Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Research Article

Inferring ecological connectivity between populations of *Opsanus beta* (Goode & Bean, 1880) from the southern Gulf of Mexico and the South-western Atlantic coast

Barbara Maichak de Carvalho[1], José Antônio Martínez Pérez[2], Alfonso Aguilar-Perera[3], Virginia Noh Quiñones[3], Acácio Ribeiro Gomes Tomás[4], Jean Vitule[1] and Alejandra Volpedo[5]

[1]Programa de Pós-Graduação em Engenharia Ambiental, Departamento de Engenharia – UFPR, Laboratório de Ecologia e Conservação (LEC), Brazil; [2]Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Laboratorio de Zoología (L 221); [3]Departamento de Biología Marina Facultad de Medicina Veterinaria y Zootecnia Universidad Autónoma de Yucatán, México; [4]Laboratório de Estudos Estuarinos, Centro do Pescado Marinho, Instituto de Pesca, APTA-SAA, Santos, SP, Brazil and [5]CONICET-Universidad de Buenos Aires, Instituto de Investigaciones en Producción Animal (INPA)/Centro de Estudios Transdisciplinarios del Agua (CETA) Facultad de Ciencias Veterinarias Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina

Cite this article: Carvalho BM, Pérez JAM, Aguilar-Perera A, Noh Quiñones V, Tomás ARG, Vitule J, Volpedo A (2022). Inferring ecological connectivity between populations of *Opsanus beta* (Goode & Bean, 1880) from the southern Gulf of Mexico and the South-western Atlantic coast. *Journal of the Marine Biological Association of the United Kingdom* **102**, 597–603. https://doi.org/10.1017/S0025315422000935

Received: 17 May 2022
Revised: 26 September 2022
Accepted: 11 October 2022
First published online: 1 December 2022

Key words:
Ballast water; Batrachoididae; bioinvasion; estuaries; Gulf of Mexico; shape

Author for correspondence:
Barbara Maichak de Carvalho,
E-mail: bmaicarvalho@gmail.com

Abstract

Otoliths are an excellent tool in studies on ecological connectivity of fish species populations. *Opsanus beta* is an invasive species introduced on the Brazilian coast, but not native from the Gulf of Mexico. The present study aimed to compare the otolith contours of specimens collected in Mexico (Celestún, CEL) and in two Brazilian estuaries (Santos Bay, STB, and Paranaguá Estuarine Complex, PEC). In the laboratory, 99 otoliths were extracted, photographed and compared using wavelet analysis. The otolith contours varied between sites (39 from CEL, 26 from STB and 34 from PEC). The linear discriminant analysis correctly reclassified 87.9% of otoliths by sites, with the best reclassifications in the CEL (97.36%), followed by PEC (88.23%) and SBT (73.07%). MANOVA showed significant differences in otolith contours between sites ($F = 5.37$; $P < 0.005$). The otolith contour from CEL was significantly different from those from the PEC and SBT. However, the otolith contour of the two Brazilian estuaries did not significantly differ among them (MANOVA, $P > 0.005$). Our results indicate *O. beta* populations on the Brazilian coast are connected, and probably isolated from the Mexican population.

Introduction

In teleost fish, otoliths are calcium carbonate structures, mainly formed by aragonite, which are located in the inner ear and comprise three pairs called sagittae, asteriscus and lapillus. These structures, which belong to the sensory and balance system (Schulz-Mirbach *et al.*, 2019), are inert, i.e. after deposition there is no resorption of otoliths. Due to this characteristic, otoliths are excellent tools for ichthyological studies as they preserve information of fish's life history (Popper *et al.*, 2011). Otolith morphology can be influenced by environmental factors and by gene flow processes occurring during fish migrations (Vignon & Morat, 2010; Cerna *et al.*, 2019). Through trace elements deposited in otoliths, it is possible to identify patterns of habitat use of fish species. Recent studies have applied this latter technique to exotic (non-native) fish species for their management and prevention of dispersal in recently colonized environments (Morissette & Whitledge, 2022).

Exotic species occur in an area far from their natural limits of distribution (Blackburn *et al.*, 2019; Vitule *et al.*, 2019). Colonization of new environments depends on the ability these species have to adapt to new environmental forces, production of fertile offspring and dispersal of recruits in the new environment (Richardson *et al.*, 2000; Wonham *et al.*, 2000; Olenin *et al.*, 2017). Species introductions occur by accident, but various human activities are pathways, or vectors, for many introductions (Castro *et al.*, 2016; Ojaveer *et al.*, 2018). Translocation of oil platforms is one of these activities, when companies displace their platforms from one place to another without removing the biofouling, and their translocation can disperse various species, which have reduced migratory capacity. Another route of introduction is ballast water, which disperses species along maritime routes of commercial ships, causing habitat homogenization and environmental imbalance (Boltovskoy & Correa, 2015; Dimitriou *et al.*, 2019; Watkins *et al.*, 2021). Aquaculture also favours species introduction by accidental escapes (Encarnação *et al.*, 2021). The number of registered exotic species has increased in the marine environment (Tempesti *et al.*, 2020; Encarnação *et al.*, 2021). The same pattern of increase in introduced species has also been documented in the South-western Atlantic, and along the Brazilian coast (Schmidt *et al.*, 2020). Together, these species, such as *Omobranchus punctatus* and *Opsanus beta*, have expanded their geographic distribution in recently colonized areas

(Caires *et al.*, 2007; Lasso-Alcalá *et al.*, 2011; Tomás *et al.*, 2012; Contente *et al.*, 2015; Carvalho *et al.*, 2020).

Opsanus beta (Goode & Bean, 1880) (family Batrachoididae) is a native and endemic fish of the Gulf of Mexico (Collette, 2002), common in estuaries and intertidal regions of the shallow inner shelf (Greenfield *et al.*, 2008). It is cryptic, territorial, sedentary and performs short migrations (Collette, 2002; Greenfield *et al.*, 2008). It is an opportunistic and generalist species feeding on molluscs, crustaceans, fish (Franco-Lopez *et al.*, 2017), and presents a short life cycle reaching up to 6 years of age in its natural distribution area (Malca *et al.*, 2009). It has parental care, with females laying adherent eggs in the substrate. The males fertilize the eggs, and after hatching, they protect the juveniles in their mouths (Gallardo-Torres *et al.*, 2004).

Opsanus beta was first recorded on the Brazilian coast in the Paranaguá Estuarine Complex (PEC) (Caires *et al.*, 2007) and Santos Bay (STB) (Tómas *et al.*, 2012). Recent studies have recorded *O. beta* in Guanabara, Sepetiba, Guaratuba and Laguna bays (Carvalho *et al.*, 2020, 2022; Cordeiro *et al.*, 2020; Almeida-Tubino *et al.*, 2021, respectively). Ballast water and/or an association with an oil platform are the most plausible vectors, which have introduced *Opsanus beta* in the Brazilian coast. This study aimed to compare the shape contours in otoliths of *O. beta* from the Brazilian coast and from the southern Gulf of Mexico as a basis for future studies on their stock and management in recently colonized regions.

Materials and methods

Study area

Fishers speared *O. beta* specimens in areas adjacent to the Celestún Lagoon (CEL), on the northern coast of the Yucatan Peninsula, Mexico (Figure 1), and in two estuaries on the south-eastern-south Brazilian coast (Figure 2). CEL is a tropical estuary ~22 km long and 2 km wide, with an average depth of 1.5 m and connected to the Gulf of Mexico by a narrow channel ~460 m wide (Figure 1). The salinity inside the lagoon varies between 3.1 and 37.4 with the diurnal tide (Gutiérrez-Mendieta & Lanza Espino, 2019).

On the Brazilian coast, specimens were collected in Santos Bay (STB – 23°59′06″S 46°18′42″W, Figure 2A), located about 80 km from São Paulo, with a representative portion of the coast dominated by mangroves. Humid weather and water temperature range between 20–30 °C, and salinity ranges from 20–35 (Porcaro *et al.*, 2014). The Paranaguá Estuarine Complex (PEC – 25°26′43″S 48° 39′58″W, Figure 2B), with an area of ~551.8 km^2, is a subtropical environment composed of mangroves, marshes and shallows, salinity and temperature vary seasonally from 0–32 and from 18–30 °C, respectively (Lana *et al.*, 2001; Mizerkowski *et al.*, 2012). In PEC, the specimens were captured with traps and in STB with hook and line fishing.

Sample processing

After sampling, fish specimens were taxonomically identified, measured in total length (TL, in centimetres, from the snout to the margin of the tail) with a scaled table and weighed in total weight (TW, in grams) with an electronic scale. The sagittae otoliths were extracted from each fish, cleaned, packed dry, and numbered according to geographic location.

Otolith contour analysis

Each otolith was photographed, and from the images obtained otoliths were measured in length (OL, in mm) and height (OH, in mm). The wavelet function was used to define the otolith contour (Parisi-Baradad *et al.*, 2010; Sadighzadeh *et al.*, 2014) (Figure 3B). The 'wavelets' are the result of the expansion of a signal in a family of functions representing the expansions and translations of a mother function, this being: $\Psi s(x) = 1/s\Psi(\varphi/s)$, where Ψ function with local support in a limited amplitude on the abscissa axis; φ lower step filter; s scale parameter (Mallat,

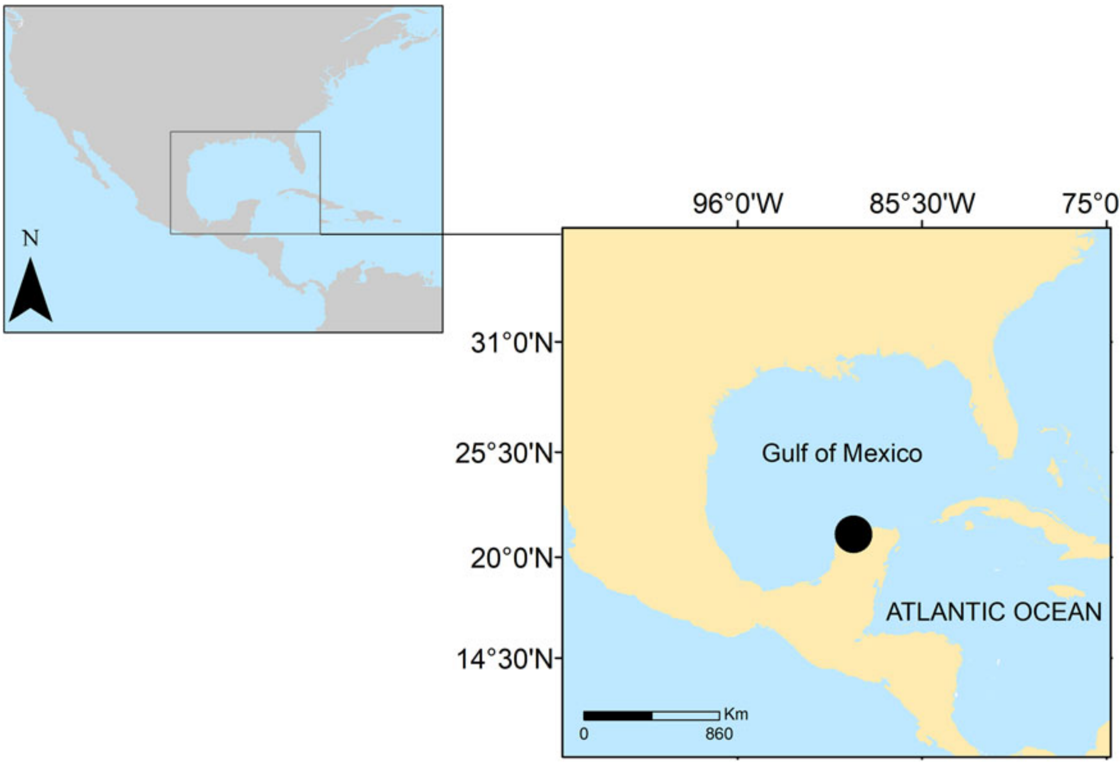

Fig. 1. Sampling site of *Opsanus beta* in Laguna de Meléstun, northern coast of the Yucatan Peninsula, Mexico, in the Gulf of Mexico (black circle).

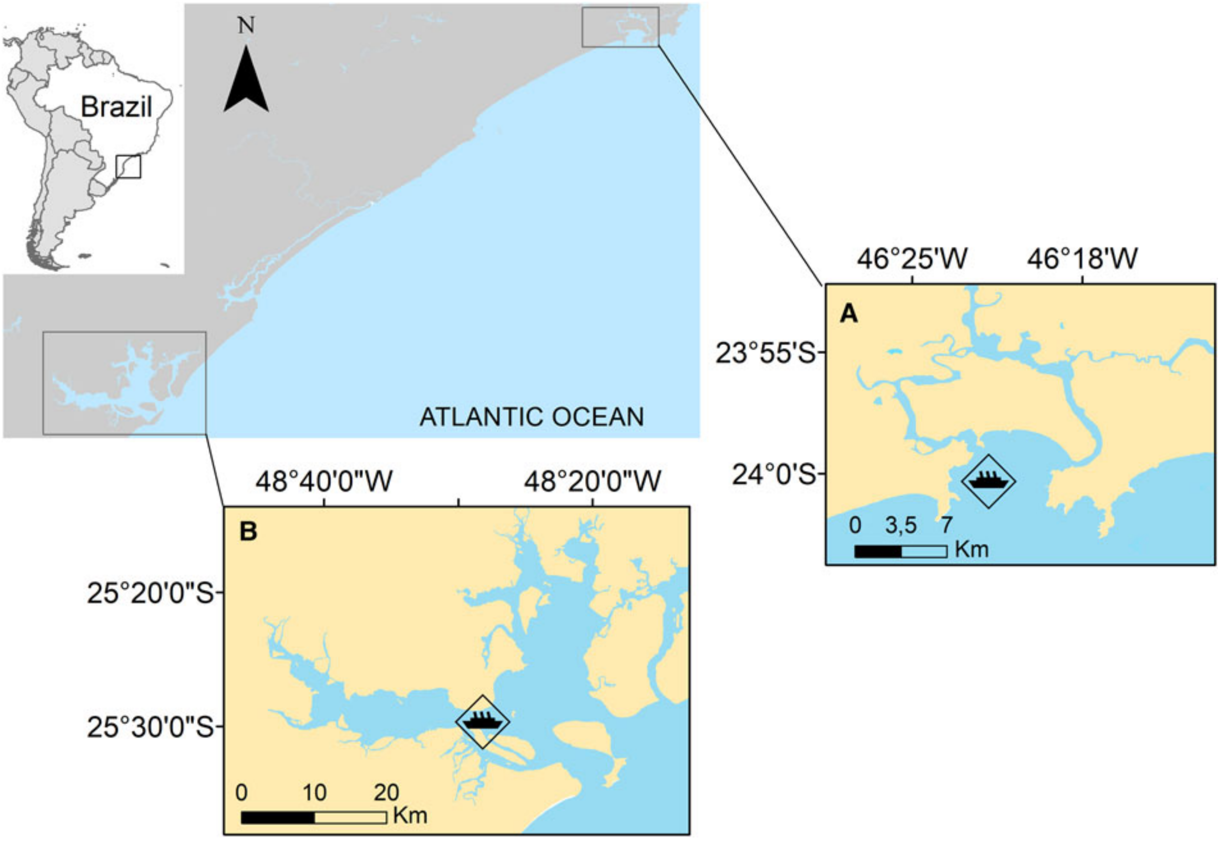

Fig. 2. Sampling sites of *Opsanus beta* in Brazil. (A) Santos Bay (23°59′06″S 46°18′42″W) and (B) Paranaguá Estuarine Complex (25°26′43″S 48°39′58″W). The ship represents port activity in the region.

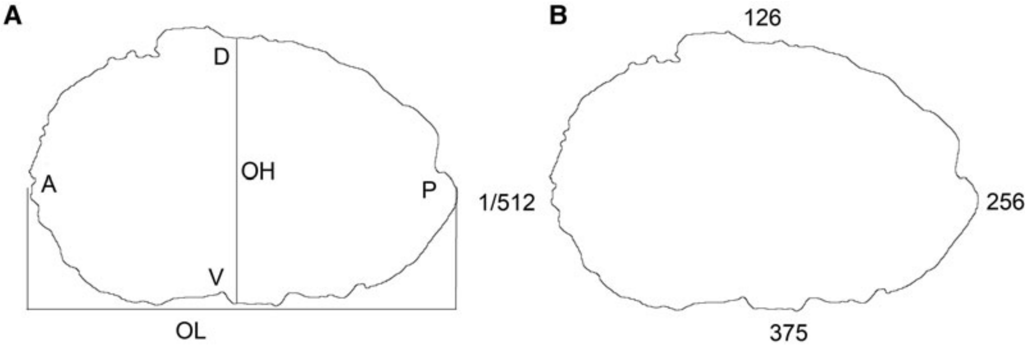

Fig. 3. (A) Otolith sagitta of *Opsanus beta*. A, anterior; D, dorsal; P, posterior; V, ventral region of the otoliths; OL, otolith length; OH, otolith height. (B) Otolith contour using 512 equidistant points.

1991). The wavelet analysis allows for measurement of similar points on the otolith (Lombarte & Tuset, 2015). A total of 512 points, with equidistant coordinates from each otolith, were extracted with the rostrum as the contour origin (Parisi-Baradad *et al*., 2010). The fourth and fifth wavelet are more appropriate for identifying stocks or populations (Sadighzadeh *et al*., 2014; Abaad *et al*., 2015). Image processing was performed using AFORO (http://isis.cmima.csic.es/aforo/).

Principal component analysis (PCA), based on the variance-covariance matrix, was applied to reduce wavelet functions without losing information (Tuset *et al*., 2015, 2016). Principal components (PCs) that explain data variability were selected by the Broken–Stick method (Gauldie & Crampton, 2002). Subsequently, the effect of fish size allometry was removed using the residual of the linear regression between the significant principal components and the otolith length. From these, a new PCA was run (Stransky & MacLellan, 2005) to check for variations in the otolith contour for each site: Celestún, STB and PEC. A Linear Discriminant Analysis (LDA) was applied between sites to verify the correct percentage of otolith reclassification. A multivariate analysis of variance (MANOVA) was performed, with the length and height of otoliths and the PC without the effect of allometry, to check for differences in the shape of otoliths collected in CEL, STB and PEC. All statistical analyses were performed using the Past program.

Results

Ninety-nine otoliths of *O. beta* from CEL, STB and PEC were analysed (Table 1). The reconstruction of the otolith contour

Table 1. Mean and standard deviation of fish total length (TL, cm), otolith length (OL, mm) and otolith height (OH, mm) of *Opsanus beta* by site and 'N' number of specimens

Site	N	LT	OL	OH
CEL	39	26.41 ± 1.87	7.87 ± 0.64	5.06 ± 0.59
STB	26	20.82 ± 3.02	6.93 ± 0.90	3.97 ± 0.62
PEC	34	21.34 ± 3.20	7.25 ± 1.25	4.02 ± 0.69

CEL, Celestun; STB, Santos Bay; PEC, Paranaguá Estuarine Complex.

using wavelets 4 and 5 showed high variability in the contour of the three analysed sites. This variability was observed in the dorsal, ventral and posterior regions (Figure 4).

PCA showed high variability in the otolith shape (Figure 5), with PC1 explaining 90.09% and PC2 explaining 5.78% in otolith shape variability. Along PC1 are distributed more elongated otoliths, with irregular margins, and straight posterior region, and on PC2 are distributed more rounded otoliths, with crenulated and irregular margins and sharp posterior region. Otoliths of *O. beta* from Brazil were more distributed along PC1, while those from the Mexican coast along PC2 (Figure 5).

The LDA showed 87.88% correct reclassification of otoliths among sites. CEL showed the highest reclassification percentage (97.36%), followed by PEC (88.23%) and SBT (73.07%) reclassification (Table 2). MANOVA evidenced a significant difference in otolith shape between sites ($F = 5.37$; $P < 0.005$). Otolith shape of CEL was significantly different from those from STB and PEC ($P < 0.005$). However, the otolith

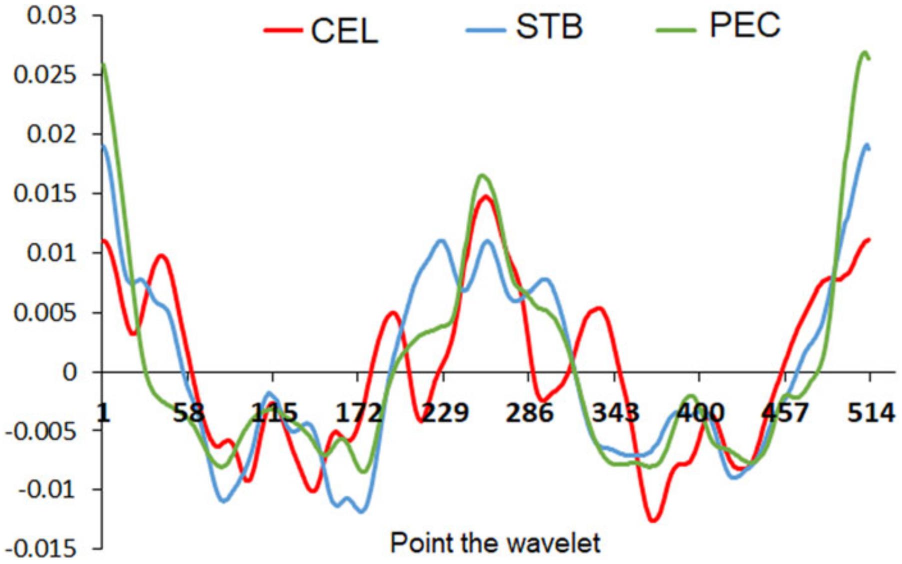

Fig. 4. Contour decomposition of the otolith sagitta of *Opsanus beta* collected in Celestun – Mexico, Santos Bay (STB) and Paranaguá Estuarine Complex (PEC) – Brazil.

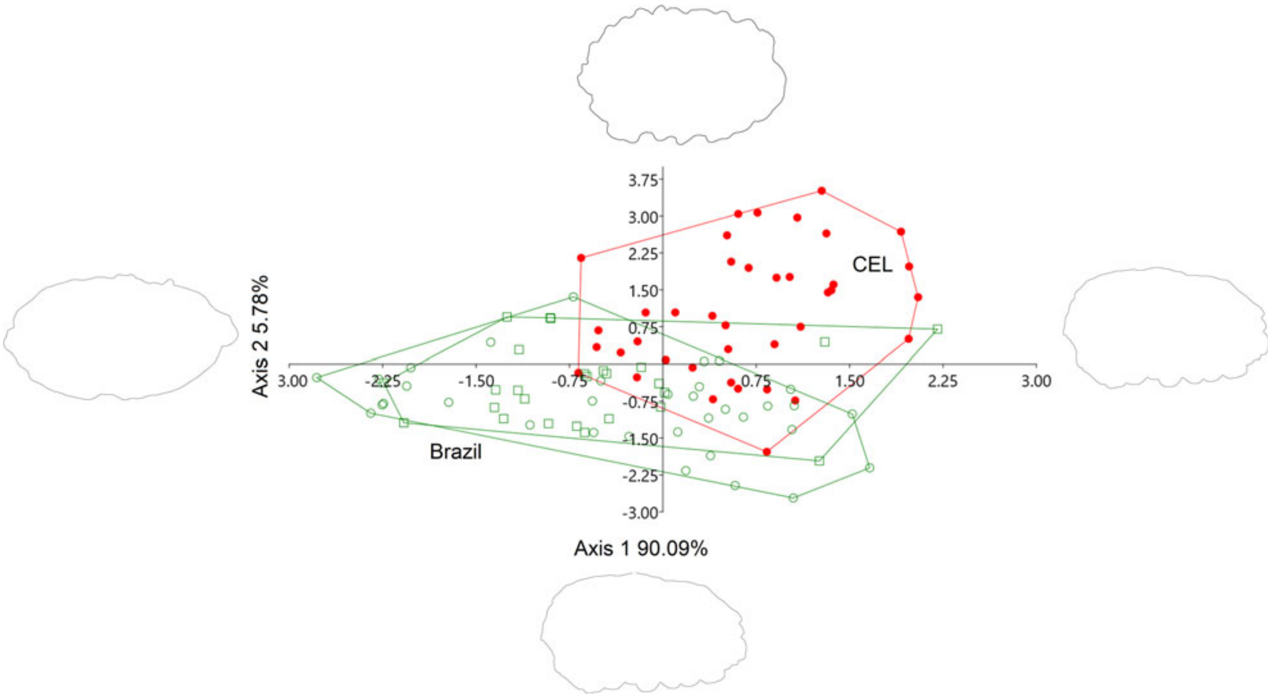

Fig. 5. Principal component analysis (PCA) scatterplot for the otolith contour of *Opsanus beta* from Mexico (CEL – red circle) and Brazil (STB – open square; PEC – open circle). The contours of the most frequent otoliths in each axis of the PCA.

Table 2. Reclassification of the otolith sagitta of *Opsanus beta* between Celéstun Lagoon (CEL, Mexico), Santos Bay (SBT, Brazil) and Paranaguá Estuarine Complex (PEC, Brazil) by the linear discriminant analysis (LDA)

Sites	CEL	STB	PEC	Total
CEL	38 (97.36%)	0	1 (2.63%)	39
STB	1 (3.84%)	19 (73.07%)	6 (23.07%)	26
PEC	1 (2.94%)	3 (8.82%)	30 (88.23%)	34
Total	40	22	37	99

shape of STB and PEC did not differ significantly among them ($P > 0.005$).

Discussion

Our results showed that shape otolith contours of *O. beta* differed between the populations from Mexico and Brazil. Populations exposed to different environmental parameters have a differentiated otolith shape, as observed for *O. beta* and other estuarine and marine species (Capoccioni *et al.*, 2011; Hoff *et al.*, 2020; Maciel *et al.*, 2021). The population of *O. beta* on the Mexican coast lives in a tropical, eutrophic environment, with diurnal tidal variations, and with three well-defined seasons (dry, rainy and windy). Meanwhile, the Brazilian populations of *O. beta* are located within subtropical estuaries, with very similar rainfall, photoperiods and dominated by semidiurnal tides, which differ greatly from the environmental forces in the Mexican estuary (Spalding *et al.*, 2007; Gutiérrez-Mendieta & Lanza Espino, 2019).

Along with the environmental influence, the ecological fish connectivity of populations influences the otolith shape, in which connected populations have similar otolith shape (Ibañez *et al.*, 2017; Soeth *et al.*, 2019). This latter suggests that populations of *O. beta* on the Mexican coast and those established on the Brazilian coast are not connected. In this context of ecological connectivity, a plausible reason of *O. beta* introduction in Brazil is the soybean industry. The soybean is the third most exported product through marine vessels from Brazil to Mexico and the USA, the native region of *O. beta*. This transport consequently would facilitate the constant pressure of propagules coming through the ballast water on the soybean cargo ships at the Brazilian ports. If there was an introduction of *O. beta* on the Brazilian coast from Mexico, these specimens could not establish properly due to potential competition with the already established *O. beta* population, showing no connectivity between the Brazilian and Mexican populations. However, based on our results, it is not possible to know if the population of *O. beta* actually comes from Mexico's population.

The similarity between *O. beta* otoliths from the PEC and STB suggests two hypotheses. First, the Brazilian *O. beta* populations probably have a common origin. Second, Brazilian *O. beta* populations are either well connected or are subjected to very similar environmental conditions. PEC and STB showed very similar salinity, water and air temperature, geological formations, vegetation and photoperiod. These latter parameters exert similar forces on *O. beta* populations, which could be reflected in the shape of their otoliths (Lessa *et al.*, 2018).

Migration between populations could also make the shape of otoliths very similar, as observed in other estuarine and marine fish species (Ibañez *et al.*, 2017; Soeth *et al.*, 2019; Kikuchi *et al.*, 2021). However, *O. beta* is a cryptic, territorial species, with a strong parental care and no larval dispersal (Collette, 2002; Gallardo-Torres *et al.*, 2004; Greenfield *et al.*, 2008). These latter life history characteristics raise questions about the occurrence of migrations and natural dispersions of *O. beta* between PEC and STB. Does the similarity of their otoliths between these sites occur by a natural ecological connectivity? Or are these fish populations connected by human pathways? The ports of Paranaguá and Santos are located in the PEC and in STB, respectively, and both are important for the international and domestic cabotage trade (Cutrim *et al.*, 2017; Beuren *et al.*, 2018). The Brazilian legislation does not determine as mandatory the disposal of maritime cabotage service of ballast water in oceanic areas prior to docking at ports (NORMAM 20/2014). It is possible that the cabotage fleet is introducing *O. beta* populations in Santos Bay and in the PEC through ballast water, making the otoliths of these two populations similar.

The analysis of the shape of otolith contours is an important tool which helped to determine if populations of *O. beta* on the Brazilian coast are connected, but it is not possible to determine whether a migration occurs either naturally by larval dispersion and/or through fish adult migration or these fish come associated with cabotage activities. We further recommend studies involving otolith chemistry to describe possible migration pathways between these *O. beta* populations and to elucidate the influence of the cabotage fleet on its dispersion on the Brazilian coast occurs. Future studies could help understand, and potentially provide information to control, the introduction of *O. beta*, preventing it from establishing in north-eastern Brazil, a region where no records of *O. beta* are available yet.

Acknowledgements. BMC is thankful to the National Council for Scientific and Technological Development (CNPq # 153090/2019-7). Virginia Nóh-Quiñones helped processing otolith samples and images in Mexico. ARGT is thankful to Sao Paulo Research Foundation (FAPESP #2018/04099-5). JRSV is thankful to National Council for Scientific and Technological Development (CNPq) for the constant research productivity grants provided to JRSV (PQ #302367/2018-7 and #303776/2015-3). AVV thank to CONICET (PIP 11220200103264CO), Universidad de Buenos Aires (UBACYT UBACYT 2020 Mod I. 20020190100069BA) and Agencia Nacional de Promoción Científica y Técnica (ANPCyT PICT 2019-0388).

References

Abaad M, Tuset VM, Montero D, Lombarte A, Otero-Ferrer JL and Haroun R (2015) Phenotypic plasticity in wild marine fishes associated with fish-cage aquaculture. *Hydrobiologia* **765**, 343–358.

Almeida-Tubino MFA, Salgado FLK, Uehara W, Utsunomia R and Araújo FG (2021) *Opsanus beta* (Goode & Bean, 1880) (Acanthopterygii: Batrachoididae), a non-indigenous toadfish in Sepetiba Bay, south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* **101**, 1–9.

Blackburn TM, Bellard C and Ricciard A (2019) Alien *vs* native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment* **17**, 1–5.

Boltovskoy D and Correa N (2015) Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America. *Hydrobiologia* **746**, 81–95.

Caires RA, Pichler HA, Spach HL and Ignácio JM (2007) *Opsanus brasiliensis* Rotundo, Spinelli & Zavalla-Camin, 2005 (Teleostei: Batrachoidiformes: Batrachoididae), a junior synonym of *Opsanus beta* (Goode & Bean, 1880), with notes on its occurrence in the Brazilian coast. *Biota Neotropical* **7**, 1–6.

Capoccioni F, Costa C, Aguzzi J, Menesatti P, Lombarte A and Ciccotti E (2011) Ontogenetic and environmental effects on otolith shape variability in three Mediterranean European eel (*Anguilla anguilla*, L.) local stocks. *Journal of Experimental Marine Biology and Ecology* **397**, 1–7.

Carvalho BM, Ferreira Junior AL, Fávaro LF, Artoni RF and Vitule JRS (2020) Human facilitated dispersal of the gulf toadfish *Opsanus beta* (Goode & Bean, 1880) in the Guaratuba Bay, southeastern Brazil. *Journal of Fish Biology* **97**, 1–5.

Carvalho BM, Freitas MO, Lapuch I, Volpedo AV and Vitule JRS (2022) Age, growth, and ontogenetic variation in the sagitta otolith of *Opsanus beta* (Goode & Bean, 1880), a non-native species in a wetland of international importance. *Latin American Journal of Aquatic Research* **50**, 1–11.

Castro MCT, Fileman TW and Hall-Spencer JM (2016) Invasive species in the Northeastern and Southwestern Atlantic Ocean: a review. *Marine Pollution Bulletin* **116**, 1–7.

Cerna F, Saavedra-Nievas JC, Plaza-Pasten G, Niklitschek E and Morales-Nin B (2019) Ontogenetic and intraspecific variability in otolith shape of anchoveta (Engraulis ringens) used to identify demographic units in the Pacific Southeast off Chile. *Marine and Freshwater Research* **70**, 1794–1804.

Collette BB (2002) Batrachoididae. In Carpenter KE (ed.), *The Living Marine Resources of the Western Central Atlantic. v. 2: Bony Fishes Part 1 (Acipenseridae to Grammatidae)*, vol. **5**. Norfolk, Virginia, USA: FAO Species Identification Guide for Fishery Purposes (American Society of Ichthyologists and Herpetologists Special Publication), pp. 1026–1042.

Contente RF, Brenha-Nunes MR, Siliprandi CC, Lamas RA and Conversani VRM (2015) Occurrence of the non-indigenous *Omobranchus punctatus* (Blenniidae) on the São Paulo coast, south-eastern Brazil. *Marine Biodiversity Records* **8**, 1–4.

Cordeiro BD, Bertoncini AA, Abrunhosa FE, Corona LS, Araújo FG and Santos LN (2020) First report of the aliengulf toadfish *Opsanus beta* (Goode & Bean, 1880) on the coast of Rio de Janeiro – Brazil. *BioInvasions Records* **9**, 1–8.

Cutrim SS, Robles LT, Galvão CB and Casaca AC (2017) Domestic short sea shipping services in Brazil: competition by enhancing logistics integration. *International Journal of Shipping and Transport Logistic* **9**, 280–303.

Dimitriou AC, Chartosia N, Hall-Spencer JM, Kleitou P, Jimenez C, Antoniou C, Hadjioannou L, Kletou D and Sfenthourakis S (2019) Genetic data suggest multiple introductions of the lionfish (*Pterois miles*) into the Mediterranean Sea. *Diversity* **11**, 1–12.

Encarnação J, Teodósio MA and Morais P (2021) Citizen science and biological invasions: a review. *Frontiers in Environmental Science* **8**, 1–14.

Franco-López J, González AGS, Arenas LGA, Sánchez CB, Escorcia HB, Pérez JAM, Rodríguez EP and Legorreta JLV (2017) Ecología y reproducción de *Opsanus beta* (Actinopterygii: Batrachoididae) en la Laguna de Alvarado, Veracruz, México. *Revista de Biologia Tropical* **65**, 1381–1396.

Gallardo-Torres A, Martinez-Perez JA and Lezina BJ (2004) Reproductive structures and early life history of the gulf toadfish, *Opsanus beta*, in the Tecolutla estuary, Veracruz, Mexico. *Gulf and Caribbean Research* **16**, 109–113.

Gauldie RW and Crampton JS (2002) An eco-morphological explanation of individual variability in the shape of the fish otolith: comparison of the otolith of *Hoplostethus atlanticus* with other species by depth. *Journal of Fish Biology* **60**, 1204–1221.

Greenfield DW, Winterbottom R and Collette BB (2008) Review of the toadfish genera (Teleostei: Batrachoididae). *Proceedings of the California Academy of Sciences* **59**, 665–710.

Gutiérrez-Mendieta FJ and Lanza Espino GL (2019) Physicochemical characterization of Mexican coastal lagoons, current status, and future environmental scenarios. In *Mexican Aquatic Environments*, pp. 77–91. https://doi.org/10.1007/978-3-030-11126-7_3

Hoff NT, Dias JF, Zani-Teixeira ML and Correia AT (2020) Spatio-temporal evaluation of the population structure of the bigtooth corvina *Isopisthus parvipinnis* from Southwest Atlantic Ocean using otolith shape signatures. *Journal of Applied Ichthyology* **36**, 1–12.

Ibañez AL, Hernández-Fraga K and Alvarez-Hernández S (2017) Discrimination analysis of phenotypic stocks comparing fish otolith and scale shapes. *Fisheries Research* **185**, 6–13.

Kikuchi E, Cardoso LG, Canel D, Timi JT and Haimovici M (2021) Using growth rates and otolith shape to identify the population structure of *Umbrina canosai* (Sciaenidae) from the Southwestern Atlantic. *Marine Biology Research* **17**, 272–285.

Lana PC, Marone E, Lopes RM and Machado EC (2001) The subtropical estuarine complex of Paranaguá Bay, Brazil. In Seeliger U and Kjerfve B (eds), *Coastal Marine Ecosystems of Latin America,* Ecological Studies, vol. **144**. Berlin: Springer-Verlag, pp. 131–145.

Lasso-Alcalá O, Nunes JLS, Lasso C, Posada J, Robertson R, Piorski NM, Tassell JV, Giarrizzo T and Gondolo G (2011) Invasion of the Indo-Pacific blenny *Omobranchus punctatus* (Perciformes: Blenniidae) on the Atlantic Coast of Central and South America. *Neotropical Ichthyology* **9**, 571–578.

Lessa GC, Santos FM, Filho PWS and Corrêa-Gomes LC (2018) Brazilian estuaries: a geomorphologic and oceanographic perspective. In Lana PC and Bernardino AF (eds), *Brazilian Estuaries: A Benthic Perspective*. Berlin: Springer, pp. 1–38.

Lombarte A and Tuset VM (2015) Morfometria de otólitos. In Volpedo A and Vaz-dos-Santos AM (eds), *Métodos de Estudos com Otólitos: Princípios e Aplicações*. Buenos Aires: CAFP-BA-PIESCI, pp. 1–12.

Maciel TR, Vianna M, Carvalho BM, Miller N and Avigliano E (2021) Integrated use of otolith shape and microchemistry to assess *Genidens barbus* fish stock structure. *Estuarine, Coastal and Shelf Science* **261**, 1–9.

Malca E, Barimo JF, Serafy JE and Walsh PJ (2009) Age and growth of the gulf toadfish *Opsanus beta* based on otolith increment analysis. *Journal of Fish Biology* **75**, 1750–1761.

Mallat S (1991) Zero crossings of a wavelet transform. *IEEE Transactions on Information Theory* **37**, 1019–1033.

Mizerkowski BD, Hesse K, Ladwig N, Machado EC, Rosa R, Araújo T and Koch D (2012) Sources, loads and dispersion of dissolved inorganic nutrients in Paranaguá Bay. *Ocean Dynamics* **62**, 1409–1424.

Morissette O and Whitledge GW (2022) Listening with the invasive fish ear: applications and innovations of otolith chemistry analysis in invasive fish biology. *Environmental Biology of Fishes* **105**, 1–17.

Ojaveer H, Galil BS, Carlton JT, Alleway H, Goulletquer P, Lehtiniemi M and Zaiko A (2018) Historical baselines in marine bioinvasions: implications for policy and management. *PLoS ONE* **13**, 1–49.

Olenin S, Gollasch S, Lehtiniemi M, Sapota M and Zaiko A (2017) Biological invasions. In Snoeijs-Leijonmalm P (ed.), *Biological Oceanography of the Baltic Sea*. Dordrech: Springer Science Business Media, pp. 1–40.

Parisi-Baradad V, Manjabacas A, Lombarte A, Olivella R, Chic Ò, Piera J and García-Ladona E (2010) Automatic taxon identification of teleost fishes in an otolith online database. *Fisheries Research* **105**, 13–20.

Popper AN and Fay RR (2011) Rethinking sound detection by fishes. *Hearing Research* **273**, 25–36.

Porcaro RR, Zani-Teixeira ML, Katsuragawa M, Namiki C, Ohkawara MH and Favero JM (2014) Spatial and temporal distribution patterns of larval sciaenids in the estuarine system and adjacent continental shelf off Santos, Southeastern Brazil. *Brazilian Journal of Oceanography* **62**, 149–164.

Richardson DM, Pysek P, Rejmánek M, Barbour MG, Panetta FD and West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**, 93–107.

Sadighzadeh Z, Valinassa T, Vosugi G, Motallebi AA, Fatemi MR, Lombarte A and Tuset VM (2014) Use of otolith shape for stock identification of John's 74 snapper, *Lutjanus johnii* (Pisces: Lutjanidae), from the Persian Gulf and the Oman Sea. *Fisheries Research* **155**, 59–63.

Schulz-Mirbach T, Ladich F, Plath M and Heb M (2019) Enigmatic ear stones: what we know about the functional role and evolution of fish otoliths. *Biological Reviews* **94**, 457–482.

Soeth M, Spach HL, Daros FA, Adelir-Alves J, Almeida ACO and Correia AT (2019) Stock structure of Atlantic spadefish *Chaetodipterus faber* from Southwest Atlantic Ocean inferred from otolith elemental and shape signatures. *Fisheries Research* **211**, 81–90.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, Mcmanus E, Molnar J, Recchia CA and Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**, 573–584.

Stransky C and Maclellan SE (2005) Species separation and zoogeography of redfish and rockfish (genus *Sebastes*) by otolith shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2265–2276.

Tempesti J, Mangano MC, Langeneck JL, Lardicci C, Maltagliati F and Castelli A (2020) Non-indigenous species in Mediterranean ports: a knowledge baseline. *Marine Environmental Research* **161**, 1–12.

Tomás ARG, Tutui SLS, Fagundes L and Souza MR (2012) *Opsanus beta*: an invasive fish species in the Santos estuary, Brazil. *Boletim do Instituto de Pesca* **38**, 349–355.

Tuset VM, Imondi R, Aguado G, Otero-Ferrer JL, Santschi L, Lombarte A and Love M (2015) Otolith Patterns of Rockfishes from the Northeastern Pacific. *Journal of Morphology* **276**, 458–469.

Tuset VM, Otero-Ferrer JL, Omez-Zurita JG, Venerus LA, Stransky C, Imondi R, Orlov AM, Ye Z, Santschi L, Afanasie PK, Zhuang L, Farré M, Love MS and Lombarte A (2016) Otolith shape lends support to the sensory drive hypothesis in rockfishes. *Journal of Evolutionary Biology* **29**, 2083–2097.

Vignon M and Morat F (2010) Environmental and genetic determinant of otolith shape revealed by a non-indigenous tropical fish. *Marine Ecolology Progress Series* **411**, 231–241.

Vitule JRS, Occhi TVT, Kang B, Matsuzaki SI, Bezerra LA, Daga VS and Padial AA (2019) Intra-country introductions unraveling global hotspots of alien fish species. *Biodiversity and Conservation* **28**, 3037–3043.

Watkins HV, Yan HF, Dunic JC and Côté IM (2021) Research biases create overrepresented "poster children" of marine invasion ecology. *Conservation Letters* **14**, 13.

Wonham MJ, Carlton JT, Smith DJ and College W (2000) Fish and ships: relating dispersal frequency to success in biological invasions. *Marine Biology* **136**, 1111–1121.