSP, CSP, SSP/PR, and SC. The observed findings among locations and between years, could be explained by a long-term genetic variation affecting *I. parvipinnis* otolith's shape driven by temporal and spatial differences in the environmental conditions of the study area. However, it should be take into account that phenotypic plasticity supports fish adaptability to natural or anthropogenic induced environmental change by modification in their physiology and behavior, which may not be related to genetic changes, leading to changes in their reproduction, morphology or survival that mitigate the effects of environmental variation (Lindsey, 1981). Thus, the detection of those population differences cannot usually be taken as evidence of genetic differentiation (Swain and Foote, 1999). Thus, changes in *I. parvipinnis* population structure due to human pressure, such as pollution, overfishing (shrimp fishery pressure), habitat destruction, climate change and other anthropogenic influences affecting the coastal and estuarine ecosystems (Arkoosh et al., 1998; Blaber et al., 2000; Koenigstein et al., 2016) should also be considered. The structure of a fish stock results from its interaction with human-induced and natural changes in the environment (Cochrane and Garcia, 2009). However, it is difficult to interpret phenotype-environment associations once their source can be generated by many processes, as mortality, adaptation, ontogeny, and biogeographic processes (McLachlan and Ladle, 2011). But, otolith shape changes could simply occur as result of differences in the growth rate of distinct population-units (Pérez and Fabré, 2013) subject to distinct fishing pressure efforts. Indeed, and probably as result of the shrimp (*Xiphopenaeus kroyeri*) overfishing in the SE-S Brazil, a more than 10-fold reduction in the fishery catch of this

species was observed during the last 20 years (from 4.4 ton in 1998 to 273 kg in 2018) by the Fishery Institute of São Paulo state (PMAP-IP, 2018).

Although the uni- and multivariate analyses of both otolith shape descriptors in the year of 1975 presented some significant regional differences, the leave-one-out cross-validation presented very low percentages of correct reclassification for all locations, suggesting the existence of a single panmictic population. These findings support some older studies regarding the population structure of other sciaenid species also occurring in this study area. *Macrodon ancylodon* collected from São Paulo, Paraná, and Northern of Santa Catarina recorded a single otolith morphotype based on otolith's morphological characteristics of concavity, the presence of denticulations, sulcus acoustic position and format of otoliths (Yamaguti, 1979). Moreover, regarding their width and length, otoliths from *Cynoscion jamaicensis* did not present significant differences between Santa Catarina and Rio Grande do Sul (Spach and Yamaguti, 1989c). It is important to note that the lack of differences between small and meso spatial distances, regarding the otolith's shape analyses, is not conclusive and it does not guarantee that a population substructure could exist under environmental homogeneity conditions (Stransky et al., 2008). However, samples from 2018/2019 showed significant differences among locations, with CAP analysis showing the formation of four main phenotypic groups – NSP, CSP, SSP/PR, and SC. It is known that both genetic and environmental conditions control otolith shape. So, factors such as temperature, salinity, food supply and other physical, chemical and geological water properties, and their respective temporal and latitudinal variations, influences fish growth rate, and consequently otolith shape (Cardinale et al., 2004; Campana, 2005a; Capoccioni et al., 2011). Likewise, the influence of the estuarine systems of Cananéia-Iguape and Paranaguá was used by Daros et al. (2016b) and Soeth et al. (2019) to justify the observed the population structure of *Stegastes fuscus* (Pomacentridae) across the South of São Paulo and Santa Catarina states, and of *Chaetodipterus faber* (Ephippidae) in the Brazilian coast between Espírito Santo and Santa Catarina states, respectively, through the use of otolith chemical and shape signatures. This could, at least, support the similarities observed in the present work between SSP and PR for 2018/2019. However, with

nearly 700 km of coast, the hereby study area comprises a variety of environment types, as mangroves, estuaries, sandy or rocky beaches, under different oceanographic conditions. Oceanographic processes in SC are dominated by the Brazilian Coastal Current, flowing northward and bringing waters from the Río de La Plata, Uruguai-Argentina border (Campos et al., 2008), and by the upwelling events in the Cabo de Santa Marta Grande (Mazzini and Barth, 2013). Itajaí-Açú river can also exert some influence in this location, mainly due to the large continental runoff events (Schettini et al., 2005). In addition, PR and SSP locations are exposed to the influence of two great estuarine systems: the Paranaguá Bay and Cananéia-Iguape. The first one, whose structural properties are typical for a marine ingression environment, contributes with freshwater input close to 200 m³/s, is considered as one of the least impacted coastal systems in Southeastern Brazil (Marone et al., 2005). The second one, is located in a Biosphere Reserve (UNESCO) which suffered important environmental changes since the opening of the Valo Grande artificial channel in the 19th century, which led to a contribution of the Ribeira de Iguape river, which presents an outflow varying from about 300 to more than 1,200 m³/s of freshwater (Mahiques et al., 2009). The CSP presented the largest portion from the continental shelf, restricting the area to coastal events, and the influence of three minor rivers, Una, Guaraú, and Peruíbe (Tessler et al., 2006), while the NSP is exposed to seasonal intrusions of the South Atlantic Central Water (SACW), a cold and salty water transported along the continental slope by the Brazil Current (Castro, 2014), besides the coastal events. Together, these factors can result in the observed *I. parvipinnis* population structure in 2018. Moreover, consideration needs to be given to environmental changes that occurred at these locations over 45 years. In fact, all estuarine ecosystems and coastal systems influenced by minor rivers have suffered intense changes in their outfalls and coastal geomorphology from the 1970s to the present due to urbanization processes (Angulo et al., 2006; Klein et al., 2006; Mahiques et al., 2009; Tessler et al., 2006), which can explain the observed regional morphological variations of otoliths within the temporal window of the hereby study. Recently, it has been demonstrated that otolith chronologies are an effective method to assess long-term trends and drivers of growth in fishery species (Martino et al., 2019).

As an important bycatch fish from shrimp fisheries in the SE-S Brazilian coast (IBAMA, 2009; Branco et al., 2015), *I. parvipinnis* has some aspects from its biology already studied (Chaves et al., 1998; Giannini and Paiva Filho, 1990, 1994; Romero et al., 2008; Soares, 1983, 1989) and their otoliths were previously characterized and described in the study area (Rossi-Wongtchowski et al., 2014). However, as far it is known, this is the first study about its population structure. Although there is no directed fishing effort for this species, *I. parvipinnis* is vulnerable to the intensive shrimp capture in the coastal region (Coelho et al., 1988), which may have an indirect impact on its population dynamics. Moreover, there is annually a close season for shrimp fishing, but its establishment did not consider the life cycles of the bycatch fish (Souza and Chaves, 2007). For this reason, studies addressing the population structure of non-target species can provide important basic biological information to support sustainable management actions from an ecosystem viewpoint. This work also highlights on the importance of historical otolith collections in fisheries science. Otolith shape analysis provided valuable information about the spatial and temporal changes of *I. parvipinnis* population structure in the Brazilian SE-S waters, suggesting a change from a single panmictic population in the past to a metapopulation structure in the present days. Although very unlikely, since EFDs are not sensitive to allometric differences, and SIs were properly detrended (Cardinale et al., 2004), some of the hereby observed regional variation in 2018/2019 could be biased by the size range asymmetries, namely for CSP and SC, the larger and smaller fish respectively. It is known that otoliths morphometry can variate allometrically with fish size, even within a geographic population unit (Zhao et al., 2017). Indeed, ontogenetic and size-class effects were detected in otolith's morphological features of *I. parvipinnis* (Rossi-Wongtchowski et al., 2014). However, adopting different methods, such as otolith elemental composition and genetics, several authors successfully studied the population structure of other sciaenid fishes (e.g. *Argyrosomus japonicus*: Ferguson et al. (2011) and Barnes et al. (2016); *Cynoscion guatucupa* and *Micropogonias furnieri*: Volpedo and Cirelli (2006) and Sabadin et al. (2010); and *Atractoscion aequidens*: Henriques et al. (2018). Thus, a more conclusive scenario needs to be draw using alternative and compli-

mentary approaches, such as genetics, parasites fauna, otolith chemistry and other natural tags.

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6 Historical and contemporary population structure of the bigtooth corvina *Isopisthus parvipinnis* in the Southwest Atlantic Ocean inferred from otolith elemental signatures

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Abstract

Otolith microchemistry is a powerful tool to investigate natal philopatry, habitat connectivity and population dynamics of fish. In this study, otolith microchemistry was used to investigate the long-term spatial shifts of the population structure of *Isopisthus parvipinnis*, an economically and ecologically important Brazilian fish species, usually caught as bycatch of shrimp fisheries. Otoliths were analyzed from juvenile individuals (66 - 139 mm TL), regarding historical (1975) and contemporary (2018/2019) samples, collected in five subareas [São Paulo: North - NSP, Center - CSP and South – SSP; Paraná (PR) and Santa Catarina (SC)] of the shallow waters off the coast of the South Brazil Bight. Informative trace elements from whole otoliths were obtained using flame atomic absorption spectrometry (^{43}Ca , ^{23}Na and ^{88}Sr) and inductively coupled plasma mass spectrometry (^{137}Ba , ^{59}Co , ^{65}Cu , ^7Li , ^{26}Mg , ^{55}Mn , ^{60}Ni , and ^{85}Rb). Univariate and multivariate statistics were performed in single and multi-elemental data in terms of element:Ca ratios. The main informative element:Ca ratios were Co:Ca, Cu:Ca, Li:Ca, Mg:Ca, Ni:Ca and Na:Ca for the historical samples; and Cu:Ca, Mg:Ca, Mn:Ca, Na:Ca, and Rb:Ca for the contemporary samples. Multivariate analysis showed spatial differences in otolith chemical composition over the years. Samples from 1975 presented an overall low reclassification rate (58%), suggesting the existence of two population units: (1) SP + PR; and (2) SC. However, samples from 2018/2019 discriminated four distinct population units with a good overall reclassification (80%): (1) NSP; (2) CSP; (3) SSP + PR; and (4) SC. The hereby data corroborates and refines the population structure scenario of *I. parvipinnis* recently described using complimentary phenotypic tags. This study also showed the effects of the temporal variability of the oceanographic conditions, anthropogenic influence and climate change in the coastal ecosystems in the chemical signatures of fish otoliths.

Keywords: Sciaenidae, otolith fingerprints, population units, temporal shifts.

6.1 Introduction

A proper understanding of the fish population structure and dynamics is necessary for the sustainable management of a fishery (Begg and Brown, 2000). Once population units may respond differently to exploitation, they must be managed separately to optimize their yield (Galli and Norbis, 2013). The accurate knowledge of the population structure can have significant impacts, including the mediation of species in a response to fishing pressure and environmental changes, which plays a key role in the species persistence (Kerr et al., 2017).

Several natural tags, such as otolith's shape and its chemical composition, body meristic and morphometric characters, and the presence and prevalence of parasites, among others, have been commonly used in fisheries biology, providing evidences for stock discreteness (Poulin and Kamiya, 2013; Moreira et al., 2020; Moura et al., 2020). Therefore, otolith chemical analysis can be pointed as a successful approach to infer about fish population structure, helping to solve questions as migration patterns, habitat use and connectivity, or fish dynamics and even dietary patterns, where environmental heterogeneity exists (Daros et al., 2016b; Adelir-Alves et al., 2018; Soeth et al., 2020). Nevertheless, coastal systems still represent a challenge for the understanding of chemical signatures once they embrace an inherent variability of environments and are under influence of human action and climate change (Cheung et al., 2013; Wheeler et al., 2016; Araújo et al., 2018).

Otoliths are calcified structures located in the fish inner ears, whose function is related to hearing, balance and three-dimensional orientation of fish (Popper et al., 2005). Otoliths are metabolically inert structures, which cannot be reabsorbed and chronologically record the chemical and physical environmental information through chemical elements incorporated in the aragonite matrix, being used as proxies to understand where fishes spent their different life stages (Campana and Thorrold, 2001). The SBB encompass a great variety of estuarine and coastal ecosystems (Biolo et al., 2019), which can provide different microchemical signatures in fish otoliths. In the estuarine and coastal waters of the South Brazil Bight (SBB), otoliths were successfully used to assess estuarine depen-

dency and habitat use of *Micropogonias furnieri* (Albuquerque et al., 2012), *Centropomus parallelus* (Daros et al., 2016a) and *Cathorops spixii* (Carvalho et al., 2020); connectivity and population structure of *Stegastes fuscus* (Daros et al., 2016b) and *Abudefduf saxatilis* (Adelir-Alves et al., 2018) from coastal systems of São Paulo, Paraná and Santa Catarina (25°S – 26.5°S); stock structure and life-time movements of *Chaetodipterus faber* from Espírito Santo to Santa Catarina states, from 20°S to 28°S (Soeth et al., 2019, 2020); and fish stocks and nursery areas of *Genidens genidens* (Maciel et al., 2020).

Croakers are fishes belonging to the Sciaenidae family (order: Perciformes) with over 250 species worldwide (Nelson, 2006), from which more than 20 can be found in the marine coastal and estuarine waters of the Western Atlantic Ocean (Menezes, 2011; Spier et al., 2018). They are also one of the most important demersal fisheries resources in the shallow waters of the SSB (Gianinni and Paiva Filho, 1990; Haimovici, 2005; Souza et al., 2008). *Isopisthus parvipinnis* (Cuvier, 1830) is one of the main demerso-pelagic species from Sciaenidae family being caught as bycatch of the artisanal fisheries in Brazil, primarily in the SE-S regions. Commonly known as “bigtooth corvina” (in Portuguese: *tortinha* or *pescadinha*), *I. parvipinnis* is widely distributed at the western Atlantic Ocean, from Costa Rica to Southern Brazil, until Santa Catarina State (Socorro and Miranda, 2015). It represents 6% of the artisanal discards (Freire and Pauly, 2015), and depending on its size, *I. parvipinnis* can also be used as bait, or sold as mixture or individually (Graça Lopes et al., 2002). The bigtooth corvina is a seasonal species usually found on the inner continental shelf at 23°S (Rossi-Wongtschowski and Paes, 1993). *I. parvipinnis* can be classified as piscivorous or carcinophage and its feeding habits are related to ontogeny and season (Soares, 1989; Santos et al., 2016). This species can migrate between the mangroves in the region of Guaratuba Bay, Southern Brazil and the open sea at Paraná State, 26°S (Chaves et al., 1998). The reproductive period of the species in the northern Santa Catarina (Southern Brazil) coincides with the season closure of the shrimp fishery (Souza and Chaves, 2007). Recruitment appears to occur between summer-autumn to winter in the northeast Brazil (Romero et al., 2008). The population structure of *I. parvipinnis* was recently studied in the SE-S Brazil through otolith shape (Hoff et al., 2020a)

and body geometric morphometrics (Hoff et al., 2020b), revealing a complex metapopulational scenario with discrete population units.

Complementary to previous studies and other methodological approaches, this work aims to investigate the long-term stability of the population structure of *I. parvipinnis* in the South Brazil Bight (23°S to 25.5°S) using trace elements recorded in otoliths collected in a temporal window of 43 years apart (1975 vs 2018/2019); and, secondly, and for the first time, the spatial-temporal variations in the chemical composition of otoliths, as environmental time-lag recorders, were evaluated taking into consideration the long-term effects of human activities and climate change on the marine ecosystem.

6.2 Material and Methods

6.2.1 Fish sampling and otolith preparation

Juvenile fish (total length < 159 mm: age at first maturity according to Romero et al. (2008)) were caught from commercial and research vessels in the shallow waters of the SBB (from 23°S to 29°S) in five sampling areas: Northern (NSP), Center (CSP), and Southern (SSP) of São Paulo, Paraná (PR) and Santa Catarina (SC) (Fig. 21). Individuals were collected by the Oceanographic Institute of the University of São Paulo, between September and November 1975 during the Nectonic Fauna research project (FAUNEC), and were archived at the ColBIO (Coleção Biológica Edmundo Ferraz Nonato IO-USP) (for more details see Lamas and Soares (2019)); and (ii) between September 2018 and May 2019 by local fishermen, immediately frozen and thereafter processed at the laboratory. For both sampling periods an otter trawl was used.

Individuals selected for otolith elemental analysis was restricted to a size range between 66 and 139 mm TL (Table 12) to minimize phenotypic variations resulting from ontogenetic processes (Campana et al., 2000). Fish were identified through meristic and morphometrics characters to the species level (Menezes and Figueiredo, 1980). Total length (TL, 0.1 mm) and body weight (W, 0.01 g) were measured for each individual. Sagittal otoliths were carefully extracted, cleaned from organic tissues, washed with distilled water and stored dry in plastic tubes.

Right otoliths were previously cleaned in an ultrasonic bath with ultrapure water (H_2O Milli-Q-Water: $> 18.2 \text{ M}\Omega\cdot\text{cm}$ at 25°C) for five minutes, followed by an immersion in 3% (v/v) of ultrapure hydrogen peroxide (H_2O_2 : Honeywell Fluka, TraceSELECTTM, $\geq 30.0\%$) for 15 minutes to remove biological residues, and thereafter superficially decontaminated in 1% (v/v) of nitric acid (HNO_3 : Honeywell Fluka, TraceSELECTTM, $\geq 69.0\%$) for 10 seconds (Rooker et al., 2001). Thereafter, otoliths suffered a triple immersion in ultrapure water (H_2O : Milli-Q-Water $> 18.2 \text{ M}\Omega\cdot\text{cm}$ at 25°C) for five minutes, were dry in a laminar flow cabinet hood and stored in decontaminated Falcon tubes (Patterson et al., 1999).

Figure 21: Sampling locations of *Isopisthus parvipinnis* juvenile individuals collected in 1975 (squares) and 2018/2019 (stars) in the South Brazil Bight from 23°S to 26.9°S , between São Paulo and Santa Catarina states

6.2.2 Otolith elemental analysis

Otoliths were weighted on an analytical balance (OM, 0.0001 g), dissolved for 15 min in $100 \mu\text{L}$ of ultrapure nitric acid (HNO_3 : Honeywell Fluka, TraceSELECTTM, $\geq 69.0\%$) and diluted with ultrapure water (H_2O : Milli-Q-Water $> 18.2 \text{ M}\Omega\cdot\text{cm}$ at 25°C) to a final volume of 5 mL (2% of HNO_3 v/v and 0.2% of TDS m/v) (Soeth et al., 2019).

Table 12: States, locations and their respective code, period of capture, sample size (n), total length (TL, mm) and otolith mass (OM, mg) of *Isopisthus parvipinnis* used in this study. For TL and OM, mean and standard deviation are presented. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, Santa Catarina – SC

States	Location	Code	Period	n	TL (mm)	OM (mg)
São Paulo	Ubatuba	NSP	Sep. and Nov. 1975	30	109±12	26.39±6.64
	Peruíbe	CSP	Sep. and Nov. 1975	30	108±14	27.89±8.14
	Cananéia	SSP	Sep. and Nov. 1975	30	109±14	28.97±8.67
Paraná	Paranaguá	PR	Sep. and Nov. 1975	30	109±14	30.06±9.22
São Paulo	Ubatuba	NSP	Nov. 2018	30	110±11	30.74±7.38
	Peruíbe	CSP	Nov. 2018	30	134±5	46.29±4.03
	Cananéia	SSP	Oct. 2018	30	113±7	32.95±4.95
Paraná	Paranaguá	PR	Sep. 2018	30	112±11	32.83±7.30

Multi-elemental analyses were performed by Solution-Based Inductively Coupled Plasma Mass Spectrometry (SB-ICP-MS) using an iCAPTM Q instrument (Thermo Fisher Scientific, Bremen, Germany) equipped with a concentric glass nebulizer, a Peltier-cooled baffled cyclonic spray chamber, a standard quartz torch and a two-cone interface design (sample and skimmer nickel cones). High-purity (99.9997%) argon (Gasin II, Leça da Palmeira, Portugal) was used as the nebulizer and plasma gas. The equipment control and data acquisition were made through the Qtegra software (Thermo Fisher Scientific). Indium (^{115}In), Scandium (^{45}Sc), Terbium (^{159}Tb) and Yttrium (^{89}Y) were monitored as internal standards to minimize the effect of plasma fluctuations or different nebulizer aspiration rates among samples (Moura et al., 2020). The limits of detection (LODs) were calculated as the concentration corresponding to three times the standard deviation of 10 sample blanks. However, calcium, sodium and strontium, because of their high concentrations in the aragonite matrix, were determined by Flame Atomic Absorption Spectrometry instrument (FAAS) instrument (Perkin Elmer, Überlingen, Germany). In order to avoid possible sequence effects, samples were analyzed randomly.

A preliminary analysis detected 20 trace elements, but the concentration of 8 of them (^{75}As , ^{111}Cd , ^{52}Cr , ^{98}Mo , ^{121}Sb , ^{82}Se , ^{205}Tl , ^{66}Zn) were consistently under the LODs, and therefore they are excluded from analyses. The remaining 12 trace elements (^{137}Ba , ^{43}Ca , ^{59}Co , ^{65}Cu , ^7Li , ^{26}Mg , ^{55}Mn , ^{23}Na , ^{60}Ni , ^{208}Pb , ^{85}Rb and ^{88}Sr), commonly

used for fish population assessment purposes (Campana et al., 2000; Moreira et al., 2018; Soeth et al., 2019), were identified as useful biogeochemical tags to *I. parvipinnis*. The SMR Fish Otolith (n. 22) from NIES (National Institute for Environmental Studies) was used for accuracy control, with recovery values between 83% and 90%. Precision of replicate analyses of individual elements was below 10%. Twelve elements were above the LOD: ^{137}Ba ($0.032 \mu\text{g.L}^{-1}$), ^{43}Ca ($2.384 \mu\text{g.L}^{-1}$), ^{59}Co ($0.001 \mu\text{g.L}^{-1}$), ^{65}Cu ($0.020 \mu\text{g.L}^{-1}$), ^7Li ($0.002 \mu\text{g.L}^{-1}$), ^{26}Mg ($0.268 \mu\text{g.L}^{-1}$), ^{55}Mn ($0.010 \mu\text{g.L}^{-1}$), ^{23}Na ($0.138 \mu\text{g.L}^{-1}$), ^{60}Ni ($0.016 \mu\text{g.L}^{-1}$), ^{208}Pb ($0.003 \mu\text{g.L}^{-1}$), ^{85}Rb ($0.005 \mu\text{g.L}^{-1}$), and ^{88}Sr ($0.006 \mu\text{g.L}^{-1}$). Concentrations of trace elements originally in $\mu\text{g.element.L}^{-1}$ solution were transformed to $\mu\text{g.element.g}^{-1}$ otolith, and finally to $\mu\text{g.element.g}^{-1}$ calcium (Higgins et al., 2013).

6.2.3 Statistical analysis

Prior to statistical analysis, data were checked for normality (Shapiro-Wilk's test), homoscedasticity (Levene's test) and the presence of outliers (Grubbs' test). The relationship between elemental concentration and fish size (expressed as otolith mass and used as covariate) was tested with Analysis of Covariance (ANCOVA). For all the element:Ca ratios that showed a negative (Ba:Ca, Li:Ca, Mg:Ca, Mn:Ca, Na:Ca, Pb:Ca, Sr:Ca) or positive (Co:Ca, Cu:Ca, Ni:Ca) relationship with OM (ANCOVA, $P < 0.05$), individual data was weight-detrended by subtraction of the common within-group linear slope (Campana et al., 2000). Differences in single elemental fingerprints among locations and years were explored by a Two-Way Analysis of Variance (Two-Way ANOVA), respectively, followed by a Tukey's *post-hoc* test if significant ($P < 0.05$). Differences in multi-elemental fingerprints among locations and years were tested using an overall and pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) based on the Euclidean distance measure using 9999 random permutations. A Canonical Analysis of Principal Coordinates (CAP) based on Euclidian distances was performed to visualize regional differences in each year. Variables which most contributed to each axis, based on the Pearson correlation ($r > 0.50$), were displayed in CAP two-dimensional plots. Reclas-

sification accuracy of the discriminant functions for each location were evaluated through the percentage of correctly re-classified individuals to the origin using a leave-one-out cross-validation (Hoff et al., 2020a).

All statistical analyses were performed using Past - Version 4.03 and PRIMER 7 + PERMANOVA software, with a statistical level of significance (α) of 0.05.

6.3 Results

Six element:Ca ratios (Ba:Ca, Cu:Ca, Li:Ca, Mg:Ca, Mn:Ca, and Sr:Ca) presented significant differences among locations, between years, and for the interaction between them; but Pb:Ca resulted only in significant differences among locations and years (Two-Way ANOVA, $P < 0.05$, Table 13). The other four element: ratios (Co:Ca, Na:Ca, Ni:Ca and Rb:Ca) did not presented any differences between years (Two-Way ANOVA, $P > 0.05$, Table 13), but differences among locations and locations x years were observed (Two-Way ANOVA, $P < 0.05$, Table 13).

Li:Ca and Sr:Ca detected significant differences between years in SSP, PR and SC; Ba:Ca and Mg:Ca were able to detected temporal differences for all locations, except SC and NSP respectively (Tukey's *post-hoc* test, $P > 0.05$; Fig. 22).

Regarding the year 1975, six element:Ca ratios distinguished all locations from SC. The former location presented the highest levels of Mg:Ca and Pb:Ca, and the lowest levels of Co:Ca, Cu:Ca, Na:Ca, and Ni:Ca; moreover, Li:Ca was significantly higher in NSP than other locations; Ba:Ca and Sr:Ca presented the same patterns, with higher values in SSP and PR; an slight increase in Rb:Ca southwards was observed; Mn:Ca did not showed any pattern (Tukey's *post-hoc* test, $P < 0.05$; Fig. 22). In 2018/2019, Ba:Ca, Mn:Ca and Rb:Ca presented values significantly higher in SC compared to other locations while Co:Ca and Ni:Ca presented the lowest values in the same region; Li:Ca was significantly higher in NSP, PR and SC; Mg:Ca was able to differentiate among locations, with a latitudinal increase in concentration from NSP to SC; Cu:Ca showed values significantly lower for NSP/SSP/PR than for CSP and SC; and Na:Ca presented significant differences between NSP, CSP and SSP/PR/SC; Pb:Ca was only detected in CSP and SC, with much

Table 13: Two-Way ANOVA comparisons among the five sampling locations regarding the chemical composition of *Isopisthus parvipinnis* otoliths collected in 1975 and 2018/2019. Statistically significant differences ($P < 0.05$) were marked in bold

	Ba:Ca					Co:Ca				
	DF	SS	MS	F	P	DF	SS	MS	F	P
Year	1	29477	29477	174.2	< 0.000	1	0.0205	0.0205	0.3514	0.5538
Location	4	17719	4429.7	26.18	< 0.000	4	29.862	7.4654	128.2	< 0.000
Interaction	4	14975	3743.7	22.13	< 0.000	4	2.8357	0.7089	12.18	< 0.000
Within	287	48560	169.2			287	16.706	0.0582		
Total	296	110568				296	49.435			

	Cu:Ca					Li:Ca				
	DF	SS	MS	F	P	DF	SS	MS	F	P
Year	1	6.8509	6.8509	45.08	< 0.000	1	0.2463	0.246	31.74	< 0.000
Location	4	4.2744	1.0686	7.032	< 0.000	4	0.3217	0.08	10.37	< 0.000
Interaction	4	24.288	6.072	39.96	< 0.000	4	0.151	0.038	4.865	< 0.000
Within	271	41.184	0.152			286	2.2191	0.008		
Total	280	77.142				295	2.942			

	Mg:Ca					Mn:Ca				
	DF	SS	MS	F	P	DF	SS	MS	F	P
Year	1	9181.7	9181.7	284.8	< 0.000	1	1851.8	1851.8	101.4	< 0.000
Location	4	9145.9	2286.5	70.91	< 0.000	4	2494.5	623.62	34.16	< 0.000
Interaction	4	5683.1	1420.8	44.06	< 0.000	4	1708.1	427.03	23.39	< 0.000
Within	287	9253.7	32.243			287	5239.6	18.256		
Total	296	33363				296	11323			

	Na:Ca					Ni:Ca				
	DF	SS	MS	F	P	DF	SS	MS	F	P
Year	1	2.58E+05	2.58E+05	1.463	0.2275	1	7.3276	7.3276	0.6257	0.4296
Location	4	6.40E+06	1.60E+06	9.087	< 0.000	4	3935.9	983.97	84.02	< 0.000
Interaction	4	6.60E+06	1.65E+06	9.377	< 0.000	4	241.86	60.465	5.163	< 0.000
Within	287	5.05E+07	1.76E+05			287	3361.3	11.712		
Total	296	6.38E+07				296	7548.7			

	Pb:Ca					Rb:Ca				
	DF	SS	MS	F	P	DF	SS	MS	F	P
Year	1	3.3757	3.3757	788.8	< 0.000	1	0.001	0.001	2.454	0.1183
Location	4	0.4424	0.1106	25.84	< 0.000	4	0.0298	0.0074	17.91	< 0.000
Interaction	4	0.037	0.0093	2.163	0.0732	4	0.006	0.0015	3.589	< 0.000
Within	287	1.2283	0.0043			287	0.1192	0.0004		
Total	296	5.0685				296	0.156			

	Sr:Ca									
	DF	SS	MS	F	P					
Year	1	7.18E+06	7.18E+06	53.85	< 0.000					
Location	4	1.97E+07	4.92E+06	36.89	< 0.000					
Interaction	4	3.37E+06	8.42E+05	6.316	< 0.000					
Within	287	3.83E+07	1.33E+05							
Total	296	6.86E+07								

lower values compared to 1975; and Sr:Ca presented the same pattern observed in 1975, with higher values in SSP and PR (Tukey's *post-hoc* test, $P < 0.05$; Fig. 22).

Regarding the multi-elemental fingerprints, the PERMANOVA analysis showed significant differences between years and among sampling locations, and also detected a significant interaction between both factors (overall PERMANOVA, $P < 0.05$; Table 14). Pairwise analysis showed significant differences among all locations for both years, except between SSP and PR, also for both years comparisons (pairwise PERMANOVA, $P > 0.05$, Table 14).

Regarding the historical samples, CAP showed some overlap between samples from SP and PR, but a clear distinction of SC samples (Fig. 23, 1975). Vector overlays indicated that group separation was primarily driven by Ni:Ca ($r = -0.94$), Co:Ca ($r = -0.93$) and Cu:Ca ($r = -0.54$) on CAP Axis 1, and by Sr:Ca ($r = -0.91$) and Ba:Ca ($r = -0.83$) on CAP Axis 2. The leave-one-out cross validation presented low overall reclassification success of 58%, highlighting SC samples which were all fully reallocated to the original location (100%) and NSP samples that reached 70% of correct reclassification, contrary to CSP and SSP (Table 15).

The overall reclassification success increased to 80% in 2018/2019, with reclassification percentages increased for all sampling locations, mainly in NSP (97%) and CSP (87%; Table 15). Again, samples from SC were all fully reclassified (100%), while SSP and PR samples were reallocated mainly between them. CAP results were similar again, with the three locations from São Paulo well distinguished, but with an overlap between SSP and PR samples (Fig. 23, 2018/2019). Vector overlays indicated that group separation was primarily driven by Mg:Ca ($r = -0.64$), Mn:Ca ($r = -0.71$), Rb:Ca (Pearson, $r = -0.66$), Cu:Ca (Pearson, $r = -0.68$), Ba:Ca (Pearson, $r = -0.82$), Ni:Ca ($r = 0.56$), Co:Ca (Pearson, $r = 0.59$), and Sr:Ca (Pearson, $r = 0.35$) on CAP Axis 1, and by Mg:Ca (Pearson, $r = 0.62$), Cu:Ca (Pearson, $r = -0.37$), Sr:Ca (Pearson, $r = 0.37$) on CAP Axis 2.

Figure 22: Element:Ca ratios in otoliths of *Isopisthus parvipinnis* collected in the South Brazil Bight in 1975 and 2018/2019. Locations sharing the same letter (year 1975) or number (year 2018/2019) do not show any statistical difference (Two-Way ANOVA, Tukey's *post-hoc* tests, $P > 0.05$). Significant time differences in each location are shown by an asterisk (*) (Two-Way ANOVA, Tukey's *post-hoc* tests, $P < 0.05$). Data are presented as mean values μ SE. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

Table 14: Overall and pairwise PERMANOVA comparisons among the five sampling locations regarding the chemical composition of *Isopisthus parvipinnis* otoliths collected in 1975 and 2018/2019. Significant statistical differences ($P < 0.05$) were marked in bold

Overall PERMANOVA						Pairwise PERMANOVA				
Source	SS	DF	MS	F	P	NSP	CSP	SSP	PR	SC
Year	9.99E+06	1	9.99E+06	30.1	0.0001	NSP		0.0152	0.0001	0.0001
Location	2.74E+07	4	6.86E+06	20.676	0.0001	CSP	0.0001		0.0001	0.0002
Interaction	8.23E+06	4	2.06E+06	6.1994	0.0001	SSP	0.0001	0.0002		0.9031
Residual	9.54E+07	287	3.32E+05			PR	0.0001	0.0001	0.9367	0.0001
Total	1.40E+08	296				SC	0.0005	0.0001	0.0001	0.0001
						2018/2019				

1975

Table 15: Jackknifed cross-validation reclassification matrices obtained from otolith's elemental composition of *Isopisthus parvipinnis* from all sampling locations for the years 1975 and 2018/2019. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, Santa Catarina – SC

1975						
Original location	Predicted location					% correct
	NSP	CSP	SSP	PR	SC	
NSP	21	7	0	2	0	70
CSP	12	9	5	4	0	30
SSP	0	7	13	10	0	43
PR	3	1	11	15	0	50
SC	0	0	0	0	29	100
Total						58

2018						
Original location	Predicted location					% correct
	NSP	CSP	SSP	PR	SC	
NSP	29	0	0	1	0	97
CSP	4	26	0	0	0	87
SSP	0	2	18	10	0	60
PR	1	2	10	17	0	57
SC	0	0	0	0	28	100
Total						80

Figure 23: Canonical analysis of principal coordinates (CAP) plots from otoliths chemical composition analysis of *Isopisthus parvipinnis* collected in the five sampling locations in the South Brazil Bight in 1975 and 2018/2019. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR, and Santa Catarina – SC

6.4 Discussion

The hereby otolith elemental composition of *I. parvipinnis* recorded significant regional and temporal variations. All single element:Ca ratios showed significant regional differences within years, but not necessarily for all locations. Regarding the multivariate analysis, the correct reallocation of individuals to the original locations was smaller in 1975 (overall 58%), compared to 2018/2019 (overall 80%), where an increment for the reclassification rates were observed for all locations. Moreover, SC samples reached a full reclassification success of 100% in both periods.

An otolith is a result of fish physiological dynamics and experiential history that mediate and influence the observed patterns incorporated into the structure itself, resulting in population-specific differences in otolith chemical composition, even in chemically homogeneous conditions (Sturrock et al., 2015; Walther, 2019). Taking into consideration the elemental signatures recorded in 1975, two population units were recorded: one including SP and PR states, but already suggesting an initial segregation between NSP/CSP and SSP/PR, and SC, a fully isolated population. Similar results were observed for the populations of other sciaenid species studied on the coastal zone of the South Brazil Bight during the 1970s and 1980s based on body and/or otolith shape (e.g. *Cynoscion jamaicensis*, Spach and Yamaguti (1989b,c); *Macrodon ancylodon*, Yamaguti (1979); *Micropogonias furnieri*, Vazzoler (1971); *Nebris microps*, Paiva Filho and Cergole (1988). However, at present (2018/2019), and 43 years later, four main population units, NSP, CSP, SSP/PR, and SC, were clearly depicted regarding *I. parvipinnis* population structure.

The study area, with about 700 km of coastline, covers a wide variety of aquatic ecosystems, under influence of different climatic and oceanographic features and anthropogenic activities (Biolo et al., 2019): NSP and SC are exposed to seasonal intrusions toward the coast by the cold oceanic South Atlantic Central Water (SACW), a water mass transported by the Brazil Current along the Brazilian continental slope (Mazzini and Barth, 2013; Castro, 2014); CSP is under coastal events and minor rivers influence; and SSP and PR are under influence of great estuarine ecosystems that have been suffered intense changes throughout time due to human activity (Mahiques et al., 2009; Marone

et al., 2005). These characteristics can lead to regional geochemical differences or similarities between fish populations (Elsdon et al., 2008; Soeth et al., 2019; Moura et al., 2020). Although some hydrographic processes remain over time, such as the SACW intrusions, the biotic integrity of SBB's coastal ecosystems is a challenge (Figueira et al., 2006; Mahiques et al., 2016; Garcia et al., 2019). Therefore, it would be challenging to pinpoint the causes behind the regional and temporal otolith chemistry variability recorded in the hereby study. The accumulation of minor and trace elements in fish otoliths depends on many factors, including their concentration and bioavailability in water, physiological processes, individual somatic growth, and the affinity of the calcium carbonate otolith for different metallic species (Geffen et al., 1998; Walther, 2019). The most significant element:Ca ratios in detecting differences among locations were Ba:Ca, Co:Ca, Cu:Ca, Ni:Ca, and Sr:Ca in 1975; while all elements presented significant results in 2018/2019.

Barium and strontium are said to be more effective elements representing the surrounding water composition since they may pass through Ca channels, replacing it directly, which results in higher abundances in otoliths (Walther, 2019). These elements usually present an opposite relationship with salinity (Ba:Ca: negative; Sr:Ca: positive) which could explain higher values of Ba:Ca in SSP and PR, but not the Sr:Ca patterns observed for both periods, which seems to be influenced by ontogenetic processes, such as growth and spawning (Avigliano et al., 2015; Sturrock et al., 2015; Hüseyin et al., 2020). Likewise, Na is also essential for cellular processes (e.g., Na, K – ATPase), with a high physiological response in its regulation, and the influence of environmental factors in the otolith absorption remains somewhat unclear (Campana et al., 2000; Hamer and Jenkins, 2007; Barnes and Gillanders, 2013), as well as its profile in our study area. Lithium incorporation into biogenic calcium carbonates involves little biological control, also replacing the Ca^{+2} site in the aragonite/calcite matrices directly (Marriott et al., 2004); thus Li:Ca, is tied to environmental influences, as salinity, temperature, upwelling conditions or primary productivity, rather than to otolith specificities (Hicks et al., 2010; Sturrock et al., 2015; Grammer et al., 2017; Pan et al., 2020). So, a possible explanation for higher Li:Ca values in NSP and SC could be related to the new primary production accompa-

nying upwelling events in these locations. The presence of cobalt and nickel, as well as zinc and iron, is primarily through their physiological roles as biomolecule co-factors, rather than as result of the environment (Thomas et al., 2017); anyway Co:Ca and Ni:Ca, were significant lower in both periods, namely in SC. Mg is not correlated with either temperature or salinity in marine fish otoliths (Sturrock et al., 2012), but it is negative correlated with metabolic processes and growth rate (Sturrock et al., 2015; Grammer et al., 2017); therefore, it is expected that changes in metabolic rates caused by environmental fluctuations (e.g., temperature and food resources variations) could cause alterations in elemental assimilation rates (Grammer et al., 2017). Studies are still contradictory about the relationship between Mn concentration and temperature, but there are evidences showing a positively relation to environmental concentrations and maternal transfer (Hüssy et al., 2020). Mg and Mn presented similar patterns, showing higher values in SC that could be related to the presumably younger individuals (regarding their size) analyzed from this state in 2018/2019. Rb:Ca usually presents a negative relationship with salinity that was not observed in *I. parvipinnis* data, possible due to interactions between Rb, salinity and physiological processes (e.g., ionic balance or osmoregulatory pathways), interchanging it with K^+ , that may render Rb more or less available for incorporation into the otolith (Evans, 2008, 2010; Hicks et al., 2010). Copper is involved in the activity of many essential enzymes and is required in oocyte formation in vertebrates (Sturrock et al., 2013); nevertheless, peaks of Cu and Pb coinciding with the most industrialized locations and under intense port activity – CSP and SC – could be an indicative of environmental contamination (Friedrich and Halden, 2010).

Unlike other chemical elements, such as Cu, Zn, Ni, Co, and Cr, which are essential in trace amounts but toxic in higher doses, Pb has no known nutritive function in fish, but it is toxic at low levels, interfering with essential nutrients of similar characteristics as Ca and Zn (Mager, 2011; Wood, 2011). However, lead is a trace metal less frequently investigated due to its analytical challenges for quantification (Walther, 2019). Higher Pb concentrations in 1975 could be a result of an intense occupation of the coast of the South Brazil Bight, beginning in the 1950s. Since that, it was observed many in-

interferences in the study area, such as sandy extraction from beaches and dunes, changes in rivers course, works of canalization, dredging, and sea walls, and contamination from different sources as port activity, industrial and domestic sewage discharge (Angulo et al., 2006; Klein et al., 2006; Tessler et al., 2006; Azevedo et al., 2009; Araújo et al., 2018). Associated with the establishment of new environmental policies in the 1980s (Moura, 2016), which led to better conservation conditions and surveillance, these changes could be reflected in Pb behavior in *I. parvipinnis* otoliths. Those temporal variations in Pb concentration were also registered in sediment cores: a reduction in SSP and PR from the 1970s to 2000-2010s (Mahiques et al., 2013; Conrad and Sanders, 2017) in contrast to an increase in CSP (Jesus et al., 2020). Literature also shows anthropogenic impacts of oil exposure, industrial, gasoline, sewage and agriculture input not only in Pb concentration in otoliths, but also in Ba, Mg, Mn, Na, Sr, and Zn ones (Spencer et al., 2000; Geffen et al., 2003; Morales-Nin et al., 2007; López-Duarte et al., 2016; Vrdoljak et al., 2020).

Anthropogenic climate changes have been addressed to affect the marine biodiversity, ecosystems, fisheries, and ecosystem services, mainly after the 1950s (Barnett et al., 2001; Pörtner, 2008; IPCC, 2019). Literature has already reported evidences of an increase in sea surface temperature in South Atlantic Ocean mainly after the 1980s (Lumpkin and Garzoli, 2011; Araújo et al., 2018) and its consequences in the ichthyofauna of a transitional zone between the tropical and subtropical regions in Southeastern Brazil (Araújo et al., 2018). Changes in temperature, oxygen depletion and other ocean biogeochemical properties (e.g., pH or pCO₂), influence fish life cycles and their distribution, abundance and composition of fish communities, since there is a direct relationship between ocean conditions and the ecophysiology of marine organisms (Cheung et al., 2013; Koenigstein et al., 2016; Kuczynski et al., 2017). Once physiological processes (e.g., ion transport, homeostasis, osmoregulation, growth or gonad development) can modify blood and otolith composition, and are often distressed by those environmental changes, such that otolith size and chemistry respond both directly and indirectly to anthropogenic climate changes (Heuer and Grosell, 2014; Sturrock et al., 2015; Walther, 2019).

The analysis of multi-elemental chemical signatures fully discriminated SC samples (100% of reclassification success), indicating a distinct population unit in both periods. The coastal zone of the Santa Catarina state, the southernmost region of our study area, is under influence of important oceanographic processes: wind-driven South Atlantic Central Water intrusions towards the coast take place in a large portion of the shelf, nearly 28.5°S (Castro et al., 2006); and the cold (14° – 17°C) and less salty (33.0 – 34.0) water transported by the Brazil Coastal Current, consisted of waters from the Argentina continental shelf, near the Río de la Plata mouth, and the Brazil-Malvinas Confluence (Campos et al., 1996, 1999; Souza and Robinson, 2004). As a consequence, SC waters are nutrient enriched, being classified as mesotrophic or even reach eutrophic conditions during some periods of the year, which increases new regional production (Simonassi et al., 2010) and possibly affects Li:Ca ratios, as described previously.

Alternative research methods can provide different scenarios about the population structure of marine fishes. A holistic approach is recommended when we deal with species and/or areas whose characteristics are not fully understood. An improvement in the reclassification rates has been observed when using otolith elemental signatures compared to otolith shape for several species (Moreira et al., 2018, 2019; Soeth et al., 2019). Regarding *I. parvipinnis*, those rates slightly increased from whole-body morphometry (79%; Hoff et al. (2020b)) to otoliths shape (42% in 1975, and 81% in 2018/2019; Hoff et al. (2020a)), and, finally, to otolith chemical composition (58% in 1975, and 80% in 2018/2019; present study). Compared with the previous data from otolith shape (Hoff et al., 2020a), the present study allowed to detect significant differences between SC and other locations in both periods, clearly detached as an isolated population unit for both periods, and increased the regional cross-validation reclassification success.

In conclusion, this multi-elemental otolith approach showed regional differences between *I. parvipinnis* individuals indicating the presence of distinct population units that underwent significant temporal and latitudinal changes. Moreover, a limited connectivity of SC population with the units located northwards and the decrease in the degree of adult populations mixing along the SBB over time was also recorded. The hereby results

also have important implications for the management of coastal ecosystems, essential for fisheries maintenance, as the noticeable anthropogenic interferences in fish population structure and the possible extension of this study to other fishery resources of higher economic value.

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7 General discussion

Isopisthus parvipinnis is a demerso-pelagic Sciaenidae and a structurer of coastal ecosystems and of trophic framework of the demersal ichthyofauna, inhabiting Central and South Americas, from 11°N to 33°S. Although this work involves the southern area of distribution of the species, it was possible to verify that the population structure of *I. parvipinnis* underwent temporal changes, in the order of 40 years, and spatial changes in this southern area.

A comparison among reclassification success values from each method (SIs + EFDs, body morphometry, otolith microchemistry) applied in the study of the *Isopisthus parvipinnis* population structure is presented in Figure 24. An improvement in overall reclassification was observed from otolith shape (42%) to otolith microchemistry (55%) in 1975; and from body shape analysis (79%) to otolith shape (81%), which was equal to otolith microchemistry, in 2018/2019. The location Center of São Paulo (CSP) was best discriminated by otolith shape in 1975 while the South of São Paulo (SSP) and Paraná (PR) were best differentiated by otolith microchemistry and body shape in contemporaneous samples.

The results of the analysis of morphological aspects of the otoliths and body, and otoliths microchemistry used to evaluate population structure of *I. parvipinnis* provided a similar overall scenario, although with slight differences. Data from 1975 suggested the existence of a panmictic population for otolith shape analysis or two (SP/PR, SC) population units for otolith microchemistry. On the other hand, for 2018/2019, body morphometric analyses discriminated five population units, not necessarily homogeneous, whereas otolith shape and chemical composition distinguished four population units: NSP, CSP, SSP/PR, and SC.

Studies on body morphometry are generally conducted in fish species which present a stiffer body due to their better swimmer or migratory abilities, as *Atherinops affinis* (O'Reilly and Horn, 2004), *Trachurus japonicus* (Kanaji et al., 2010), and *Diplodus vulgaris* (Kaouèche et al., 2013). It is possible that even taking care in obtaining the morphological data and thus using correct information, *I. parvipinnis* body geomet-

Figure 24: The cross-validation reclassification analysis of the *Isopisthus parvipinnis* population structure correctly allocated (%) to their respective collection location in each year based in all methods used in this work: body morphometry (red), otolith shape (yellow), and otolith elemental composition (blue). The proportional population unit composition is indicated by the gradient colors in each pie chart. Legend: North of São Paulo – NSP, Center of São Paulo – CSP, South of São Paulo – SSP, Paraná – PR

ric analysis may have been biased by its soft body, especially the elasticity of the body wall in the abdominal cavity region. Meristic characteristics could improve this research, as observed in other Sciaenid species studies (Paiva Filho and Cergole, 1988; Spach and Yamaguti, 1989a; Galli and Norbis, 2013). Still, the form of body relative growth of the species could present another source of variation, despite the limitation of a range of specimen lengths for analysis.

Different and complementary approaches have been successfully used to assess the population structure of several fish species, providing an holistic approach for the species knowledge and management, as observed for *Trachurus picturus* (Moreira et al., 2017, 2019; Vasconcelos et al., 2018) and *Chelidonichthys lucerna* (Ferreira et al., 2019) in the NE Atlantic Ocean; *Chaetodipterus faber* and *Cynoscion guatucupa* in SW Atlantic Ocean (Sabadin et al., 2010; Soeth et al., 2019); *Argyrosomus japonicus* in southern Australia (Ferguson et al., 2011); *T. japonicus* in NW Pacific Ocean (Kanaji et al., 2010). Distinct methods can result in different responses, but their combination allows to obtain more robust information on fish stock structure (Biole et al., 2019).

The techniques employed hereby provided a phenotypic marker representative of the entire life-history of fish prior to capture. However, they are not enough to explain where or when the development of such phenotypic distinction among locations occurred (Moreira et al., 2019; Soeth et al., 2019). Therefore, a better understanding of *I. parvipinnis* movement patterns and spawning components in the South Brazilian Bight would be achieved using similar techniques of finer temporal resolution, as the laser ablation ICP-MS applied to otolith elemental composition.

Regarding the management consequences, despite some signs of improvement in the management of some fisheries in the developed world (Pitcher and Cheung, 2013), it is known that fisheries management has often been ineffective as a result of models focused on the maximization of single target species captures, ignoring important factors such as habitat, predators, prey of the target species and other ecosystem components and interactions (King and McFarlane, 2003; Pikitch et al., 2004). In recent years, a growing concern over issues, as bycatch species, impacts of gear on habitat and the impacts of cli-

mate changes on the natural regulation of populations, has led agencies to develop more holistic approaches to the assessment and management of the marine resources (King and McFarlane, 2003). Hence, an ecosystem-based fishery management approach was proposed as an attempt to implement management practices focused on sustain healthy marine ecosystems and the fisheries, they support rather than a particular species, which include target and non-target species (Pikitch et al., 2004). Nevertheless, it was observed a widespread failure among countries adopting the key features of this concept (Pitcher and Cheung, 2013). On the other hand, as an important element of the shrimp bycatch, *I. parvipinnis* is not a direct target for management. Few situations are reported for the southwest Atlantic region where regulation of a target species also benefits the main bycatch species (Souza and Chaves, 2007; Pina and Chaves, 2009), a clear knowledge gap.

The species studied plays an important role in the trophic structure of ecosystems (Santos et al., 2002; Soares et al., 2008; Miotto et al., 2017), besides being commonly captured as bycatch by shrimp fishery trawl in the Brazilian southeastern and southern coast (Graça Lopes et al., 2002; Branco and Verani, 2006; Santos et al., 2006; Spier et al., 2018). The species have little importance as a fishery resource, but participate in the annual Brazilian fishery production (MPA, 2011). A diagnosis of the specific causes for the new population structure found in the southern area of the species distribution could not be made, but some could be listed and discussed. Therefore, the population aspects of *I. parvipinnis* studied here are essential for understanding the life-strategies of these species, and hence develop effective ecosystem management measures.

8 Conclusions

The conclusions of this study can be looked at three different points of view, regarding (1) the hypotheses established at the beginning of this study, (2) the methods applied to the evaluation of the *Isopisthus parvipinnis* population structure, and (3) the suggestions for future studies.

1.Regarding the hypotheses:

The first hypothesis, that *Isopisthus parvipinnis* presents different phenotypic population units in the Southwest Atlantic Ocean, was confirmed once all approaches detected the existence of at least three population units in 2018/2019.

The second hypothesis, about the temporal and spatial maintenance of *Isopisthus parvipinnis* population structure from 1975 to 2018/2019, was refuted since otolith shape and elemental composition provided information about the existence of a single panmictic population in 1975 and three or four population units in 2018/2019: one in the North of São Paulo, a second population unit in the Center of São Paulo, a third one grouping the estuary influence zones in the South of São Paulo and Paraná, and a fourth unit at Santa Catarina state, the latter being distinct only evaluated only in shape analysis.

The last hypothesis, about the capability of natural tags in distinguishing phenotypic population units of *Isopisthus parvipinnis*, was also confirmed since the three natural tags tested in this work (body morphometry, otolith shape and elemental composition) were able to detect phenotypic differences among the coastal areas of the three Brazilian states and five locations, even presenting different results.

2.Regarding the methods:

The population structure of *Isopisthus parvipinnis* was assessed by three different approaches – body morphometry, otolith shape, and otolith chemical composition –, which responded to latitudinal and temporal variations.

It can be said that there is a hierarchy of the tools used in this study to the assessment of population structure of *I. parvipinnis*. While body morphology suffers

general influences from the environment and, particularly some variation of expansion and retraction of the abdominal region, due to its sagging, the morphometry and shape of the otoliths use a structure that is conserved and inert, despite the reproductive processes and the diet. More accurately, otolith microchemistry was complementary and best responded to the observed variations.

3.Regarding the future studies:

Since the use of body morphometry, otolith shape, and otolith elemental composition were successful in the analyses of the *Isopisthus parvipinnis* population structure in the SW Atlantic Ocean, some suggestions for future studies could be made, such as:

[3.1] Incorporate data from meristic characters and condition factor in body geometric morphometrics analysis;

[3.2] Study the existence of otolith's shape differences among individuals of *Isopisthus parvipinnis* related to sex, maturity stages, body and otolith weight relationship, and between adults and young;

[3.3] Expand this study through the all distribution area of *Isopisthus parvipinnis*;

[3.4] Finally, this work encourages the use of biological collections once they can provide valuable information on long-term studies.

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