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Are landmarks analysis adequate to identify fish assemblages in a subtropical ecosystem? Study of case for the Araçá Bay (São Sebastião, Brazil).

VERSÃO CORRIGIDA

Tese apresentada ao Instituto Oceanográfico da Universidade de São Paulo, como parte dos requisitos para obtenção do título de "Doutor em Ciências", Programa Oceanografia, Área de Oceanografia Biológica.

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ABSTRACT

This thesis is part of the project *“Biodiversity and functioning of a subtropical coastal ecosystem: a contribution to integrated management*” funded by FAPESP – São Paulo Research Foundation – Process 2011/50317-5. Known as *Biota Araçá,* this project was performed in order to evaluate the diversity and the functionality of a subtropical tidal flat located at the northern coast of São Paulo State, a high diversity area. Our study, based on landmark analysis of fish body shape and otoliths shape, was conducted at the University of São Paulo in collaboration with researchers from the Institut de Ciències del Mar (Consejo Superior de Investigaciones Cientificas, Barcelona, Spain). The thesis was organized in five chapters. In the first one, we present a historical review about the use of morphology as a tool for the Science. Initially this theme was to supply my curiosity about *“how the shape of organisms contributed to the development of biodiversity studies”*. The second chapter shows the dependence of the fish assemblages’ morphological structure according to the samplers utilized. For that, nine fishing gears were used to sample the Araçá fish assemblages and we determined which samplers are more useful to represent the total fish morphological variability of the area. Given the heterogeneity and complexity of habitats of Araçá Bay, we supposed that some habitats have major influence in the morphological diversity. Therefore, the aim of the third chapter was to determine how fish diversity techniques reveal the ichthyofauna of the three main habitats of Araçá Bay: intertidal, inner/outer sublittoral, marginal shallow sublittoral (elected as results of the previous chapter). Here we emphasize the importance of abundance data and morpho-functional approaches to understand fish habitat complexities, and consequently, the ecosystem functioning. Thus, we present the more sensible habitats in case of the Araçá’s environmental degradation. During the development of our study, one question emerged: *“are sagittae landmarks able to describe the fish assemblage biodiversity as well as are fish body shapes?”* To answer this question, in the fourth chapter, the morphological correspondence between fish body shapes and otolith *sagittae* shapes were assessed. We investigated 43 species using different shape descriptors, attempting to habit, diet, swimming type, and hearing capabilities. Other specific questions were answered: 1- which method: shape indices, wavelets or landmarks, better discriminate species classification and, 2- which one shows the ecological significance of otoliths? In the last chapter, considerations are presented taking in account our initial question *“Are landmarks analysis adequate to identify fish assemblages in a subtropical ecosystem?”* The conclusion is that the method is a useful tool to describe fish body and otolith shapes as well as to define fish assemblages in highly diverse ecosystems.

Keywords: fish body, *sagittae* otoliths, morphofunctional diversity, morphometric geometric, landmark analysis, habitat uses, multiple fishing gears.

RESUMO

Esta tese é parte do projeto “*Biodiversidade e funcionamento de um ecossistema subtropical: uma contribuição ao manejo integrado*” financiado pela FAPESP – Fundação de Amparo a Pesquisa do Estado de São Paulo – Processo 2011/ 50317-5. Conhecido como *Biota Araçá*, este projeto foi desenvolvido com o objetivo de avaliar a diversidade e a funcionalidade de uma planície de maré subtropical localizada no litoral norte do Estado de São Paulo, uma área de alta diversidade. Nosso estudo, baseado na análise de pontos homólogos relacionados à forma dos corpos de peixes e à forma de otólitos, foi conduzido na Universidade de São Paulo com a colaboração de pesquisadores do Institut de Ciències del Mar (Consejo Superior de Investigaciones Cientificas, Barcelona, Espanha). A tese está organizada em cinco capítulos. No primeiro, apresentamos uma revisão histórica sobre o uso da morfologia como ferramenta para a Ciência. Inicialmente, este tema surgiu a partir da nossa curiosidade sobre "*como a forma dos organismos contribuiu para o desenvolvimento dos estudos de biodiversidade*". O segundo capítulo mostra a dependência da estrutura morfológica das assembléias de peixes de acordo com os amostradores utilizados. Para isso, nove artes de pesca foram empregadas para amostrar as assembléias de peixes do Araçá e, foi analisado quais delas foram mais úteis para representar a variabilidade morfológica total das espécies presentes na área. Dada a heterogeneidade e complexidade dos habitats da Baía do Araçá, supusemos que alguns deles apresentariam maior influência na diversidade morfológica da ictiofauna. Assim, o objetivo do terceiro capítulo foi analisar como as técnicas utilizadas na avaliação da diversidade de peixes revelam esta diversidade nos três principais habitats da Baía do Araçá: entremarés, sublitoral interno/externo, sublitoral marginal raso (eleitos a partir dos resultados obtidos no capítulo anterior). Aqui, enfatizamos a importância dos dados de abundância e de abordagens morfofuncionais para entender as complexidades dos habitats para os peixes e, conseqüentemente, o funcionamento do ecossistema. Ainda aqui, apresentamos os habitats mais sensíveis no caso de uma degradação ambiental do Araçá. Durante o desenvolvimento do estudo, uma questão emergiu: *“pontos homólogos em sagittae são capazes de descrever a biodiversidade da assembléia de peixes, assim como o são as formas corporais?”* Para responder esta questão, no quarto capítulo, avaliamos a correspondência morfológica entre formas corporais de peixes e formas de otólitos *sagittae*. Nós investigamos 43 espécies utilizando diferentes descritores de forma, com vistas aos hábitos, dieta, tipo de natação e capacidades auditivas. Outras questões específicas foram respondidas: 1- qual método: índices de forma, *wavelets* ou *landmarks*, melhor discriminam as espécies para classificação e, 2- qual deles mostra a significância ecológica dos otólitos? No último capítulo, são apresentadas considerações levando em conta nossa pergunta inicial "*A análise de pontos homólogos é adequada para identificar assembléias de peixes em um ecossistema subtropical?*" A conclusão é que o método é uma ferramenta útil para descrever formas de corpos de peixes e otólitos, bem como definir associações de peixes em ecossistemas altamente diversificados.

Palavras-chave: forma de peixes, otólitos *sagittae*, diversidade morfofuncional, morfometria geométrica, análise de pontos homólogos, usos do habitat, múltiplas artes de pesca.

1.

Shape's diversity towards ecomorphology: a historical review

1. Importance of the morphology in biological studies

Form and diversity are the two greatest subjects of natural history (GOULD, 1971; MOTTA et al., 1995). The high diversity of the living nature has been considered product of the evolutionary process, including similarities and differences among organisms, patterns of distribution and behaviours, adaptations and interactions (MAYR, 1966, 1977). According to Begon et al. (2006) the organisms were moulded by past environments and their characteristics (evolutionary baggage) reflects successes and failures of their ancestors. In this sense, the physical forces, which operate indirectly specifying the forms, provide optimal adaptation for animals' subject to their influence (THOMPSON, 1966). As said D'Arcy Thompson, in 1917, "the *organisms are well projected"* (THOMPSON, 1966).

At present and over the evolutionary time, the interaction of morphological with ecological diversities (among organisms) is the central focus of a comparative discipline named *ecological morphology* or *ecomorphology* (WINEMILLER, 1991). The ecomorphology hypothesis supports that morphological attributes of an organism should reflect its ecology and, thus indicate habits or adaptations to different habitats (VAN DER KLAAUW, 1948; WINEMILLER, 1991). Bock (1990) explained, "*Ecomorphology is primarily concerned with analyses of the adaptiveness of morphological features and all dependent correlated topics such as the comparisons of adaptations in different organisms, modifications of adaptive features due to competition and other causes, structure of ecological communities, diversity within taxa, etc"*. Winkler's (1988) definition is: *"Ecomorphology deals with the covariation of morphology and ecology".*

Morphology has been considered a predictor of the way-of-life (KARR AND JAMES, 1975). The shape of an organism can determine the niche occupied (GATZ, 1979), hence diverse morphologies are indicatives of distinct ecological and adaptive strategies (NORTON et al., 1995). Therefore, the communities are structured by biotic and abiotic processes which ecological niches (habitat use and relationships) and organization can variate in space and time (MOTTA et al., 1995; NORTON et al., 1995). Nowadays, the ecomorphology is an useful tool for biological studies related to: a) structure of communities, share of resources, ecological niche description; b) intra and interspecific interactions (predation, defence and competition); c) biodiversity; and, d) population dynamics (relative and absolute growth, ontogeny, description and identification of populations) (MOTTA; KORTSCHALL, 1992; MOTTA et al., 1995; RECASENS; LOMARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; TUSET et al., 2014; FARRÉ et al., 2013, 2015, 2016a). Moreover, the overall body shapes and common characteristics have been used to define biological groups phylogenetically related through morphometric geometric methods (ZELDITCH et al., 2003; PRICE et al. 2012), widely employed in the biology and palaeontology fields (ELEWA, 2010).

Research's on morphology have not been surveyed by a historical review so this chapter has as objective to scrutinize the ancient literature, showing (1) the contribution of the forms on the biodiversity discovery and (2) on animal sciences' development, according to the different thoughts, (3) presenting the shift from an evolutionary vision to an ecological approach and, in addition, (4) creating the theoretical base for the sequential chapters.

2. Historical survey about measuring the morphological variability

The first classification system based on resemblance of morphological characters (form and structure) in order to establish phylogenetic relationships emerged from the **comparative anatomy** (QUEIROZ, 2005). Due to the high diversity of living organisms, many philosophers were encouraged to study anatomy. Aristotle (384-322 *b.C. – before Christ* or 2,402-2,340 *ybp* - *years before present*) was the pioneer concentrating his dissections studies in other vertebrates than humans (MOORE, 1990; SINGER, 1996; CHAGAS, 2001). Aristotle investigated and compared shapes and structures and, besides the morphology, studied growth, physiology, behaviour and ecology of most than 500 mammals, birds, fishes, reptiles, amphibians, insects and cephalopods species (BLITS, 1999; REVERÓN, 2015). However, it cannot be said that Aristotle established an evolutionist principle because he expressed clearly: *"…man produces man, the plant produces the plant, according to the material constituting of everything*", never thinking about an animal common ancestor (CRIVELLATO; RIBATTI, 2007). Using a comprehensive scope with rigorous and systematic methods, Aristotle wrote several books (as *History of Animals, Parts of Animals, Generation of Animals, Motion of Animals, Progression of Animals, Parva Naturalia* and *De Anima*) and was considered "the Zoology's father" (BLITS, 1999). Nevertheless, he followed the inductive reasoning and his scientific theories were elaborated from observations.

The principle of **inductivism** was substantiated by singular observations generating an equal number of trues and after that, generalized to everything (VIANA, 2007). To discover patterns of resemblance within major groups of animals, Aristotle recognized and used homologous structures and analogous functions (BLITS, 1999). Thus, **homologous structures** presenting the same anatomic pattern and embryonic origin, translate organisms' adaptations to different environment types and reflecting a divergent evolution, while **analogous structures** differing in anatomic patterns and do not having the same embryonic origin, perform the same function in different living beings (COLE, 1944). Afterward, Richard Owen (1804-1892) defined homology in 1843 as *"the same organ in different animals under every variety of form and function"*. The Owen's concept of homology remains an important concept and helped biology in relation to public understanding (HARRISON, 1993).

Aristotle's writings also originated the Ichthyology (from the greek *ikhthus*, meaning fish) science, as he recognized about 115 fish species (MOYLE; CECH, 1988). Around 2,000 years later, in the 16th century, Guillaume Rondelet (1507-1572) summarized all the knowledge about fishes at that moment, and published the first ichthyological text, including drawings based on Aristotle's' writings (Figure 1). At the same time, Hippolito Salviani (1514-1572) published the first regional faunal paper and an Italian treatise with 92 fish species, followed by Pierre Belon (1517-1564) with the first modern systematic treatise on fish according anatomical characteristics (MOYLE; CECH, 1988). However, the Ichthyology's father was Petrus Artedi (1705-1735) through his standard methods for making counts and measurements of anatomical features, which contributed to Carl von Linné (1707-1778) refinement of the principles of taxonomy (MERRIMAN, 1938; BROBERG, 1987).

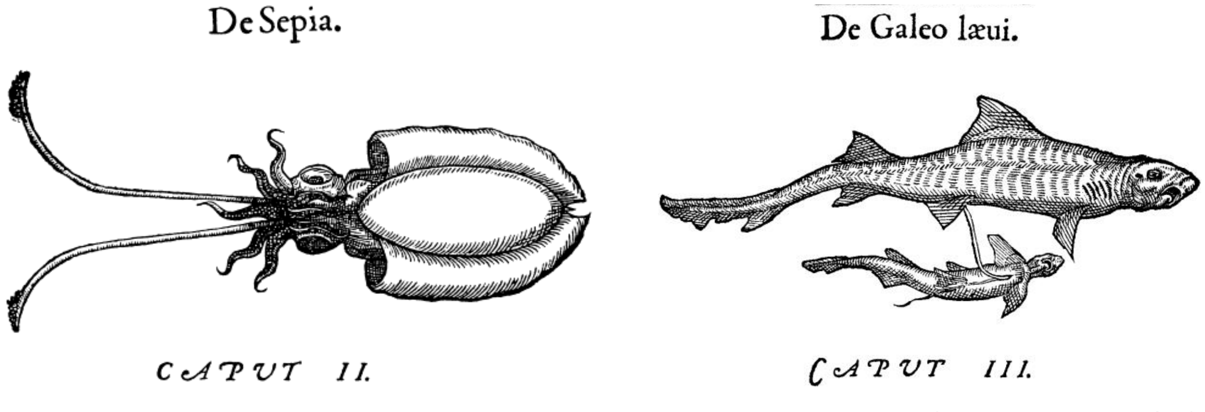


Figure 1. Rondelet's Illustrations based on Aristotle's descriptions of an adult sepia (left side), and a young dogfish (*Mustelus laevis*) still attached by the umbilical cord to its mother (right side) (Modified of BLITS, 1999).

René Descartes (1596-1650), the mathematician who developed the analytical geometry, considered the living organisms as complexes machines whose structures were associated to functions: *"…But in my opinion, all things in nature occur mathematically"*. Thus, he developed an extensive physiological description of animal bodies, in which he explained the functions of life as a purely mechanical way, without appeal to a soul or vital principle (HATFIELD, 1992, 2015). Since these descriptions, the Physiological Science (from the greek *physis*, meaning functioning) was born. In Brazil, the understanding about animals and plants started in 1638 with the arrival of the german naturalist George Marggraf (1610-1644), who published the *Historia Naturalis Brasiliae*, ten years later.

The idea of shape evolution arose for the first time by George-Louis Leclerc (1707-1788), in France. Commonly known as Count de Buffon, he conducted an extensive work on the earth history, and his "*Histoire Naturelle*, *génerele et partuculiére*" was published in three volumes' in 1749 with the idea of species changing according to the time (a prerogative of evolution) (LOVELAND, 2004). Contemporaneous and a critic of Carl von Linné (1707-1778), Buffon believed in a natural classification method defending the principles of continuity and affinity between species, based on anatomical structure comparisons. Linnaeus, on the contrary, was engaged with the nature's diversity, using classification methods based on discontinuity and morphology as main taxonomy aspects (CAMPOS, 2010). In 1761, in the Volume IX of his *Histoire Naturelle*, Buffon described similar species between the Old World (Europe, Africa and Asia) and the New World (Americas), concluding that mammals were originated from a single centre of dispersion located in the Old World, specifically Europe. He believed that species had degenerated, in other words, the Old World species became those found in the Americas. In 1766, in the volume XIV of *Histoire Naturelle*, Buffon published the article *Dégénération des animaux,* dealing with the theory of origin of the American fauna and presenting, perhaps for the first time in history, the theory that the South American continent was in the past attached to the African continent, forming a single super-continent: *"Let us suppose, that the Old and New worlds were formerly but one continent, and that, by a violent earthquake, the ancient Atalantis of Plato was sunk ... The sea would necessarily rush in from all quarters, and form what is now called the Atlantic Ocean."* (GERBI, 1996).

Meanwhile Buffon was concerned with this theory, Linné (or Linnaeus) attempted to describe all the known natural world, by assigning a name that consisted of two parts, specifying the three kingdoms of nature, the mineral, the vegetable and the animal (NOMURA, 2011). In *Systema Naturae* (LINNÉ, 1758), he expanded the concept of the binomial nomenclature created nearly 200 years before by Johan Bauhin (1541-1613), a Guillaume Rondelet student, publishing in *Historia Plantarum Universalis*, the first international flora, containing 5,226 plants descriptions, an indicative of the great strides done about the knowledge of botany during the 16th century (CINCINNATI HISTORY LIBRARY AND ARCHIVES, 2015). Linné utilized the form of the structures to group the organisms in classes, orders, genders and species (BLUNT, 1982), also replacing previously descriptions as - *physalis amno ramosissime ramis angulosis glabris foliis dentoserratis* – by the concise and familiar names "Gender - Species" – *Physalis angulata* (MOBERG, 2008). Since the binomial nomenclature was officially adopted in January 1, 1758, when Linné published the 10º edition of his work, it is in use until the present days. Regarded as an exceptional mind, Linnaeus is the "Taxonomy's father", having described 4382 animal species and about 7000 plants (NOMURA, 2011).

During that time, the natural history had as one of its great goals the development of a natural classification system based on hidden laws of the form of organisms, which could reflect the way they were "built". Completely subordinate to function, Georges Cuvier (1769-1832) was the first to classify the animal kingdom based on a structural and morphological point of view, expanding Linnaeus's taxonomy by grouping classes into phyla, and arranging both fossils and living species in this taxonomy (RUDWICK, 1997). Cuvier (1818) preserved the natural history descriptive and classificatory rigor from Linnaeus without renouncing the theoretical claims of Buffon (CAPONI, 2004). He was the great promoter of the comparative anatomy. According to him, the classification method should be grounded analysing shapes and understanding how different beings coordinate their different functions (SMITH, 1993; FARIA, 2015).

Until then, all naturalists believed in **creationism** as species origin and, in consequence, in **fixism**. As a defender of fixism, Cuvier realised that fossils were the organic remains of extinct animals, believing that the fossilized species had no connection with those of his time. Thus, he created the catastrophism theory to explain that the geological and biological changes on the planet have never occurred by gradual changes but by sudden and violent ones, stablishing the extinction as a fact (by comparing fossils pieces with actual species) (PALMER, 1999). Unlike fixists, the defenders of the **transformism** believed that species had changed over time in response to certain circunstances, such as the Count de Buffon and Jean-Baptiste Pierre Antoine de Monet, the Chevalier of Lamarck (CAPONI, 2009). Jean-Baptiste Lamarck (1744-1788), the naturalist early proponent of the idea that biological evolution proceeded in accordance with natural laws, and the creator of the "Theory of the progression of animals", admitted that species undergone changes in a constant progression towards the more complexity and advancement, stating that the transformation of an organ was passed down from generation to generation, changing the species (PACKARD, 1901). For Cuvier the term "analogy" just refered to similarities of functions while for Étienne Geoffroy Saint-Hillaire (1772-1844), a naturalist with formalistic conception, the analogy was based on structural correspondence between distinct organisms, which all vertebrates were modifications of a common archetype. The debate of Cuvier and Geoffroy theoretical views was named "controversy of analogues" (APPEL, 1987).

The morphological school at the time, called **functionalism**, compared organisms owning certain features with others of the same type, and types with resemblance belonged to the same species. The "**type concept**" was an attempt to explain the true forms of organic bodies (STEINER, 1984). For Cuvier, an organism was compounded by a functional system, where each component acquired its specific position according to its function. For Johann Wolfgang von Goethe (1749-1832), the poet philosopher who accepted both the holistic nature of an organism as the functionality of its parts, the bodies were in continuous transformation, another way to see the "type" (RADL, 1988). Goethe' typologism played a paradigmatic role in the science of biological form and the name gave to this new manner of research was "**morphology**", published in 1796 (STEINER, 1984; LEVIT; REINHOLD; HOßFELD, 2015).

Later, Goethe in the 1817 *Zur Morphologie* defined it as "the theory of form, formation and transformation of organic bodies" (STEIGERWALD, 2002; OPITZ, 2004). To compare differences and similarities between various organic structures, two basic and different methodologies were employed: **idealistic** (constructionist, structuralistic) and **evolutionary** (historical) (LEVIT; REINHOLD; HOßFELD, 2015). The structuralist method, commonly outlined in works of Goethe, Cuvier and Geoffroy, presupposed that two characters of two different taxa are homologous, since they are located in a similar structural position, expressing a similar structural concept. On the other side, the evolutionary morphology used morphological data of all sorts in an evolutionary context (historical, often phylogenetic) and was connected mainly with the names of the anatomist Carl Gegenbaur (1826-1903) and Ernst Haeckel (1834-1919) (LEVIT; REINHOLD; HOßFELD, 2015).

It was common to explain such homologies by supposing that the Creator (God) used a certain pattern, which he modified in different ways. Despite Goethe’s theory had been developed on these lines, he sometimes argued that the Creator modified the pattern by direct influence of the environment. Goethe used the word “metamorphosis” (meaning, in this context, transmutation of species) in the sense of “evolution of species” as a valuable but dangerous idea, since it “leads to formlessness” as said by himself (WELLS, 1967). Goethe was certainly not thinking in evolution of species, however he inspired both Darwinian and Lamarckian evolutionism as well as ‘counter-revolutionary’ idealistic morphology (LEVIT; REINHOLD; HOßFELD, 2015).

Erasmus Darwin (1731-1802), the Charles Darwin’s paternal grandfather, was the founder of the modern evolutionism and proposed the **transmutations of species** including the laws of organic life (artificial, natural and sexual selections). Unfortunatelly, his book *Zoonomia: the laws of organic life* published in 1792 was not well understood at that time (SALGADO-NETO, 2009). Indeed, the first well understood theory about organic evolution was presented by Jean Baptiste Lamarck (BURKHARDT, 1977, 2013). In the 1809 *Phylosophic Zoologique*, Lamarck presented his explanation about the species origin, called “**Theory of inheritance of acquired characters**” based on: the use and disuse of organs; and the inheritance of acquired traits (MAYR, 1972; CORSI, 1988). According to him two intrinsic abilities allowed the animals to vary and the evolution to take place: the first was the “*Le pouvoir de vie”* - the force that led to increasing complexity and was responsible for the evolution of the major life forms (hence **homologous structures**); the second was the *“L'influence des circonstances”* - the adaptive force responsible for the animals’ adaptation to their environment (hence **analogous structures**) (MAYR; PROVINE, 1980). Lamarck claimed that the organs form, structure and functioning were affected by environmental effects according to the use or disuse of a characteristic which lead to its progressive inheritance or loss. In turn, that implied in the inheritance of acquired characteristics albeit did not exist a clear mechanism related to these acquisitions (BARD, 2011). Continuous and extra use of particular organs make them more efficient while the continued disuse of some other organs leads to their degeneration and ultimate disappearance. Therefore for him, influenced by Goethe, the extinction did not exist (BURKHARDT, 2013). Lamarck told: *"I could prove it is not the form, either of the body or of its parts, that gives rise to habits and way of life of animals, but it is contrary, the habits, the way of life, and all the other influential circumstances that have with time constituted the form of the body and the parts of animals. With new forms, new faculties have been acquired, and little by little nature has arrived at the state where we see it at present"* (LAMARCK, 1801; BURKHARDT, 2013). The most famous Lamarck's' example was the giraffes stretching their necks to reach leaves high in trees, strengthening and gradually lengthening their necks. These giraffes would have the offspring with slightly longer necks (also known as "soft inheritance"). Although Lamarck's theory was considered speculative, with low impact and acceptance (BURKHARDT, 1977; MARTINS; MARTINS, 1996; MAGNER, 1979), it was important to the understanding of the process of species origin related to environmental influences.

The preparation of these previous theories and the processes of their verification and refutation produced the biggest revolution in biology, determining the current paradigm of Biology. Perhaps no one has influenced our knowledge of life on Earth as much as the English naturalist Charles Darwin (1809-1882). Darwin's principal innovation was the mechanism of **natural selection**, which explained how populations of living forms adapt to changes in their environment by assuming that natural selection operated on occasional variations (GISSIS; JABLONSKA, 2011). This resulted in what Darwin called "*descent with modification*" which gathered a lot of coherent evidences about the transmutation of species (FERREIRA, 2007). During the Beagle journey between 1832-1836, Darwin collected lot of data about the variety of organism forms (livings and fossils). A considerable portion of species examined and described were new to science, especially those collected in South America (DARWIN, 1859). When studying the wildlife from the Galápagos Islands, he noticed that the finches (Figure 2) from the different islands besides to be similar, showed wide variations in their size, beaks and claws from island to island (i.e. their beaks were different depending on the local food source). Returning to England, Darwin began reflecting on his observations and experiences and concluded that, because the islands are so distant from the mainland, the finches that arrived there in the past had changed over time. Over the next two years, Darwin developed the basic outline of his groundbreaking theory of evolution through natural selection (BATESON, 1979).

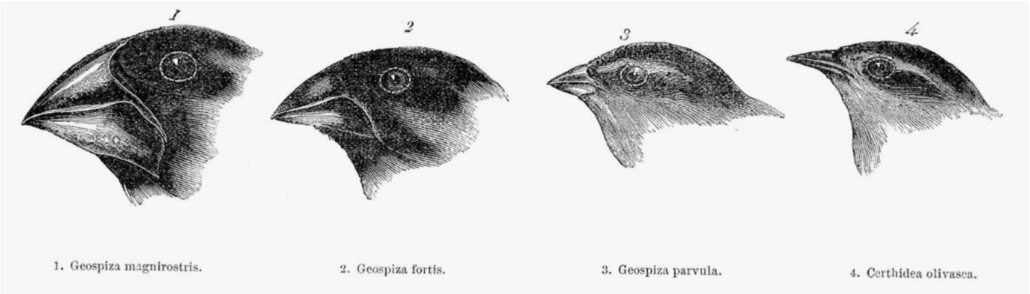


Figure 2. Darwin's drawings of the different heads and beaks he found among the finches on the Galapagos Islands (Source: Darwin Online).

On the Origin of Species may never have been written, let alone published, if it had not been for Alfred Russel Wallace (1823-1913), another British naturalist who independently proposed a strikingly similar theory in 1858 (KUTSCHERA; NIKLAS, 2004; COOPERMAN; MASCI; O'CONNELL, 2009). Together, Darwin and Wallace published in 1858 some manuscripts in the Journal of the Linnaean Society about the hypothesis of descent with modification by means of natural selection (DARWIN, 1859). This hypothesis has five fundamental assertions, *reproduction*: all organisms produce more offspring than their environments can support; *variability*: intraspecific variability of most characters exists in abundance; *struggle for life*: competition for limited resources leads to a struggle for life (Darwin) or existence (Wallace); *inheritance*: descent with heritable modification occurs; and *natural selection*: as a result, new species evolve into being, with its "consequences" divergence of character and the extinction of less improved forms (RAUP, 1994; KUTSCHERA; NIKLAS, 2004). They included evidences of homologies between humans and other mammals, suggesting that men were the transformation from monkeys and God was not involved with the universe and life's creations (FREEMAN, 1977).

In 1859, Darwin published *On the Origen of Species by means of a Natural Selection*, his most important publication which settled the theoretical framework of evolutionary biology and the end of the fixist concept of the species. In this context, the study of comparative anatomy undergoes a substantial change in the concept of the organization of animals since it began to consider the interaction between phenotypic features with the external environmental conditions acting on them (DARWIN, 1859; ALLEN, 1907). The typological concept of anatomy is abandoned, and the modern concept of **phylogenetic morphology** becomes a key element in the study of evolutionary lines. Therefore, the species transformation through time, as species became modified and diverge to produce multiple descendant species are now referred as evolution (MEYER; KEAS, 2003; LOSOS, 2013). And, how the traits could be inherited through generations was explained from the principles proposed by Gregor Johann Mendel (1822-1884), in 1866 (MIKO, 2008). Mendelian analysis has revealed the further fact, unsuspected by Darwin, that recombination of existing genetic units could both produce as modify new inheritable variations, and this has important evolutionary consequences (HUXLEY, 1942).

It is important to recognize that “natural selection” is not synonymous of “evolution” (FUTUYMA, 2009). Evolution can occur by processes other than natural selection (especially genetic drift), and natural selection can occur without any evolutionary change (as when natural selection maintains the *status quo* by eliminating deviants from the optimal phenotype) (PERETÓ; BADA; LAZCANO, 2009). On the other hand, the natural selection is the only known mechanism to cause adaptive evolutions (FUTUYMA, 2009; PIANKA, 2011; VITT; PIANKA, 2014). **Adaptation** is the important concept that link morphology and ecology, whereby members of a population become better suited to some characteristics of their environment, changing attributes that affects their survival or reproduction (FUTUYMA, 2009). By the way, the **sexual selection** (another of the aspects described by Darwin, in 1859) is the process of choosing morphological and behavioral characteristics that led to the successful crossing, where the features evolution gives reproductive advantages to the organisms (RUNDLE; CHENOWETH; BLOWS, 2006; JONES; RATTERMAN, 2009). At this moment, regarding to studies on environment adaptability, some ecological rules began being formulated.

Joel Asahp Allen (1838-1921) showed that other influences than natural selection operate powerfully in the differentiation of specific forms. He described trends of geographical character variation that became known as Allen's Law, one of the most famous of the so-called "**ecogeographical rules**" (ALLEN, 1877) beside the Bergman's Law, from Carl Georg Lucas Christian Bergmann (1814-1865). Through morphological characters comparison and the assumption of correlation between the phenotype and the physical habitat, the Allen-Bergmann's rule indicated the existance of a lower surface/volume ratio in homothermous animals of cold waters (NUDDS; OSWALD, 2007).

Another rule of shape transformation was formulated by the naturalist and mathematician D'Arcy Thompson (1860-1948), suggesting that physical forces exert direct and immediate influence in shaping organisms as they grow (GOULD, 1971). This is the guiding concept of 1917 *On Growth and Form*, where Thompson showed that changes on biological form are both modeled and described as mathematical diffeomorphisms (transformations that are smooth and that have smooth inverse), which he called as *cartesian transformations* (BOOKSTEIN, 1991, 1997). D'Arcy Thompson introduced the study of form-comparisons with a latent variable, which have been studied by biologists as homology (BOOKSTEIN et al., 1985; ELEWA, 2010). The Thompson's homology rule refers to parts of different organisms that are correspondents, whereas the Cartesian transformation acts distorting a picture or other specifically geometric representation form (Figure 3) (BOOKSTEIN, 1977, 1991; BOOKSTEIN et al., 1985). This approach, as Thompson pointed out, gives a clearer view of what Darwin (1859) referred to as **correlation of characters** (ARTHUR, 1984).

After the Evolution's theory formulation, there was a stagnation in the appearance of new concepts in morphology. The morphology science lost strength during almost forty years. Just in the middle of the twentieth century, Hans Heinrich Böker (1886-1939) in his 1935 book *Vergleichende biologische Anatomie der Wirbeltiere* (*Comparative biological anatomy of vertebrates*) incorporated the direct observation of animals under natural conditions to morphological studies, and established that form is derived from function; thus, function always precedes form (DUTTA, 1982). Despite the direct observation importance, Böker's principles were rejected by considering only functional aspects of form and neglecting the influence of genetics and the convergence. In this context, the quality of morphological studies began to be improved, developing essential principles for the **ecomorphology** (or ecological morphology) formulation.

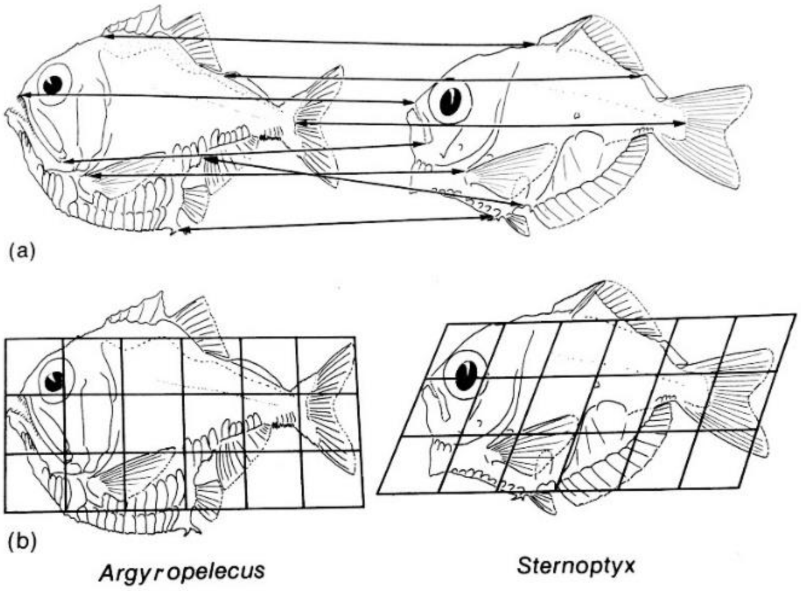


Figure 3. D’Arcy Thompson example of homology as a smooth deformation, displaying the correspondence of homologous points (a) and by a Cartesian grid transformation (b) (Source BOOKSTEIN et al., 1985).

Until Theodosius Grygorovych Dobzhansky (1900-1975) published in 1937 *Genetics and the origin of species,* it was believed that all members of one species had practically identical genes (FORD, 1977). Dobzhansky was the most influent evolutionist at his time and his most significant contribution to science doubtless was the formulation and popularization of the modern synthesis of evolutionary theory (DOBZHANSKY, 1973; KALINOWSKI; LEONARD; ANDREWS, 2010). Evolution was defined as "a change in the frequency of an allele within a gene pool", and according him it was through mutations in genes that natural selection took place, and new species arose (BARAHONA; AYALA, 2005). To Darwin, the difference between species and varieties was that species are delineated by gaps in morphology that persist when they overlap in space, whereas varieties are less definite, and show intermediates (MALLET, 2010). Theodosius Dobzhansky, Ernst Walter Mayr (1904-2005) and Julian Huxley (1887-1975) judged Darwin’s species ideas as inadequate and promoted the “Modern Synthesis” view of species (MALLET, 2010; FONSECA, 2006). “Modern Synthesis” was a movement which championed Darwinian natural selection as compatible both with Mendelian genetics and with the data on natural biodiversity, in which species were characterized by ‘reproductive isolation’ from others (varieties as geographic subspecies do not) (DOBZHANSKY 1935, 1937; MAYR, 1940, 1942,1963).

In 1942, with *Systematics and the Origin of Species* (MAYR, 1942) and *Evolution, the modern synthesis* publications (HUXLEY, 1942), the theoretical scope of neoDarwinism (or synthetic theory of evolution) was formulated based on population genetics, ecology, paleontology, biogeography, and morphology in a second plane (FONSECA, 2006). Mayr proposed that the species was a fundamental category of biological organization and was the first taxonomist to introduce the *biological species concept* (BOCK, 2005; QUEIROZ, 2005; MALLET, 2010; POLISELI; OLIVEIRA; CRISTOFFERSEN, 2013). **Species** were defined as agroupments of reproductive populations (reproductively isolated from other groups) with the same characteristics that occupies a specific niche in the nature (MAYR, 1982). His work on species and speciation helped scientists to understand the progress and mechanisms of evolution from one species to another, and the importance of the species unit as "the keystone of evolution". *"Without speciation, there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution"*, said Mayr (MEYER, 2005). The speciation caused by geographic separation of populations (**allopatry**), such as by rivers or valleys, prohibited homogenizing gene flow between them and accumulated mutations over time. To Mayr this might lead to the divergence of such populations from each other, and reproductive isolation might arise as a simple product of these separate evolutionary histories (LENSKI, 2005; MEYER, 2005).

As significant as the investigations of D’Arcy Thompson, in the 1920’s Julian Huxley was pioneer in the quantitative investigation of **allometric growth** (GOULD, 1971; GALL, 2011, PACKARD, 2012). Huxley investigations considered the organism shape as a fundamental feature of its overall design, and an obvious aspect of the individual shape was that it markedly changed many times, and in a continuous manner, throughout its **ontogeny** (STRAUSS, 1993). Huxley's fundamental deduction about body form was his "law" of the constant differential growth ratio (HUXLEY, 1942). In genetics, this mechanism was used to clarify any facts and theoretical constructions in the framework of classical biology, such as morphology and embryology (GALL, 2011). A common point of view among Huxley and Mayr was that natural selection and mutations were complementary processes.

However, the evolutionary taxonomy school, whose vision was based on the works of Mayr and associates, was completely broken by Emil Hans Willi Hennig (1913-1976) with the proposal of phylogenetic systematics, in 1950 *Fundamentals of a Theory of Phylogenetic Systematics* (HENNIG, 1966). Henning grounded different classificatory schools of the XX century providing the understanding of the organic diversity at the light of evolution (SANTOS; KLASSA, 2012). In *Phylogenetic Systematics*, the phylogenetic systematic (or cladistic) corresponded to a biological classification reflecting the kinship between the living beings by using the common ancestry concept to identify the monophyletism (HENNIG, 1966). To constitute a natural clade, the kinship relations were established through refined observation on homologous characters, discriminating them among primitives (plesiomorphic) and derivatives (apomorphic). In this sense, the sharing of apomorphies allowed distinguishing homologies from adaptive convergences and thus, monophyletic groups were determined (SANTOS; KLASSA, 2012). Hennig is commonly referred as the father of Phylogenetic Systematics due to his contribution with a great paradigm to the taxonomy history and systematisation of the biological diversity.

In 1943, Robert Gustav Adolf Remane (1898-1976), a morphologist, and Wilhelm Kühnelt (1905-1988), a terrestrial ecologist (SCHALLER, 1990), published separately their concepts of *“Lebensform”* (form of live) based on observations about morphological analogies of organisms distant phylogenetically, produced by adaptive processes to similar environmental factors (MOTTA et al., 1995). Remane (1952) described the criteria by which homologues were to be recognized and his work was very influent (RIEPPEL, 2013). The 1952 *Die Grundlagen des natfirlichen Systems, der vergleichenden Anatomic und der Phylogenetik* (*"The foundations of the natural system, of comparative anatomy and phylogenetics"*) was explicitly dedicated to the foundations of systematic, phylogenetic and the concept of homology (ZACHOS; HOßFELD, 2006). Six criteria were proposed by him, being the three principles related to: - position: *“Homology can be recognized by similar position in comparable systems of features”*; - structure: *“Similar structures can be homologized without reference to similar position, when they agree in numerous special features”;* - transition: *“Even dissimilar structures of different position can be regarded as homologous if transitional forms between them can be proved so that in considering two neighboring forms, the first and second conditions are fulfilled. The transitional forms can be taken from* *ontogeny of the structure or can be true systematically intermediate forms."* (ZACHOS; HOßFELD, 2006; WHEELER, 2012).

Subsequently, despite environmental constraints, Cornelis Jakob van der Klaauw (1893-1972) connected the morphology to ecology and used it to define the relationship between body structure and environment. Van der Klaauw was able to make the concept of holism operational by introducing the functional component in functional morphology (DUBBELDAM, 2007). In its 1948 *Ecological Morphology* publication, van der Klaauw introduced two new cohering concepts: - the ***functional component***: skeletal elements together performing a specific function should be considered as a unit with a certain degree of independence; and, - the ***holism***: the various functional components should fit together within the whole of the skull (DUBBELDAM, 2007). Thence, the connection between morphological features of the organism began to be linked with their ecological and functional habits within ecosystems and, on the 1950's, morphology studies focused in functional aspects. That was significant to the establishment of a basis for the development of future studies.

The evolutionary morphology concepts emerged in 1965 with *Adaptation and the form-function complex* by Walter Joseph Bock (1933-) and Gerd von Wahlert (1925-) who presented the "**form and function complex**" and suggested that any component of the life history of the organisms' results of adaptation determined by the interaction of organism with the environmental conditions. They distinguished form, function, faculty and biological role, as follows: - *form:* defined as the material configuration of a feature; - *function:* as its action, or how the feature works; - *faculty:* comprising a form-function complex; and, - *biological role:* defined as the action or the use of the faculty by the organism in the course of its life, with reference to the environment where it lives (BOCK; VON WAHLERT, 1965; BOCK, 1969; BOCK, 1994). The biological adaptation had been interpreted as an interaction between the organism and its environment, and was used in three different ways in evolutionary studies: - *universal adaptation:* as the bond between living organisms and their environment and was an absolute property of life that can neither increase or decrease; - *physiological adaptation:* as the ability of tissues to modify phenotypically in response to environmental stimuli and a special case of the general principle that the phenotype was an expression of the genotype in a particular environment; and, - *long-term* *evolutionary adaptation:* as the hereditary adjustment of an organism to a particular set of environmental conditions (BOCK; VON WAHLERT, 1965).

In parallel to the evolutionary morphology development, ecologists perceived that the species morphology was also important to analyze competition, coexistence relationships, habitat differentiation and to elucidate the ecological structure of communities. Thus, the **Ecological** Science introduced new concepts and theories as ecological niches, resource partitioning, habitat differentiation, adaptations and competition within communities (HUTCHINSON, 1959; MACARTHUR; WILSON, 1967; MACARTHUR, 1968; SCHOENNER, 1974). Thereby, studies on morphology, function and ecology of species showed a growing trend in the half century.

In 1959 *Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?* George Evelyn Hutchinson (1903-1991) focused attention on a problem that is central to all ecological theory: what determines the number of species in a particular ecosystem? (HUTCHINSON, 1959; SLOBODKIN; SLACK, 1999; KEARNEY et al., 2010). Among all of his ideas, one received most attention: how species (of similar features) can have their utilization of limiting resources and still avoid interspecific competition sufficiently to coexist in the same community (BROWN, 1981). Hutchinson helped to build the best insights into species **richness** and **community ecology**, which further developed the formal notion of **ecological niche** (LOVEJOY, 2011). Initially, the niche concept was originated on a subjective way in the natural history by Joseph Grinnell (1877-1939) in 1917, and was subsequently employed in quantitative ecology (PATTEN; AUBLE, 1980). In collaboration with his students, in particular with Robert MacArthur (1930-1972), Hutchinson developed the first comprehensive mathematical theory to explain species richness and other mathematical models to depict the various interacting component parts of an ecosystem (BENSON, 2000). The ecological niche was defined by him as "***hypervolume** in a multidimensional ecological space*", determined by species requirements to reproduce and survive (POLECHOVÁ; STORCH, 2008). The *n-dimensional hypervolume* could be subdivided in two categories: - *fundamental niche:* the full range of conditions (biotic and abiotic) and resources in which one species could survive and reproduce free of interference from other species; and – *realized niche:* a narrower niche resultant of pressure from interactions with other organisms (i.e. inter-specific competition), to which the species would be mostly highly adapted (SCHOENER, 1974, 1986; GRIESEMER, 1992). In other words, ecological niche was the position of an organism within an environmental gradient involving both abiotic conditions exploited by the organisms (e.g. temperature, pH, moisture, solar radiation, humidity, soil texture) as well as biotic interactions (e.g. predators, parasites, competitors), both important for a species persistence (PINTO-COELHO, 2009). For that, adaptations to different ecological conditions and habitat uses require morpho-functional body variations in order to perform relevant behaviors as swimming, habitat choice, prey selection, and anti-predator responses (WAINWRIGTH, 1996; KARPOUZI; STERGIOU, 2003; LANGERHANS; REZNIK, 2010). After Hutchinson' contribution, the Ecology promised to become a fully mathematized and experimental discipline (BROWN, 1986). This new perspective revitalized Ecology as a science.

Later, MacArthur together with other Hutchinson' student, Edward Osborne Wilson (1929-), built a general theory to explain how distance and area combine to regulate the balance between immigration of new species to the island and the extinction of species already present (MACARTHUR; WILSON, 1967). MacArthur and Wilson published in 1967 *Theory of Island Biogeography* the first principles of ecology and population genetics used to provide mathematical models which helped to explain the biotic diversity patterns and the species distribution in archipelagos (HAMILTON, 1968; BROWN, 1986). In 1968, MacArthur stablished a parallelism between niche and phenotype, in the sense that both are intrinsic character reflections of the organisms (PINTO-COELHO, 2009).

When two species differentiate their niches, they tend to compete less strongly, and thus facilitate their coexistence. According to Thomas William Schoener (1943-), in 1974 *Resource Partitioning in Ecological Communities* the niche overlap between similarly species varies in response to food availability, habitat spatial distribution and time (e.g. feeds at different times of the day), all of them fundamental to community organization (SCHOENER, 1974). He developed resource-partitioning studies, which the major purpose was to analyze the limits placed by the interspecific competition on the number of species that could stably coexist (SCHOENER, 1974).

According to this new scientific trend, ecologists passed to interpret morphophological variations among species as different adaptations to the environment, and incorporated the measurements of morphological traits for their analysis in order to clarify evolutionary and ecological questions (HUTCHINSON,

1959; KEAST; WEBB, 1966; MACARTHUR, 1968; SCHOENER, 1974). The term "ecomorphology" was coined by James Richard Karr (1948-) and Francis Crews James (1930-) in his 1975 *Ecomorphological configurations and Convergent Evolution*, where they examined the relationship between morphological features and environmental aspects strictly from the ecological side, in particular related to the structure of communities (KARR; JAMES 1975; Bock, 1994).

The following years finally linked vertebrate morphology and ecology establishing the foundations of the modern ecomorphology. Ecomorphological studies began to focus on the casual consequences of anatomical differences between species and the ecology of the organism (WAINWRIGHT; REILLY, 1994). A series of papers by Walter Joseph Bock (1933-) (BOCK, 1977, 1990) clarified several important points and set a conceptual framework for interpreting the ecological and evolutionary implications of functional morphological observations. The first paper (BOCK, 1977) was important to reinstate the ecomorphology on the perspective of form-function complex and differentiates concepts: - *functional morphology:* deals with the functional properties of the morphological structures; and, - *ecomorphology:* deals with the biological role of structures in the environment and throughout the evolution.

In the 1980's, studies relating the functional design showed how variations in intra and interspecific performance molded the fitness distributions in communities', as Earl Werner and Donald Hall (WERNER; HALL, 1974, 1977, 1979) working on sunfishes, and Peter Raymond Grant (1936-) and his wife working on Galapagos' finches (GRANT, 1968, 1986; GRANT; GRANT, 1989, 1993, 1996). **Fitness** involves the ability of the organism to survive and reproduce in their environments, having as consequence of success the gene's contribution to the next generation. When no differences in fitness occurs, natural selection cannot act and adaptation cannot occur (ORR 2009), the reason why recents ecomorphologic studies have incorporated phylogenetic hypothesis.

Joseph Felsenstein (1942-) evaluated the species differences and relationships between individuals or populations through **phylogenetic inferences** analyzing heritable traits (such as the DNA sequences) and historical evolution of characters (FELSENSTEIN, 1983). Joe Felsenstein in 1982 *Numerical Methods for Inferring Evolutionary Trees* and in 1983 *Statistical Inference of Phylogenies* used methods of phylogenetic variables to estimate the interspecific correlation among characters noting divergence patterns when sister species evolved independently of their ancestors (FELSENSTEIN, 1982, 1983; WAINWRIGHT; REILLY, 1994). Felsenstein (1983) defined **phylogeny** as a branching tree diagram showing the course of evolution in a group of organisms. However, the phylogeny concept was first introduced by Ernst Haeckel in 1820, when he proposed a link with ontogeny and said: “ontogeny recapitulates phylogeny” (RICHARDSON; KEUCK, 2002).

Even as Felsenstein, George Lauder cautioned the difficulty of determine adaptive processes when historical information is ignored. In this framework, Lauder brought a phylogenetic approach to the study of functional morphology. In 1981 *Form and Function: structural analysis in evolutionary morphology* he stated the relative importance of phylogenetic constraints in the functional morphology evolution (BROOKS; MCLENNAM, 1991). Furthermore, it could be assessed by examining emergent structural or functional traits within a phylogenetic framework and test hypothesis of phylogenetic constraints comparing general properties among clades (BROOKS; MCLENNAM, 1991). In 1990 *Functional Morphology and Systematics,* Lauder contributed with biomechanical studies to define the physical constraints which organisms must work beyond to explain how the phylogenetic analysis on both form and function allows to know the historical pathways taken during transformations of the organismal design (BROOKS; MCLENNAM, 1991).

As exposed, over life, the influence of ecological factors may cause morphological changes and the selection on these characters leads to changes in gene frequencies and extinction or speciation of a taxon (MOTTA et al., 1995). In other words, the speciation is the evolution mechanism of living organism’s (DARWIN, 1859; FARKAS et al., 2015). Although speciation process is hard to observe, replicate and manipulate in the wild (GRAS et al., 2015), the last detection was published by Andrew P. Hendry (1968-) and his colleagues, in 2000 *Rapid Evolution of Reproductive Isolation in the Wild: Evidence from Introduced Salmon* describing a fast process of sympatric speciation since an ecological isolation.

3. Quantitative techniques for measuring morphological variability

More than exploring the interactions between intrinsic characteristics of individuals (or taxonomic units) and their environment, the ecomorphology is a developing field of the organismal biology and ecology (NORTON et al., 1995). The addition of phylogenetic components to the ecomorphology studies resolved the statistical dilemma of the nonindependence of characters for those taxa which share a trait due to common ancestry (MOTTA et al., 1995). Species relationships could be ordered as phylogenetic trees using anatomical and molecular traits, according their character differentiation.

Per advent of computing in the 60’s many possibilities emerged for the objective classification in quantitative biology (SOKAL, 1966). Robert Rueven Sokal (1926-2012), Peter Sneath (1923-2011) and James Rolhf (1936-) were pioneers in the development of **numerical taxonomy** methods, initially performing their researchs independently (SNEATH, 1995). The numerical taxonomy was the biological classification system where taxonomic units were grouped into taxa by using numerical methods supported by the character states (SNEATH; SOKAL, 1973; HULL, 1988). It used all characters without ignoring any bad character initially rejected by the conventional taxonomy (SOKAL, 1963; SOKAL; SNEATH, 1963). The relationships among characters were inferred without regard to whether character states was derived (apomorphic) or primitive (plesiomorphic) (SOKAL; SNEATH, 1963; HART; REYNOLDS, 2008). The development of numerical taxonomy involved many problems because inevitably led to a re-examination of the bases of phylogenetic reasoning and to attempts the reconstruction of phylogenetic sequences (SOKAL; CAMIN, 1965).

The 1963 *Principles of Numerical Taxonomy* publication was a preliminary exposition of this new field, when Sokal and Sneath determined as a fundamental principle the strict segregation of phylogenetic speculation from taxonomic procedure. *Taxonomic affinity* was determined as the similarities based on observable characters of taxa, so-called **phenetic** similarities (SOKAL, 1963). To represent the taxa, Sokal and Sneath (1963) used the **Operational Taxonomic Unit (OTU)** as observation of organisms that means species, genus or a group of undetermined evolutionary relationship.

The 1965 *Fundamental problems in numerical taxonomy* published by William Thomas Williams (1913-1995) and M. B. Dale, was the first critic analysis about numerical taxonomy and introduced greater rigor into methodology development (SNEATH, 1995). Williams and Dale (1965) presented viewpoints on monothetic *versus* polythetic classifications, hierarchical *versus* nonhierarchical classifications, and metric (quantitative) *versus* nonmetric (qualitative) resemblance coefficients (ROMESBURG, 2004).

The Numerical Taxonomy progressed quickly, and in sequence Sokal and Rolf (1966) published *Random Scanning of Taxonomic Characters* performing experiments with group identification based on the random sampling of morphology, and introducing image analysis to process electronic data. Sneath, in 1967, published *Trend surface analysis of transformation grids* in order to quantify the D'Arcy Thompson's transformation grids approach to shape analysis through application of trade surface analysis.

Over the years, the measurements and analyses of shape variations were improved and named **morphometrics**, accompanied by the development of rigorous multivariate statistical methods (ROHLF; MARCUS, 1993). Initially, the shape of species was assessed underpinned on linear measurements methods (STRAUSS; BOOKSTEIN, 1982; WINEMILLER, 1991). Although important to the scientific development, the traditional morphometrics studies presented biases by allometry and size effects, the distances between the measurements were difficult to standardize, and mainly, the exact geometric structure of the shape was not preserved (ADAMS et al., 2004). Researchers as Fred Bookstein (1947-), Richard Arthur Reyment (1926-), Richard E. Strauss (1950-) and Paul Ralph Ehrlich (1932-) pursued applying this numerical approach to quantify organisms shape variation.

In the late 1980's, these approaches were synthetized through efforts of Bookstein and contributions of David George Kendall (1918-2007), Kanti Mardia (1935-) and Ian L. Dryden, Colin Goodall and James Rohlf, resulting in a formulation and subsequent development of the **geometric morphometrics** (GM) (WHEELER, 2012), considered as a 'revolution' in the field (ROHLF; MARCUS, 1993). The geometric morphometrics consists in the analysis of Cartesian geometric coordinates between morphological structures rather than linear, outline or volumetric variables, which enable to describe complex morphological structures in more detail (such as general body shape) (FARRÉ et al., 2016a).

In the 1990's, techniques from mathematical statistics, multivariate biometrics, non-Euclidean geometry and computer graphics were combined in a coherent new system of tools for the complete quali and quantitative analysis, the **landmark-based method** (homologous coordinate points in anatomical structures of interest, defining the geometric shape of the object) (BOOKSTEIN, 1996). More formally, a *landmark configuration is a discrete sample from a homology mapping across pairs of specimens* (that literature is summarized in BOOKSTEIN et al., 1985). When important biological information (i.e. the presence of barbel in fish) cannot be defined using landmarks, an additional type of coordinate points can be used to define the shape of boundary curves or of not fixed structures, and are named semilandmarks (BOOKSTEIN, 1991, 1997).

In landmark-based analysis (including the semilandmarks), the non-shape information is removed from the coordinates of landmarks (by scaling or translation) to compare the shapes (KENDALL, 1977). In general, the shapes are scaled to unit centroid size and rotating to minimize the distances between corresponding landmarks (square root of the summed squared distances of each landmark to the centroid). The landmark configuration is rotated to minimize the deviation between it and a reference, typically the mean shape. Because shape space is curved, analyses are done by projecting shapes onto a tangential space. In other words, the Cartesian coordinates of anatomical landmarks are quantified by the unification of a rigorous statistical theory with analytical procedures for superimposing landmark configurations for all specimens in a common coordinate system (FARRÉ et al., 2016a). Among the superimposition techniques, the Procrustes analysis has been considered the most complete method to provide the uniform components of the shape variation (**partial** or **relative warps**) for each analyzed object (i.e. specimens or species). The resulted warps are utilized as shape variables in the multivariated statistical analysis. The interpretation of the shape patterns is given through graphical representation of the results plotted in a morphological space (**morphospace**). The pattern of clustering the samples in the morphospace represents the similarities and differences of the shapes, which can reflect phylogenetic relationships (WALKER, 2000; ZELDITCH; SHEETS; FINK, 2003; PRICE et al., 2012). Conventional multivariate statistical methods such as multivariate analysis of variance and multivariate regression can be used to test statistical hypotheses about shape (ROHLF; SLICE, 1990; ROHLF; BOOKSTEIN, 1990; BOOKSTEIN, 1991; MARCUS; BELO; GARICA-VALDECASAS, 1993; MARCUS et al., 1996; WALKER, 2000; ELEWA, 2004, 2010). The power of this method lies in the ability to detect and visualize shape differences more clearly than classical approaches (CLABAUT et al., 2007; LOMBARTE et al., 2012; FARRÉ et al., 2013, 2015, 2016).

Because landmark-based GM methods possess more powerful statistical support, they have been considered one of the most appropriate methods to quantify the shape variation between structures (ADAMS; ROHLF; SLICE, 2004; ADAMS;

OTAROLA-CASTILLO, 2013). Systematics, phylogeny, paleontology, taxonomy and evolutionary biology are among the main research fields using GM, most of them analyzing differences in bony structures (i.e. skulls, jaws, dentitions, vertebrae, otoliths, etc.) or in overall body shapes in order to answer evolutionary, taxonomic, ecological or biological hypothesis (FARRÉ et al., 2016).

Fishes have been one of the most researched zoological groups by means of GM methods due to the great phenotypic plasticity. The analysis comprises since overall body shape (CLABAUT et al. 2007; COSTA; CATAUDELLA, 2007; ANTONUCCI et al., 2009; YOUNG; SNOEKS; SEEHAUSEN, 2009; PARK et al., 2013; CHAPMAN et al., 2015; FAULKS et al., 2015; PRICE et al., 2015; FARRÉ et al., 2016; PÉREZ-QUIÑÓNEZ et al., 2017) to specific structures as otoliths (MONTEIRO et al., 2005; PONTON, 2006; LOMBARTE et al., 2010, TUSET et al., 2016, IBAÑEZ; HERNÁNDEZ-FRAGA; ALVAREZ-HERNÁNDEZ, 2017), skulls (WINTZER; MOTTA, 2005; COOPER; MASCI; O'CONNELL, 2009) or fins (WAINWRIGHT; BELLWOOD; WESTNEAT, 2002; STANGE et al., 2016). The purposes cover from taxonomic differentiation among species (VALENTIN; SÉVIGNY, CHANUT, 2002; LANGERHANS et al., 2003; IBAÑEZ; CHOWX; O'HIGGINS, 2007; IBAÑEZ; HERNÁNDEZ-FRAGA; ALVAREZ-HERNÁNDEZ, 2017) to phylogenetic relationships and evolution processes (RÜBER; ADAMS, 2001; CLABAUT et al., 2007; MUSCHICK; INDERMAUR; SALZBURGER, 2012; KLINGENBERG; MARUGÁN-LOBÓN, 2013). Regarding to ecology and biodiversity approaches, the landmark GM method has been successfully employed in studies related to: reconstruction of the trajectory of morphological diversification using fossils (FRIEDMAN, 2010; MARRAMÀ; GARBELLI; CARNEVALE, 2016); complex phenotype–environment associations (WAINWRIGHT; RICHARDS, 1995; KASSAM; SATO; YAMAOKA, 2002; WAINWRIGHT; BELLWOOD; WESTNEAT, 2002; LANGERHANS; CHAPMAN; DEWIT, 2007); resource partitioning (KASSAM et al., 2003); biological invasion success (AZURRO et al., 2014); ontogenetic dynamics (ZELDITCH et al., 2003); diversity measure and communities structure (LAYMAN; LANGERHANS; WINEMILLER, 2005; RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; FARRÉ et al., 2013; TUSET et al., 2014; FARRÉ et al., 2015; 2016b).

Among other zoological groups studied by means of the GM application are dinossaurs (YATES et al, 2010; SERB et al., 2011; BRUSATTE et al., 2012; HEDRICK;

DODSON, 2013; KLINGENBERG; MARUGÁN-LOBÓN, 2013); reptiles (CLAUDE et al., 2003, 2004; BONNAN et al., 2008; PIERCE; ANGIELCZYK; RAYFIELD, 2008), amphibians (ADAMS; ROHLF, 2000; BUSKIRK, 2009; KALIONTZOPOULOU, 2011; ORIZAOLA et al., 2013), birds (MARUGÁN-LOBÓN; BUSCALIONI, 2004; KULEMEYER et al., 2009; BHULLAR et al., 2012), and mammals (MARCUS; HYNGST-ZAHER; ZAHER, 2000; MONTEIRO-FILHO; MONTEIRO; REIS, 2002; PEREZ; BERNAL; GONZALEZ, 2006; DRAKE, 2011; GUNZ et al., 2012; LU et al., 2014).

This above overview gave us a complete overview of the theme, and was useful to situate our study in the context of the area of *Form and Functional* studies.

2.

Optimal fishing samplers to reveal the morphological structure of a fish assemblage in a subtropical tidal flat

Abstract

Species morphological characters are essential for assessing the functional structure of fish assemblages, since differences between them are indicative of distinct ecological strategies. Globally, tidal flats are relevant to fish assemblages by offering feeding, refuge, and reproduction grounds. To analyze the morphological structure of the fish assemblage present in a tidal flat in the Brazilian coast, we performed samplings using nine different fishing gears. To describe the fish shapes and verify the morphological variability of the assemblage it was applied the geometric morphometric method. A total of 106 teleost species of a wide variety of shapes and belonging to 47 families, were identified. Here, we assessed the influence of each gear on the morphological diversity of the fish assemblage. The results indicated that beach seine, otter trawl, marginal encircling gillnet, and fish traps, together, were the most effective gears to represent the maximum morphological variability of fish inhabiting tidal flats. Moreover, the assemblage showed high morphological redundancy, which increases ecosystem resilience.

1. Introduction

Tidal flats are of vital relevance for many fish species who enter this ecosystem during flood tides for feeding, refuge, growth and reproduction (CLARIDGE; POTTER; HARDISTY, 1986; ROBERTSON; DUKE, 1990; POTTER et al., 1997; MORRISON et al., 2002; SEMENIUK, 2005; LUGENDO et al., 2006; NAGELKERKEN, 2009). This use may occur only during parts of their life cycles (i.e., nursery grounds), on a daily or seasonal basis (i.e., pathways in diadromous migrations) for spawning or pursuing preferred prey items, or throughout their entire life span (WHITLATCH, 1980; LENANTON, 1982; NAGELKERKEN et al., 2000; FRANCO et al., 2006; ADAMS et al., 2006). Many artisanal fisheries depend upon these specific coastal habitats, where the recruitment occurs (LENANTON; POTTER, 1987; BECK et al., 2001; NAGELKERKEN et al., 2002; DOHERTY; FOWLER, 2004; LIPCIUS et al., 2008; SEITZ et al., 2014; SUNDBLAD et al., 2014; SHEAVES et al., 2014; GROL; RYPEL; NAGELKERKEN, 2014; UNSWORTH et al., 2014). Moreover, tidal flats provide ecosystem services to millions of people worldwide, consequently, the knowledge about composition and structure of fish assemblages become indispensable for the fishing activity management (WORLD BANK, 2004; MILLENNIUM ECOSYSTEM ASSESSMENT, 2005; SALAS et al., 2011; MACKINNON; VERKUIL; MURRAY, 2012). In this sense, how fishing gears select fish sizes and shapes is a key question for fisheries management (RECASENS et al., 1998; LIANG et al., 2014; ALÓS et al., 2014).

Particularly, the Araçá Bay (southeastern Brazil) is a tidal flat ecosystem (≈ 500,000 m²) with highly diverse habitats occupied by many types of organisms. There, more than 1,364 species have been recorded, with 56 novel species catalogued, as well as 16 threatened species (AMARAL et al., 2015). In this last category, they are ten benthic species (three polychaetes, five echinoderms, and two enteropneusts); one bird, the Royal Tern (*Thalasseus maximus*); one sea turtle, *Chelonia mydas*; and five marine fishes, including the dusky grouper (*Epinephelus marginatus*), the mutton snapper (*Lutjanus analis*), the cubera snapper (*Lutjanus cyanopterus*), and two rays, the chola guitarfish (*Rhinobatos percellens*) and the spiny butterfly ray (*Gymnura altavela*) (AMARAL et al., 2010; AMARAL et al., 2015; BRASIL, 2014; LAMAS; ROSSI-WONGTSCHOWSKI; CONTENTE, 2016; CONTENTE; ROSSI-WONGTSCHOWSKI, 2017). In addition to this biodiversity, many fish species (e.g., sardines, snooks, white mullets, mojarras, groupers, and croakers) are important supporting artisanal fishing activities. One of the most abundant fish species in Araçá, the Clupeidae *Sardinella brasiliensis*, is the main Brazilian fishery resource with great ecological importance. It acts as a link in coastal food webs, transferring energy from plankton and small organisms to larger fishes and other organisms posted at higher trophic levels (GANIAS, 2014). The higher phytoplankton concentration inside the bay than in adjacent areas (CIOTTI et al., 2015), attracts clupeid and engraulid juveniles in abundance, allowing larger piscivores to enter the bay (MATSUURA, 1998; CONTENTE; ROSSI-WONGTSCHOWSKI, 2017). In adittion, high concentrations of mature sardine spawners are frequently found in the region surrounding Ilhabela Island and the São Sebastião Channel (Figure 1), close to Araçá bay (MATSUURA, 1998). Moreover, the Araçá contains areas with the last remaining mangroves along the northern coast of São Paulo State, attesting its vitality and social-ecological importance (SCHAEFFER-NOVELLI et al., 2018).

Morphological characters of fish species are essential for assessing the function structure of an assemblage (SCHOENER, 1974), since fish morphological differences indicate distinct ecological strategies (NORTON; LUCZKOVICH; MOTTA, 1995). For that reason, morphological techniques have been used to measure temporal and spatial patterns of biodiversity, helping to evaluate the influence of environmental and biological factors in a community’s organization. This provides extremely useful information that can be used to predict structural alterations following disturbances (WINEMILLER, 1992; MOTTA; NORTON; LUCZKOVICH, 1995). The results of fish morphology studies have demonstrated the relevance of this method to detect variation in diversity between ecosystems (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; FARRÉ et al., 2013, 2015; TUSET et al., 2014) and to explain the success of biological invaders (AZZURRO et al., 2014; SMITH et al., 2016). In tropical and subtropical ecosystems, fish biodiversity includes widely variable forms. However, most studies on this subject have been performed based on a single gear (ARAÚJO et al., 2002; BARLETTA et al., 2008; MIRANDA et al., 2008; ROCHA; FERNANDEZ; PAIVA-FILHO, 2010; CONTENTE; STEFANONI; SPACH, 2011; JUNIOR et al., 2012; SOETH et al., 2015; WORK; CODNER; GIBBS, 2017), even though different gears perform better for specific components. The use of a single gear often underestimates the species richness and the morphological diversity of the system, thereby contributing to an inaccurate assessment of its health (DIEKMANN et al., 2005; GARCIA et al., 2012). Therefore, it is important to combine gears to ensure that most possible compartments and assemblages were included (BAKER et al., 2016). Among the factors that can affect the gear selection are depth, substratum type, vegetation type and density, wood or other types of structures (i.e., artificial reefs) (CLEMENT; PANGLE; UZARSKI, 2014).

Recently, in Araçá Bay, Contente and Rossi-Wongtschowski (2017) used multiple sampling methods and showed that this approach improved the characterization of the fish assemblage composition; however, that study did not cluster the fishing gears in relation to their catch similarity. Here, our main goal was to perform a morphological analysis of the fish assemblage structure. We believe that the morphological diversity is an adequate approach for knowing how fishing gears influence fish assemblage data since the body shape is related to many functional and ecological traits (i.e., swimming, search for food, striking and capturing prey, evading predators, migration, courtship dances, defending territories and spawning) (KEAST; WEBB, 1966; WAINWRIGHT; RICHARD, 1995; LANGERHANS et al., 2004; CLABAUT et al., 2007; LOMBARTE et al., 2012; WALKER, 2010; AZZURRO et al., 2014). To achieve this, we used the same fishing samplers as Contente and Rossi-

Wongtschowski (2017) to verify how they influence the diversity of the morphological set, and to determine which samplers are most representative of the total morphological diversity, independent of fish abundance.

2. Material and Methods

2.1. Study area

Araçá Bay (23°48'52"S; 45°24'17"W) is a small and semi-secluded coastal area on the north coast of São Paulo State (Southwestern Atlantic Ocean) (Figure 4). The sediment is mostly sandy-muddy (AMARAL et al., 2010) and its hydrodynamics is driven by tides under the action of low-amplitude waves (DOTTORI; SIEGLE; CASTRO, 2015). The bay is exposed to the São Sebastião Channel dynamics, a highly energetic region influenced by wind flows (CASTRO; MIRANDA, 1998). The bay is considered a natural nursery (AMARAL et al., 2015), which shelters a high diversity of organisms, and contains the last remaining mangrove of the northern coast of the São Paulo State. Araçá bay is under pressure of the São Sebastião Port (SBP) and of oil leaks by the Almirante Barroso Terminal (Petrobrás). In addition, it is exposed to other constant anthropic effects, such as irregular occupations, domestic sewage, and the presence of one sea outfall. Since its construction in 1936, the SBP has been expanded through successive landfills, two of which (in 1987 and 1994) covered part of the bay, changing the original configuration of the nearby beaches (ALBUQUERQUE, 2013). In 2009, a new port expansion project was proposed, involving the construction of a concrete slab covering 75% of the area (CPEA, 2011), which would affect all ecosystem processes (PARDAL-SOUZA et al., 2016).

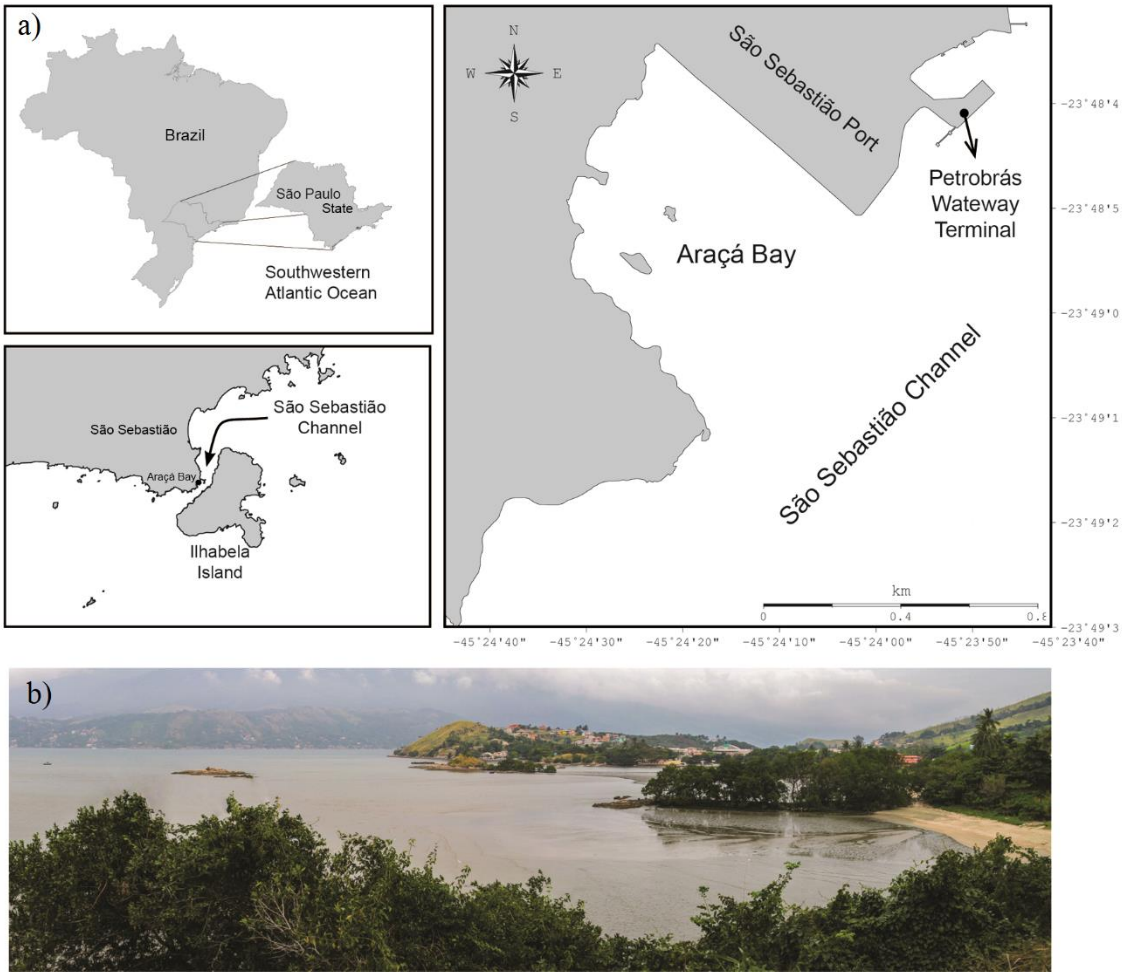


Figure 4. a) Araçá Bay location, bordering São Sebastião Channel, north shore of São Paulo State, Brazil; b) Top view of the Araçá bay (Source: Gabriel Monteiro).

2.2. Sampling

Four 12-days sampling campaigns (Permits nos. 5218, 5553, 5866 and 6104, authorized by Brazil’s Chico Mendes Institute for Conservation), were carried out between March 2013 and January 2014 along the Araçá Bay. To consider the main habitats of the bay, samplings were performed using nine gears of regional common use, as follows:

- Otter trawls (Figure 5A) were carried out from one small boat equipped with two nets (9.5 m opening x 6.7 m sac; 10 mm mesh between nodes), one on each boat side. Seven fishing deployments were performed for five minutes each in the sublittoral zone bordering the SSC, following random direction but not overlapping.
- Beach seine net (Figure 5B) (15 m length x 4 m sac; 5 mm mesh between nodes) was conducted by two fishermen with the net mouth opening toward the beach front. This procedure was repeated in the all Araçá sandy beaches.

- Encircling gillnet 1 (Figure 5C) (590 m length x 3 m height; 30 mm mesh between nodes) were employed using a canoe where the fisherman spread the net in a circle, being the initial marked by an indicator buoy. The procedure was accomplished twice, one in each half of the bay (right and left sides).
- Encircling gillnet 2 (Figure 5D) (590 m length x 3 m height; 30 mm mesh between nodes) was spread in a "J" format in the sideways of the bay, near the rocky shores.
- Large gillnet (Figure 5E) was a single nylon net arranged in "L" maintained during 12 hours (Larger portion = 154 m length x 3.3 m height, small portion = 87.75 m length x 3.15 m height; 50 mm mesh between nodes, in both). A fisherman performed fish removal every 6 hours.
- Small gillnet (Figure 5F) (154 m length x 2.6 m height; 32 mm mesh between nodes) was arranged in parallel in front of the mangrove, between the two islets present at the bay core. A fisherman performed fish removal every 6 hours.
- Cast net (Figure 5G) with 4 m of radius and 30 mm between nodes. The bay was divided into six zones and three random launches were made in each one.
- Fish traps (Figure 5H) (80 cm length x 53 cm height x 37 cm width; 1.5 cm of mesh) were placed consecutively along the right rocky shore, for 48 hours. Fish removal was performed every 6 hours.
- Hook and line (not illustrated) were used along the sampling period, being sardines and shrimps as lures, in the border of the SSC.

More details regarding samplings, gear design, and operation are described in Contente and Rossi-Wongtschowski (2017), however we considered the encircling gillnet as two different gears because they were employed in two distinct habitats (the inner shallow sublittoral and the marginal shallow sublittoral). The samplings occurred on consecutive nights, on a quarterly basis.

During high tide in Araçá Bay, four habitats are recognized: intertidal habitat (mean depth ± standard deviation 0.6 ± 0.3 m), marginal shallow sublittoral habitat (0.8 ± 0.4 m), inner shallow sublittoral habitat (1.2 ± 0.5 m), and outer sublittoral habitat (8.4 ± 4.1 m) with soft and rocky bottoms. Active gears and gillnets were used at soft-bottoms, intertidal, and sublittoral habitats. Fish trap, and hook and line were used over the rocky bottoms at the outer sublittoral.

Fishes were identified as described by Figueiredo and Menezes (1978, 1980, 2000), Menezes and Figueiredo (1980, 1985), and Carpenter (2002a, 2002b, 2002c), and classified according Eschmeyer and Fong (2015a, 2015b). All fresh specimens were measured to the nearest 1.0-mm total length (TL). Structures such as fins, barbels, cutaneous appendages, and extended fin rays were fixed with formalin and trapped in a white background base using entomological pins. Standardized images (around 4,000) of the left side of the body were obtained for all species (ROSSI-WONGTSCHOWSKI; SILIPRANDI; CONTENTE, 2015). Samples with 10 fish per species, fitted into 10-mm intervals of TL, were obtained. Vouchers were deposited and catalogued at the Zoological Museum of the University of São Paulo (LAMAS; ROSSI-WONGTSCHOWSKI; CONTENTE, 2016).

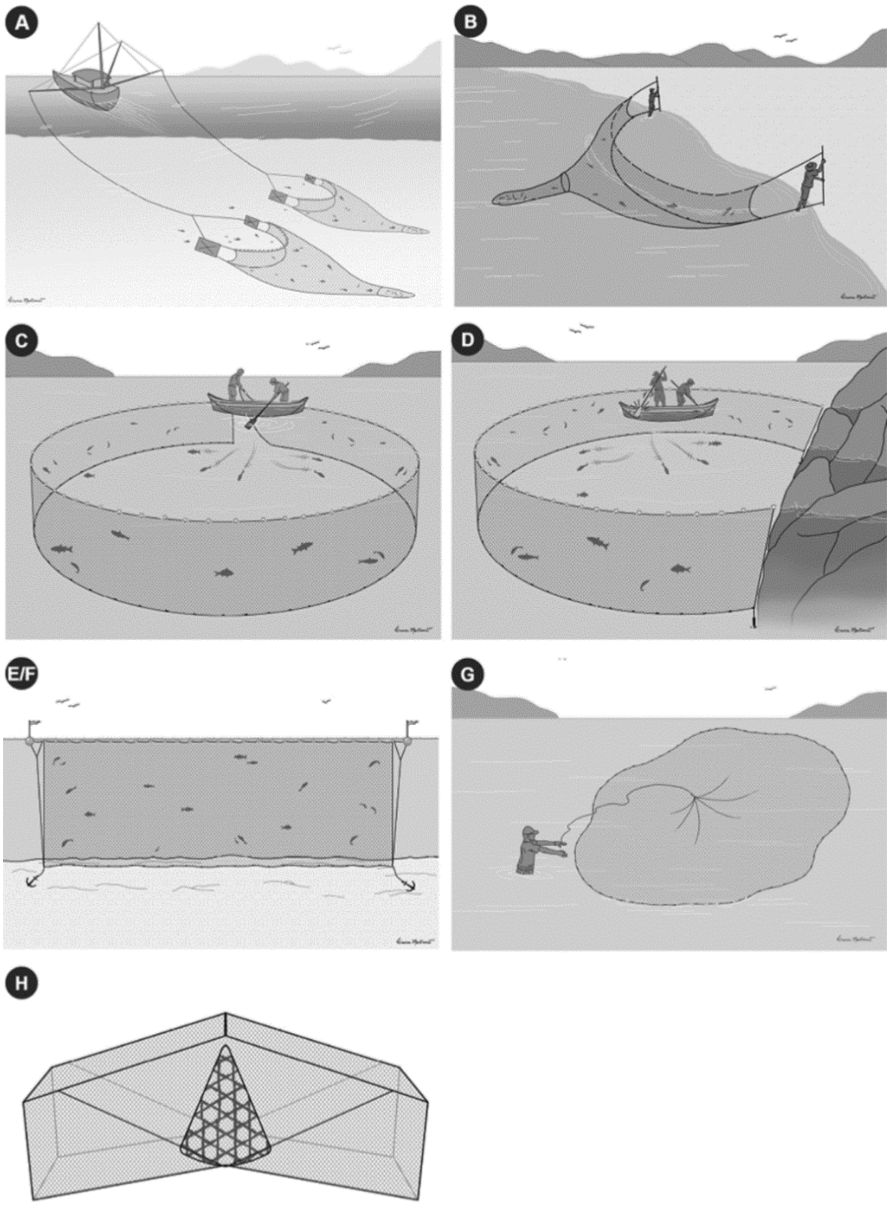


Figure 5. Schemes of fishing gears employed in sampling fish faunal diversity in Araçá Bay: a) otter trawl; b) beach seine; c) encircling gillnet 1; d) encircling gillnet 2; and f)

large and small gillnets; g) cast net; h) fish trap; and hook and line, not illustrated. (Source images: Ichthyofauna and Growth Laboratory – LABIC, University of São Paulo, designer: Laura Montserrat).

2.3. Geometric morphometric data and analysis

The geometric morphometric method was used to quantify and describe the shapes of species and to represent morphological variability within morphospaces (BOOKSTEIN, 1991; ROHLF; BOOKSTEIN, 2003; LOMBARTE et al., 2012; TUSET et al., 2014). Fish morphometric data were obtained considering 27 landmarks and semilandmarks (Figure 6) (following RECASENS; LOMBARTE; SÁNCHEZ, 2006; FARRÉ et al., 2013, 2015, 2016; TUSET et al., 2014; SMITH et al., 2016). For each species, a consensus image (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012) was built from the composed samples (10 fish images) using tpsDig, v.2.16 (ROHLF, 2001). The landmarks and semilandmarks were digitalized, rotated, scaled (to unit centroid size), and translated. Then, a generalized least-square superimposition (GLS) procedure (generalized Procrustes) was applied using tpsRel 1.24 (ROHLF, 2001). A thin-plate spline representation was used to fit the interpolated function to an average map (consensus configuration) of the profile shape, resulting in uniform components of the shape variation (relative warps, RW). Finally, a relative warp analysis allowed changes in shapes to be visualized (ROHLF; BOOKSTEIN, 2003). According to Recasens, Lombarte and Sánchez (2006) and Lombarte et al. (2012), the first eight RWs explain more than 95% of the total morphological variability and describe each species. The morphospaces based on qualitative data (presence/absence) were generated using only three warps, since they represented around 70% of the variability, allowing the structural complexity of the fish assemblage of each gear and all gears together to be discerned. The Euclidean distances between all pairs of aligned and scaled specimens in the tangential plane, and the Procrustes distances between all pairs of specimens in the Kendall shape space, were compared using TpsSmall 1.33 (ROHLF, 2015). The correlations indicated minimal variation between all fishing gears ($r > 0.9999$).

2.4. Measuring morphological diversity

Three morphological indices were estimated for each fishing gear and all gears together based on the presence/absence data matrix. The Morphological Richness

Index, MR= ∑jCC (FARRÉ et al., 2013), Morpho-geometric Diversity Index, EMI= ∑jCC/(N-1) (RECASENS et al., 2006; LOMBARTE et al., 2012), and Morphological Disparity, MD= ∑jRWj^2/(N-1) (ZELDITCH; SHEETS; FINK, 2003; ANTONUCCI et al., 2009) were calculated and classified by hierarchical agglomerative cluster analysis using the Euclidean distance (where, CC is the cluster coefficient, j is the species, N is the total number of species, and RWj represents the species relative warps).

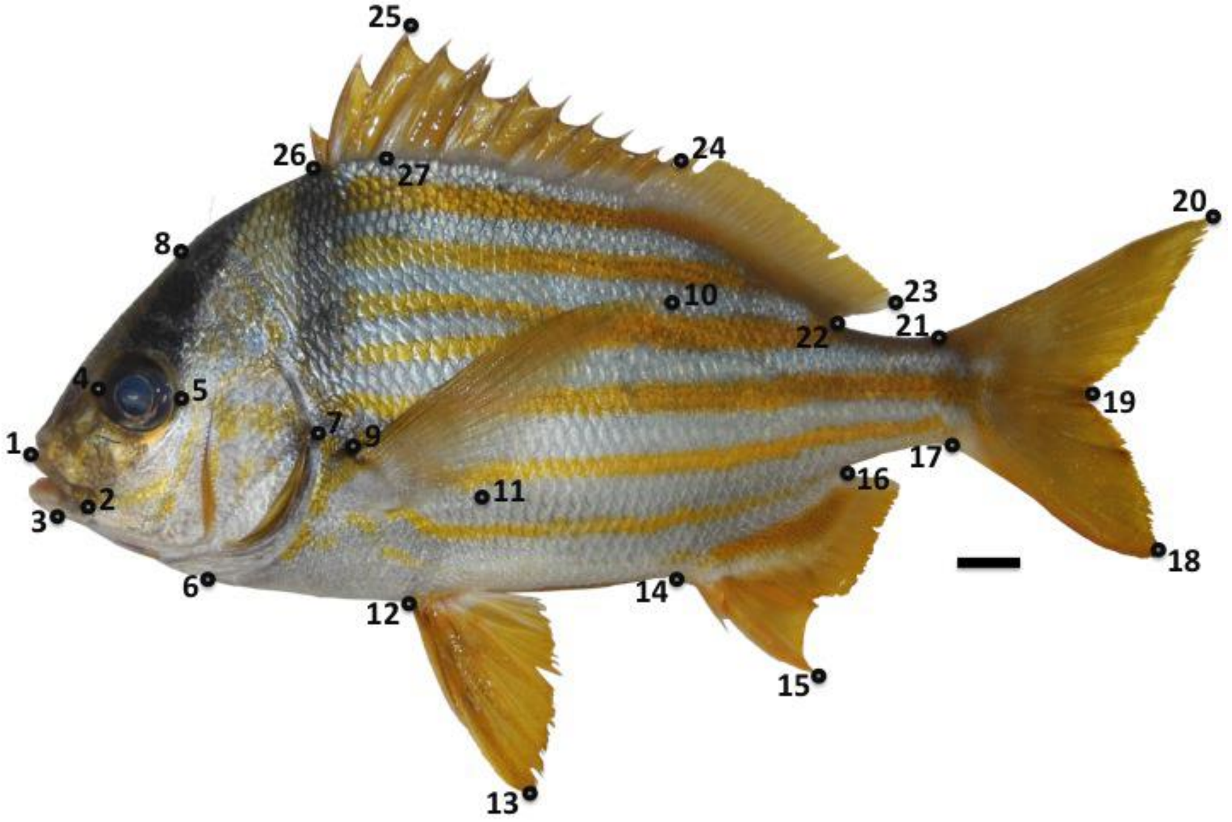


Figure 6. Landmarks and semilandmarks used in the geometric morphometric analysis. Morphological meanings: **1** and **2**, the mouth position and size in relation to the head and body size; **3**, the presence and size of sensorial barbells; **4** and **5**, the size and position of the eyes in relation to the head and body size; **6 to 8,** the relative head size (height and width) respect to the body size; **9 to 11**, the size, shape and position of pectoral fins; **12** and **13**, the size, shape and position of pelvic fins; **14 to 16,** the size, shape and position of the anal fin; **17 to 21**, the shape and size of the peduncle and of the caudal fin; **22** and **23**, the second dorsal fin position and ending; **24**, the presence of one or two dorsal fins; **25** and **26**, the first dorsal fin position and starting; **27**, the maximum height of the body shape.

2.5. Statistical analysis

To explore the influence of the gears on the morphological structure of the fish assemblage, a redundancy analysis (RDA) was performed on all nine fishing gears (LEGENDRE; LEGENDRE, 1998). This technique uses one matrix showing the presence/absence of each species for each fishing gear (predictor variables) to quantify their variation in a matrix of response variables (the first two relative warps of all species). The explained variance was derived from the sum of squares on a regression (RICHARDS; JOHNSON; HOST, 1996).

3. Results

3.1. Composition and morphological structure of the fish assemblage

Overall, 106 teleost species (Supplementary Material, SM 1), belonging to 47 families were identified. The most common species were: *Harengula clupeola, Sardinella brasiliensis* (Clupeidae), *Eucinostomus argenteus, Diapterus rhombeus* (Gerreidae), *Atherinella brasiliensis* (Atherinopsidae), *Mugil curema* (Mugilidae), and *Haemulopsis corvinaeformis* (Haemulidae).

Morphological analyses revealed a wide variety of shapes, such as, anguilliform (i.e., *Gymnothorax ocellatus*), fusiform (i.e., *E. marginatus*), elongated (i.e., *Hemiramphus brasiliensis*), oblong (i.e., *Prionotus punctatus*), oval (i.e., *Lagocephalus laevigatus*), asymmetrical flatfish (i.e., *Citharichthys macrops*), and seahorse (i.e., *Hippocampus reidi*). In the general morphospace, the first axis (RW 1, 37.5% of the total variance) was related to the position of the first dorsal fin and body shape; elongated for positive values, and higher bodies, laterally compressed for negative values (Figure 7). The second axis (RW 2, 25.4%) defined elongated fish shapes with the first dorsal fin distant to the head (positive values), and benthic fishes with dorsal-ventral flattened shapes or elongated dorsal and anal fins (negative values) (Figure 7). The third axis (RW 3, 7.8%) expressed the pelvic fin position, gave positive values when anterior and near to the scapular girdle, or negative values when the pelvic fin was posterior or modified (Figure 7). Within the convex hull, two major groups were identified: one formed by demersal species, such as grunts (Haemulidae), mojarras (Gerreidae), and croakers (Sciaenidae), and another formed by active swimmers, such as clupeids, engraulids, and neotropical silversides (Atherinopsidae) (Figure 8). The remaining species tended to disperse in the morphospace depending on their morphological specialization and on the relative warp used to represent the external variability (Figure 8A with the first and second warps; 8B with the first and third warps). The species located in the peripheral morphospace provided the highest morphological dispersion and variability of the fish assemblage, i.e., eel-like fishes (Anguilliformes), flatfishes (Pleuronectiformes), porcupinefishes (Diodontidae), halfbeaks (Hemiramphidae), seahorses (Syngnathiforms), and some carangids.

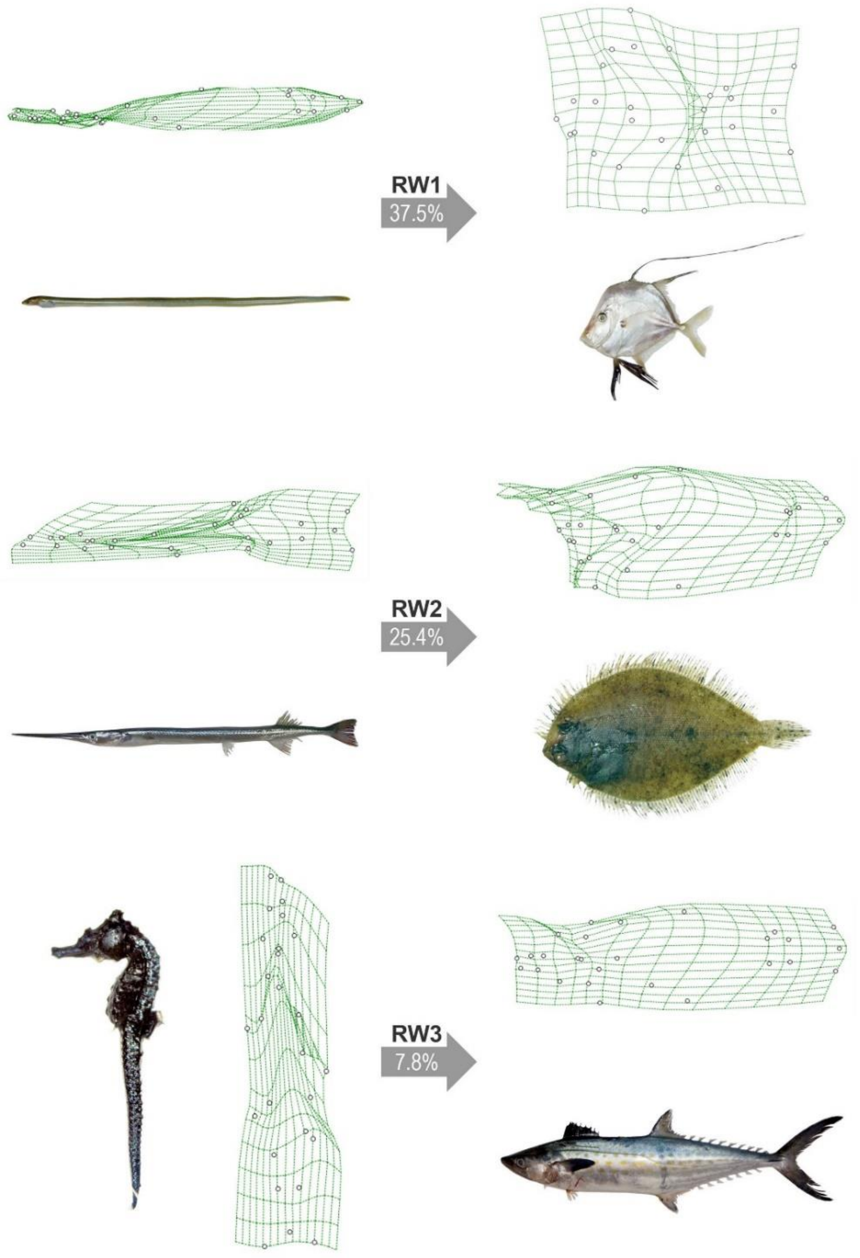


Figure 7. Morphological changes and variance explained for the relative warps 1 to 3 using the thin-plate spline.

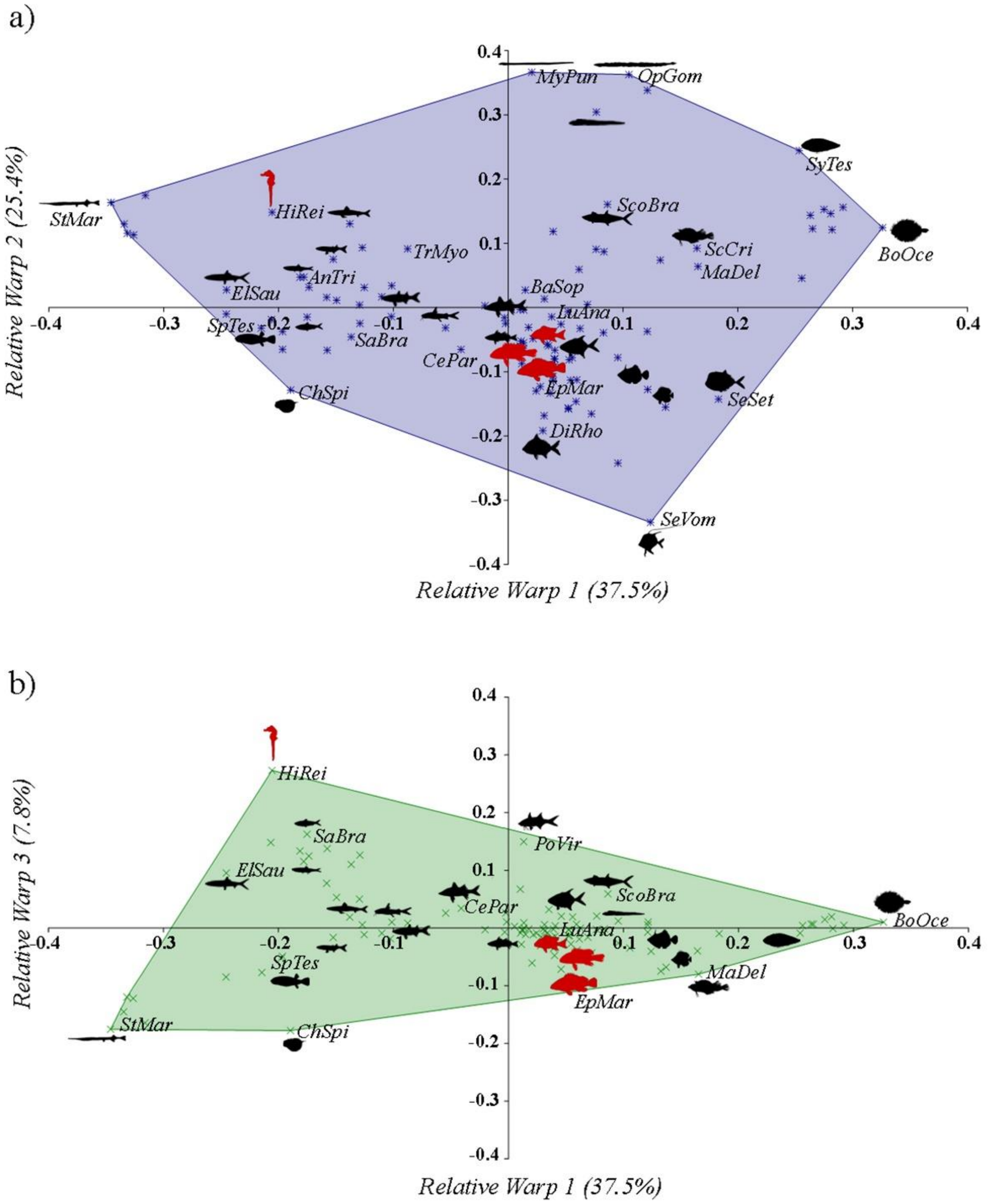


Figure 8. General morphospace represented by shape variation using the relative warps: a) 1 and 2; b) 1 and 3. Threatened species (*Hippocampus reidi, Lutjanus analis, L. cyanopterus* and *Epinephelus marginatus*) are highlighted in red.

3.2. Morphological variability according to each gear

Otter trawl and beach seine (both active gears) captured a higher number of species (53 and 52, respectively) and the highest diversity of body shapes. Otter trawl morphospace (Figure 9) was composed mainly by flatfishes (*Bothus ocellatus*, *Syacium papillosum, Citharichthys spilopterus*), fusiform bodies moderately compressed (*Micropogonias furnieri, Haemulon steindachneri, Diplodus argenteus*) or much laterally compressed (*Oligoplites saurus, Hemicaranx amblyrynchus, Stephanolepis hispidus*), and by oval bodies (*L. laevigatus, Sphoeroides greeleyi, Sphoeroides testudineus*). The beach seine morphospace (Figure 9) was composed by eel-like fishes (*Myrophis punctatus, Ophichthus gomesii*), fishes with a pointed snout (*H. brasiliensis, Hyporhamphus roberti, Strongylura marina*), very specialized shapes (as the seahorse *H. reidi*), cylindrical elongated bodies (*Synodus foetens, Trachinocephalus myops*), fusiform adapted to live hidden or burrowed (*Malacoctenus delalandii, Ctenogobius boleosoma, Bathygobius soporator*), and some clupeid forms (*Opisthonema oglinum, H. clupeola, S. brasiliensis*). The inner encircling gillnet (Figure 9) also caught demersal species, similar to the otter trawl, but mainly mojarras (*E. argenteus, Eucinostomus melanopterus, Eucinostomus gula*), weakfishes (*Cynoscion jamaicensis, Cynoscion leiarchus, Menticirrhus americanus*), snooks (*Centropomus parallelus, Centropomus undecimalis*), and mugillids (*Mugil liza, M. curema*). The marginal encircling gillnet (Figure 9) capture was much similar to that of the inner encircling gillnet; however, fish shapes with higher mobility were captured (*Caranx latus, Trachinotus carolinus, Selene setapinnis, Selene vomer, Pomatomus saltatrix*). The cast net (Figure 9) operated on intertidal, marginal shallow sublittoral and inner shallow sublittoral habitats, and contributed with the most variable morphologies in comparison to the other gears. Indeed, it was an important way in capturing clupeid species. Among passive gears, fish trap (Figure 10) caught shapes adapted to life in rocky bottoms (*Chaetodon striatus, Nicholsina usta, Mycteroperca acutirostris, E. marginatus*), and some of these were also obtained by hook and line (Figure 10). Hook and line operated mainly on reef-associated species (*Scartella cristata, Labrisomus nuchipinnis*). Additionally, the small gillnet (Figure 10) allowed the capture of demersal species associated with muddy bottoms, such as the catfish (*Genidens genidens*) and the threadfin (*Polydactylus virginicus*). The large gillnet (Figure 10) caught fishes adapted to diverse habitats, and represented the only gear that fished the pelagic species *Anchoviella lepidentostole*, and *Tylosurus acus*. Beach seine, fish trap, hook and line, and marginal encircling gillnet registered the occurrence of three threatened species: the longsnout seahorse (*H. reidi*), the dusky grouper (*E. marginatus*), and the cubera snapper (*L. cyanopterus*). Adult and juvenile forms of the mutton snapper (*L. analis*), another threatened species, were recorded by most of the gears, except by the cast net and the fish traps.

3.3. Effect of fishing gear on the fish diversity estimates

The morphological indices indicated that the beach seine and otter trawl aggregated the highest morphological disparity (MD = 0.057 and 0.053, respectively) and morphological richness (MR = 7.03 and 6.35, respectively), whereas the inner encircling gillnet (MD = 0.042 and MR = 3.36) and the small gillnet (MD = 0.045 and MR = 3.63) attained higher values of morpho-geometric diversity (EMI = 0.160 and 0.158, respectively), indicating less redundancy of external morphology (Table 1).

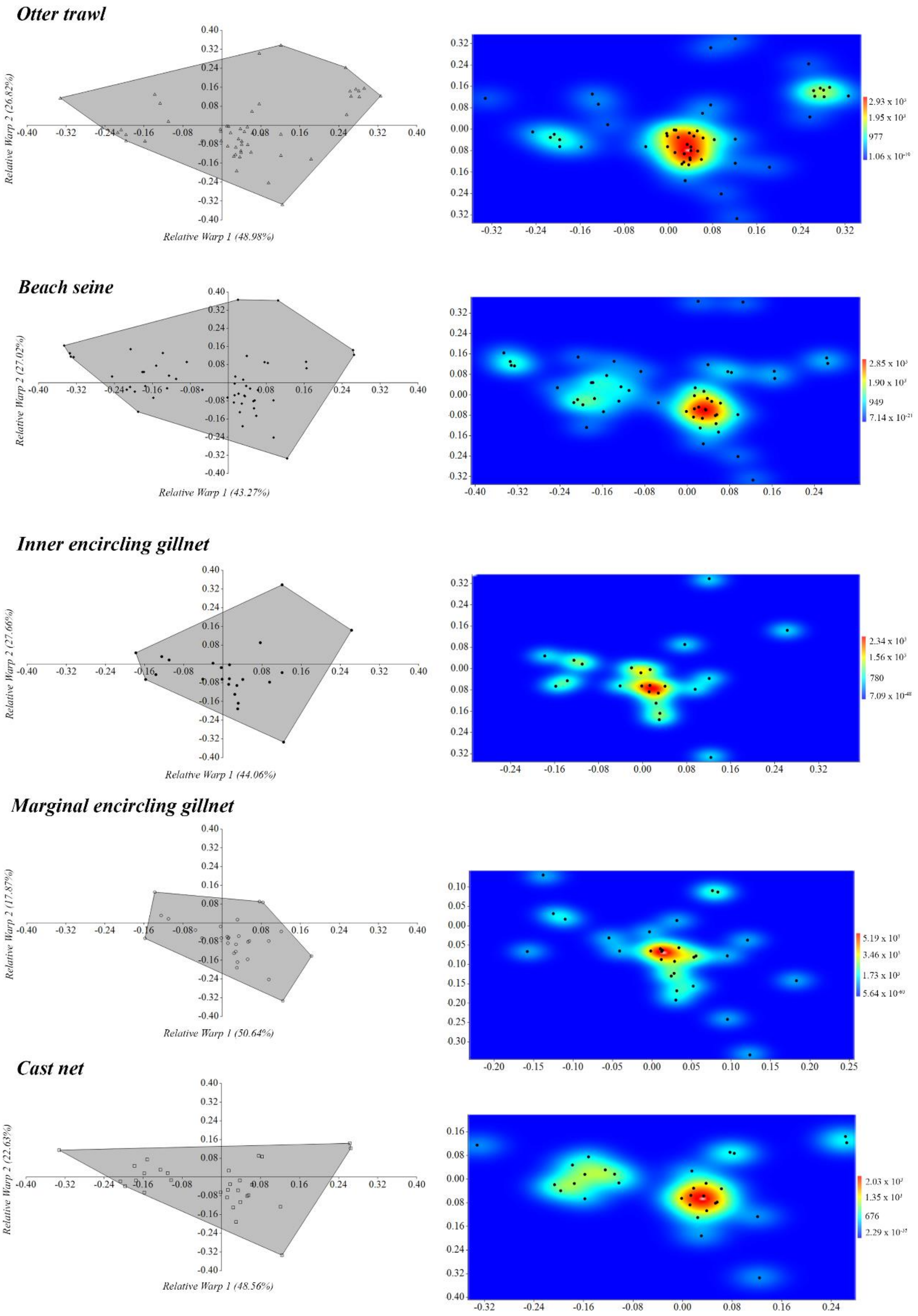
The RDA demonstrated that the morphological structure of the Araçá fish assemblage is expressed by a combination of fish shapes caught by complementary gears (Monte Carlo test, Pseudo-F= 0.260, P< 0.001) (Figure 11, Table 2). RDA1 attained 14.2% of the total inertia, and was mainly correlated to RW2 (r= 0.405, while r= -0.338 for RW1). The marginal encircling gillnet, fish trap, and beach seine were better correlated to RW1 (r= -0.193, r= -0.142 and r= 0.103, respectively). In contrast, the second RDA2 axis only explained 6.5%, and was correlated to both relative warps (r= 0.273 for RW1, and r= 0.229 for RW2). However, the otter trawl best defined the RDA2 axis (r= -0.123).

Table 1 - Morphological diversity indices estimated using incidence-based data for all fishing gears grouped and for each fishing gear: MD, morphological disparity; MR, morphological richness; EMI, morpho-geometric diversity.

Fishing gears	Morphological		
	MD	MR	EMI
Active gears			
Otter trawl	**0.053**	**6.35**	0.122
Beach seine	**0.057**	**7.03**	0.141
Inner encircling gillnet	0.042	3.36	**0.160**
Marginal encircling gillne	0.031	3.36	0.124
Cast net	0.044	4.16	0.149
Passive gears			
Large gillnet	0.038	3.42	0.149
Small gillnet	0.045	3.63	**0.158**
Hook and line	0.025	1.38	0.138
Fish trap	0.037	1.64	0.149
All	0.052	11.68	0.112

Table 2. Scores of explanatory variables in the redundancy analysis. In bold are the fishing gears representing some major fish shape variations.

Fishing gears	F1	F2
Beach seine	**0.103**	-0.038
Otter trawl	-0.080	**0.123**
Inner encircling gillnet	-0.006	-0.012
Marginal encircling gillnet	**-0.193**	-0.066
Large gillnet	0.001	0.011
Small gillnet	0.046	-0.039
Cast net	-0.019	-0.054
Hook line	-0.033	-0.003
Fish trap	-0.142	**-0.089**



Otter trawl

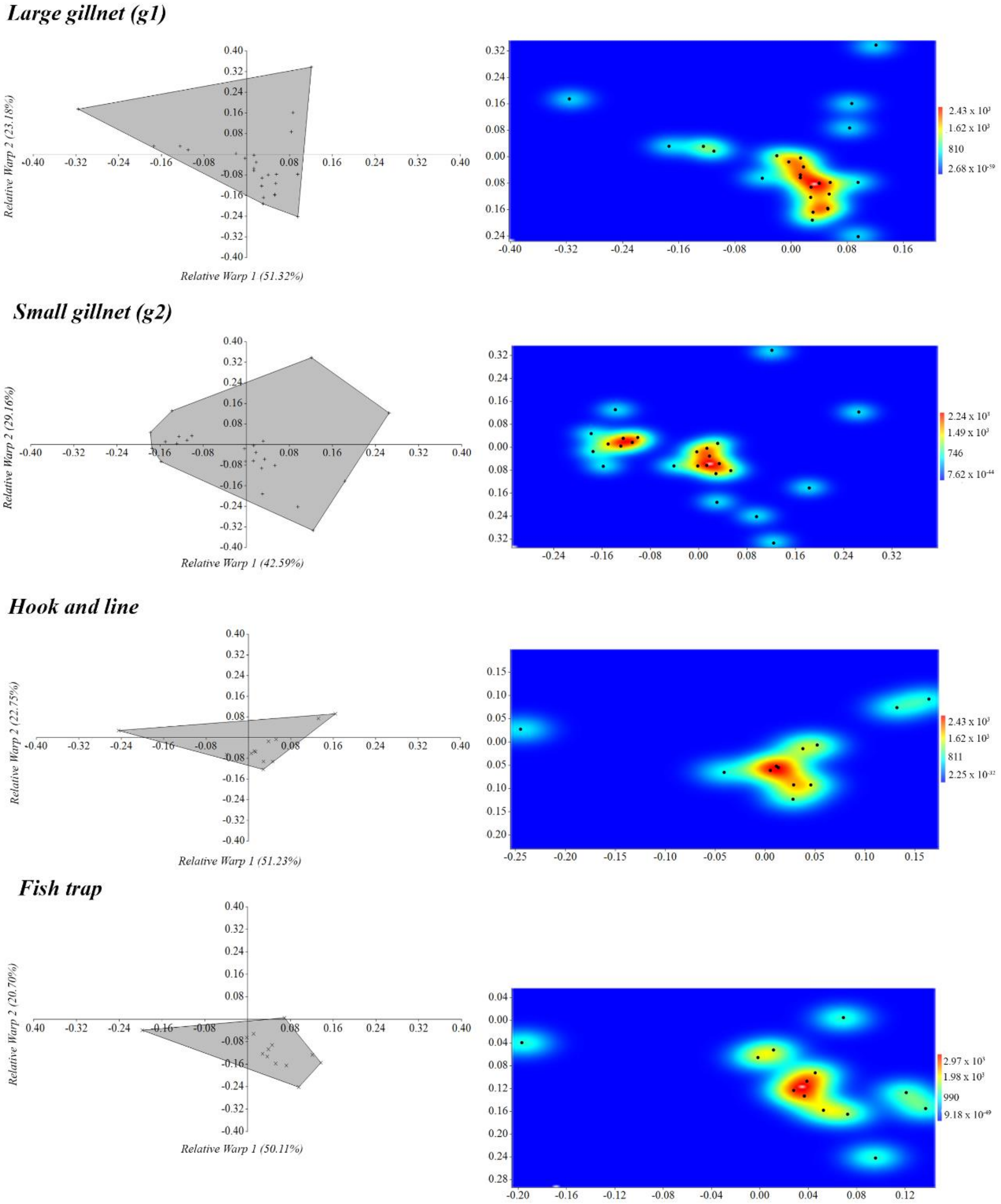
Beach seine

Inner encircling gillnet

Marginal encircling gillnet

Cast net

Figure 9. Morphospaces and Kernel density using the first and second relative warps for each active fishing gears (otter trawl, beach seine, inner encircling gillnet, marginal encircling gillnet and cast net).


Large gillnet (g1)

Small gillnet (g2)

Hook and line

Fish trap

Figure 10. Morphospaces and Kernel density using the first and second relative warps for each passive fishing gears (large gillnet, small gillnet, hook and line and fish trap).

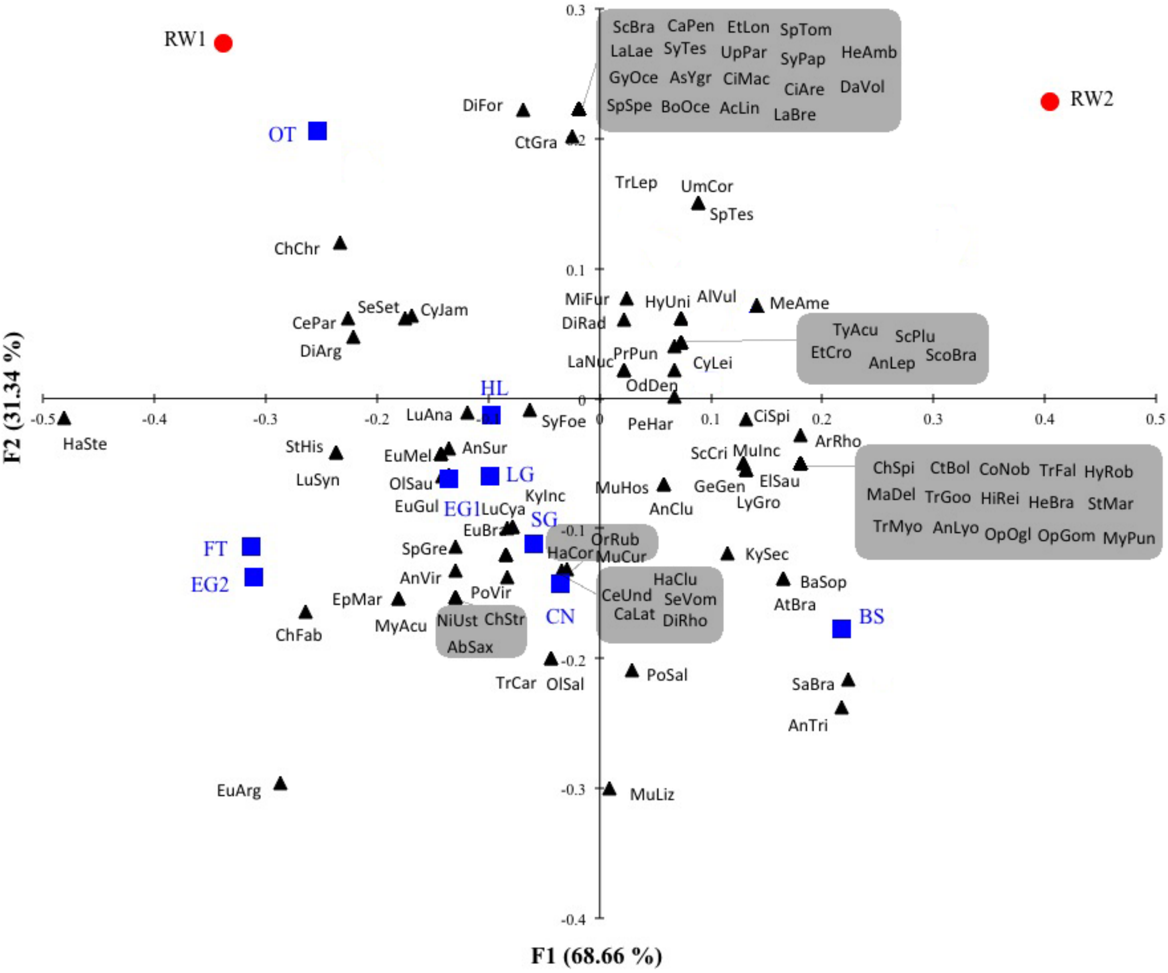


Figure 11. Redundancy analysis (RDA): individual species-gear relationships explained by morphological shape variability, using incidence data.

4. Discussion

Our findings demonstrate that some of the samplers (beach seine, otter trawl, marginal encircling gillnet, and traps) best represent the wide morphological diversity of these fauna which use the resources offered by this tidal flat. Each one of these fishing gears contributed in emphasizing a specific portion of the morpho-functional structure of the assemblage, showing species that perform distinct ecological functions in the studied ecosystem (RICKLEFS, 2010; ARANTES, 2014; LEITÃO et al., 2016). The active fishing gears (i.e. beach seine, otter trawl, and encircling gillnets) were less selective and more precise at revealing the fish spatial distribution and habitat use (BROADHURST et al., 2006). In turn, the capture of traps was directly dependent on fish behavior and morphology (HAYES; FERRERI; TAYLOR, 2010; ALÓS; PALMER; ARLINGHAUS, 2012; ALÓS et al., 2014). Beach seine was crucial to represent the richness, comprising the largest extent of morphological and taxonomical variabilities. Commonly used to capture mid-water and bottom-dwelling fishes (BUTCHER et al., 2005; DEMBKOWSKI; WILLIS; WUELLNER, 2012), beach seine captured the majority of small-to-medium species as well as elongated and active ones, such as halfbeaks (*Hyporhamphus roberti, H. unifasciatus and Hemiramphus brasiliensis*), which possess long premaxillae's that probe the substrate to find preys (HOBSON, 1975). Likewise, beach seine retained many small shapes, probably because it was operated at the intertidal zone and close to mangrove spots, an area of advantageous conditions for feeding and refuge. Highly specialized species (peripheric in the morphospace) could also be recorded by beach seine, like the sea horse *(H. reidi*), nowadays considered threatened by the loss and degradation of some of their preferred habitats, particularly mangroves, caused by the use of coastal areas.

Species situated at the periphery of the morphospace provided more morphological variability, meaning that they are less abundant and more sensible to anthropogenic perturbations (LOMBARTE et al., 2012; FARRÉ et al., 2016). In contrast to beach seine, otter trawl mainly captured flatfishes (flounders) and oval shapes (pufferfishes) (both peripheral species), besides some demersal fusiforms (croackers) with great importance for local fishermen. However, otter trawl *per se* would slightly underestimate the fish morphological variability since it did not sample many small pelagic species at the surface. In a complementary way, the marginal encircling gillnets and traps caught the fusiform shapes centrally located at the morphospace but associated with rocky bottoms.

Worldwide, coastal shallow sandy areas (including tidal flats) are recognized as important nurseries and growth grounds for fish (MCLACHLAN, 1983; ELLIOTT; DEWAILLY, 1995; BECK et al., 2001; GILLANDERS et al., 2003; ADAMS et al., 2006; FAUNCE; SERAFY, 2006; WRIGHT et al., 2010; FAVERO; DIAS, 2015; LE LUHEME et al., 2017). The peculiar presence of small mangrove spots in Araçá Bay, the habitats heterogeneity and its hydrodynamics, provide shelter and food for juveniles of many species, including important commercial ones, besides being a natural refuge for some threatened species, such as the snappers *L. analis* and *L. cyanopterus*, and the dusky grouper *E. marginatus* (LAMAS; ROSSI-WONGTSCHOWSKI; CONTENTE, 2016; CONTENTE; ROSSI-WONGTSCHOWSKI, 2017). Gibson (1994), Vasconcelos et al. (2013), and Le Pape and Bonhommeau (2015) consider this kind of ecosystem as a nursery ground, and according to Nagelkerken et al. (2015) and Sheaves et al. (2014), this characteristic renders a substantial importance for its conservation.

In conclusion, as fish vulnerability is strongly dependent on their shape, body size, behavior and habitat (EHLINGER, 1990; WILEMAN, 1996; BOURKE; MAGNAN; RODRÍGUEZ, 1997; DOMENICI; BLAKE, 1997; FULTON; BELLWOOD, 2005; FULTON; BELWOOD; WAINWRIGHT, 2005; DOMENICI et al., 2008; LANGERHANS; REZNIK, 2010; ALÓS et al., 2014), the catch effectiveness depends on the gear type selected (BAYLEY; HERENDEEN, 2000; NEWMAN et al., 2012; WALKER et al., 2017). Consequently, biodiversity studies with a reduced number of samplers can underestimate the morpho-functional richness, and therefore, cause inaccurate assessment of the ecosystem. According to Selig et al. (2014), due to the high richness recorded in Araçá, it has greater resilience to environmental stress than other similar communities with lower richness. Nevertheless, caution is needed since few is known about the population conditions of the Brazilian ichthyofauna, being most of the species classified as “deficient data” (BRASIL, 2014). Although the spatial distribution of species in the hole morphospace was similar to other coastal fish assemblages (LAYMAN et al., 2007; FARRÉ et al., 2013, 2014, 2016; TUSET et al., 2014), the Araçá assemblage showed high morphological redundancy, which could be considered a resistance of the ecosystem in avoiding the biodiversity loss (MICHELI et al., 2014; MOUILLOT et al., 2016). During the harbor expansion predicted for the future, the morphological analysis would be an useful tool to monitor the fish assemblage and possibly to detect structural changes, as demonstrated for other sites (WAINWRIGHT; RICHARD, 1995; LAYMAN; LANGERHANS; WINEMILLER, 2005; LOMBARTE et al., 2012; OLIVER et al., 2015). Even though morphological analysis is efficient to diagnose both species composition and assemblage structure, it must be employed together with a functional diversity analysis to determine resilient are the habitats of the Araçá ecosystem.

3.

How diversity indicators reveal fish habitats use

Abstract

Fish assemblages in intertidal (IH), inner/outer sublittoral (IOS) and marginal shallow sublittoral (MSS) habitats within a subtropical tidal flat were sampled with specific fishing gears. The objective was to test if these habitats contain similar fish assemblages (in terms of abundance, diversity and morpho-functional structure), and to establish what habitat/s will be more sensitive if a hypothetical environmental degradation would occur. Fish assemblages associated with these habitats were significantly different in terms of diversity, abundance, and morpho-functional structure. The intertidal habitat presents a larger number of specimens and greater morpho-functional diversity being strongly dominated by pelagic species. The inner/outer sublittoral supported similar number of species but lesser abundance being dominated by benthopelagic and benthic species. The marginal shallow sublittoral showed a distinct morpho-functional diversity from the other two habitats. Juveniles of sardines, silver mojarra, white mullet and all stages of the Brazilian silversides dominated the IH habitat, while IOS was mainly dominated by barbel drum, silver mojarra and the roughneck grunt. At the MSS, were abundant the caitipa mojarra, the southern weakfish, and the flagfin mojarra. The three habitats serve the species in a functionally distinct manner, as nursery, food supply or protection. IH habitat is essential in the tidal flat being an important feeding source for all fish assemblages. In case of it would be damaged, the whole ecosystem functioning would be very affected.

1. Introduction

The variability among living organisms and the ecological processes from which they are part has been defined as “biodiversity” (MAGURRAN, 1988, 2004; COLWELL, 2009; MAGURRAN; MCGILL, 2011). Biological diversity includes the variability within and between species and within and between ecosystems (MAGURRAN; MCGILL, 2011). Therefore, it spans over a range of organizational levels: ecological, taxonomic, phylogenetic, morphological and functional (WALKER, 1992; NORTON; LUCZKOVICH; MOTTA, 1995; WAINWRIGTH, 1996; MAGURRAN, 2004; OLSSON; EKLÖV, 2005; WILLIS; WINIEMILLER; LOPEZ-FERNANDEZ, 2005; PETCHEY; GASTON, 2006; ELLIOT et al., 2007; MOUCHET et al., 2010; PETCHEY; BELGRANO, 2010; LOMBARTE et al., 2012; PRICE et al., 2012; BOOKSTEIN, 2013; FARRÉ et al., 2013; DREISS et al., 2015; ZHU et al., 2017).

At the species level, diversity corresponds to multiple forms of adaptation and integration with the habitat complexity (HUTCHINSON, 1957; MACARTHUR; MACARTHUR, 1961; GARPE; ÖHMAN, 2007; GAILLARD et al., 2010). The presence of species, its functional role, abundance and distribution are determined by resources available in the environment (as food, shelter, predation) (MANNA; REZENDE; MAZZONI, 2013) and influence the ecosystem properties since they act in concert with abiotic factors (i.e. temperature, depth, bottom type, disturbances) (HOOPER et al., 2005). In return, the habitat structural heterogeneity provides a wide variety of microhabitats and niche spaces, which may support higher richness and morphological diversity (WILLIS; WINEMILLER; LOPEZ-FERNANDEZ, 2005; KOVALENKO; THOMAZ; WARFE, 2012). However, although the organization and the biological interactions are determined by local characteristics of the habitat, the organisms functional attributes (morphological, physiological, reproductive or behavioral) are the major mediators of the ecosystem functioning (PETCHEY; GASTON, 2002).

The structural complexity of habitats has been linked to fish species richness in both freshwater and marine environments. Many studies examined distinct components such as topography and depth (JENNINGS; GRANDCOURT; POLUNIN, 1996; WALKER; JORDAN; SPIELER, 2009; KOMYAKOVA; MUNDAY; JONES, 2013; DARLING et al., 2017), rugosity (GRATWICKE; SPEIGHT, 2005; BEJARANO et al., 2015), substratum type - which includes live cover of corals and algae - (BELL; GALZIN, 1984; CHABANET et al., 1997; MUNDAY; JONES; CALEY, 1997; OHMAN; RAJASURIYA, 1998; PRATCHETT; WILSON; BAIRD, 2006; KOMYAKOVA; MUNDAY; JONES, 2013; TREBILCO et al., 2015), current flows and exposure (DOMINICI-AROSEMENA; WOLFF, 2005; FLOETER et al., 2007; GREGOR; ANDERSON, 2016). All these structural elements are associated not only with increased richness or abundance, but also with recruitment success and survival (CONNELL; JONES, 1991; SHEAVES et al., 2015), fish sizes distribution (ROGERS; BLANCHARD; MUMBY, 2014; DARLING et al., 2017; STAMOULIS et al., 2018), predation strategies or predator avoidance (BEJARANO et al., 2015; NAGELKERKEN et al., 2015; MURRAY; STILLMAN; BRITTON, 2016; GREGOR; ANDERSON, 2016), and morpho-functional differentiation (WILLIS; WINEMILLER; LOPEZ-FERNADEZ, 2005; PRICE et al., 2012; LOMBARTE et al., 2012; FARRÉ et al., 2015). In freshwater ecosystems conservation, woody debris and rocky habitats had been added in habitats to facilitate fish spawning and feeding (MANNY et al., 2010). The results obtained in the Detroit River suggest that the reproduction of the walleye (*Sander vitreus*) and the white sucker (*Catostomus commersoni*) at this spawning ground occurs when the bottom substrates are composed by rocks and gravels, providing protection to the deposited fish eggs (MANNY et al., 2010). In addition, the structurally complex mangrove roots increase the surface area available for epiphytic colonization, providing foraging habitats for fish while giving refuge against large fishes and crabs (LAYMAN et al., 2007; MACKENZIE; CORMIER, 2012). Coral-reefs, a highly productive habitat with physical hydrodynamic and complexity, create rich environments for fish niche partitioning and specialization, mainly related to predation strategies and predator avoidance (PRICE et al., 2012). Likewise, cold-water corals (scleractinian, antipatharian, gorgonian and stylasterid) represent complex habitats at deep-sea, acting as nursery grounds and adult habitat for *Sebastes spp* and offering protection against predators (ROBERTS et al., 2009; BAILLON et al., 2012). In this way, the knowledge about how assemblages are structured have been mandatory to understand the relationship between biodiversity and ecosystems functioning, as well as the environmental consequences of biodiversity loss (NAEEM, 2002).

Despite the generalized use of ecological measures in charactering biodiversity (i.e., species richness), they are insufficient to reveal the effect of natural or anthropic changes due to their little predictive power about the community’s structure and its functioning (WEBB, 2000; PETCHEY, 2004; CIANCIARUSO et al., 2009). Phylogenetic and taxonomic species relationships and their morphofunctional traits have been considered most robust estimates to investigate diversity and perturbations (PETCHEY; GASTON, 2006; LOMBARTE et al., 2012). Nevertheless, to estimate the phylogenetic diversity of a assemblage it is necessary to have the sequencing of various genes (WEBB, 2000) and this information is not available for many species, although several research groups are working on this subject. Taxonomic indices measure the relatedness of species within a community based on taxonomic hierarchy, by comparing the average path length among pair of species (WARWICK; CLARKE 1995, 1998; CLARKE; WARWICK, 1998, 2001b). Due to it practicality, taxonomic indices are most common in biodiversity studies. Their major advantages of them are the independence of sampling effort (AZEVEDO et al., 2017), the capacity to assess anthropogenic effects and to determine the extent and rate of environmental change

(LEONARD et al., 2006; O’CONNELL; O’CONNELL; HASTINGS, 2009; LEFCHECK et al., 2014; BARJAU-GONZÁLEZ et al. 2016).

Alternatively, other diversity indices have been developed based on morphological and functional distances between two species and their spatial distribution within a convex hull (SCHOENER, 1974; TILMAN, 2001; PETCHEY; GASTON, 2006; RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; FARRÉ et al., 2016). The functional diversity allows to better understand the coexistence of mechanisms among species, characterizing their functional responses and identifying anthropogenic effects on biological communities (ZHU et al., 2017). This approach focuses on species functional traits to couple the community dynamics with ecosystem functioning (HOOPER et al., 2005). A clear example is the body size, which is an indicator explaining variations in fish assemblage structures (PETCHEY; BELGRANO, 2010; EMMRICH et al., 2011) and where small juveniles-sized representatives are more abundant closer to the shoreline occupying habitats which provide food and shelter (HYNDES et al., 2003).

In marine tidal flat ecosystems, the available information about its biodiversity and their habitats influence on the structure of fish assemblages is scarce, mainly in regional scale. Many studies show the relevance of tropical coastal mangroves as nursery and feeding grounds for juveniles of commercial importance fish species (CHONG et al., 1990; KRUMME, 2003; DIAS et al., 2016; WHITFIELD, 2016; LE LUHEME et al., 2017), as well as the abundance decrease of lesser mobile species with distance increase related to low tides (MORRISON et al., 2002). In Brazil, the information about the ichthyofauna in tidal flats is recent (VENDEL et al., 2003; SPACH et al., 2004; DOLBETH et al., 2016; SILVA-JUNIOR et al., 2016; AZEVEDO et al., 2017; MÉRIGOT et al., 2017; VITULE et al., 2017; CONTENTE; ROSSI-WONGTSCHOWSKI, 2017). So, there are not historical data regarding the diversity and abundance of species in these ecosystems. But, precisely due to its high biodiversity, tidal flats have special social, economic and ecological relevance providing food, subsistence and recreation for the surroundings artisanal communities. A clear example is the Araçá Bay, a tidal flat area in the southeastern Brazil, characterized by high complexity which supports high biodiversity and provide food and refuge (for spawning and nursery) for many fish and crustaceans species, including commercial ones (AMARAL et al., 2016; CONTENTE; ROSSI-

WONGTSCHOWSKI, 2017). Recently, Contente and Rossi-Wongtschowski (2017) have analyzed the fish assemblage structure of this bay under a classical ecological approach, finding high fish diversity.

Given its habitats heterogeneity, we believe that some zones of Araçá Bay should have major influence in the overall diversity of the bay, and their conservation and protection should be priorititized. In order to examine this idea, the aim of this study was to determine the diversity in the three main habitats of Araçá Bay (intertidal, inner/outer sublittoral, marginal sublittoral), establishing the most sensitive in case of a hypothetical environmental degradation.

2. Material and Methods

2.1. *Sampling*

This study was performed in a subtropical tidal flat of the southeastern Brazilian region, the Araçá Bay (~0.5km²), at the Western Atlantic Ocean (Figure 12). Data were collected during four research campaigns, carried out between March 2013 and January 2014, at twelve consecutive nights and during high tides. Standardized samplings were performed using three active gears: otter trawl, beach seine and marginal encircling gillnet (the more representative; see Chapter 2). All details of the sampling are available in Contente and Rossi-Wongtschowski (2017).

Fishing gears were used according to each habitat characteristics, which influence on its effectiveness. Otter trawl was used at the inner and outer sublittoral (IOS), beach seine tows were employed at the five sandy beaches of the bay in the intertidal habitat (IH) (average depth = 0.6 ± 0.3 m), and marginal encircling gillnets were performed in the marginal shallow sublittoral habitat (MSS) (average depth = 0.8 ± 0.4 m) (Figure 1).

Otter trawling was performed by a commercial pink-shrimp trawler with 8 meters (m) long and 100-HP traction power, provided with twin-gear trawl (each one with 9.5-m long, attached to 30 kg flat wood otter boards). The net mouth was approximately 1.0m high when in activity, covering 70-80% of the water column. Four random and independent transects were performed in the inner sublittoral habitat (mean depth = 1.2 ± 0.5 m – standard deviation) and three in the outer sublittoral one (mean = 8.4 ± 4.1 m) (interface with the São Sebastião Channel, mean depth= 30 m). The geographic position was noted at the beginning and the ending of each tow. The tows distances were calculated by the trigonometric equation referred by Sparre and Venema (1997). The swept area was estimated as follow: [2 (two nets) × distance of the haul (m) × 0.5 (X_2) × 9.5 m (length of the fishing line)] assuming 0.5 as the fraction of the net ground-rope (X_2) effectively opened during the draw (PAULY, 1980; BARLETTA et al., 2008). The mean swept area by otter trawl was 2237 ± 1201 m^2.

Beach seine was 20-m wide, 3-m high with a 15-m long bag, and 5 mm of mesh size between knots. The tows locations were haphazardly selected (minimum distance from each other = 25 m). The swept area was estimated using Google Earth, based on the path of the tow covered with a GPS device (± 3 m). The mean swept area by beach seine was 362 ± 136 m^2.

Marginal encircling gillnet was 3-m high and 590-m long with a mesh size of 3 cm between knots. Two haphazard operations were performed with two fishermen in a canoe selecting an area and surrounding it with the net blocking the entire water column. Using oars, they produced noise on the sides of the canoe for 20 minutes driving the fishes towards the net. The area of the encircling was estimated using Google Earth, based on the path covered with an auxiliary canoe and a GPS device. The mean swept area by marginal encircling gillnet was 4272 ± 5021 m^2.

Fishes were identified according Figueiredo and Menezes (1978, 1980, 2000), Menezes and Figueiredo (1980, 1985), and Carpenter et al. (2002a, 2002b, 2002c); and, classified according to Eschmeyer, Fricke and Van der Laan (2014) and Eschmeyer and Fong (2015a; 2015b). Fresh specimens were measured to the nearest 1.0-mm total length (FTL). Standardized images (around 4,000) of the left side of the fish body of all species were obtained for morphological purposes (details in Chapter 2). The specimens were photographed in a white background base, being the structures (as fins, barbels, cutaneous appendages, and extended fin rays) trapped in with entomological pins and hardened with formalin. Samples including 10 fishes fitted into 10-mm intervals, were composed.

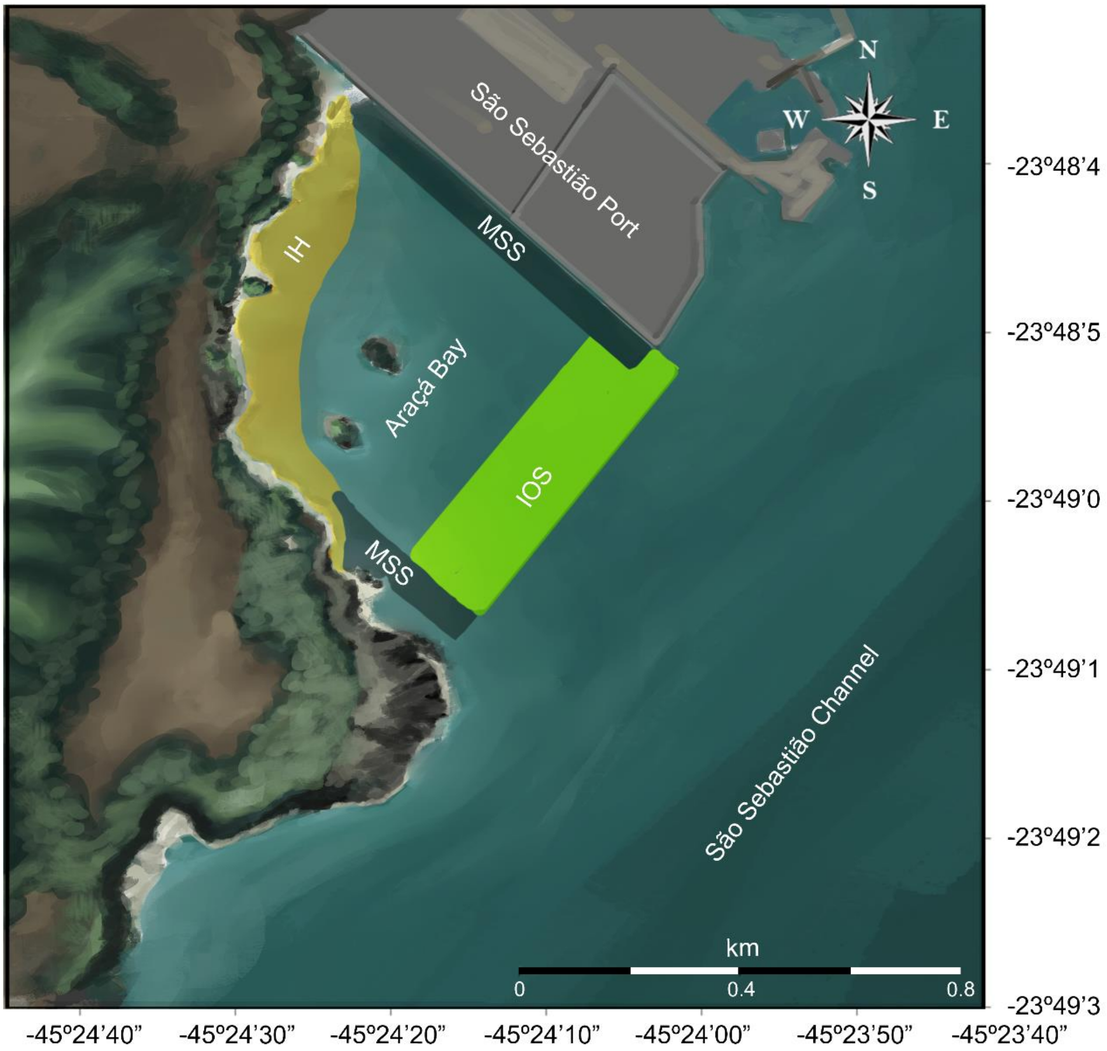


Figure 12. Araçá Bay. Habitats where the standardized samplings were performed, using three active gears: otter trawl at the inner/outer sublittoral (IOS), beach seine at the intertidal habitat (IH), and marginal encircling gillnet at the marginal shallow sublittoral (MSS).

2.2. Fish composition and habitat

The species abundance was expressed as number of fish × m^{-2} (density). Initially, abundance data were transformed by square root in order to equalize the weight between species and reduce the effect of the dominant ones. A Similarity Percentages Breakdown (SIMPER - One-way) procedure (CLARKE; WARWICK, 1994; CLARKE et al., 2014) was conducted to assess the average percent contribution of the species (at least 70%) to the dissimilarity among habitats (Bray-Curtis dissimilarity matrix) (WARWICK; CLARKE, 1995; CLARKE; WARWICK, 1998, 2001a; CLARKE et al., 2014).

2.3. *Morphological diversity*

The morphological structure of the fish assemblage of each habitat was investigated applying geometric morphometric analysis (GMA) (BOOKSTEIN, 1991; ROHLF; MARCUS, 1993; LOMBARTE et al., 2012; TUSET et al., 2014). To analyze the morphological features, samples containing 10 fish images were used to build one representative image to each species, the *"consensus"* (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012), by means of tpsDig, v.2.16 (ROHLF, 2010). Only one consensus image of each species was used. Fish shapes were described considering 27 landmarks and semilandmarks with anatomical, ecological and taxonomic senses (following RECASENS; LOMBARTE; SÁNCHEZ, 2006; FARRÉ et al., 2013, 2015, 2016; TUSET et al., 2014; SMITH et al., 2016). A generalized least-square superimposition (GLS) procedure (generalized Procrustes) was applied using tpsRel 1.24 (ROHLF, 2001) to digitalize, rotate, scale (to unit centroid size), and translate the landmarks and semilandmarks. For each species, the uniform components of shape variation (*relative warps, RW*) were obtained as result of a thin-plate spline representation applied to fit the interpolated function to an average map (consensus configuration), which were utilized to compare the deformations between specimen's shape.

According to Rohlf and Marcus (1993), Recasens, Lombarte and Sánchez (2006) and Lombarte et al. (2012), major morphological variability can be visualized by the first eight RWs. Morphospaces were plotted using PAST software v.3.16 (Paleontological Statistics software package, HAMMER; HARPER; RIAN, 2001) in two-dimensional charts of the first and second relative warps representing about 70% of the total morphological variation. Moreover, morphological indices were estimated taking into account the first eight relative warps based in both incidence and abundance data for each habitat. They were classified by hierarchical agglomerative cluster analysis using the Euclidean distance (where, CC is the cluster coefficient, j is the species, N is the total number of species, and RWj represents the species relative warps), being: i) Morphological Richness Index (MR= ∑jCC) (FARRÉ et al., 2013); ii) Morpho-geometric Diversity Index (EMI= ∑jCC/(N-1)) (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012); and, iii) Morphological Disparity (MD= ∑jRWj^2/(N-1)) (ZELDITCH; SHEETS; FINK, 2003; ANTONUCCI et al., 2009). Directly related to richness, the MR index quantifies the diversity of distinct morphologies within an assemblage (FARRÉ et al., 2013, 2016). Complementary, MD index measures and defines the morphospace size and configuration, while EMI determine the degree of species clustering within the morphospace (LOMBARTE et al., 2012; FARRÉ et al., 2013, 2016).

2.4. Functional Diversity

The functional strategy of each fish species was described using eight categorical traits, the biologically most representative to their fitness within the assemblage (VIOLLE et al., 2007) (Table 3).

Involving multiple traits, the ***body shape*** affects fish stability in the water column and its swimming ability influencing the behavior, the efficiency in preys' search and capture, evasion of predators, defense of territories and spawning (WALKER, 2010). ***Body shapes*** were ranked through seven ordered categories: anguilliform, asymmetrical flatfish, elongated, fusiform, horse, oblong and oval (FARRÉ et al., 2013, 2016; RIERA et al., 2017). Based on species composition, their ***swimming abilitys*** were separated in seven categories: amiiform, anguilliform, balistiform, carangiform, diodontiform, subcarangiform and tetraodontiform.

Fish size and ***mobility*** determine the amount of energy needed to maintain the body mass (RIERA et al., 2017). Therefore, ***fish size*** was ranked into five categories: <100 mm, >100-200 mm, >200-300 mm, >300-400 mm and >400 mm.

Mobility was ranked in three categories: sedentary (including territorial species), roving, and high mobile (including migratory species). The ***burying ability*** was specified (yes or no).

Diet provide understanding about prey-predator relationships besides feeding links between species (MOUILLOT et al., 2014). The ***diet*** was described based on the main items consumed by each species according to Halpern and Floeter (2008), leading to ten trophic categories: diurnal planktivore, nocturnal planktivore, macroalgae browser, scrappers, omnivores, colonial sessile invertivore, mobile benthic invertivores, sand invertivores, strict piscivores and macrocarnivores (i.e. fish, crustaceans, cephalopods).

The ***environment*** (exclusively marine or other) was obtained from Fishbase (FROESE AND PAULY, 2017). The ***vertical distribution*** in the water column establishing the ecological niche occupied by the species was ranked in four ordered categories: pelagic, benthopelagic, endobenthic (i.e. species owning burying ability) and epibenthic (i.e. species living above the substrate). A functional-trait matrix was prepared with the species categorization (Supplementary Material, SM 2).

A Principal Coordinates Analysis (PCoA) was performed after the nominal variables of the matrix were transformed to binary presence/absence variables (VILLÉGER; NOVACK-GOTTSHALL; MOUILLOT, 2011; CLAVERIE; WAINWRIGHT, 2014; MOUILLOT et al., 2014; FARRÉ et al., 2016) using R Program version 3.3.1. Finally, the resulting PCoA axis were considered as the new traits to compute the functional diversity indices (VILLÉGER; MASON; MOUILLOT, 2008).

The functional diversity estimates were: 1- ***Functional Evenness (Feve)***, that quantifies how the abundance is distributed in a functional trait space in order to allow effective utilization of the available resources (MASON et al., 2005). Besides being weighted by the species abundance, *Feve* is not biased by the richness. Its values range between 0 and 1, decreasing when the abundance among species is not evenly distributed or their functional distances are irregular (VILLÉGER; MASON; MOUILLOT, 2008). 2- ***Functional Divergence (Fdiv)***, that determines how far high species abundances are from the functional space center. This index ranges from 0 and 1, high values indicating low resource competition (MASON et al., 2005; RIERA et al., 2017; VILLÉGER; MASON; MOUILLOT, 2008). 3- ***Rao Quadratic Entropy (RaoQ)***, that evaluates changes in the abundance-weighted sum of pairwise functional distance among functional entities (PLASS-JOHNSON et al., 2016). Low functional richness indicates that some of the resources available to the community are unused (MASON et al., 2005). 4- ***Functional Redundancy (FR)***, corresponding to the number of species per functional entity (FE) within a community or, the number of unique combinations of the categorical functional traits previously selected (MOUILLOT et al., 2014). In this analysis, the number of categories for some traits was reduced to a crude categorization in order to avoid the induction of low functional redundancy (few species in each FE) (MOUILLOT et al., 2014). Finally, the functional trait spaces were built using the coordinates of the first and second PCoA axis for each species with the average abundance transformed in the third axis.

Table 3. Functional traits and categories used to describe each species (COLGATE; LYNCH, 2004; HALPERN; FLOETER, 2008; FARRÉ et al., 2013, 2016).

Functional trait	Code	Definition	Functional trait	Code	Definition
Body shape	Fu	Fusiform	*Diet*	MAC	Macrocarnivores
	El	Elongated		PIS	Strict piscivores
	Ob	Oblong		MINV	Mobile benthic invertivores
	Ov	Oval		SAND	Sand invertivores
	Sy	Symmetrical flatfish		SINV	Colonial sessile invertivores
	Ang	Anguilliform		DPLA	Diurnal planktivores
	As	Asymmetrical flatfish		NPLA	Nocturnal planktivores
	Ho	Horse		SCRP	Scrapers
				MALG	Macroalgae browser
Swimming type	Ang	Anguilliform		OMNI	General Omnivores
	Dio	Diodontiform			
	Sub	Subcarangiform	*Vertical distribution*	P	Pelagic
	Car	Carangiform		BP	Benthopelagic
	Bal	Balistiform		EPIB	Epibenthic
	Tet	Tetraodontiform		ENDB	Endobenthic
	Ami	Amiiform			
			Environment	Em	Exclusive marine
Fish size	S	Small 0-100 mm		Oe	Other environments
	SM	Small-Medium >101-200 mm			
	M	Medium >201-300 mm	*Motility*	S	Sedentary or territorial
	ML	Medium-Large >301-400 mm		R	Roving
	L	Large >401 mm		H	High mobile or migratory
Burying ability	Y	Yes			
	N	No			

2.5. Taxonomic Diversity

Two taxonomic measurements were calculated considering the ‘‘weighted’’ taxonomic differences among species (WARWICK; CLARKE, 1995; CLARKE; WARWICK, 1998, 2001a, 2001b): the ***taxonomic diversity (Δ)*** and the ***taxonomic distinctness (Δ*)***. To obtain these estimations, the species were placed within a taxonomic hierarchy, based on the Linnean classification: class, order, family, genus and species according Eschmeyer and Fong (2015). The indices were obtained through the multivariate software package PRIMER (Plymouth Routines in Multivariate Ecological Research) v. 7.0 (CLARKE et al., 2014).

2.6. Ecologic diversity

To obtain a diversity overview of the community, classical ecological measures were predicted for each habitat: i) **species richness (S)**; ii) **Margalef’s richness** ($d = (S-1)/Log(N)$) (MARGALEF, 1958); iii) **Shannon’s diversity** ($H' = -\sum(pi*Log(pi))$) (SHANNON; WEAVER, 1949); iv) **Simpson** ($S' = 1-\sum(Ni*(Ni-1))/(N*(Ni-1))$) (SIMPSON, 1949); and, v) **Pielou’s evenness** ($J' = H'/Log(S)$) (PIELOU, 1975). These indices were calculated through the multivariate software package PRIMER (Plymouth Routines in Multivariate Ecological Research) v. 7.0 (CLARKE et al., 2014).

3. Results

3.1. Fish composition and habitat

A total of 232,854 fish (average density = 41.35 n/m²; transformed average density = 11.23 n/m²) representing 87 species, 41 families and 12 orders were collected (Table 4). In IH, a strong presence of *Sardinella brasiliensis* and *Harengula clupeola* juveniles' schools in the intertidal zone was obtained representing 97% of the average density (39.87 n/m²) or 38% of the transformed average density (3.12 n/m²), and contributing to more than 30% of the dissimilarities among habitats (Table 5; Figure 13). When sardines' values were excluded, the most abundant species were juveniles of the silver mojarra *Eucinostomus argenteus* (0.36 n/m²), the white mullet *Mugil curema* (0.31 n/m²), and adult and juveniles of the Brazilian silversides *Atherinella brasiliensis* (0.37 n/m²). Besides sardines, other 23 fish species pertaining to 17 families and 9 orders appeared exclusively in IH, such as the sea horse *Hippocampus reidi*, the gobies *Bathygobius soporator and Ctenogobius boleosoma,* the blenny *Malacoctenus delalandii*, the eels *Myrophis punctatus* and *Ophichthus gomesii,* the halfbeaks *Hyporhamphus roberti roberti* and *Hemiramphus brasiliensis*, and the seabream *Archosargus rhomboidalis.*

The specific richness of IOS habitat was similar to that of IH, but the variability of benthic and benthopelagic species groups was higher in the first one due the occurrence of flounders (i.e. *Etropus crossotus, Citarichthys arenaceus, Symphurus tesselatus, Syacium papillosum, Bothus ocellatus*), puffers (i.e. *Sphoeroides greeleyi, S. testudineus, Lagocephalus laevigatus*), barbfish *Scorpaena brasiliensis,* and the flying gurnard *Dactylopterus volitans.* In IOS habitat, among the most abundant species were the barbel drum *Ctenosciaena gracilicirrhus* (0.15 n/m²), the silver mojarra (0.18 n/m²), and the roughneck grunt *Haemulopsis corvinaeformis* (0.15 n/m²), contributing with about 15% of the dissimilarities with MSS (Table 5). For almost covering the entire water column, also occurred exclusive pelagic species as the Atlantic bumper *Chloroscombrus chrysurus,* the bluntnose jack *Hemicaranx amblyrynchus,* and the barracuda *Sphyraena tome.*

MSS and IOS habitats showed similar species due to their proximity and the use of otter trawls close to the rocks. In the marginal shallow zone of the bay, were abundant the caitipa mojarra *Diapterus rhombeus* (0.07 n/m²), the southern weakfish *Cynoscion jamaicensis* (0.04 n/m²), and the flagfin mojarra *E. melanopterus* (0.04 n/m²). Moreover, an important species diversity associated with rocky shores appeared with the presence of the black margate *Anisotremus surinamensis,* the cubera snapper *Lutjanus cyanopetrus*, and the barbu *Polydactylus virginicus.*

Table 4. Contribution of species by habitat. IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat; ATD, average transformed density; AD, average density (*Continue*…).

Order	Family	Species	IH		IOS		MSS	
			ATD	AD	ATD	AD	ATD	AD
Albuliformes	Albulidae	*Albula vulpes*	0.1289	0.0196	0.0321	0.0011		
Anguiliformes	Ophichthidae	*Myrophis punctatus*	0.0637	0.0041				
		Ophichthus gomesii	0.0747	0.0056				
	Muraenidae	*Gymnothorax ocellatus*			0.0321	0.0012		
Atheriniformes	Atherinopsidae	*Atherinella brasiliensis*	0.3795	0.2228				
Aulopiformes	Synodontidae	*Synodus foetens*	0.0550	0.0030	0.0348	0.0015	0.0260	0.0008
Aulopiformes		*Trachinocephalus myops*	0.0707	0.0050				
Beloniformes	Belonidae	*Strongylura marina*	0.0707	0.0062				
	Hemiramphidae	*Hemiramphus brasiliensis*	0.1100	0.0121				
		Hyporhamphus roberti	0.0678	0.0046				
		Hyporhamphus unifasciatus	0.1350	0.0262	0.0203	0.0004		
Clupeiformes	Clupeidae	*Harengula clupeola*	1.4218	25.1988	0.0264	0.0007	0.0317	0.0010
		Opisthonema oglinum	0.0672	0.0045				
		Sardinella brasiliensis	1.6985	14.7757				
	Engraulidae	*Anchoa lyolepis*	0.0775	0.0065				
		Anchoa tricolor	0.1075	0.0197				
Elopiformes	Elopidae	*Elops saurus*	0.0983	0.0097				
Perciformes	Blenniidae	*Scartella cristata*	0.0597	0.0036				
	Carangidae	*Caranx latus*	0.0508	0.0026			0.0271	0.0007
		Chloroscombrus chrysurus			0.0291	0.0009	0.0664	0.0044
		Hemicaranx amblyrhynchus			0.0256	0.0007		
		Oligoplites saliens	0.0546	0.0031			0.0153	0.0002
		Oligoplites saurus	0.1327	0.0392	0.0189	0.0004	0.0187	0.0004
		Selene setapinnis			0.0272	0.0008	0.0606	0.0037
		Selene vomer	0.0550	0.0030	0.0231	0.0006	0.0347	0.0014
		Trachinotus carolinus	0.1109	0.0150			0.0172	0.0003
		Trachinotus falcatus	0.1440	0.0278				
		Trachinotus goodei	0.1583	0.0378				
	Centropomidae	*Centropomus parallelus*			0.0198	0.0004	0.0246	0.0008
		Centropomus undecimalis	0.0559	0.0032			0.0271	0.0007
	Ephippidae	*Chaetodipterus faber*	0.0807	0.0077	0.0281	0.0008	0.0276	0.0009

Table 4. Contribution of species by habitat. IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat; ATD, average transformed density; AD, average density (*Continue*…).

Order	Family	Species	IH		IOS		MSS	
			ATD	AD	ATD	AD	ATD	AD
	Gerreidae	*Diapterus rhombeus*	0.1434	0.0327	0.0846	0.0119	0.0768	0.0184
		Eucinostomus argenteus	0.3604	0.2023	0.1862	0.0488	0.0234	0.0006
		Eucinostomus gula	0.0828	0.0093	0.0585	0.0045	0.0542	0.0029
		Eucinostomus melanopterus	0.0700	0.0055	0.0414	0.0025	0.0421	0.0036
		Eugerres brasilianus					0.0295	0.0009
	Gobiidae	*Bathygobius soporator*	0.0720	0.0067				
		Ctenogobius boleosoma	0.1230	0.0240				
	Haemulidae	*Anisotremus surinamensis*					0.0451	0.0021
		Conodon nobilis	0.0799	0.0064				
		Haemulon steindachneri			0.0244	0.0006	0.0426	0.0021
		Haemulopsis corvinaeformis	0.1128	0.0155	0.1571	0.0452	0.0172	0.0003
		Orthopristis ruber	0.0849	0.0078	0.0700	0.0069	0.0381	0.0014
	Kyphosidae	*Kyphosus incisor*					0.0513	0.0026
		Kyphosus sectatrix	0.0800	0.0068				
	Labrisomidae	*Malacoctenus delalandii*	0.0645	0.0042				
	Lutjanidae	*Lutjanus analis*	0.0471	0.0022	0.0336	0.0012	0.0323	0.0011
		Lutjanus cyanopterus					0.0363	0.0013
		Lutjanus synagris			0.0339	0.0013		
	Mugilidae	*Mugil curema*	0.3133	0.1809	0.0215	0.0005	0.0456	0.0025
		Mugil liza	0.0652	0.0043			0.0140	0.0002
	Mullidae	*Upeneus parvus*			0.0617	0.0038		
	Polynemidae	*Polydactylus virginicus*					0.0438	0.0020
	Pomatomidae	*Pomatomus saltatrix*	0.0471	0.0022			0.0084	0.0001
	Sciaenidae	*Ctenosciaena gracilicirrhus*			0.1576	0.0691		
		Cynoscion jamaicensis			0.0568	0.0051	0.0410	0.0027
		Larimus breviceps			0.0195	0.0004		
		Menticirrhus americanus	0.0670	0.0048	0.0276	0.0008		
		Micropogonias furnieri			0.0426	0.0021		
		Umbrina coroides	0.1136	0.0181	0.0244	0.0006		
	Serranidae	*Diplectrum formosum*			0.0331	0.0013		
		Diplectrum radiale	0.0550	0.0030	0.0429	0.0023		
	Sparidae	*Archosargus rhomboidalis*	0.1129	0.0128				
		Calamus penna			0.0229	0.0005		
		Diplodus argenteus			0.0189	0.0004		
	Sphyraenidae	*Sphyraena tome*			0.0187	0.0003		
	Trichiuridae	*Trichiurus lepturus*			0.0281	0.0008		
	Uranoscopidae	*Astroscopus y-graecum*			0.0187	0.0003		
Pleuronectiformes	Achiridae	*Achirus lineatus*			0.0185	0.0003		
	Bothidae	*Bothus ocellatus*			0.0206	0.0004		
	Cynoglossidae	*Symphurus tessellatus*			0.0371	0.0016		
	Paralichthyidae	*Citharichthys arenaceus*			0.0338	0.0012		
		Citharichthys macrops			0.0310	0.0010		
		Citharichthys spilopterus	0.0727	0.0055	0.0492	0.0029		
		Etropus crossotus	0.0731	0.0060	0.0719	0.0060		
		Etropus longimanus			0.0187	0.0003		
		Syacium papillosum			0.0345	0.0013		
Scorpaeniformes	Dactylopteridae	*Dactylopterus volitans*			0.0346	0.0016		
	Scorpaenidae	*Scorpaena brasiliensis*			0.0232	0.0005		
	Triglidae	*Prionotus punctatus*	0.0679	0.0047	0.0447	0.0023		
Syngnathiformes	Syngnathidae	*Hippocampus reidi*	0.0471	0.0022				
Tetraodontiformes	Diodontidae	*Chilomycterus spinosus*	0.0643	0.0043				
	Monacanthidae	*Stephanolepis hispidus*			0.0232	0.0006		
	Tetraodontidae	*Lagocephalus laevigatus*			0.0194	0.0004		
		Sphoeroides greeleyi	0.0789	0.0075	0.0239	0.0006		
		Sphoeroides spengleri			0.0293	0.0009		
		Sphoeroides testudineus	0.0464	0.0022	0.0261	0.0007		

Table 5. Results of the SIMPER routine. Test of dissimilarities between pairs of habitats, based on abundance data (transformed density). Species are in decreasing order of contribution. IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat; δi, mean dissimilarity between the habitats; δi%, contribution of each species to mean dissimilarity.

IH *vs.* IOS		**IH *vs.* MSS**		**IOS *vs.* MSS**	
δi = 78.39		**δi = 87.18**		**δi = 64.32**	
Species	***δi %***	**Species**	***δi %***	**Species**	***δi %***
S. brasiliensis	16.62	*S. brasiliensis*	18.67	*E. argenteus*	5.14
H. clupeola	13.66	*H. clupeola*	15.28	*C. gracilicirrhus*	4.98
A. brasiliensis	3.71	*A. brasiliensis*	4.17	*H. corvinaeformis*	4.42
M. curema	2.86	*E. argenteus*	3.70	*E. crossotus*	2.27
E. argenteus	1.71	*M. curema*	2.94	*U. parvus*	1.95
T. goodei	1.55	*T. goodei*	1.74	*K. incisor*	1.62
C. gracilicirrhus	1.54	*T. falcatus*	1.58	*C. spilopterus*	1.55
T. falcatus	1.41	*H. unifasciatus*	1.48	*A. surinamensis*	1.42
C. boleosoma	1.20	*A. vulpes*	1.42	*P. punctatus*	1.41
H. unifasciatus	1.12	*C. boleosoma*	1.35	*P. virginicus*	1.38
O. saurus	1.11	*O. saurus*	1.29	*D. radiale*	1.35
A. rhomboidalis	1.11	*U. coroides*	1.25	*M. furnieri*	1.34
T. carolinus	1.09	*A. rhomboidalis*	1.24	*C. chrysurus*	1.18
H. brasiliensis	1.08	*H. brasiliensis*	1.21	*S. tesselatus*	1.17
A. tricolor	1.05	*A. tricolor*	1.18	*L. cyanopterus*	1.15
E. saurus	0.96	*E. saurus*	1.08	*D. volitans*	1.09
A. vulpes	0.95	*H. corvinaeformis*	1.05	*S. papillosum*	1.09
U. coroides	0.87	*T. carolinus*	1.03	*L. synagris*	1.07
K. sectatrix	0.78			*C. arenaceus*	1.07
C. nobilis	0.78			*S. setapinnis*	1.06
				D. formosum	1.05
				G. ocellatus	1.01
				A. vulpes	1.01
				O. ruber	1.01
				C. macrops	0.98
				E. brasilianus	0.93
				S. spengleri	0.92
				T. lepturus	0.89

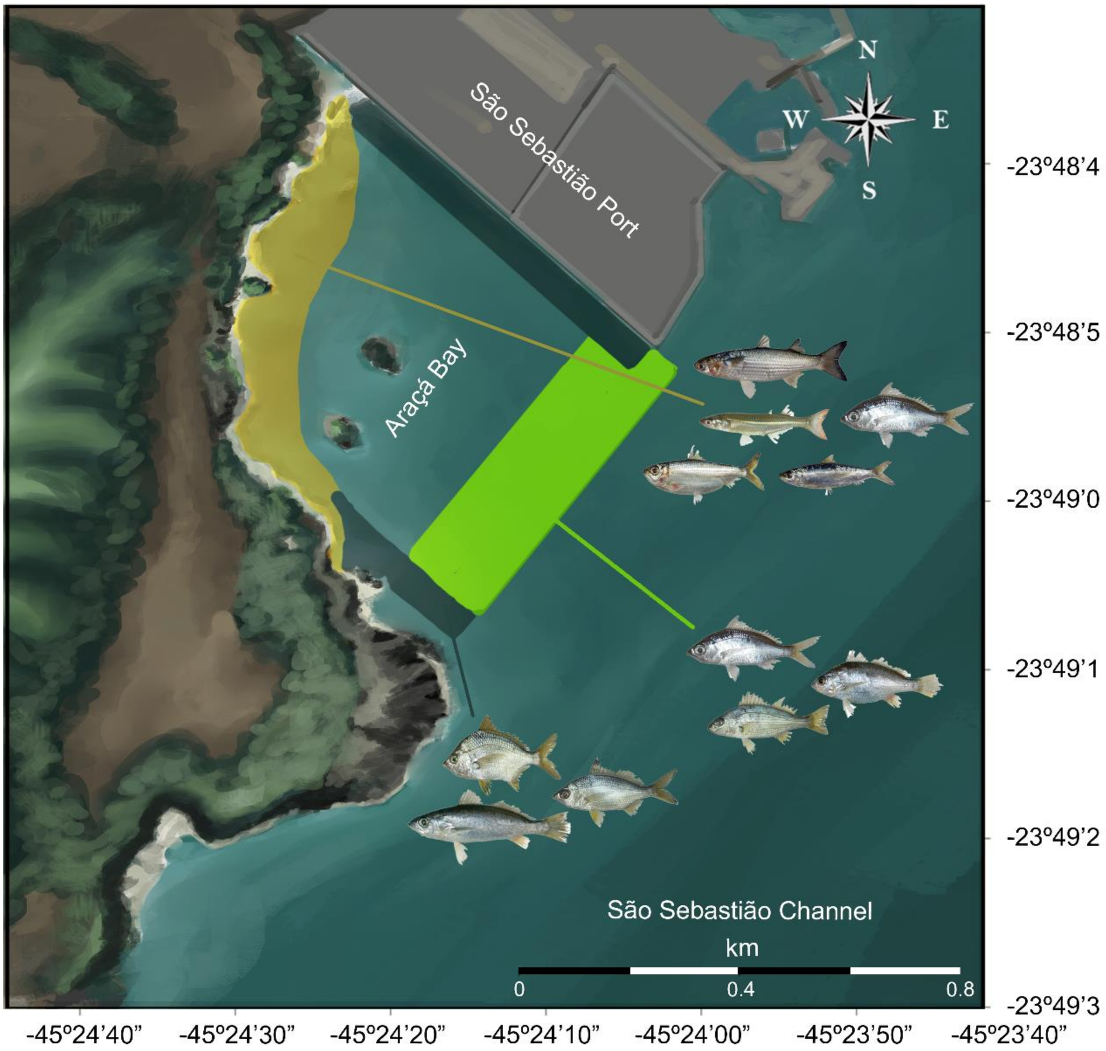


Figure 13. Main species contribution to the dissimilarity between habitats regarding to composition and density. In the intertidal habitat, were abundant *Sardinella brasiliensis, Harengula clupeola, Eucinostomus argenteus, Atherinella brasiliensis,* and *Mugil curema*. In the inner/outer sublittoral habitat, *Ctenosciaena gracilicirrhus, E. argenteus,* and *Haemulopsis corvinaeformis*. In the marginal shallow sublittoral habitat, the most abundant ones were *Diapterus rhombeus, E. melanopterus,* and *Cynoscion jamaicensis.*

3.2. Morphospaces of fish assemblages

The first eight relative warps represented 96.8% of the total morphological variability. The morphospaces were built using the first two *RWs* which explained around 70% of the total morphological variability (Supplementary Material, SM 3). The species distribution within morphospaces occurred according their morphological characteristics. The RW1 axis (41.71%) corresponds to the position and type of fins, and the head size. Positive values are associated to species with elongated anal fin which begins at the anterior half of the body, long and continuous dorsal fin, short or absent pectoral fins, and small heads (i.e. Pleuronectiformes, Anguiliformes, Elopiformes, Aulopiformes, Beloniformes) (Figure 14). In opposition, negative values represent species with short anal fins beginning at the posterior half of the body, and with large heads in proportion to the body size (i.e. Percifomes, Scorpaeniformes, Clupeiformes, Tetraodontiformes, Albuliformes). The RW2 axis (28.58%) defined the relation between height and length of the body, characterizing the general shape profile. Positive values indicated oval, oblong and deep-bodies laterally compressed (i.e. Perciformes, Scorpaeniformes, Pleuronectiformes), while negative ones represented elongated shapes (i.e. Beloniformes, Aulopiformes, Elopiformes) (Figure 14).

Perciformes was the most diverse order both in the intertidal and sublittoral habitats, adding high degree of morphological redundancy. Located at the center of the morphospaces, they have oval (i.e. Sparidae, Ephippidae), oblong (i.e. Gobiidae, Uranoscopidae, Labrisomidae) and fusiform shapes (i.e. Sciaenidae, Lutjanidae), some being laterally compressed (i.e. Carangidae). At the periphery, fish orders owning extreme morphological traits were poorly represented (i.e. Trichiuridae) unless they had been important to define the size of the morphological space (Figure 14).

The IH habitat presented morphospace expanded by species with positive RW1 and negative RW2 values, featured by elongated shapes, short dorsal fins beginning at the half of the body, and big heads such as Beloniformes (Belonidade, Hemiramphidae), Clupeiformes (Engraulidae), Aulopiformes (Synodontidae), Elopiformes (Elopidae) and by Anguilliformes representatives pertaining to the Ophichthidae family (Figure 15). Instead, in the IOS habitat occurred more fishes with positive RW2 values, with oval, oblong and deep-bodies laterally compressed mainly represented by Perciformes, and by flattened shapes with elongated dorsal and anal fins, the Pleuronectiformes (Figure 16). The morphospace of the MSS habitat was restricted to fishes with “common fish shape”, basically Perciformes, except one Synodontidae and one Clupeidae (Figure 17).

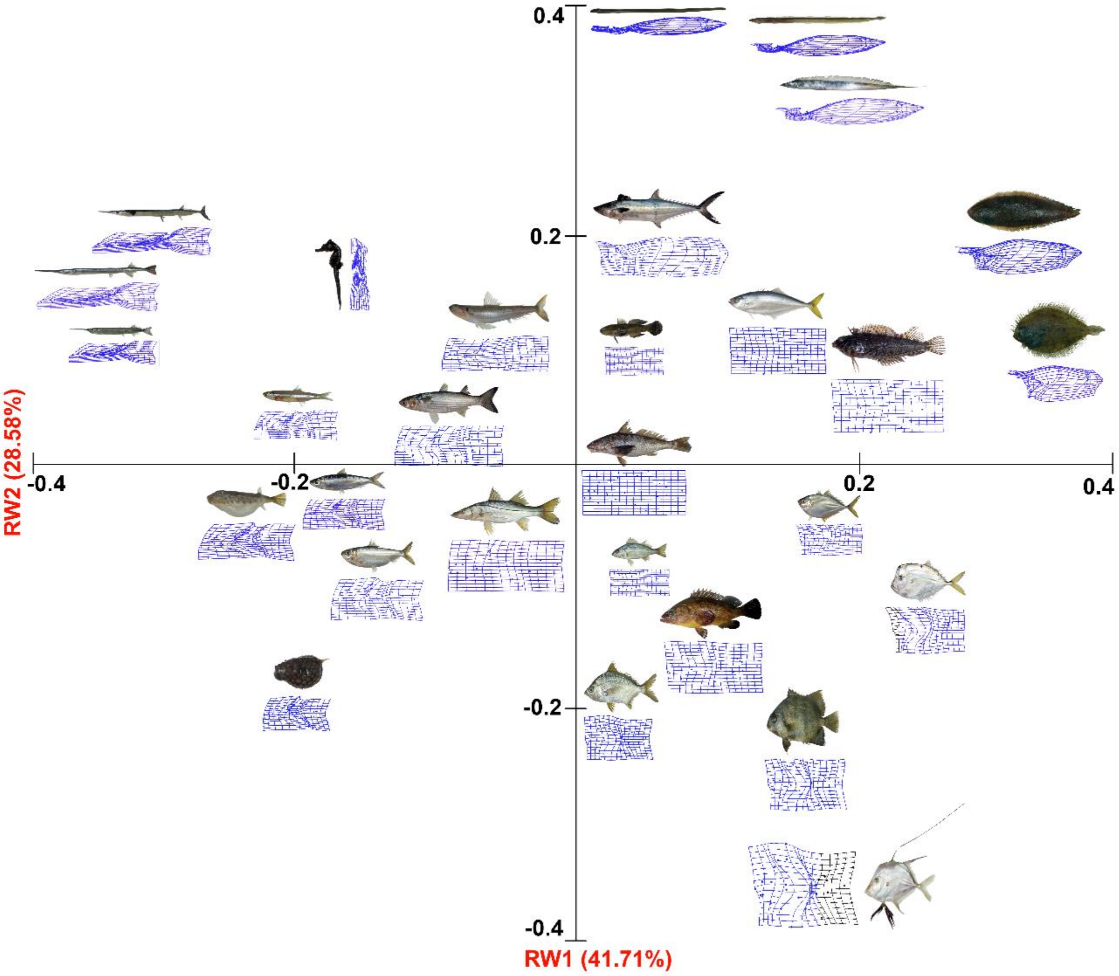


Figure 14. Deformation grid (thin-spline) of fish shapes representatives. Correspondence of the relative warp 1 (RW1, 41.71%) and relative warp 2 (RW2, 28.58%) values to explain the morphological variability among species.

3.3. *Functional spaces of fish assemblages*

Functional spaces were constructed according to fish species functional traits (Supplementary Material, SM 2). In all cases, they were built using the first and second PCoA values representing 35.9% of the total functional variability (Figures 15, 16 and 17). The PCoA1 axis (21.1 %) was associated with body shape, vertical distribution in the water column and species mobility. On the lower right side were positioned the fishes with oblong, oval (Tetraodontiformes: Tetraodontidae, Diodontidae; Scorpaeniformes: Triglidae, Scorpaenidae), elongated (Beloniformes: Hemiramphidae, Belonidae) and fusiform bodies (Perciformes: Sciaenidae, Gerreidae, Haemulidae, Serranidae). These species live in the benthopelagic domain and present medium mobility (or roving). Displayed on the upper right side were positioned fishes mostly fusiforms (Perciformes: Pomatomidae, Carangidae; Albuliformes: Albulidae;

Clupeiformes: Clupeidae), despite few elongated representatives (Atheriniformes: Atherinidae; and Elopiformes: Elopidae). These species present pelagic habits and high mobility. At the left side, were arranged species with asymmetrical flat shapes (Pleuronectiformes: Achiridae, Bothidae, Paralichthyidae, Cynoglossidae), anguilliforms (Anguiliformes: Ophichtidae, Muraenidae), sea horse (Syngnathiformes: Syngnathidae) and oblong ones (Perciformes: Bleniidae, Labrisomidae). These species present endobenthic (burying ability) and epibenthic sedentary habits. The PCoA2 axis (14.8 %), related to swimming type and diet, revealed negative values for benthic invertivores (sand invertivores, mobile benthic invertivores and colonial sessile invertivores, i.e. Pleuronectiformes, Perciformes: Gobiidae, Syngnathiformes, Anguiliformes), strict piscivores (i.e. Aulopiformes: Synodontidae; Perciformes: Uranoscopidae) and scrapers (i.e. Perciformes: Bleniidae). These species present anguilliform, balistiform, amiiform and diodontiform swimming types. In contrast, positive values were occupied by macrocarnivores (i.e. Perciformes: Sciaenidae, Centropomidae, Lutjanidae), omnivores (i.e. Perciformes: Sparidae, Mugilidae), macroalgae browsers (i.e. Perciformes: Kyphosidae), and diurnal (i.e. Perciformes: Carangidae, Sparidae; Clupeiformes: Engraulidae) or nocturnal (i.e Clupeiformes: Clupeidae) planctivores species, presenting carangiform and subcarangiform locomotion.

Like the morphospaces, the IH showed richer functional groups where pelagic species strongly dominated (Figure 15). The functional space of the intertidal habitat was featured by fifteen main groups (Table 6). Although pelagic species with carangiform and subcarangiform locomotion remained well represented, sedentary species with balistiform and diodontiform locomotion also dominated the intertidal assemblage. Regarding sizes, small (0-100 mm) to small-medium (101-200 mm) fishes were the most common within all assemblages, but mainly in the intertidal habitat. Instead, medium (201-300 mm) to large (>401 mm) fishes occupied the inner-outer sublittoral and the marginal shallow sublittoral. In the IOS functional space (Figure 16), eleven groups were revealed (Table 6). Roving species with fusiform shapes and subcarangiform swimming type dominated the IOS assemblage while the highly mobility species suffered a significant reduction on the functional space. The functional space of the MSS assemblage (Figure 17) was composed by eight groups, prevailing fusiform roving species with subcarangiform locomotion (Table 6)

Table 6. Functional groups revealed by the studied habitats (IH, intertidal habitat; IOS, inner/outer sublittoral; MSS, marginal shallow sublittoral).

Functional Groups	**IH**	**IOS**	**MSS**
1- high mobility planktivores pelagic species (i.e. *Sardinella brasiliensis, Oligoplites saliens, Chloroschombrus chrysurus*)	x	x	x
2- high mobility macrocarnivores pelagic species (i.e. *Strongylura marina, Caranx latus, Selene vomer, Sphyraena tome*)	x	x	x
3- high mobility invertivore pelagic species (i.e. *Trachinotus carolinus, Hemicaranx amblyrynchus*)	x	x	x
4- roving macroalgae browser pelagic species (i.e. *Hemiramphus brasiliensis, Pomatomus saltatrix*)	x		x
5- roving omnivores pelagic species (i.e. *Atherinella brasiliensis, Hyporhamphus unifasciatus*)	x	x	
6- roving planktivore benthopelagic species (i.e. *Archosargus rhomboidalis*)	x		
7- roving macrocarnivores benthopelagic species (i.e. *Menticirrhus americanus, Micropogonias furnieri, Gymnothorax ocellatus*)	x	x	x
8- roving macroalgae browser benthopelagic species (i.e. *Kyphosus sectatrix*)	x		
9- roving omnivores benthopelagic species (i.e. *Mugil curema, Diapterus rhombeus, Stephanolepis hispidus*)	x	x	x
10- roving invertivores benthopelagic species (i.e. *Ortopristhis ruber, Eucinostomus argenteus, Chilomycterus spinosus, Sphoeroides greeley*)	x	x	x
11- roving invertivores epibenthic species (i.e. *Dactylopterus volitans*)		x	
12- roving macrocarnivores epibenthic species (i.e. *Prionotus punctatus*)	x	x	
13- sedentary scrappers epibenthic species (i.e. *Scartella cristata*)	x		
14- sedentary invertivore epibenthic species (i.e. *Bathygobius soporator, Hippocampus reidi*)	x		
15- sedentary invertivores endobenthic species (i.e. *Syacium papillosum, Achirus lineatus, Etropus crossotus, Myrophis punctatus*)	x	x	
16- sedentary strict piscivores endobenthic species (*Synodus foetens, Astroscopus y-graecum*)	x	x	x

3.4. Comparing diversity indices

The three habitats (IH, MSS and IOS) showed high fish variability in morphology, taxonomic group, specific richness, dominance and functional traits (Tables 7, 8). Abundance data aggregated very important information, evidencing that the habitat influences the diversity estimates. Despite the notable biodiversity (H' = 3.27; d= 23.42) of the IH habitat, mostly of the species abundance was not equally distributed (J' = 0.82; S' = 1.81) and sardines dominated (Table 7). IOS habitat showed higher diversity because richness and abundance values remained in balance (d= 68.24; H' = 3.73) (Table 7). The equitability (J' = 0.97) prevailed in MSS, caused lower diversity (H'= 3.27; S' = 40.55) in comparison to the two other habitats (Table 7). Accompanying the specific diversity, the IOS comprised higher taxonomic diversity (Δ = 161.5) and presented more redundant shapes (lower value of EMI = 0.0003) (Table 7). The opposite occurred for the intertidal zone where the fish shapes were less redundant (EMI = 0.0045) besides very diverse, presenting varied phylogenetic relationships (Δ* = 92.73) (Table 7). Regarding to functional diversity results, the assemblages also showed variations (Table 8). Feve evidenced broad occupation of the functional space by biological entities in IOS (Feve = 0.61), indicating the well use of the resources. By contrast, the MSS functional space was underused suggesting low competition (Fdiv = 0.92) among the biological entities. The RaoQ designated the IH as the habitat with more distinct species abundance (RaoQ = 0.68) while MSS showed similar abundances but distant inside the functional space (Fdis = 2.14, RaoQ = 4.75). According to the functional redundancy, among the three habitats, IOS (FR = 1.60) was more stable and resilient against the loss of ecosystem functioning.

Table 7. Ecological, taxonomic, and morphological indices estimates for each habitat (IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat). S, richness; d, Margalef’s richness index; H’, Shannon’s diversity index (log e); S’, Simpson index; J’, Pielou’s evenness index; Δ, taxonomic diversity; Δ*, taxonomic distinctness; MD: morphological disparity; MR: morphological richness; EMI: morphogeometric diversity.

Habitats	Ecological					Taxonomic		Morphological		
	S	**d**	**J'**	**H' (log e)**	**S'**	**Δ**	**Δ***	**MD**	**MR**	**EMI**
IH	52	24.42	0.82	3.23	1.04	96.68	92.73	0.009	0.23	0.0045
IOS	53	68.24	0.94	3.73	1.81	161.50	89.02	0.002	0.02	0.0003
MSS	29	1,170	0.97	3.27	40.55	3.23	79.72	0.001	0.01	0.0005

Table 8. Functional indices estimates for each habitat (IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat). (*Feve,* Functional Evenness; *Fdiv,* Functional Divergence; *FR,* Functional Redundancy; *RaoQ,* Rao Quadratic Entropy).

Habitats	***Feve***	***Fdiv***	***FR***	***RaoQ***
IH	0.54	0.81	1.53	0.68
IOS	0.61	0.88	1.60	3.40
MSS	0.53	0.92	1.45	4.75

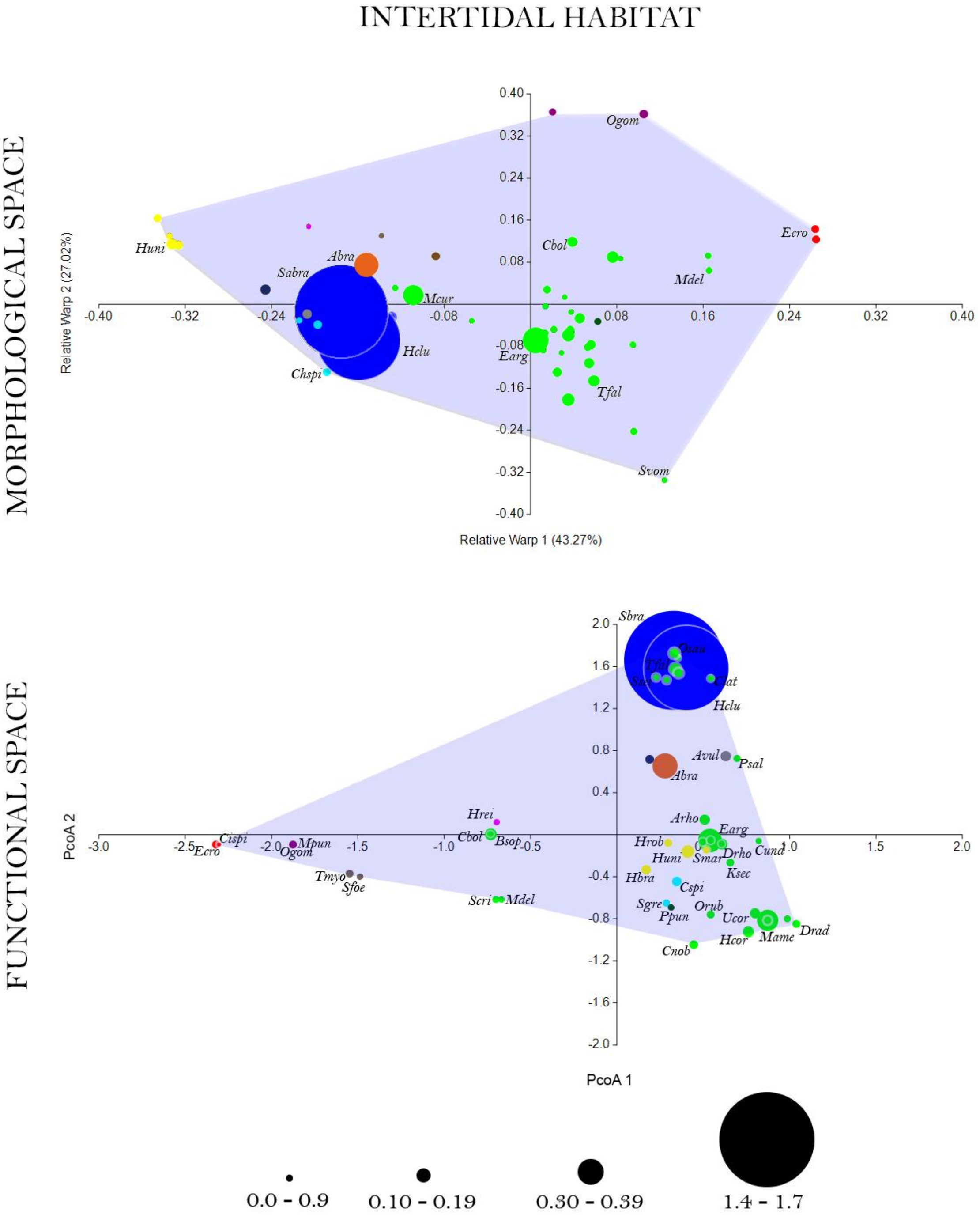


Figure 15. Representation of the morphological and functional spaces for the intertidal habitat. In the morphological space, axes are represented by the first (RW1) and second (RW2) relative warps. In the functional spaces, the axes are represented by the first (PcoA1) and second (PcoA2) values. Ball sizes represent the transformed abundance (square root) of species within the habitats. Colors represent the orders the species belong: Albuliformes (gray), Anguiliformes (violet), Atheriniformes (orange), Aulopiformes (brown), Beloniformes (yellow), Clupeiformes (blue), Elopiformes (dark blue), Perciformes (green), Pleuronectiformes (red), Scorpaeniformes (dark green), Syngnatiformes (magenta), and Tetraodontiformes (cyan). Species acronyms are shown in Supplementary Material 1.

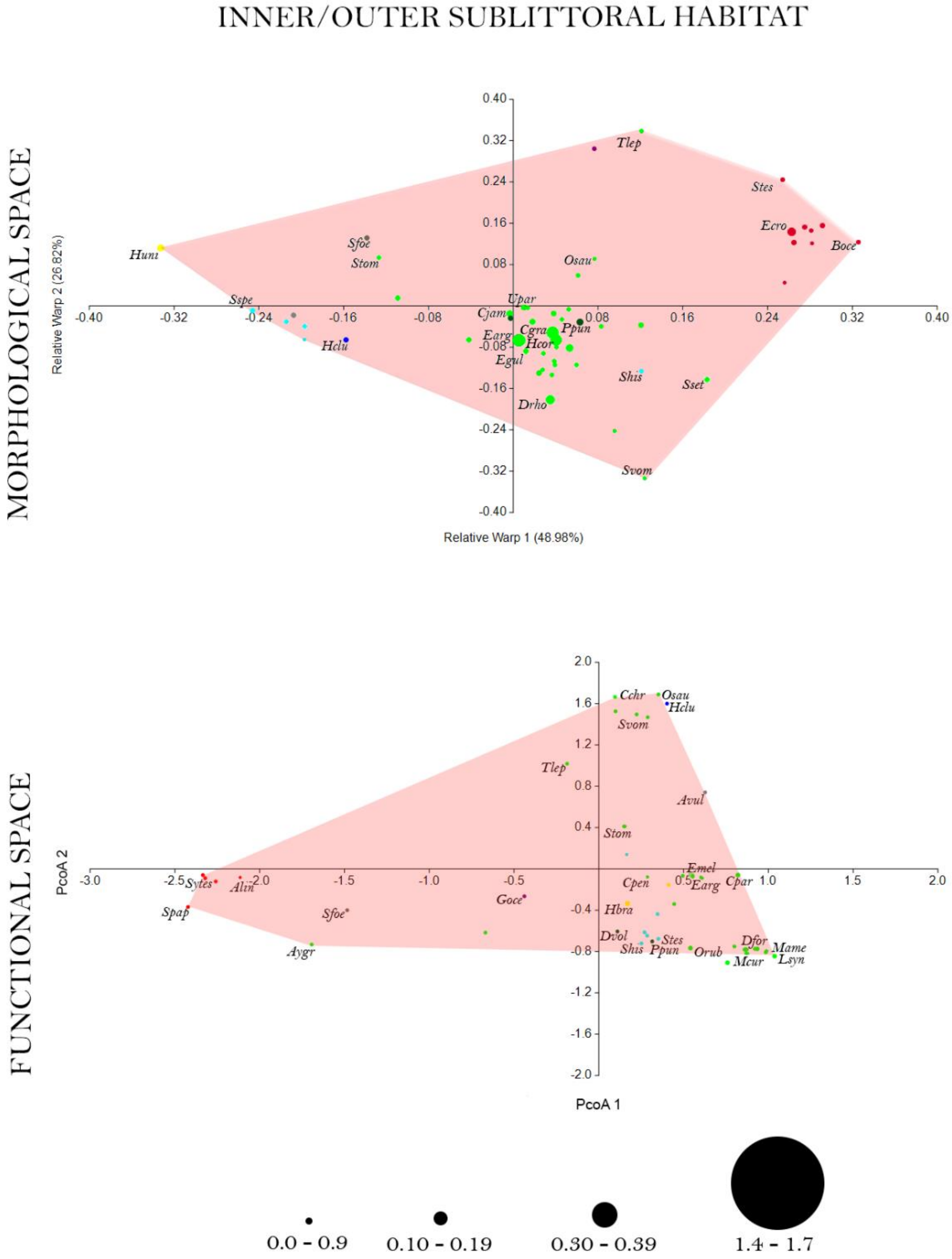


Figure 16. Representation of the morphological and functional spaces for the inner/outer sublittoral habitat. In the morphological space, axes were represented by the first (RW1) and second (RW2) relative warps. In the functional spaces, the axes were represented by the first (PcoA1) and second (PcoA2) values. Ball sizes represent the transformed abundance (square root) of species within the habitats. Colors represent the orders the species belong: Albuliformes (gray), Anguiliformes (violet), Atheriniformes (orange), Aulopiformes (brown), Beloniformes (yellow), Clupeiformes (blue), Elopiformes (dark blue), Perciformes (green), Pleuronectiformes (red), Scorpaeniformes (dark green), Syngnatiformes (magenta), and Tetraodontiformes (cyan). Species acronyms are shown in Supplementary Material 1.

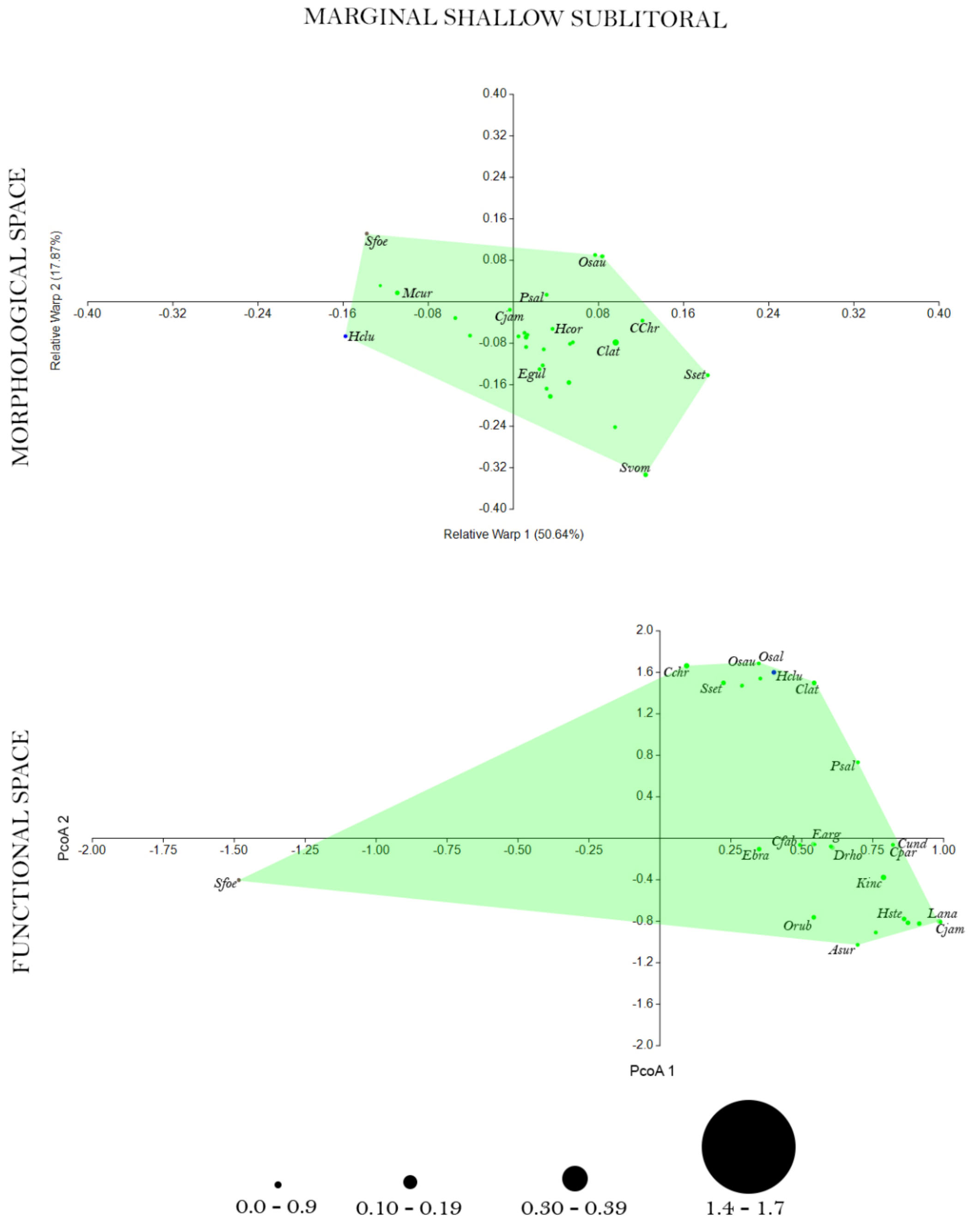


Figure 17. Representation of the morphological and functional spaces for the marginal shallow sublittoral habitat. In the morphological space, axes were represented by the first (RW1) and second (RW2) relative warps. In the functional spaces, the axes were represented by the first (PcoA1) and second (PcoA2) values. Ball sizes represent the transformed abundance (square root) of species within the habitats. Colors represent the orders to species belong: Albuliformes (gray), Anguiliformes (violet), Atheriniformes (orange), Aulopiformes (brown), Beloniformes (yellow), Clupeiformes (blue), Elopiformes (dark blue), Perciformes (green), Pleuronectiformes (red), Scorpaeniformes (dark green), Syngnatiformes (magenta), and Tetraodontiformes (cyan). Species acronyms are shown in Supplementary Material 1.

4. Discussion

Our results reveal that habitat characteristics influence fish distribution and abundance in the Araçá tidal flat ecosystem and, fish with distinct ecological strategies are connected to specific components of the area. To assess fish assemblages, fishing gears were chosen considering their better performances according to depth, substratum type, vegetation presence and density, since it is known that different gears has distinct species selectivity (RICKER, 1969; BEAMESDERFER; RIEMAN, 1988; HOVGARD; LASSEN, 2000; LAYMAN; SMITH, 2001; MCCLANAHAN; MANGI, 2004; CAROL; GARCÍA-BERTHOU, 2007; SHOUP; RYSWYK, 2016).

Initially, to have a diversity overview of the community, classical ecological indices were applied to each of the three habitats: IH, intertidal habitat; IOS, inner/outer sublittoral habitat; and the MSS, marginal shallow sublittoral habitat. These indices alone were insufficient to define the diversity of the species according their habitat preferences related to feeding and body size (WEBB, 2000; PETCHEY, 2004; CIANCIARUSO; SILVA; BATALHA, 2009). However, they were enough to reveal similar richness distribution between IH and IOS habitats, although the abundance has been higher in the first one. On the other side, taxonomic indices contributed to understand the degree of phylogenetic relationships among species inside each habitat. At IH and IOS, the species were related at genus level while in MSS, at family level. Considering that habitat perturbations can cause biodiversity loss (BARNOSKY et al., 2011) and that species sensitivity is phylogenetically conserved (HELMUS et al., 2010), high values of taxonomic indices indicated higher environmental integrity in IH and IOS (ROQUE et al., 2013),

As expected, the species distribution within the morphospaces occurred according to their morphological features, explaining 96.8% of the total morphological variability adapted to the habitat ecological conditions. At IH habitat, elongated and fusiform shapes adapted to live at the water surface prevailed, with short dorsal fins beginning at the half of the body, and prolonged heads. Most of these species were small to small-medium sized. At IOS habitat, the fish bodies were adapted to live on the bottom, presenting flattened shapes with elongated dorsal and anal fins, oval, oblong and deep-bodies laterally compressed; their sizes were small-medium to large. At MSS, basically occurred fusiform shapes with adaptations to explore rock shores. Morphological indices (MD, MR and EMI) revealed a decreasing in ecomorphological diversity from IH toward IOS and MSS, being the high value of first one explained by the high abundance of *Sardinella brasiliensis.*

Fish features living into the Araçá Bay are equivalent to other studies in shallow-water habitats along the Brazilian coast, mainly small-bodied and large-bodied pelagic fishes (i.e. sardines juveniles, anchovies, largehead hairtail), and benthopelagics (i.e. mojarras juveniles, silversides, snooks, croakers, grunts) (ARAÚJO; SANTOS, 1999; MUTO; SOARES; ROSSI-WONGTSCHOWSKI, 2000; FAVARO; LOPES; SPACH, 2003; PESSANHA et al., 2003; RUEDA; DEFEO, 2003; AZEVEDO et al., 2007; ARAÚJO et al., 2008; BARLETTA et al., 2008; ROCHA; FERNANDEZ; PAIVA-FILHO, 2010; VILAR; SPACH; JOYEUX, 2011; DIAS et al., 2011). Some of them use the bay throughout their entire life cycles (i.e*. E. argenteus, M. curema and D. rhombeus*) inhabiting the IH, IOS and MSS habitats, and supporting a regular use of the bay by piscivores which feed on them (CONTENTE; ROSSI-WONGTSCHOWSKI, 2017).

Similarly, in very different ecosystems of the world, fish species assemblages differ according to their complexity (CONNOLLY, 1994). In a shallow intertidal creek within the saltmarsh area of the Ria Formosa coastal lagoon (Portugal), gobiids and young-of-the-year silversides dominate the unvegetated habitat, while seagrass are dominated by a diverse group of species, in particular syngnathids and small labrids, revealing different habitat preferences (RIBEIRO et al., 2012). The ichthyofauna of the Kariega Estuary (South Africa) associated with an intertidal creek and adjacent eelgrass beds had similar fish diversities, mainly dominated by mugilids, sparids, clupeids, atherinids and gobiids. However, the most notable difference between habitats is the dominance of mugilids in the creek and their scarcity in the eelgrass (PATERSON; WHITFIELD, 2000). The same occur in intertidal mudflats of the temperate Australian embayment, where atherinids, mugilids, gobiids, tetraodontids, pleuronectids, and clupeids present differences in abundances varying between the mangroves and mudflats habitats (HINDELL; JENKINS, 2004). Thus, fish distribution and abundance directly depend on habitat characteristics.

The partitioning of the species into functional groups (according HALPERN; FLOETER, 2008) allowed to reveal 15 groups in IH, 11 groups in IOS, 8 groups in MSS. Vertical distribution, mobility and diet were the most relevant characters which in association with the body features, partitioned the species. Unless it is common to summarize many species into few functional groups, in this study we considered it not appropriated, mainly in the IH habitat. In this sense, the great deal of functional groups was attributed to the high morphological divergence among species and of their feeding habits. According to Hutchinson (1959) approach, this is expected in highly heterogeneous ecosystems such as the Araçá bay. In addition, the values of the functional indices (Feve, Fdiv and FR and RaoQ) confirmed how these functional groups use the habitat resources.

Together, the morphological and functional approaches were most robust to achieve our objectives. In general, morpho-functional variations are interpreted as adaptations to different ecological conditions (NORTON et al., 1995; WAINWRIGTH; RICHARD, 1995; UNDERWOOD, 1997; SVANBÄCK; EKLÖV, 2002), and habitat uses (WAINWRIGHT; BELLWOOD, 2002; FULTON, 2007; AGUILAR-MEDRANO et al., 2011, 2013). The link between these features and ecology patterns reflected the fish's abilities to perform relevant behaviors as swimming, habitat preference, prey selection, and anti-predator response (WAINWRIGTH, 1996; KARPOUZI; STERGIOU, 2003; LANGERHANS; REZNIK, 2010). The combination of these factors provided us to classify species in functional groups and determnine which of them are more vulnerable to habitat changes.

The proximity of IH to the remaining mangrove vegetation, the presence of two islets, the low hydrodynamics, and the constant changes in the granulometry (DOTTORI; SIEGLE; CASTRO, 2015; ALCÁNTARA-CARRIÓ et al., 2017) support the high abundance of pelagic fishes, the high specific richness and their varied ecological strategies. According to Christensen and Persson (1993), and Layman and Smith (2001) the habitat complexity is extremely important, serving to reduce the action of major predators, and offering greater protection. This is in accordance to the function of nursery, feeding and growth grounds attributed by Contente and Rossi-Wongtschowski (2017) to the Araçá Bay, and proven by the fish fauna biomass comprised by > 90 % of juveniles. Fish juveniles' abundance is mainly attributed to the rich benthic faunal composition associated to fine sand zones interspersed with large gravel banks (AMARAL et al., 2003). Likewise, that bottom complexity gives functional versatility in resources use by invertebrate feeders (both macro- and micro-predators) (BELLWOOD; HUGHES; HOEY, 2006) and may be the key driver of the IH fish diversity.

IH presents many functional groups but little functional redundancy. Since functional redundancy acts as biological insurance against diversity loss (DUFFY et al., 2001; LOREAU; MOUQUET; GONZALEZ, 2003; BRANDL et al., 2016) we could suppose that IH is most vulnerable to disturbances, even so with high-species diversity (MOUILLOT et al., 2014).

Regarding IOS, it presents higher functional redundancy than the other two habitats. It similarity with IH is due to some functional groups and species composition, reinforcing the idea of ecological connection between them. For instance, some species have their early development in IH habitat (i.e. *Etropus crossotus, Citharichthys spilopterus and Prionotus punctatus*), while the adult phase occurs in the IOS. That connection between a most sensitive habitat (IH) with a more resilient one (IOS) reveals the ability of the ecosystem to assimilate few impacts, compromising its functionality (MANNA; REZENDE; MAZZONI, 2013; BRANDL et al., 2016). Depending on the habitat interference, some species can adapt their functional roles and fill gaps in the ecosystem functions (HALPERN; FLOETER, 2008).

Differences in abundances of key species have important consequences to understand how human activities may affect biological communities (DULVY; SADOVY; REYNOLDS, 2003; HALPERN; FLOETER, 2008). For example, in the IH, the extirpation of the functional group “roving macroalgae browser pelagic species” with a single one, not abundant but vulnerable species (*Hemiramphus brasiliensis*), would have relatively little consequence to the ecosystem. In contrast, the loss of functional groups as “high mobility planktivores pelagic species” comprised by the abundant sardine shoals and five less abundant species would cause profound impacts on the overall habitat structure and its functioning (BELLWOOD; HOEY; CHOAT, 2003). Sardine shoals enter IH probably in pursuiting food and shelter (SACCARDO; ROSSI-WONGTSCHOWSKI, 1991; ROSSI-WONGTSCHOWSKI; SACCARDO; CERGOLE, 1995; MATSUURA, 1998; CASTELLO, 2000; PAIVA; MOTTA, 2000; CERGOLE; DIAS-NETO, 2011). Although being a highly mobile species, sardines increase significantly the partitioning of resources within IH. It functional role is rarely filled by other species.

The port expansion project by constructing a concrete slab covering 75% of the Araçá area (CPEA, 2011) would change the enlightening and sedimentation rate (ALCÁNTARA-CARRIÓ et al., 2017; TURRA et al., 2017), which negatively would affect the photosynthetic capacity of the primary producers (CIOTTI; FERREIRA; GIANNINI, 2018). This scenario would generate benthic biomass loss (TURRA et al., 2017), and consequently would destabilize the food web, inducing the loss of the fish diversity inhabiting intertidal and sublittoral zones (IH and IOS). Habitat-generalist species such as the mojarras and mullets living in those habitats have more ability to explore other functionally distinct habitats. In the case of a future degradation of the bay, these species can easily be coping with the local loss of a food item or of the habitat area. In contrast, for the habitat-specialist's such as gobies, sea horses, and eels living in the intertidal zone (IH), it would be harder mainly for being highly local attached, possessing reduced mobility and relying on their particular habitat for feeding, sheltering, and breeding (WONG et al., 2013).

Following Kovalenko, Thomaz and Warfe (2012) and Massicotte et al. (2015), monitoring, restoring or protecting areas with high microhabitat variability (habitat heterogeneity) is of great importance for slowing current trends of decreasing biodiversity in coastal ecosystems.

Anyway, to maintain the functioning of the Araçá ecosystem, management decisions regarding to area loss need a holistic view of the ecological function of each habitat. A clear perspective of the role of habitats complexity is critically important to prevent and mitigate potential impacts in the ichthyofauna, which directly affect the subsistence of local artisanal communities. In order to preserve the resilience of the Araçá marine fish assemblages, conservation policies based on quantitative data and morpho-functional estimates are crucial. Rice et al. (2013) reinforce the importance to maintain the abundance of key-species in particular functional groups.

Our findings support the idea that Araçá Bay must be protected as a whole. Nevertheless, to maintain the most part of its fish diversity we believe that the maintenance of IH is a priority and it has to be monitored.

Although we have not reported our results seasonally, but considering the major occurrence of juveniles and fish diversity, we suggest the autumn-winter months as the better time to conduct future monitoring programs.

4.

Fish body shapes and otolith shapes: are them morphologically correspondent?

Abstract

Otolith morphologies are indicative of fish ecological patterns. Their shapes indicate the fish development varying with sex, age and habitat. Moreover, otoliths perform an important role in fish hearing, with vestibular and acoustic functions. To quantify the morphological correspondence between otolith shapes and fish body shapes of 43 species collected in a tidal flat on the Brazilian coast, we analysed different shape descriptors: shape indices, wavelets and landmarks. We found that otolith shapes are related to fish habit, diet, swimming type, and sound production capability. The results showed positive morphological correspondence between fish body shape and otolith shape, considering the morphological distances obtained using the landmark method and the wavelets representation. Landmarks analysis plus the aspect ratio of the otolith weight was the better method to species discrimination as well as to recognize ecological aspects of the species analysed.

1. Introduction

Teleostean otoliths are calcium carbonate concretions, composed basically by aragonite crystals and protein organic material (PLATT; POPPER, 1981). Although typical of other vertebrates, fish present three pairs of otoliths (*lapillus, asteriscus* and *sagittae*) which are located at the inner ear in distinct otolithic organs (utricle, lagena and saccule, respectively) (POPPER; LU, 2000). The *sagittae* are the largest pair in marine species and commonly analysed by research proposals. Associated to the semicircular canals and the ampullae, otolithic organs possess a doble function: vestibular (balance) and acoustic (auditory) (POPPER; FAY, 1993), playing an important role in fish hearing. A sensory epithelium (*maculae*) made up of ciliary bundles surrounds the otoliths, and is connected through a depression in the mesial surface called *sulcus acusticus* (LOMBARTE; FORTUÑO, 1992; TORRES; LOMBARTE; MORALES-NIN, 2000). Relative motions between the sensory epithelium and the otoliths result in bending of the ciliary bundles and stimulation of the auditory nerve (POPPER; LU, 2000). Thus, both the frequency sensitivity, the mechanical efficiency in hearing and the fish orientation in the 3-dimensional space are closely tied to the shape, the relative size of the otoliths and their sensory maculae (GAULDIE, 1988).

The surface structure and the general otoliths outline are species-specific and reflect phylogenetic patterns (NOLF, 1985; NOLF; STERBAUT, 1989). They have been used as tool for: prey-predators identification (FITCH; BROWNELL, 1968; BOWEN, 2000; BARRETT et al., 2007; MILLÉ et al., 2016), fish species identification in palaeontology (CARPENTER; ERICKSON; HOLLAND, 2003; REICHENBACHER et al., 2007; NOLF, 2013), ecomorphological studies (VOLPEDO; ECHEVERRÍA, 2003; LOMBARTE; CRUZ, 2007; LOMBARTE et al., 2010; TUSET et al., 2010, 2016), climate variability effects assessments (GEFFEN et al., 2011; ROUNTREY et al., 2014), fish aging (CARDINALE; ARRHENIUS; JOHNSSON, 2000; WOYDACK; MORALES-NIN, 2001; CAMPANA; THORROLD, 2001; CAMPANA et al., 2016; CRAIG et al., 2017), and stocks identification (CAMPANA; CASSELMAN, 1993; CARDINALE et al., 2004; HÜSSY et al., 2016; MAPP et al., 2017).

Otolith shape reflects phenotypic stages of fish development, varying with sex, age and habitat where the fish lives (GAULDIE, 1988; CAMPANA et al., 1995, AGUIRRE; LOMBARTE, 1999; TORRES; LOMBARTE; MORALES-NIN, 2000; VOLPEDO; ECHEVERRIA, 2003; KEATING et al., 2014). Especially the *sulcus acusticus* area is a morpho-functional characteristic (PLATT; POPPER, 1981), since the increase of the ostial area is correlated with an increase in the amount of horizontal-oriented sensory cells (POPPER; COOMBS, 1982) responsible for the hearing skills (LOMBARTE; FORTUÑO, 1992; RAMCHARITART; GANNON; POPPER, 2006). Relatively large otoliths belong to groups considered specialists in sound production, while small otoliths belong to groups that rely on bright or contrasting colour patterns for visual communication (CRUZ; LOMBARTE, 2004; LOMBARTE; CRUZ, 2007). Most sagittae of pelagic fishes are characteristically long with a prolonged rostrum while benthic fishes present rounded otoliths (VOLPEDO; ECHEVERRÍA, 2003; LOMBARTE et al., 2010). Luminous species have slightly larger otoliths than non-luminous ones in the same family for living where acute colour vision is probably impossible (PAXTON, 2000). Bottom and littoral fishes have better auditory capabilities than the pelagic ones (LYCHAKOV; REBANE, 2000).

In addition to morphology, biological (ontogeny and physiology) and environmental factors can also influence the morphometry and the microstructure of the *sagittae* (GAULDIE, 1988; CAMPANA et al., 1995; AGUIRRE; LOMBARTE 1999; TORRES; LOMBARTE; MORALES-NIN, 2000; VOLPEDO; ECHEVERRIA, 2003).

Individuals of the same species inhabiting different areas may present different growth rates, affecting the general shape of that structure (CAMPANA; CASSELMAN, 1993; REICHENBACHER et al., 2009). Often, changes on growth rates are due to water temperature variation, depth and food availability (LOMBARTE; LLEONART, 1993; TUSET et al., 2003; MÉRIGOT; LETOURNEUR; LECOMTE-FINIGER, 2007); however, it is practically unknown how the morphological variability influences the process of sound detection (POPPER; LU, 2000; LOMBARTE et al., 2010).

Recently, the development of digital techniques using shape analysis have offered new possibilities for biological research by means of morphometric features of fish and otoliths. In addition to the commonly used indices i.e. form-factor, circularity, rectangularity, roundness, ellipticity, eccentricity (CAMPANA; CASSELMAN, 1993; TUSET et al., 2003), many shape descriptors have been proposed, such as the Fourier decompositions of the otolith or the *sulcus acusticus* outlines (BIRD et al., 1986; CASTONGUAY et al., 1991; TORRES; LOMBARTE; MORALES-NIN, 2000; DEVRIES; GRIMES; PRAGER, 2002; GAULDIE; CRAMPTON, 2002; CARDINALE et al., 2004; FERGUSSON et al., 2011; KEATING et al., 2014; HUSSY et al., 2016), the wavelets transform and the curvature scale space analysis (PARISI-BARADAD et al., 2005, 2010; TUSET et al., 2015), and the landmark shape analysis (MONTEIRO et al., 2005; PONTON, 2006; JAVOR; LO; VETTER., 2011; LOMBARTE et al., 2010; VIGNON; MORAT, 2010; TUSET et al., 2016). Although applied in diverse research areas, most of them (except wavelets) were developed for stocks discrimination since this is an important question for fishery resources management.

Morphological and morphometric otolith characters arguably constitute an important instrument for species identification, but each shape descriptor has its particularities (ROSIN, 2003). For example, shape indices are useful to biologically interpret interspecific morphological changes in otoliths in order to determine the groups separation, although it is not a good descriptor of intraspecific variability (MONTEIRO et al., 2005). Fourier is an efficient method to describe outline shapes, independent of the otolith position, however do not detect subtle differences (CADRIN; FRIEDLAND, 1999). In turn, landmarks analysis is more sensitive, but the use of few homologue points may be a problem (ROLHF; MARCUS, 1993). On the other hand, a fine wavelets analysis becomes computationally intensive, but is particularly relevant to identify otoliths having local contour alterations. Such imperfections alter the Fourier transform globally, while the wavelet transform is only altered locally (PARISI-BARADAD et al. 2010). Therefore, it is reasonable to suppose that these methods, used to measure the high morphological variability of otoliths and their specificity, may be also used to quantify their correspondence with fish body shapes.

The main objectives of the present study were to test the potential of the otolith methods for estimating species classification and their ecological significances, by applying shape indices, a geometric morphometric method and the wavelets transform, and to quantify the morphological correspondence between otolith shapes and fish body shapes among the studied species.

2. Material and Methods

2.1. Sampling

Sagittae otoliths of 43 species belonging to the families Albulidae, Atherinopsidae, Carangidae, Centropomidae, Chaetodontidade, Clupeidae, Engraulidae, Ephippidae, Gerreidae, Gobiidae, Haemulidae, Hemiramphidae, Kyphosidae, Lutjanidae, Mugilidae, Muraenidae, Paralichthydae, Polynemidae, Pomatomidae, Sciaenidae, Serranidae, Sparidae, Synodontidae and Triglidae were obtained during samplings in the Araçá Bay (north coast of São Paulo State, Brazil), between March 2013 and January 2014 (Table 8). The fish total length (FTL, mm) of all specimens was measured. The *sagittae* were removed, cleaned, dried and stored. A total of 430 left s*agittae* were analysed, being ten otoliths per species. The left otoliths were positioned with the mesial surface (*sulcus acusticus* side) upwards and the *rostrum* to the right (Figure 18A).

Table 9. Species analysed in this study, their taxonomical classification (order and family) and the acronym used for each one.

Order	**Family**	**Species**	**Acronym**
Albuliformes	Albulidae	*Albula vulpes*	Avul
Anguiliformes	Muraenidae	*Gymnothorax ocellatus*	Goce
Clupeiformes	Engraulidae	*Anchoa tricolor*	Atri
Clupeiformes	Clupeidae	*Harengula clupeola*	Hclu
Clupeiformes	Clupeidae	*Sardinella brasiliensis*	Sbra
Aulopiformes	Synodontidae	*Synodus foetens*	Sfoe
Gobiiformes	Gobiidae	*Bathygobius soporator*	Bsop
Gobiiformes	Gobiidae	*Ctenogobius boleosoma*	Cbol
Pleuronectiformes	Paralichthydae	*Citharichthys macrops*	Cmac
Pleuronectiformes	Paralichthydae	*Citharichthys spilopterus*	Cspi
Pleuronectiformes	Paralichthydae	*Etropus crossotus*	Ecro
Atheriniformes	Atherinopsidae	*Atherinella brasiliensis*	Abra
Beloniformes	Hemiramphidae	*Hemiramphus brasiliensis*	Hbra
Beloniformes	Hemiramphidae	*Hyporhamphus unifasciatus*	Huni
Mugiliformes	Mugilidae	*Mugil curema*	Mcur
Scorpaeniformes	Triglidae	*Prionotus punctatus*	Ppun
Perciformes	Centropomidae	*Centropomus parallelus*	Cpar
Perciformes	Centropomidae	*Centropomus undecimalis*	Cund
Perciformes	Serranidae	*Diplectrum formosum*	Dfor
Perciformes	Serranidae	*Diplectrum radiale*	Drad
Perciformes	Serranidae	*Epinephelus marginatus*	Emar
Perciformes	Pomatomidae	*Pomatomus saltatrix*	Psal
Perciformes	Carangidae	*Chloroscombrus chrysurus*	Cchr
Perciformes	Carangidae	*Selene vomer*	Svom
Perciformes	Lutjanidae	*Lutjanus analis*	Lana
Perciformes	Lutjanidae	*Lutjanus synagris*	Lsyn
Perciformes	Gerreidae	*Diapterus rhombeus*	Drho
Perciformes	Gerreidae	*Eucinostomus argenteus*	Earg
Perciformes	Gerreidae	*Eucinostomus gula*	Egul
Perciformes	Gerreidae	*Eucinostomus melanopterus*	Emel
Perciformes	Gerreidae	*Eugerres brasilianus*	Ebra
Perciformes	Haemulidae	*Haemulon steindachneri*	Hste
Perciformes	Haemulidae	*Haemulopsis corvinaeformis*	Hcor
Perciformes	Haemulidae	*Ortopristhis ruber*	Orub
Perciformes	Sparidae	*Archosargus rhomboidalis*	Arho
Perciformes	Sciaenidae	*Ctenosciaena gracilicirrhus*	Cgra
Perciformes	Sciaenidae	*Cynoscion jamaicensis*	Cjam
Perciformes	Sciaenidae	*Menticirrhus americanus*	Mame
Perciformes	Sciaenidae	*Micropogonias furnieri*	Mfur
Perciformes	Polynemidae	*Polydactylus virginicus*	Pvir
Perciformes	Kyphosidae	*Kyphosus sectatrix*	Ksec
Perciformes	Chaetodontidae	*Chaetodon striatus*	Cstr
Perciformes	Ephippidae	*Chaetodipterus faber*	Cfab

2.2. Otolith size parameters

Morphometrics were made by taking digital images from the mesial surface of the otoliths with a Carl Zeiss AxioCam ICc3 video camera coupled to a Carl Zeiss Discovery V.12 Stereomicroscope and a computer. The processing, calibration and measurements were performed using the AxioVision package programme. The otolith length (OL, mm) was measured as the greater distance along the longitudinal axis

(Figure 18B). The otolith height (OH, mm), was the largest perpendicular distance of the dorsoventral otolith. The otolith area (OA, mm²), was considered as the *sagitta* surface area; and the otolith perimeter (mm) as the length of its contour. The *sulcus acusticus* length (SL, mm), its height (SH, mm) and its area (SA, mm²) were measured following the same precepts. All otoliths were weighted (OW, g). For each species, the allometric relationship between the otolith measures and FTL was calculated using the standard equation $y= ax^b$, thus fitted by logarithmic-transformation (log10) in order to homogenize the residuals. Each morphometric variable *y* (OL, OW, OH, OA, OP, SL, SH, SA) was transformed into the term *z* according to $z= (x_0\, x^{-1})^{b}$, where *z* is the value of *y* if FLT is x_0, x_0 is the original total length of the fish, and *b* is the allometric parameter relating the dependent variable <u>y</u> (OL, OW, OH, OA, OP, SL, SH, SA) to the independent variable <u>x</u> (FTL). For each species, the reference fish total length was the mean value of FTL of the specimens (LOMBARTE; LLEONART, 1993). The multivariate normality was tested by Mardia's Multivariate Skewness (111.6, p-value < 0.005) and Kurtosis (303.6, p-value < 0.005). Once the data were standardized, species and families' otolith morphometries were compared using a Permutational Multivariate Analysis of Variance (One-way PERMANOVA - Euclidean Similarity Index, 9999 permutations).

To verify the influence of adaptive components in the otolith shape, the morphometric data were compared by means of One-way Permanova (Euclidean Similarity Index, 9999 permutations) and using four categorical traits that describe biologically each species (COLGATE; LYNCH, 2004; HALPERN; FLOETER, 2008; FARRÉ et al., 2013, 2016): habit type (pelagic, benthopelagic, epibenthic, endobenthic), sound production (yes, no), swimming type (anguilliform, balistiform, carangiform, diodontiform, subcarangiform) and diet (diurnal planktivore, nocturnal planktivore, macroalgae browser, omnivores, colonial sessile invertivore, mobile benthic invertivores, sand invertivores, strict piscivores and macrocarnivores) (Table 9). These analyses were performed in PAST (Palaeontological Statistics, ver. 1.81; HAMMER; HARPER; RIAN, 2001).

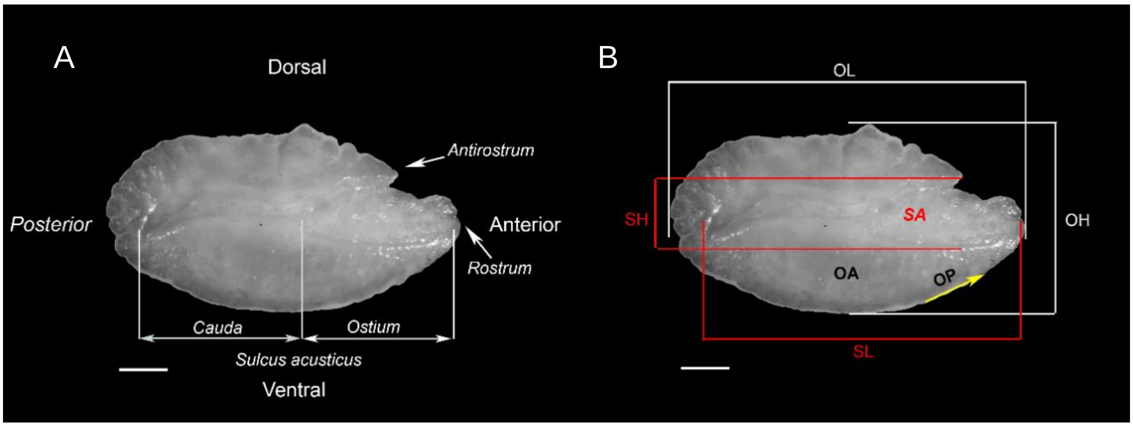


Figure 18. A) Mesial surface of a *sagitta* (*Centropomus undecimalis*) illustrating features analysed. B) Linear measurements obtained from each *sagitta*: OL, length (mm); OH, height (mm); OA, area (mm²); OP, perimeter (mm); SL, sulcus length (mm); SH, sulcus height (mm); SA, sulcus area.

2.3. Otolith Shape Indices

Shape otolith descriptors were obtained by combining size parameters of the *sagittae* (RUSS, 1990; TUSET et al., 2003): AR = $OH/OL,$ compactness (C) = OP^2/OA, form factor (FF) = $(4\pi * OA)/OP^2$, and rectangularity (R) = $OA/(OL * OH)$. Compactness provides information about the similarity of the structure to a perfect circle, having as minimum value 4π (or 12.57). Rectangularity measures the distinction of width and length with respect to the area, being 1.0 the value of a perfect square. Form-factor range from 1.0 when it is a perfect circle, and < 1.0 when the surface area is irregular. Moreover, other aspect ratios were obtained: ARw = OW/OL, ARsa = SA/OA, ARsh = SH/SL, and were independently compared using a Permutational Multivariate Analysis of Variance (Two-way PERMANOVA - Euclidean Similarity Index, 9999 permutations), by species and habits. These analyses were performed in PAST (Palaeontological Statistics, ver. 1.81; HAMMER; HARPER; RIAN, 2001).

Table 10. Categorical traits used to describe biologically each species (habit type, sound production, swimming type, and diet). MAC: macrocarnivores, PIS: strict piscivores, MINV: mobile benthic invertivores, SAND: sand invertivores colonial sessile, SINV: invertivores, DPLA: diurnal planktivores, NPLA: nocturnal planktivores, MALG: macroalgae browser, OMNI: general omnivores.

Species	Acronym	Habit	Sound Production	Swimming type	Diet
Anchoa tricolor	Atri	Pelagic	No	Carangiform	DPLA
Atherinella brasiliensis	Abra	Pelagic	No	Carangiform	OMNI
Chloroscombrus chrysurus	Cchr	Pelagic	No	Carangiform	DPLA
Harengula clupeola	Hclu	Pelagic	No	Carangiform	NPLA
Hemiramphus brasiliensis	Hbra	Pelagic	No	Subcarangiform	MALG
Hyporhamphus unifasciatus	Huni	Pelagic	No	Subcarangiform	OMNI
Pomatomus saltatrix	Psal	Pelagic	No	Carangiform	MAC
Sardinella brasiliensis	Sbra	Pelagic	No	Carangiform	NPLA
Selene vomer	Svom	Pelagic	No	Carangiform	MAC
Albula vulpes	Avul	Bathypelagic	No	Carangiform	MINV
Archosargus rhomboidalis	Arho	Bathypelagic	No	Carangiform	DPLA
Centropomus parallelus	Cpar	Bathypelagic	Yes	Subcarangiform	MAC
Centropomus undecimalis	Cund	Bathypelagic	Yes	Subcarangiform	MAC
Chaetodipterus faber	Cfab	Bathypelagic	No	Carangiform	SINV
Chaetodon striatus	Cstr	Bathypelagic	No	Balistiform	SINV
Ctenosciaena gracilicirrhus	Cgra	Bathypelagic	Yes	Subcarangiform	MAC
Cynoscion jamaicensis	Cjam	Bathypelagic	Yes	Subcarangiform	MAC
Diapterus rhombeus	Drho	Bathypelagic	No	Carangiform	OMNI
Diplectrum formosum	Dfor	Bathypelagic	No	Subcarangiform	MAC
Diplectrum radiale	Drad	Bathypelagic	No	Subcarangiform	MAC
Epinephelus marginatus	Emar	Bathypelagic	No	Subcarangiform	MAC
Eucinostomus argenteus	Earg	Bathypelagic	No	Carangiform	SAND
Eucinostomus gula	Egul	Bathypelagic	No	Carangiform	SAND
Eucinostomus melanopterus	Emel	Bathypelagic	No	Carangiform	SAND
Eugerres brasilianus	Ebra	Bathypelagic	No	Carangiform	SAND
Gymnothorax ocellatus	Goce	Bathypelagic	No	Anguiliform	MAC
Haemulon steindachneri	Hste	Bathypelagic	Yes	Subcarangiform	MINV
Haemulopsis corvinaeformis	Hcor	Bathypelagic	Yes	Subcarangiform	MINV
Kyphosus sectatrix	Ksec	Bathypelagic	No	Carangiform	MALG
Lutjanus analis	Lana	Bathypelagic	Yes	Subcarangiform	MAC
Lutjanus synagris	Lsyn	Bathypelagic	Yes	Subcarangiform	MAC
Menticirrhus americanus	Mame	Bathypelagic	Yes	Subcarangiform	MAC
Micropogonias furnieri	Mfur	Bathypelagic	Yes	Subcarangiform	MAC
Mugil curema	Mcur	Bathypelagic	No	Subcarangiform	OMNI
Ortopristhis ruber	Orub	Bathypelagic	Yes	Subcarangiform	SAND
Polydactylus virginicus	Pvir	Bathypelagic	No	Subcarangiform	MINV
Bathygobius soporator	Bsop	Epibenthic	No	Diodontiform	MINV
Ctenogobius boleosoma	Cbol	Epibenthic	No	Diodontiform	MINV
Prionotus punctatus	Ppun	Epibenthic	No	Subcarangiform	MAC
Citharichthys macrops	Cmac	Endobenthic	No	Anguiliform	SAND
Citharichthys spilopterus	Cspi	Endobenthic	No	Anguiliform	SAND
Etropus crossotus	Ecro	Endobenthic	No	Anguiliform	SAND
Synodus foetens	Sfoe	Endobenthic	No	Subcarangiform	PISC

2.4. Geometric Morphology

Geometric morphology analysis was applied to quantify the morphological diversity of fish shapes and otoliths separately (BOOKSTEIN, 1991). The landmarks and semilandmarks were digitised using tpsDig software (ver. 2.16; ROHLF, 2003). After that, the cartesian grid coordinates were analysed with tpsRelw (ver. 1.49; ROLHF, 2003), where the specimens images were rotated, translated and scaled to landmark coordinates. Essentially, specific morphological characteristics passed to be represented by *relative warps* (ROHLF; MARCUS, 1993; ZELDITCH; SHEETS; FINK, 2003). Even as performed for the body shape (protocols explanations in the previous chapters), one consensus (average) configuration was obtained for each species, from ten otoliths. Thus, the geometric morphological analysis was performed using the consensus figure for each species.

The otolith outline was described by eight reference landmarks (homologous points) established in terms of straight lines according to Reichenbacher et al. (2007) (blue dots, Figure 19). To improve the representation of the otolith shape, four semi-landmarks equidistant from particular consecutive landmarks were also added according to Tuset et al. (2016) (red dots, Figure 19). Furthermore, the *sulcus acusticus* contour were characterised by means of fourteen landmarks selected according to the literature (MONTEIRO et al., 2005; LOMBARTE et al., 2010; TUSET et al., 2016). The number of points were similar for the otolith and *sulcus acusticus* contours in order to avoid influences in the relative warp estimations. Warps of the otoliths analysis were independently compared using a Permutational Multivariate Analysis of Variance (Two-way PERMANOVA - Euclidean Similarity Index, 9999 permutations), by species and habit. This analysis was performed in PAST (Palaeontological Statistics, ver. 1.81; HAMMER; HARPER; RIAN, 2001).

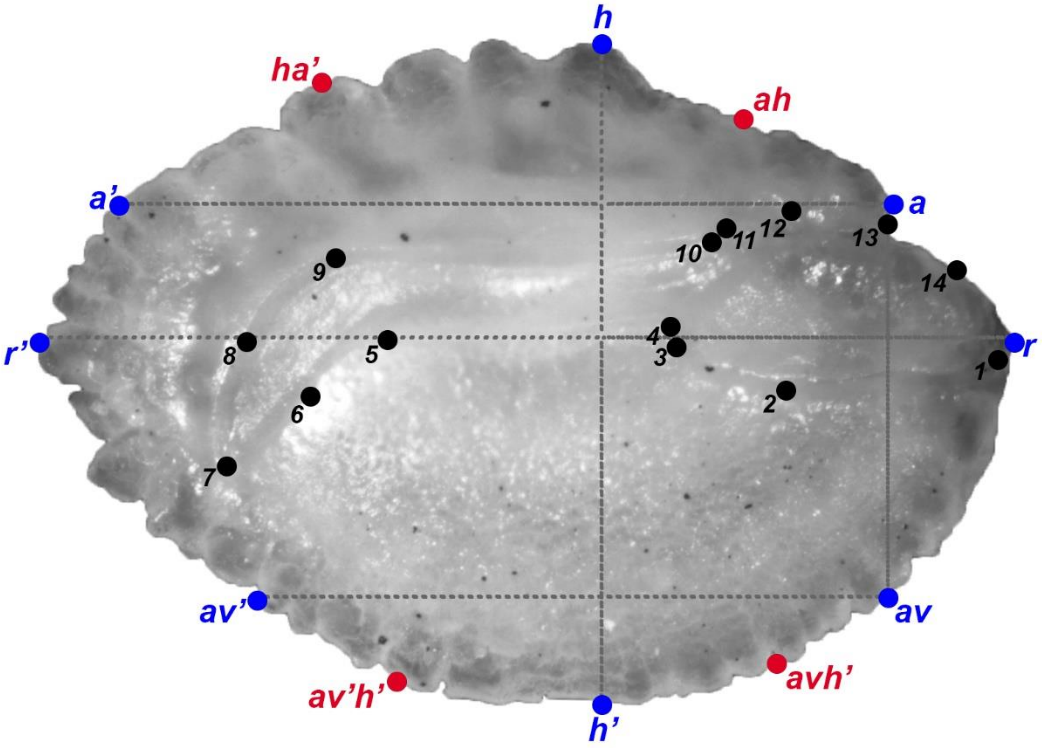


Figure 19. Mesial surface of the left otolith (*Haemulopsis corvinaeformis*) showing the landmarks and semi-landmarks used in the present study to define the otolith contour (blue and red dots, labelled by characters, respectively) and the sulcus acusticus (black dots, labelled by numbers). Otolith contour: **r** is the rostrum, **r'** the posterior projection of **r**, **a** the antirostrum and **a'** the posterior projection of **a** (if the antirostrum were absent and the ostium typically had an ostial opening, the dorsal ending of the crista dorsal was considered **a**; if the ostium was not opening, **a** was located together with **r**), **av** is the ventral projection of **a**, **av'** the posterior projection of **av**, **h** to **h'** defines the maximum height perpendicular to lines **r–r'** between the dorsal margin (**h**) and the ventral margin (**h'**), and **avh'**, **av'h'**, **ha**', **ah** are semilandmarks. Sulcus acusticus: 1 and 13 indicate the intersection between inferior and superior crista of the ostium and the excisura ostii, 2 and 12 show where the inferior and superior crista of the ostium change the curvature, 3 to 4 and 10 to 11 provide the position, size and symmetry of the constriction between the ostium and cauda, 5 and 9 indicate the place where the inferior and superior crista of the cauda change the curvature, 7 is the most distal point of the cauda and 6, 8 and 14 are semilandmarks (modified from TUSET et al., 2016).

2.5. Wavelet Transform Representation

Image processing for automatic extraction of otoliths outline was performed by the image analysis from AFORO database (http://isis.cmima.csic.es/aforo) according to Parisi-Baradad et al. (2005, 2010). Ten images of the left *sagitta* of each specimen was uploaded. Images of the mesial surface of the otolith were made against a homogeneous black background in order to guarantee a good representation of their contours. The rostral side (R) was oriented to the right side of the image. First, the external outline of the otolith was obtained by calculating the distances between 512 outline points (equidistant to each other) and the centre of gravity of the otolith image. The centre of gravity of each contour was considered as the origin of the coordinates, starting from the rostrum as input signal for the wavelets calculation. Then, wavelet transform (WT) was applied to extract useful features of the otolith outline and the irregularities of the contours were quantified and localized appropriately. Nine levels of wavelet transforms are generated, however, the level 5 (WT5) was selected to classify the studied specimens because it would represent the entire otolith shape (Figure 20). A Principal Component Analysis (PCA) and a Multivariate Linear Model were applied to the specimens WT5. Then, an appropriate discriminant analysis (LDA) was applied to the relevant Principal Components (PCs) and the average success rate was calculated using a Jacknife cross-validation method. Wavelets 5 were independently compared using a Permutational Multivariate Analysis of Variance (Two-way PERMANOVA - Euclidean Similarity Index, 9999 permutations), by species and habits. These analyses were performed in PAST (Palaeontological Statistics, ver. 1.81; HAMMER; HARPER; RIAN, 2001).

2.6. Statistical Analysis

To define the body shape of fish, twenty-seven landmarks and semi-landmarks were selected, according with was described in the chapter 2. In this sense, the eight relative warps adopted for each fish species were calculated in that analysis. The correlation between the Euclidean morphological distances obtained for the body characteristics and the otolith characteristics were analysed using a Mantel Test (Monte Carlo randomization test). Finally, Random Forest method was applied to measure the average error of classification attained by the otoliths analysing methods. These analyses were performed in the R software.

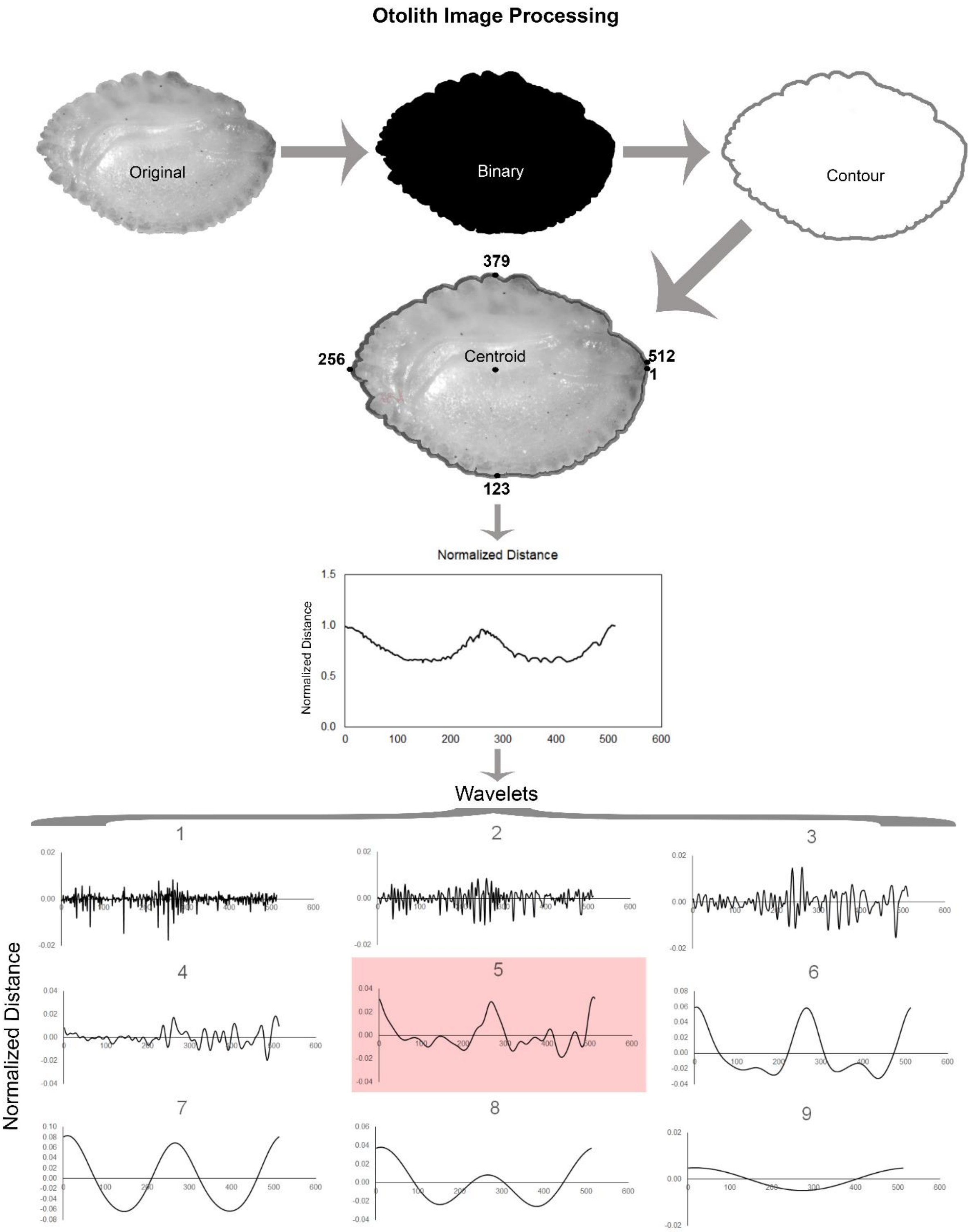


Figure 20. Wavelet transform representation from a left otolith of *Haemulopsis corvinaeformis* (modified from TUSET et al., 2016).

3. Results

3.1. Morphometry

Otolith measurements and fish sizes are positively correlated because somatic growth has influence in otolith material accretion. For each species, the measurement ranges of fish and otolith variables are summarized in Table 10. Morphometric relationships between FTL and OL, OW, OH, OA, OP, SL, SH, SA are summarized in Table 11. The coefficients between FTL and the otolith measurements were highly significant for most species, with r^2 values > 0.70 (Table 11, $p < 0.05$), except for *Archosargus rhomboidalis, Chaetodon striatus*, *Eugerres brasilianus,* and *Kyphosus sectatrix*. Permutational Multivariate Analysis of Variance (One-way Permanova) revealed significant morphologic differences between species (sequential Bonferroni significance p-value = 0.0001, $F = 203.6$) and families (sequential Bonferroni significance p-value = 0.0001, $F = 87$). Preferences for habit type and diet, sound production and swimming exert influences in the otolith format of the species and families examined (Table 12).

Table 11. Ranges of fish total length (FTL, mm) and descriptive statistic of otolith shape variables (raw data): OL, otolith length; OW, otolith weight; OH, otolith height; OA, otolith area; OP, otolith perimeter; SL, *sulcus* length; SH, *sulcus* height; and, *sulcus* area (SA) (*Continue*…).

Species	Family	FTL	OL (mm)		OW (g) * 100		OH (mm)		OA (mm²)	
		range	range	mean ± sd	range	mean ± sd	range	mean ± sd	range	mean ± sd
Albula vulpes	Albulidae	32-153	1.68 - 6.97	4.43 ± 1.59	0.07 - 3.40	1.28 ± 1.08	0.93 - 3.72	2.35 ± 0.86	1.22 - 18.46	8.73 ± 5.35
Anchoa tricolor	Engraulidae	57-98	1.77 - 2.97	2.28 ± 0.39	0.08 - 0.26	0.14 ± 0.07	1.11 - 1.72	1.35 ± 0.21	1.44 - 3.60	2.27 ± 0.77
Archosargus rhomboidalis	Sparidae	115-151	3.66 - 4.47	4.07 ± 0.26	0.72 - 0.11	0.52 ± 0.93	2.57 - 3.02	2.72 ± 0.14	6.61 - 9.28	7.66 ± 0.85
Atherinella brasiliensis	Atherinopsidae	25-151	0.79 - 4.28	2.67 ± 1.29	0.00 - 10.00	1.29 ± 3.08	0.51 - 2.58	1.59 ± 0.72	0.30 - 8.14	3.74 ± 2.91
Bathygobius soporator	Gobiidae	34-131	1.17 - 3.58	2.30 ± 0.91	0.04 - 1.01	0.32 ± 0.31	1.03 - 3.21	1.96 ± 0.71	0.98 - 8.80	3.83 ± 2.58
Ctenogobius boleosoma	Gobiidae	21-55	0.70 - 1.72	1.26 ± 0.32	0.00 - 0.10	0.03 ± 0.04	0.72 - 1.50	1.18 ± 0.26	0.41 - 1.99	1.24 ± 0.53
Centropomus parallelus	Centropomidae	214-360	8.91 - 13.94	12.00 ± 1.54	6.34 - 20.48	13.99 ± 4.42	5.47 - 8.33	7.07 ± 0.84	35.49 - 84.68	62.31 ± 14.56
Centropomus undecimalis	Centropomidae	146-382	6.20 - 8.96	7.52 ± 1.09	2.14 - 12.73	4.15 ± 3.19	3.43 - 5.11	4.16 ± 0.68	14.95 - 32.26	22.83 ± 6.95
Chloroscombrus chrysurus	Carangidae	43-193	1.31 - 4.69	3.54 ± 0.94	0.00 - 0.58	0.33 ± 0.17	0.89 - 2.47	1.92 ± 0.44	0.75 - 7.19	4.51 ± 1.79
Selene vomer	Carangidae	125-212	2.55 - 3.71	3.21 ± 0.44	0.20 - 0.54	0.38 ± 0.12	1.97 - 2.86	2.29 ± 0.33	3.42 - 6.60	5.10 ± 1.27
Chaetodipterus faber	Ephippidae	26-114	1.08 - 4.05	2.70 ± 1.10	0.00 - 0.48	0.21 ± 0.18	0.92 - 2.17	1.61 ± 0.47	0.70 - 6.50	3.46 ± 2.13
Chaetodon striatus	Chaetodontidade	128-149	4.28 - 5.38	4.78 ± 0.33	0.65 - 1.19	0.94 ± 0.18	2.24 - 2.86	2.57 ± 0.18	7.27 - 9.80	8.57 ± 0.83
Citharichthys macrops	Paralichthydae	84-134	2.58 - 2.05	2.58 ± 0.31	0.13 - 0.40	0.25 ± 0.08	1.70 - 2.29	2.07 ± 0.17	2.53 - 5.32	3.90 ± 0.77
Citharichthys spilopterus	Paralichthydae	63-191	1.86 - 4.03	2.89 ± 0.77	0.00 - 0.79	0.38 ± 0.28	1.55 - 2.74	2.07 ± 0.45	1.94 - 8.33	4.60 ± 2.33
Etropus crossotus	Paralichthydae	34-143	1.25 - 3.67	2.57 ± 0.76	0.09 - 0.74	0.33 ± 0.20	1.13 - 2.51	1.94 ± 0.42	1.02 - 6.93	3.84 ± 1.88
Ctenosciaena gracilicirrhus	Sciaenidae	42-145	4.64 - 1.45	2.66 ± 6.76	0.42 - 6.97	3.18 ± 2.43	2.24 - 5.39	3.81 ± 1.10	4.43 - 27.59	14.78 ± 8.43
Cynoscion jamaicensis	Sciaenidae	144-224	7.50 - 11.23	9.69 ± 1.25	5.08 - 13.27	9.43 ± 2.60	4.24 - 5.94	5.17 ± 0.51	24.25 - 51.67	38.64 ± 8.72
Menticirrhus americanus	Sciaenidae	48-384	2.32 - 11.62	7.80 ± 2.95	0.12 - 10.38	4.53 ± 3.47	1.31 - 4.34	3.03 ± 0.91	2.25 - 31.85	18.60 ± 10.02
Micropogonias furnieri	Sciaenidae	116-202	5.38 - 9.54	7.22 ± 1.52	3.83 - 20.28	10.65 ± 6.74	4.16 - 6.88	5.55 ± 1.06	16.08 - 46.88	29.59 ± 11.66
Diplectrum formmosum	Serranidae	49-131	2.13 - 5.45	4.37 ± 1.11	0.07 - 1.06	0.64 ± 0.35	1.10 - 2.61	2.10 ± 0.51	1.59 - 9.58	6.51 ± 2.83
Diplectrum radiale	Serranidae	95-225	4.09 - 8.64	5.76 ± 1.81	0.41 - 3.31	1.28 ± 1.00	1.77 - 3.61	2.55 ± 0.69	4.64 - 19.95	10.26 ± 6.05
Epinephelus marginatus	Serranidae	213-321	7.57 - 10.93	9.67 ± 0.90	2.18 - 5.62	4.40 ± 0.97	3.78 - 4.97	4.57 ± 0.36	18.67 - 36.67	30.02 ± 5.12
Diapterus rhombeus	Gerreidae	31-240	1.36 - 8.28	5.39 ± 2.23	0.00 - 8.37	2.68 ± 2.63	1.16 - 5.43	3.96 ± 1.30	1.04 - 29.01	15.91 ± 9.49
Eucinostomus argenteus	Gerreidae	20-151	0.91 - 4.35	2.89 ± 1.19	0.00 - 1.02	0.40 ± 0.29	0.61 - 2.78	1.84 ± 0.75	0.38 - 8.36	4.25 ± 2.80
Eugerres brasilianus	Gerreidae	152-219	5.39 - 6.79	5.88 ± 0.42	1.43 - 2.40	1.69 ± 0.28	3.21 - 3.74	3.48 ± 0.16	12.22 - 17.76	14.03 ± 1.60
Eucinostomus gula	Gerreidae	73-185	3.25 - 6.55	4.52 ± 1.36	0.42 - 2.55	1.17 ± 0.82	1.97 - 3.52	2.65 ± 0.57	4.26 - 14.55	8.46 ± 4.03
Eucinostomus melanopterus	Gerreidae	57-230	2.13 - 6.00	4.55 ± 1.27	0.15 - 3.10	1.60 ± 1.03	1.56 - 4.12	3.15 ± 0.82	2.31 - 16.31	10.44 ± 4.90
Gymnothorax ocellatus	Muraenidae	341-522	3.20 - 4.19	3.70 ± 0.33	0.63 - 1.32	0.93 ± 0.29	2.10 - 2.91	2.44 ± 0.32	5.22 - 9.31	6.80 ± 1.45
Harengula clupeola	Clupeidae	38-212	1.10 - 4.28	2.40 ± 1.23	0.00 - 0.85	0.23 ± 0.33	0.66 - 2.41	1.38 ± 0.67	0.51 - 7.09	2.78 ± 2.57
Sardinella brasiliensis	Clupeidae	45-115	1.07 - 2.11	1.74 ± 0.37	0.00 - 0.14	0.06 ± 0.05	0.69 - 0.98	0.86 ± 0.12	0.54 - 1.50	1.08 ± 0.36
Haemulopsis corvinaeformis	Haemulidae	62-178	3.61 - 8.62	6.03 ± 1.82	0.71 - 8.26	3.80 ± 2.80	2.43 - 6.09	4.13 ± 1.29	6.26 - 35.81	18.79 ± 10.71
Haemulon steindachneri	Haemulidae	105-258	5.52 - 11.13	7.99 ± 1.94	2.13 - 23.01	8.79 ± 6.44	3.95 - 7.50	5.55 ± 1.27	15.50 - 60.37	33.55 ± 15.18
Orthopristis ruber	Haemulidae	64-134	4.21 - 5.65	4.82 ± 0.52	0.47 - 1.89	1.11 ± 0.53	2.79 - 3.62	3.16 ± 0.31	8.04 - 13.88	10.63 ± 2.16
Hyporhamphus unifasciatus	Hemiramphidae	116-261	2.82 - 6.10	4.48 ± 1.22	0.33 - 3.13	1.38 ± 0.97	2.06 - 4.42	3.09 ± 0.81	4.28 - 18.13	10.13 ± 5.00
Hemiramphus brasiliensis	Hemiramphidae	116-200	2.50 - 4.30	3.51 ± 0.57	0.20 - 1.05	0.61 ± 0.26	1.84 - 2.97	2.47 ± 0.35	3.59 - 8.76	6.26 ± 1.61
Kyphosus sectatrix	Kyphosidae	280-454	6.15 - 7.76	6.71 ± 0.50	1.03 - 2.21	1.44 ± 0.37	2.59 - 3.47	3.04 ± 0.28	11.68 - 19.78	14.53 ± 2.51
Lutjanus analis	Lutjanidae	45-363	2.23 - 13.16	7.76 ± 3.01	0.12 - 19.61	6.04 ± 5.61	1.38 - 8.12	4.65 ± 1.84	2.11 - 71.96	28.10 ± 19.83
Lutjanus synagris	Lutjanidae	81-300	4.23 - 11.62	6.52 ± 2.34	0.86 - 14.05	3.94 ± 4.08	2.64 - 6.91	3.98 ± 1.41	7.85 - 55.72	20.09 ± 15.02
Mugil curema	Mugilidae	29-450	1.25 - 10.35	6.35 ± 2.81	0.00 - 9.44	3.04 ± 3.04	0.89 - 4.49	3.08 ± 1.10	0.79 - 33.30	15.65 ± 10.38
Pomatomus saltatrix	Pomatomidae	281-471	8.31 - 13.10	10.71 ± 1.20	1.69 - 5.50	2.98 ± 1.00	3.14 - 4.62	3.81 ± 0.39	19.87 - 43.48	29.79 ± 6.00
Polydactylus virginicus	Polynemidae	235-365	5.70 - 7.81	7.06 ± 0.67	1.33 - 3.03	2.36 ± 0.57	2.74 - 4.17	3.52 ± 0.40	11.77 - 20.59	17.69 ± 2.94
Prionotus punctatus	Triglidae	48-220	1.92 - 5.99	3.75 ± 1.44	0.14 - 1.84	0.70 ± 0.62	1.25 - 3.88	2.45 ± 0.91	1.62 - 15.61	7.07 ± 5.04
Synodos foetens	Synodontidae	106-238	1.98 - 4.54	3.09 ± 0.99	0.07 - 0.80	0.34 ± 0.26	1.08 - 1.98	1.53 ± 0.38	1.46 - 6.36	3.47 ± 1.85

Table 11. Ranges of fish total length (FTL, mm) and descriptive statistic of otolith shape variables (raw data): OL, otolith length; OW, otolith weight; OH, otolith height; OA, otolith area; OP, otolith perimeter; SL, *sulcus* length; SH, *sulcus* height; and, *sulcus* area (SA) (*Continue…*)

Species	**Family**	**FTL range (mm)**	**OP (mm²)**		**SL (mm)**		**SH (mm)**		**SA (mm)**	
			range	**mean ± sd**	**range**	**mean ± sd**	**range**	**mean ± sd**	**range**	**mean ± sd**
Albula vulpes	Albulidae	32-153	4.65 - 17.99	12.10 ± 4.14	1.19 - 5.47	3.45 ± 1.28	0.51 - 2.31	1.52 ± 0.62	0.23 - 5.02	2.15 ± 1.46
Anchoa tricolor	Engraulidae	57-98	4.74 - 7.99	6.18 ± 1.08	1.34 - 2.30	1.67 ± 0.32	0.47 - 0.79	0.62 ± 0.10	0.48 - 1.31	0.75 ± 0.31
Archosargus rhomboidalis	Sparidae	115-151	10.64 - 13.55	11.88 ± 0.86	2.76 - 3.70	3.29 ± 0.25	1.07 - 1.46	1.27 ± 0.14	1.48 - 2.22	1.75 ± 0.21
Atherinella brasiliensis	Atherinopsidae	25-151	2.11 - 11.71	7.34 ± 3.37	0.52 - 3.87	2.30 ± 1.22	0.13 - 0.91	0.54 ± 0.28	0.04 - 1.87	0.82 ± 0.68
Bathygobius soporator	Gobiidae	34-131	3.85 - 12.41	7.75 ± 3.04	0.77 - 2.17	1.50 ± 0.50	0.33 - 0.96	0.60 ± 0.20	0.16 - 1.11	0.59 ± 0.32
Ctenogobius boleosoma	Gobiidae	21-55	2.43 - 5.35	4.12 ± 0.97	0.43 - 1.01	0.72 ± 0.19	0.24 - 0.55	0.35 ± 0.10	0.06 - 0.34	0.17 ± 0.09
Centropomus parallelus	Centropomidae	214-360	25.69 - 38.13	32.78 ± 3.88	8.25 - 12.70	10.85 ± 1.31	2.46 - 4.30	3.28 ± 0.58	11.53 - 27.11	19.12 ± 5.37
Centropomus undecimalis	Centropomidae	146-382	15.71 - 24.17	19.68 ± 3.38	5.61 - 7.97	6.72 ± 0.94	1.29 - 2.07	1.66 ± 0.27	4.40 - 9.96	6.51 ± 2.09
Chloroscombrus chrysurus	Carangidae	43-193	3.50 - 13.38	9.69 ± 2.75	1.16 - 3.98	3.00 ± 0.79	0.37 - 0.96	0.78 ± 0.17	0.16 - 1.73	1.03 ± 0.44
Selene vomer	Carangidae	125-212	8.15 - 11.90	10.09 ± 1.44	2.01 - 3.25	2.71 ± 0.45	0.66 - 1.14	0.96 ± 0.15	0.68 - 1.45	1.09 ± 0.31
Chaetodipterus faber	Ephippidae	26-114	3.54 - 10.99	7.61 ± 2.77	0.94 - 3.53	2.38 ± 0.95	0.34 - 1.09	0.76 ± 0.27	0.13 - 1.96	0.97 ± 0.68
Chaetodon striatus	Chaetodontidade	128-149	11.76 - 14.52	12.99 ± 0.80	3.65 - 4.59	4.05 ± 0.29	1.03 - 1.71	1.41 ± 0.24	1.51 - 2.33	1.83 ± 0.29
Citharichthys macrops	Paralichthydae	84-134	6.10 - 8.81	7.66 ± 0.79	1.06 - 1.70	1.36 ± 0.20	0.38 - 0.61	0.45 ± 0.07	0.27 - 0.51	0.41 ± 0.08
Citharichthys spilopterus	Paralichthydae	63-191	5.50 - 10.96	8.07 ± 2.09	1.07 - 2.36	1.57 ± 0.48	0.32 - 0.82	0.53 ± 0.16	0.23 - 1.14	0.59 ± 0.36
Etropus crossotus	Paralichthydae	34-143	3.95 - 9.98	7.25 ± 1.92	0.53 - 1.81	1.32 ± 0.41	0.24 - 0.87	0.55 ± 0.20	0.09 - 0.81	0.47 ± 0.25
Ctenosciaena gracilicirrhus	Sciaenidae	42-145	13.58 - 4.15	7.82 ± 19.33	2.31 - 6.22	4.22 ± 1.39	1.39 - 3.62	2.53 ± 0.85	1.38 - 11.87	6.14 ± 3.97
Cynoscion jamaicensis	Sciaenidae	144-224	19.44 - 28.34	24.49 ± 2.90	6.93 - 10.35	8.91 ± 1.15	2.79 - 4.37	3.60 ± 0.50	10.09 - 26.82	18.52 ± 5.25
Menticirrhus americanus	Sciaenidae	48-384	5.92 - 27.95	18.65 ± 6.89	1.97 - 10.06	6.56 ± 2.60	0.80 - 3.89	2.52 ± 0.95	0.75 - 21.71	10.76 ± 7.19
Micropogonias furnieri	Sciaenidae	116-202	17.58 - 26.66	21.51 ± 3.80	4.71 - 8.41	6.29 ± 1.31	2.36 - 4.40	3.38 ± 0.73	6.41 - 19.92	12.17 ± 4.90
Diplectrum formmosum	Serranidae	49-131	5.21 - 13.59	10.91 ± 2.71	1.72 - 4.48	3.56 ± 0.93	0.49 - 1.52	0.92 ± 0.29	0.41 - 2.25	1.51 ± 0.62
Diplectrum radiale	Serranidae	95-225	9.72 - 20.80	14.21 ± 4.26	3.35 - 7.49	4.89 ± 1.65	0.74 - 1.65	1.08 ± 0.34	1.04 - 6.08	2.67 ± 1.76
Epinephelus marginatus	Serranidae	213-321	17.46 - 37.04	30.44 ± 5.53	6.83 - 9.57	8.58 ± 0.75	1.74 - 2.92	2.33 ± 0.35	5.37 - 10.82	8.30 ± 1.57
Diapterus rhombeus	Gerreidae	31-240	4.22 - 24.15	16.49 ± 6.24	1.17 - 7.06	4.63 ± 1.90	0.35 - 2.21	1.42 ± 0.60	0.22 - 7.21	3.83 ± 2.43
Eucinostomus argenteus	Gerreidae	20-151	2.46 - 11.92	7.79 ± 3.19	0.82 - 4.22	2.75 ± 1.15	0.26 - 1.14	0.78 ± 0.30	0.11 - 1.98	1.02 ± 0.65
Eugerres brasilianus	Gerreidae	152-219	14.86 - 19.28	16.43 ± 1.42	4.36 - 5.26	4.74 ± 0.27	1.30 - 2.21	1.70 ± 0.31	2.80 - 4.86	3.33 ± 0.61
Eucinostomus gula	Gerreidae	73-185	8.67 - 16.80	12.21 ± 3.45	3.12 - 6.26	4.36 ± 1.26	0.69 - 1.39	0.99 ± 0.24	0.99 - 3.83	2.12 ± 1.06
Eucinostomus melanopterus	Gerreidae	57-230	6.27 - 16.54	13.01 ± 3.44	1.90 - 5.56	4.19 ± 1.19	0.69 - 1.61	1.20 ± 0.30	0.50 - 4.22	2.40 ± 1.23
Gymnothorax ocellatus	Muraenidae	341-522	9.42 - 12.28	10.56 ± 1.05	2.25 - 3.50	2.67 ± 0.40	0.76 - 1.18	0.99 ± 0.13	1.01 - 2.41	1.59 ± 0.48
Harengula clupeola	Clupeidae	38-212	3.06 - 12.73	7.10 ± 3.83	0.85 - 3.74	1.99 ± 1.08	0.33 - 1.70	0.80 ± 0.49	0.17 - 3.48	1.21 ± 1.26
Sardinella brasiliensis	Clupeidae	45-115	3.07 - 6.30	5.00 ± 1.20	0.91 - 1.73	1.43 ± 0.29	0.32 - 0.59	0.47 ± 0.09	0.20 - 0.60	0.42 ± 0.14
Haemulopsis corvinaeformis	Haemulidae	62-178	10.01 - 24.30	16.71 ± 5.13	2.92 - 6.97	4.89 ± 1.44	0.98 - 2.91	1.80 ± 0.74	1.09 - 7.72	3.99 ± 2.44
Haemulon steindachneri	Haemulidae	105-258	15.19 - 30.30	22.33 ± 5.51	4.47 - 9.55	6.60 ± 1.65	1.84 - 4.12	2.98 ± 0.76	3.17 - 15.82	7.61 ± 3.92
Orthopristis ruber	Haemulidae	64-134	11.24 - 15.29	13.24 ± 1.37	3.55 - 4.65	4.07 ± 0.40	1.07 - 1.41	1.25 ± 0.13	1.78 - 3.30	2.44 ± 0.53
Hyporhamphus unifasciatus	Hemiramphidae	116-261	8.63 - 17.18	13.02 ± 3.17	2.36 - 5.36	3.73 ± 1.09	0.56 - 1.36	0.90 ± 0.28	0.73 - 4.59	2.12 ± 1.17
Hemiramphus brasiliensis	Hemiramphidae	116-200	7.86 - 12.83	10.87 ± 1.61	2.04 - 3.89	3.02 ± 0.54	0.45 - 1.00	0.71 ± 0.19	0.57 - 2.34	1.32 ± 0.53
Kyphosus sectatrix	Kyphosidae	280-454	16.64 - 23.42	19.69 ± 2.36	4.40 - 6.26	5.35 ± 0.53	1.34 - 2.06	1.69 ± 0.23	2.86 - 5.32	3.79 ± 0.72
Lutjanus analis	Lutjanidae	45-363	6.49 - 35.56	21.82 ± 8.91	1.86 - 10.52	6.22 ± 2.39	0.63 - 3.42	1.90 ± 0.75	0.56 - 20.13	7.31 ± 5.55
Lutjanus synagris	Lutjanidae	81-300	13.52 - 32.62	18.65 ± 5.81	3.35 - 9.37	5.32 ± 1.89	1.01 - 3.01	1.60 ± 0.64	1.86 - 14.68	5.21 ± 4.01
Mugil curema	Mugilidae	29-450	3.61 - 27.13	18.09 ± 7.42	1.16 - 8.72	5.40 ± 2.33	0.31 - 2.31	1.37 ± 0.67	0.18 - 6.95	3.45 ± 2.28
Pomatomus saltatrix	Pomatomidae	281-471	23.84 - 35.62	28.43 ± 3.21	7.51 - 12.11	9.86 ± 1.17	1.42 - 2.42	1.85 ± 0.29	5.73 - 15.71	9.75 ± 2.61
Polydactylus virginicus	Polynemidae	235-365	14.89 - 21.88	19.47 ± 2.26	4.62 - 6.82	5.84 ± 0.62	1.64 - 2.36	2.10 ± 0.23	3.25 - 7.81	5.81 ± 1.46
Prionotus punctatus	Triglidae	48-220	5.85 - 18.47	11.29 ± 4.46	1.58 - 5.10	3.16 ± 1.23	0.50 - 1.35	0.84 ± 0.26	0.49 - 4.18	1.78 ± 1.30
Synodos foetens	Synodontidae	106-238	5.34 - 11.72	8.25 ± 2.52	1.66 - 3.87	2.59 ± 0.85	0.41 - 0.90	0.65 ± 0.19	0.32 - 1.63	0.83 ± 0.49

Table 12. Relationships between of fish total length (FTL) and otolith shape variables, using power regression (Y=aX^b; LLEONART et al. 2000): OL, otolith length; OW, otolith weight; OH, otolith height; OA, otolith area; OP, otolith perimeter; SL, *sulcus* length; SH, *sulcus* height; and, *sulcus* area (SA) (*Continue…*).

Species	FTL - OL			FTL - OW			FTL - OH			FTL - AO			FTL - OP		
	a	b	R²	a	b	R²	a	b	R²	a	b	R²	a	b	R²
Albula vulpes	-10178	0.8575	0.98	-6.7515	2.4436	0.99	-12855	0.8539	0.99	-2.3278	16623	0.98	-0.5379	0.8357	0.97
Anchoa tricolor	-10971	0.7775	0.89	-6.6226	2.0028	0.82	-11602	0.6890	0.85	-2.4011	14676	0.88	-0.6827	0.7876	0.88
Archosargus rhomboidalis	0.1315	0.2246	0.08	-2.6454	0.2348	0.02	-0.1777	0.2882	0.22	0.0444	0.3942	0.09	0.2742	0.3763	0.20
Atherinella brasiliensis	-14839	0.9840	0.99	-116850	4.6672	0.93	-15481	0.9028	0.99	-3.1924	18995	0.99	-10060	0.9646	0.97
Bathygobius soporator	-11469	0.8114	0.99	-6.3786	2.0288	0.96	-10276	0.7117	0.97	-2.2185	14822	0.99	-0.6020	0.8020	0.97
Ctenogobius boleosoma	-13745	0.9430	0.96	-13.7830	6.2155	0.69	-12345	0.8365	0.99	-2.6861	17655	0.98	-0.7732	0.888	0.98
Centropomus parallelus	-0.8697	0.7891	0.94	-6.0812	2.1106	0.95	-0.9321	0.7214	0.95	-18835	14869	0.94	-0.0603	0.638	0.75
Centropomus undecimalis	-0.1184	0.4306	0.75	-5.7447	18646	0.96	-0.5000	0.4843	0.77	-0.7554	0.9112	0.78	0.1138	0.5106	0.76
Chloroscombrus chrysurus	-12167	0.8291	0.98	-114480	4.1523	0.90	-11185	0.6597	0.98	-2.4918	14686	0.99	-0.8631	0.868	0.98
Selene vomer	-0.7983	0.5875	0.85	-5.7178	14759	0.89	-0.9590	0.5935	0.85	-17995	11261	0.94	-0.3495	0.6091	0.84
Chaetodipterus faber	-10559	0.8215	0.97	-111100	4.4262	0.86	-0.7803	0.5490	0.96	-2.0421	14043	0.98	-0.4209	0.7216	0.97
Chaetodon striatus	-0.9297	0.7496	0.32	-8.9788	3.2354	0.63	-0.9680	0.6414	0.22	-18644	13030	0.47	-0.2729	0.6459	0.30
Citharichthys macrops	-13037	0.8448	0.92	-6.9997	2.1555	0.76	-0.8645	0.5812	0.88	-2.3071	14261	0.91	-0.6028	0.7326	0.89
Citharichthys spilopterus	-11563	0.7757	0.97	-12.5270	4.7439	0.70	-0.8966	0.5826	0.90	-2.4457	14791	0.97	-0.6128	0.7291	0.95
Etropus crossotus	-10085	0.7224	0.99	-5.4104	14711	0.94	-0.7228	0.5170	0.96	-19547	12818	0.99	-0.3785	0.6323	0.99
Ctenosciaena gracilicirrhus	-0.8785	0.7857	0.99	-6.0860	2.2883	100	-0.8663	0.7362	0.99	-19330	15601	0.99	-0.3917	0.7754	0.99
Cynoscion jamaicensis	-11112	0.9248	0.95	-5.6825	2.0489	0.87	-0.8549	0.6915	0.91	-2.1928	16644	0.95	-0.5300	0.8462	0.95
Menticirrhus americanus	-0.8624	0.7468	0.89	-6.4598	2.1370	0.99	-0.7727	0.5364	0.87	-18292	13079	0.98	-0.4094	0.7155	0.89
Micropogonias furnieri	-14585	10589	0.93	-8.4774	3.4039	0.94	-13823	0.9724	0.93	-3.0313	2.0513	0.95	-0.5721	0.871	0.90
Diplectrum formosum	-11229	0.8781	0.94	-7.1778	2.4525	0.91	-13044	0.8102	0.94	-2.6320	17039	0.94	-0.6880	0.8594	0.92
Diplectrum radiale	-10689	0.8349	0.74	-7.2418	2.4124	0.95	-13232	0.7906	0.87	-2.5256	16012	0.79	-0.6919	0.8424	0.81
Epinephelus marginatus	-0.9663	0.7936	0.88	-6.8365	2.2253	0.95	-0.9724	0.6636	0.89	-2.4035	15768	0.93	-2.8879	17758	0.95
Diapterus rhombeus	-12237	0.9146	0.99	-110350	4.3197	0.94	-10221	0.7607	0.97	-2.4218	16771	0.98	-0.6548	0.8769	0.97
Eucinostomus argenteus	-10329	0.7869	0.94	-7.4839	2.6077	0.74	-11588	0.7503	0.92	-2.3563	15402	0.93	-0.5958	0.7839	0.96
Eugerres brasilianus	-0.6127	0.6069	0.74	-4.3556	11328	0.57	-0.2718	0.3572	0.56	-10011	0.9429	0.72	-0.4883	0.7481	0.75
Eucinostomus gula	-10371	0.8045	0.92	-6.1932	19988	0.97	-0.8454	0.6044	0.95	-19959	13814	0.98	-0.5702	0.7883	0.97
Eucinostomus melanopterus	-0.9321	0.7312	0.97	-6.4841	2.1222	0.99	-0.9829	0.6813	0.98	-2.0592	14035	0.98	-0.4012	0.6972	0.98
Gymnothorax ocellatus	-0.7656	0.5073	0.85	-6.8624	18327	0.90	-14886	0.7129	0.78	-2.4775	12569	0.91	-0.4145	0.5468	0.80
Harengula clupeola	-12619	0.8090	0.99	-13.0820	4.7372	0.84	-14106	0.7648	0.99	-2.7490	15361	0.99	-0.8835	0.8535	0.99
Sardinella brasiliensis	-11435	0.7185	0.96	-15.3270	6.1100	0.82	-0.8386	0.4024	0.78	-2.0914	10976	0.91	-0.8121	0.7837	0.94
Haemulopsis corvinaeformis	-0.9449	0.8387	100	-6.3346	2.3507	0.99	-11638	0.8649	100	-2.1742	16602	100	-0.4758	0.8257	0.99
Haemulon steindachneri	-0.8232	0.7718	0.99	-6.3584	2.3392	0.97	-0.8778	0.7257	0.99	-18385	14956	0.99	-0.3624	0.7651	0.92
Orthopristis ruber	-0.0640	0.3753	0.90	-5.7355	18802	0.98	-0.1814	0.3422	0.92	-0.4084	0.7190	0.94	0.3809	0.3723	0.95
Hyporhamphus unifasciatus	-17290	10354	0.92	-8.3528	2.7952	0.92	-16213	0.9187	0.87	-3.2753	18524	0.91	-0.9925	0.9171	0.92
Hemiramphus brasiliensis	-13589	0.8555	0.88	-8.2479	2.6977	0.88	-12409	0.7341	0.86	-2.3687	14194	0.88	-0.6786	0.7704	0.85
Kyphosus sectatrix	-0.1401	0.3859	0.62	-5.7427	15535	0.87	-0.7758	0.5024	0.66	-14571	10444	0.87	-0.3561	0.6583	0.69
Lutjanus analis	-10295	0.8460	0.99	-6.7317	2.3776	0.98	-12132	0.8287	0.99	-2.3801	16641	0.99	-0.5928	0.8506	0.98
Lutjanus synagris	-10180	0.8496	0.96	-6.7429	2.4184	0.93	-12104	0.8393	0.93	-2.4133	17004	0.94	-0.2272	0.6958	0.96
Mugil curema	-0.8177	0.6947	0.95	-8.4952	2.8807	0.89	-0.7271	0.5247	0.93	-17147	12253	0.95	-0.2577	0.6504	0.91
Pomatomus saltatrix	-10517	0.8031	0.89	-6.7470	2.0096	0.82	-10965	0.6473	0.72	-19876	13342	0.83	-0.3751	0.7055	0.76
Polydactylus virginicus	-0.9649	0.7290	0.96	-6.6358	2.0099	0.95	-15181	0.8297	0.86	-2.0555	13268	0.94	-0.8812	0.8723	0.89
Prionotus punctatus	-10091	0.7638	0.99	-5.9858	18028	0.97	-11680	0.7518	100	-2.3322	15112	100	-0.5714	0.7831	0.97
Synodos foetens	-17156	0.9861	0.96	-8.3382	2.5863	0.88	-14649	0.7382	0.92	-3.3284	17181	0.95	-11915	0.9425	0.95

Table 12. Relationships between of fish total length (FTL) and otolith shape variables, using power regression ($Y=aX^b$; LLEONART et al. 2000): OL, otolith length; OW, otolith weight; OH, otolith height; OA, otolith area; OP, otolith perimeter; SL, *sulcus* length; SH, *sulcus* height; and, *sulcus* area (SA) (*Continue…*).

Species	FTL - SL			FTL - SH			FTL - AS		
	a	b	R^2	a	b	R^2	a	b	R^2
Albula vulpes	-1.2062	0.8976	0.97	-1.8668	1.0513	0.94	-3.3649	1.8740	0.98
Anchoa tricolor	-1.2351	0.7790	0.79	-1.4938	0.6865	0.73	-3.1581	1.6110	0.84
Archosargus rhomboidalis	0.2467	0.1266	0.02	-0.9072	0.4748	0.13	-1.0269	0.5968	0.20
Atherinella brasiliensis	-1.8347	1.1274	0.99	-2.2995	1.0460	0.97	-4.2704	2.1048	0.99
Bathygobius soporator	-1.0536	0.6633	0.93	-1.3945	0.6306	0.93	-2.5181	1.2169	0.94
Ctenogobius boleosoma	-1.4738	0.8503	0.83	-1.7710	0.8340	0.70	-3.5968	1.7782	0.86
Centropomus parallelus	-0.6951	0.7007	0.85	-1.9094	0.9810	0.84	-2.7702	1.6369	0.90
Centropomus undecimalis	-0.1301	0.4145	0.75	-0.8423	0.4594	0.66	-1.3563	0.9348	0.77
Chloroscombrus chrysurus	-1.2330	0.8033	0.99	-1.3219	0.5713	0.81	-3.3077	1.5487	0.98
Selene vomer	-0.9880	0.6390	0.67	-1.1266	0.4980	0.40	-2.6453	1.2025	0.79
Chaetodipterus faber	-1.0898	0.8103	0.94	-1.3525	0.6837	0.93	-3.1107	1.6755	0.95
Chaetodon striatus	-0.9134	0.7085	0.26	-1.2643	0.6552	0.04	0.1371	0.0565	0.00
Citharichthys macrops	-1.7538	0.9292	0.74	-0.2725	-0.0411	0.00	-2.8121	1.1908	0.55
Citharichthys spilopterus	-1.5047	0.8133	0.84	-1.7419	0.7025	0.63	-3.9575	1.7656	0.91
Etropus crossotus	-1.4278	0.7874	0.91	-1.9179	0.8432	0.90	-3.2417	1.4636	0.93
Ctenosciaena gracilicirrhus	-1.0299	0.8411	0.99	-1.2161	0.8218	0.92	-2.8949	1.8456	0.99
Cynoscion jamaicensis	-1.1491	0.9253	0.96	-1.6478	0.9717	0.95	-3.5712	2.1291	0.95
Menticirrhus americanus	-1.0706	0.8036	1.00	-1.3824	0.7605	0.99	-2.9212	1.6581	0.99
Micropogonias furnieri	-1.5359	1.0670	0.96	-1.9165	1.1174	0.93	-3.5578	2.1150	0.96
Diplectrum formosum	-1.2207	0.8821	0.91	-1.7668	0.8601	0.80	-3.0463	1.5959	0.94
Diplectrum radiale	-1.2747	0.8956	0.75	-1.7771	0.8260	0.70	-3.5171	1.7825	0.81
Epinephelus marginatus	-0.7895	0.7005	0.77	-2.1418	1.0190	0.63	-2.9354	1.5655	0.83
Diapterus rhombeus	-1.2870	0.9137	0.99	-1.8278	0.9247	0.93	-3.2651	1.7769	0.98
Eucinostomus argenteus	-1.1097	0.8157	0.94	-1.4179	0.6905	0.88	-2.8359	1.4694	0.92
Eugerres brasilianus	-0.4021	0.4732	0.68	-1.6793	0.8367	0.22	-2.2562	1.2187	0.53
Eucinostomus gula	-1.0122	0.7855	0.95	-1.2963	0.6152	0.78	-2.6817	1.4200	0.97
Eucinostomus melanopterus	-1.0058	0.7481	0.96	-1.2485	0.6112	0.95	-2.8421	1.4667	0.97
Gymnothorax ocellatus	-1.5895	0.7661	0.73	-1.6771	0.6352	0.56	-4.2437	1.6857	0.83
Harengula clupeola	-1.4376	0.8545	0.98	-1.9510	0.9078	0.94	-3.5143	1.7177	0.98
Sardinella brasiliensis	-1.0814	0.6414	0.87	-1.5185	0.6174	0.92	-2.5277	1.1104	0.92
Haemulopsis corvinaeformis	-0.9891	0.8161	1.00	-1.9625	1.0734	0.97	-3.1718	1.8135	0.99
Haemulon steindachneri	-0.9440	0.7886	0.98	-1.2497	0.7702	0.85	-2.7491	1.6115	0.98
Orthopristis ruber	-0.0401	0.3265	0.86	-0.6034	0.3511	0.84	-1.1292	0.7596	0.93
Hyporhamphus unifasciatus	-1.8694	1.0613	0.89	-2.3748	1.0112	0.73	-4.2845	1.9925	0.90
Hemiramphus brasiliensis	-1.5958	0.9322	0.85	-2.7886	1.1820	0.66	-4.2031	1.9333	0.73
Kyphosus sectatrix	-0.4438	0.4676	0.47	-1.5169	0.6956	0.60	-2.1060	1.0699	0.72
Lutjanus analis	-1.0784	0.8254	0.99	-1.4711	0.7713	0.95	-3.0300	1.6891	0.99
Lutjanus synagris	-1.0735	0.8343	0.94	-1.6979	0.8796	0.87	-3.1311	1.7585	0.92
Mugil curema	-0.8124	0.6626	0.95	-1.4629	0.6836	0.92	-2.3628	1.2207	0.94
Pomatomus saltatrix	-1.2151	0.8522	0.88	-1.7976	0.7960	0.48	-3.4810	1.7216	0.80
Polydactylus virginicus	-1.2382	0.8058	0.96	-1.6654	0.7986	0.88	-4.3482	2.0518	0.97
Prionotus punctatus	-1.1011	0.7720	0.99	-1.1515	0.5206	0.80	-2.7156	1.4073	0.96
Synodos foetens	-1.8467	1.0099	0.95	-2.1803	0.8903	0.84	-4.4398	1.9315	0.94

Table 13. Results of the multivariate permutational analysis (One-way PERMANOVA) performed for otolith morphometric variables by each ecological profile (SS: sum of squares).

One-way Permanova	**SS**	**F**	**P-value**
Habit	502.70	109.80	0.0001
Sound Production	502.70	252.90	0.0001
Swimming	502.70	80.05	0.0001
Diet	502.70	34.40	0.0001

3.2. Shape Indices

Shape indices showed mainly elliptic otoliths (i.e. Carangidae, Clupeidae and Engraulidae) (Figure 21). Elongated otolith patterns were seen in Kyphosidae and Pomatomidae, whilst squared *sagittae* were typical of Gobiidae fishes. Although two families had presented greater variability in its general shape: the Serranidae with fusiform and different types of elliptic shapes, and the Sciaenidae with discoidal, bullet-shape, elliptic, and pyriform shapes. In addition, aspect ratios (ARwe, ARsa, ARswi) allowed the separation of fishes with relatively large otoliths and *sulcus acusticus,* and are capable to emit sounds or possess hearing habilities (Figure 21, * in red). A summary of descriptive statistics (mean, standard deviation, minimum, and maximum) showing the results of shapes indices and aspect ratios obtained for each species are presented in Table 13. The Multivariate Analysis of Variance (Two-way Permanova) revealed significant shape differences (both for indices and aspect ratios) related to species and habit (Table 14).

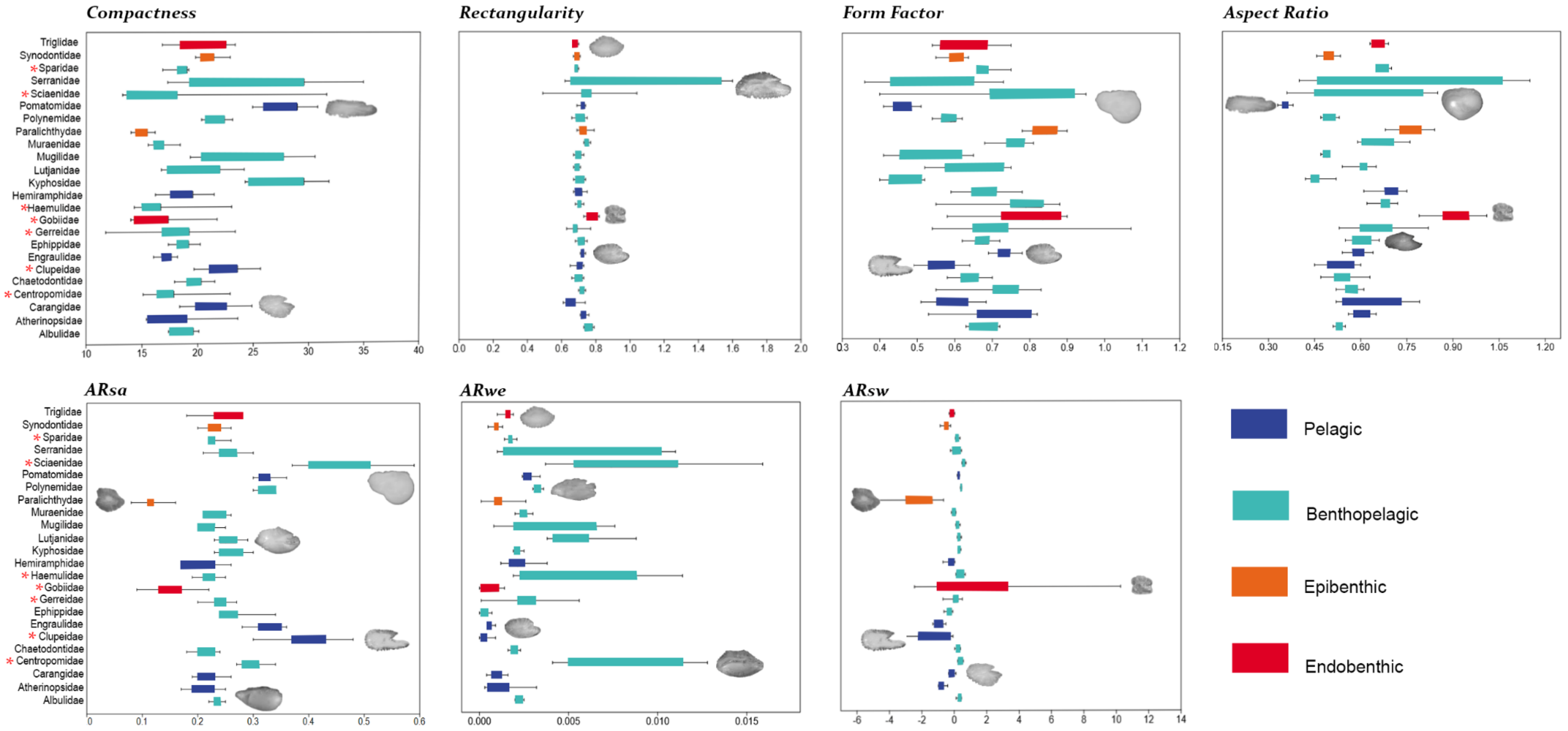


Figure 21. Representation of shape indices and aspect ratios applied to the otolith morphometries by family (* indicate fish with hearing habilities).

Table 14. Summary of descriptive statistics (mean, standard deviation, minimum, and maximum) showing the results of shapes indices and aspect ratios obtained for each species (*Continue…*).

Acronym		**AR**	**C**	**FF**	**R**	**Rwe*100**	**Rsa**	**Rswi**
Avul	mean ± SD	0.53 ± 0.01	18.62 ± 1.00	0.68 ± 0.04	0.76 ± 0.02	0.23 ± 0.02	0.24 ± 0.01	0.44 ± 0.06
	min	0.51	17.38	0.63	0.73	0.20	0.22	0.30
	max	0.55	20.09	0.72	0.79	0.25	0.25	0.50
Atri	mean ± SD	0.59 ± 0.03	17.27 ± 0.61	0.73 ± 0.03	0.72 ± 0.01	0.06 ± 0.01	0.33 ± 0.03	0.37 ± 0.03
	min	0.54	16.03	0.69	0.71	0.05	0.28	0.32
	max	0.64	18.17	0.78	0.74	0.09	0.36	0.44
Arho	mean ± SD	0.67 ± 0.02	18.47 ± 0.87	0.68 ± 0.03	0.69 ± 0.01	0.18 ± 0.02	0.23 ± 0.01	0.39 ± 0.05
	min	0.65	16.82	0.66	0.68	0.14	0.22	0.34
	max	0.70	19.14	0.75	0.70	0.21	0.26	0.49
Abra	mean ± SD	0.60 ± 0.03	17.45 ± 2.60	0.73 ± 0.09	0.73 ± 0.02	0.12 ± 0.09	0.21 ± 0.03	0.24 ± 0.02
	min	0.56	15.40	0.53	0.71	0.03	0.17	0.21
	max	0.65	23.60	0.82	0.76	0.32	0.25	0.27
Bsop	mean ± SD	0.86 ± 0.05	17.52 ± 1.75	0.72 ± 0.07	0.76 ± 0.02	0.11 ± 0.02	0.16 ± 0.03	0.40 ± 0.04
	min	0.79	15.30	0.58	0.73	0.09	0.13	0.33
	max	0.95	21.72	0.82	0.79	0.14	0.22	0.46
Cpar	mean ± SD	0.59 ± 0.01	17.57 ± 2.29	0.72 ± 0.08	0.72 ± 0.01	1.13 ± 0.06	0.31 ± 0.02	0.30 ± 0.03
	min	0.56	15.10	0.55	0.71	1.06	0.27	0.26
	max	0.61	22.91	0.83	0.74	1.28	0.34	0.36
Cund	mean ± SD	0.55 ± 0.02	17.31 ± 0.75	0.73 ± 0.03	0.72 ±0.01	0.50 ± 0.06	0.28 ± 0.01	0.25 ± 0.01
	min	0.52	16.42	0.67	0.70	0.41	0.27	0.23
	max	0.58	18.74	0.77	0.74	0.60	0.31	0.27
Cchr	mean ± SD	0.55 ± 0.02	21.74 ± 1.68	0.58 ± 0.04	0.63 ± 0.01	0.08 ± 0.05	0.23 ± 0.02	0.26 ± 0.03
	min	0.52	19.86	0.51	0.61	0.04	0.21	0.21
	max	0.56	24.87	0.63	0.65	0.16	0.26	0.29
Cfab	mean ± SD	0.60 ± 0.03	18.69 ± 0.77	0.67 ± 0.03	0.72 ± 0.02	0.05 ± 0.08	0.27 ± 0.03	0.32 ± 0.02
	min	0.55	17.35	0.62	0.68	0.01	0.24	0.29
	max	0.66	20.20	0.72	0.75	0.27	0.34	0.36
Cstr	mean ± SD	0.54 ± 0.04	19.73 ± 0.98	0.64 ± 0.03	0.70 ± 0.02	0.19 ± 0.02	0.21 ± 0.02	0.35 ± 0.05
	min	0.47	17.92	0.58	0.66	0.16	0.18	0.27
	max	0.63	21.52	0.70	0.73	0.23	0.24	0.43
Cmac	mean ± SD	0.80 ± 0.03	15.19 ± 0.67	0.83 ± 0.04	0.73 ± 0.03	0.09 ± 0.02	0.10 ± 0.01	0.33 ± 0.05
	min	0.77	14.05	0.78	0.70	0.07	0.08	0.28
	max	0.84	16.14	0.89	0.79	0.13	0.12	0.43
Cspi	mean ± SD	0.72 ± 0.03	15.02 ± 0.55	0.84 ± 0.03	0.72 ± 0.02	0.12 ± 0.09	0.12 ± 0.02	0.35 ± 0.07
	min	0.68	14.07	0.80	0.69	0.01	0.10	0.28
	max	0.77	15.72	0.89	0.75	0.26	0.16	0.48
Cbol	mean ± SD	0.94 ± 0.05	14.32 ± 0.25	0.88 ± 0.02	0.80 ± 0.02	0.01 ± 0.01	0.13 ± 0.03	0.48 ± 0.08
	min	0.87	13.99	0.85	0.77	0.00	0.09	0.36
	max	1.01	14.77	0.90	0.82	0.03	0.18	0.59
Cgra	mean ± SD	0.82 ± 0.02	13.53 ± 0.22	0.93 ± 0.02	0.77 ± 0.01	0.57 ± 0.03	0.40 ± 0.02	0.60 ± 0.05
	min	0.91	13.24	0.91	0.74	0.53	0.37	0.49
	max	0.95	13.87	0.95	0.80	0.61	0.43	0.67
Cjam	mean ± SD	0.53 ± 0.02	15.71 ± 0.14	0.80 ± 0.01	0.76 ± 0.01	0.96 ± 0.09	0.47 ± 0.01	0.40 ± 001
	min	0.51	15.46	0.79	0.75	0.87	0.47	0.38
	max	0.57	15.89	0.81	0.77	1.17	0.50	0.42
Dfor	mean ± SD	0.48 ± 0.01	19.38 ± 1.73	0.65 ± 0.06	0.67 ± 0.01	0.13 ± 0.03	0.23 ± 0.01	0.26 ± 0.04
	min	0.46	17.26	0.56	0.65	0.10	0.21	0.22
	max	0.49	22.60	0.73	0.70	0.18	0.25	0.35
Drad	mean ± SD	0.45 ± 0.04	21.17 ± 1.70	0.60 ± 0.05	0.65 ± 0.03	0.19 ± 0.03	0.25 ± 0.01	0.22 ± 0.02
	min	0.40	17.98	0.53	0.62	0.15	0.24	0.18
	max	0.53	23.50	0.70	0.70	0.26	0.28	0.26
Drho	mean ± SD	0.75 ± 0.05	18.97 ± 1.92	0.67 ± 0.06	0.67 ± 0.01	0.35 ± 0.17	0.23 ± 0.01	0.31 ± 0.05
	min	0.67	16.63	0.54	0.66	0.12	0.21	0.25
	max	0.82	23.35	0.76	0.69	0.56	0.25	0.43
Emar	mean ± SD	1.03 ± 0.20	30.62 ± 2.21	0.41 ± 0.03	1.47 ± 0.28	0.98 ± 0.19	0.28 ± 0.02	0.27 ± 0.02
	min	0.48	27.18	0.36	0.68	0.44	0.25	0.25
	max	1.15	34.87	0.46	1.60	1.10	0.30	0.31

Table 14. Summary of descriptive statistics (mean, standard deviation, minimum, and maximum) showing the results of shapes indices and aspect ratios obtained for each species (*Continue…*).

Acronym		AR	C	FF	R	Rwe*100	Rsa	Rswi
Ecro	mean ± SD	0.76 ± 0.03	14.59 ± 0.35	0.86 ± 0.02	0.72 ± 0.02	0.12 ± 0.02	0.12 ± 0.02	0.42 ± 0.07
	min	0.73	14.00	0.84	0.70	0.09	0.10	0.33
	max	0.83	15.04	0.90	0.75	0.15	0.16	0.53
Earg	mean ± SD	0.64 ± 0.02	16.61 ± 2.02	0.77 ± 0.11	0.69 ± 0.01	0.16 ± 0.15	0.24 ± 0.02	0.28 ± 0.03
	min	0.61	11.75	0.66	0.67	0.01	0.22	0.23
	max	0.70	19.18	1.07	0.72	0.53	0.27	0.32
Ebra	mean ± SD	0.59 ± 0.02	19.28 ± 0.85	0.65 ± 0.03	0.68 ± 0.01	0.29 ± 0.02	0.24 ± 0.02	0.36 ± 0.06
	min	0.56	17.91	0.61	0.66	0.26	0.21	0.27
	max	0.62	20.45	0.70	0.71	0.33	0.26	0.47
Egul	mean ± SD	0.59 ± 0.05	18.49 ± 0.98	0.68 ± 0.04	0.68 ± 0.04	0.23 ± 0.02	0.25 ± 0.01	0.23 ± 0.03
	min	0.53	16.50	0.64	0.63	0.20	0.23	0.19
	max	0.70	19.72	0.76	0.77	0.26	0.27	0.28
Emel	mean ± SD	0.69 ± 0.03	17.26 ± 0.47	0.73 ± 0.02	0.69 ± 0.01	0.31 ± 0.02	0.23 ± 0.02	0.29 ± 0.02
	min	0.65	16.72	0.69	0.67	0.28	0.20	0.24
	max	0.74	18.22	0.75	0.70	0.34	0.25	0.32
Goce	mean ± SD	0.66 ± 0.06	16.57 ± 0.78	0.76 ± 0.03	0.75 ± 0.01	0.25 ± 0.03	0.23 ± 0.02	0.37 ± 0.04
	min	0.59	15.53	0.68	0.73	0.20	0.21	0.33
	max	0.76	18.39	0.81	0.77	0.30	0.26	0.45
Hclu	mean ± SD	0.58 ± 0.02	21.44 ± 1.15	0.59 ± 0.03	0.70 ± 0.02	0.03 ± 0.03	0.40 ± 0.04	0.40 ± 0.04
	min	0.55	19.66	0.54	0.65	0.00	0.34	0.34
	max	0.60	23.46	0.64	0.73	0.09	0.47	0.47
Hcor	mean ± SD	0.68 ± 0.01	16.04 ± 1.01	0.79 ± 0.05	0.70 ± 0.01	0.53 ± 0.04	0.21 ± 0.01	0.36 ± 0.03
	min	0.66	15.08	0.69	0.69	0.49	0.19	0.32
	max	0.71	18.12	0.83	0.71	0.58	0.22	0.39
Hste	mean ± SD	0.70 ± 0.01	15.68 ± 2.61	0.82 ± 0.10	0.72 ± 0.01	0.95 ± 0.11	0.22 ± 0.01	0.45 ± 0.05
	min	0.69	14.29	0.55	0.71	0.8000	0.21	0.37
	max	0.72	23.02	0.88	0.73	1.14	0.25	0.55
Huni	mean ± SD	0.69 ± 0.04	17.76 ± 1.14	0.71 ± 0.05	0.69 ± 0.02	0.27 ± 0.04	0.21 ± 0.03	0.24 ± 0.04
	min	0.61	16.18	0.64	0.67	0.23	0.17	0.17
	max	0.75	19.77	0.78	0.73	0.38	0.26	0.30
Hbra	mean ± SD	0.70 ± 0.02	19.19 ± 1.39	0.66 ± 0.05	0.71 ± 0.02	0.16 ± 0.02	0.21 ± 0.03	0.23 ± 0.03
	min	0.66	17.63	0.59	0.67	0.12	0.17	0.19
	max	0.75	21.44	0.71	0.75	0.20	0.24	0.30
Ksec	mean ± SD	0.45 ± 0.03	26.87 ± 2.66	0.47 ± 0.04	0.71 ± 0.02	0.21 ± 0.02	0.26 ± 0.02	0.32 ± 0.03
	min	0.42	24.22	0.4	0.67	0.19	0.23	0.27
	max	0.52	31.78	0.52	0.74	0.25	0.3	0.39
Lana	mean ± SD	0.60 ± 0.08	19.16 ± 2.55	0.67 ± 0.08	0.69 ± 0.01	0.62 ± 0.11	0.26 ± 0.02	0.31 ± 0.03
	min	0.52	16.71	0.52	0.67	0.48	0.23	0.26
	max	0.75	24.14	0.75	0.71	0.88	0.29	0.34
Lsyn	mean ± SD	0.61 ± 0.02	19.72 ± 2.54	0.65 ± 0.08	0.69 ± 0.01	0.47 ± 0.10	0.26 ± 0.01	0.30 ± 0.02
	min	0.57	16.94	0.53	0.67	0.38	0.23	0.25
	max	0.65	23.90	0.74	0.71	0.62	0.28	0.33
Mame	mean ± SD	0.39 ± 0.02	20.38 ± 4.49	0.64 ± 0.13	0.74 ± 0.14	0.48 ± 0.06	0.54 ± 0.03	0.39 ± 0.02
	min	0.36	13.42	0.40	0.49	0.37	0.51	0.36
	max	0.43	31.55	0.94	1.04	0.58	0.59	0.43
Mfur	mean ± SD	0.77 ± 0.03	16.28 ± 1.11	0.78 ± 0.05	0.71 ± 0.02	1.30 ± 0.16	0.41 ± 0.02	0.54 ± 0.03
	min	0.74	15.01	0.67	0.67	1.08	0.38	0.50
	max	0.80	18.67	0.84	0.74	1.59	0.45	0.62
Mcur	mean ± SD	0.49 ± 0.01	24.17 ± 4.10	0.53 ± 0.09	0.70 ± 0.02	0.39 ± 0.25	0.22 ± 0.02	0.25 ± 0.03
	min	0.47	19.3	0.41	0.67	0.08	0.20	0.21
	max	0.50	30.52	0.65	0.73	0.76	0.25	0.29
Orub	mean ± SD	0.66 ± 0.02	16.65 ± 0.43	0.76 ± 0.02	0.69 ± 0.01	0.22 ± 0.02	0.23 ± 0.01	0.31 ± 0.01
	min	0.62	15.89	0.72	0.68	0.19	0.21	0.28
	max	0.69	17.48	0.79	0.7	0.23	0.24	0.33
Psal	mean ± SD	0.36 ± 0.01	27.38 ± 1.76	0.46 ± 0.03	0.72 ± 0.02	0.27 ± 0.03	0.32 ± 0.002	0.19 ± 0.02
	min	0.33	24.88	0.41	0.69	0.24	0.30	0.15
	max	0.38	30.74	0.51	0.74	0.34	0.36	0.21

Table 14. Summary of descriptive statistics (mean, standard deviation, minimum, and maximum) showing the results of shapes indices and aspect ratios obtained for each species.

Acronym		AR	C	FF	R	Rwe*100	Rsa	Rswi
Pvir	mean ± SD	0.50 ± 0.02	21.53 ± 0.96	0.58 ± 0.03	0.71 ± 0.03	0.33 ± 0.02	0.32 ± 0.01	0.36 ± 0.02
	min	0.47	20.30	0.54	0.66	0.30	0.30	0.33
	max	0.53	23.08	0.62	0.75	0.36	0.34	0.39
Ppun	mean ± SD	0.66 ± 0.02	20.25 ± 2.28	0.63 ± 0.07	0.68 ± 0.01	0.16 ± 0.02	0.25 ± 0.03	0.27 ± 0.03
	min	0.63	16.78	0.54	0.67	0.10	0.18	0.22
	max	0.69	23.29	0.75	0.7	0.19	0.28	0.30
Sbra	mean ± SD	0.50 ± 0.02	23.70 ± 0.97	0.53 ± 0.02	0.70 ± 0.02	0.02 ± 0.02	0.39 ± 0.03	0.33 ± 0.03
	min	0.45	22.41	0.49	0.68	0.00	0.28	0.28
	max	0.53	25.64	0.56	0.73	0.08	0.39	0.39
Svom	mean ± SD	0.71 ± 0.05	20.25 ± 1.61	0.62 ± 0.05	0.69 ± 0.03	0.11 ± 0.01	021 ± 0.02	0.36 ± 0.05
	min	0.64	18.38	0.55	0.65	0.10	0.19	0.28
	max	0.79	22.96	0.68	0.74	0.13	0.26	0.43
Sfoe	mean ± SD	0.50 ± 0.02	20.84 ± 0.96	0.60 ± 0.03	0.69 ± 0.01	0.09 ± 0.02	0.23 ± 0.02	0.25 ± 0.02
	min	0.46	19.74	0.55	0.67	0.05	0.2	0.23
	max	0.53	22.85	0.64	0.71	0.13	0.26	0.29

3.4. Geometric Morphology

The first eight warps explained 83.09% of the interspecific variability inside the morphospace, demonstrating that landmarks were appropriate to define otolith morphologies. The warps description included the general shape, dorso-ventral curvatures, the posterior region configuration, the type of rostrum when present, and the *sulcus acusticus* morphology (opening and relative size of the *ostium*, type and curvature of the cauda) (Figure 22). The first warp explained 25.14% of the variability classifying otoliths with wider ostium and concave cauda (positive axis) from otoliths with a convex cauda and narrower ostium (negative axis). Moreover, the first warp clearly discriminated the otoliths with mesial opening (left side of the plot). The second warp explained 16.85% of the variability, identifying rounded otoliths (negative axis) and enlarged shapes (positive axis). The third warp explained a similar degree of morphological variation (13.27%), but the otoliths with a lanceolate shape showed a convex cauda and wider ostium. Multivariate Analysis of Variance (Two-way Permanova) revealed significant morphologic differences in relation to the principal components of landmark analysis by species and habit (Table 14).

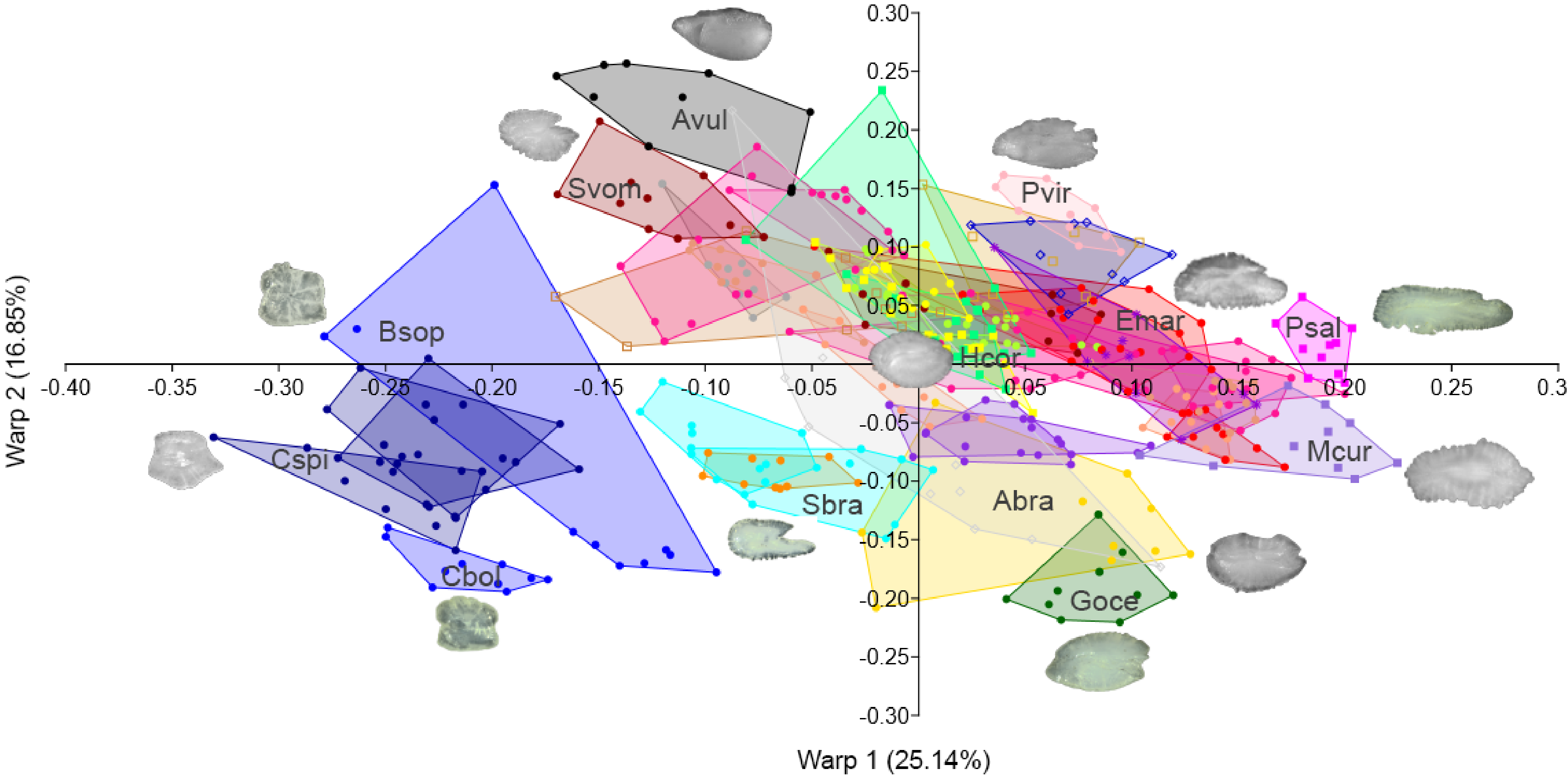
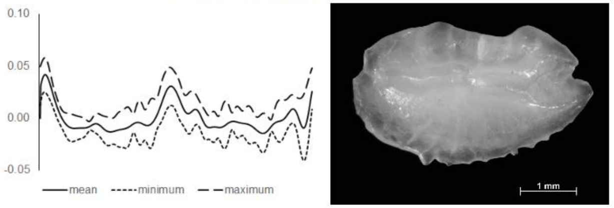


Figure 22. First and second principal components explaining the morphological variability of otolith shape when *sulcus acusticus* is included. Acronyms are presented in Supplementary Material 1 (SM 1).

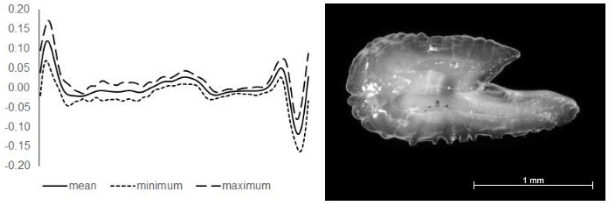
3.5. Wavelet Transform Representation

The discrimination among otolith shapes in polar coordinates is presented in Figure 23 (plates 1 to 6), evidencing the minimum, mean and maximum contour as well as the precise position of the irregularities for each species. The wavelets 5 description includes the general shape, curvatures, posterior and anterior region configuration, attempting to the development of *rostrum* and *antirostrum*, and do not considering the *sulcus acusticus* information. The first 32 PCs calculated from the 512 initial descriptors were kept and explained more than 92.87% of the variance in the otolith shapes. By means of Linear Discriminant Analysis (LDA), a Jacknife cross-validation showed that an average success in the classification rate of 76.05% was achieved. The first four axis represented 63.40% of the differences among shapes (Figure 24). The first axis explained 30.58% of the variability, identifying otoliths with *rostrum* and *antirostrum* developed (positive values) from otoliths with *rostrum* and *antirostrum* absents (negative values). The second axis explained 17.12% of the variability, classifying rounded shapes (negative values) and enlarged shapes (positive axis). The third axis (10.43%) explained elliptic otoliths with *rostrum* absent or underdeveloped and *antirostrum* developed. Multivariate Analysis of Variance (Two-way Permanova) revealed significant differences in relation to the wavelets 5 transform by species and habit (Table 14).

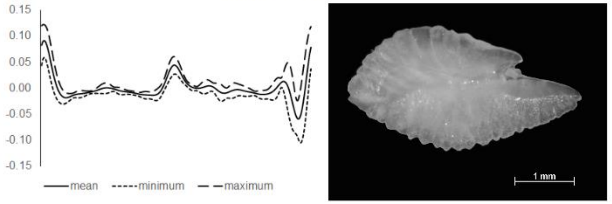
Atherinella brasiliensis **(Family Atherinopsidae)**



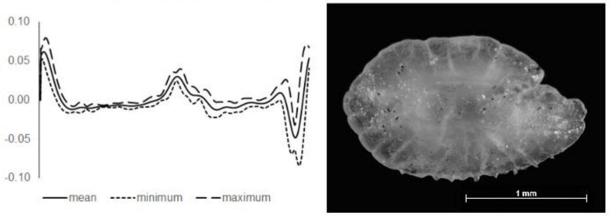
Sardinella brasiliensis **(Família Clupeidae)**



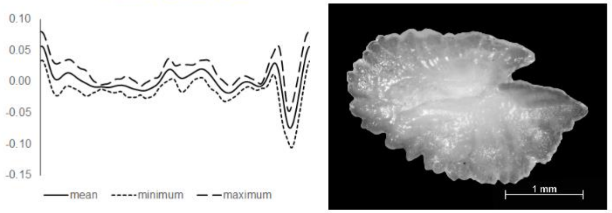
Chloroscombrus chrysurus **(Family Carangidae)**



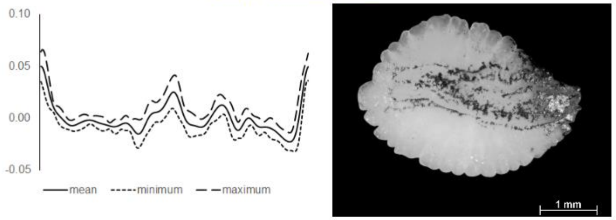
Anchoa tricolor **(Family Engraulidae)**



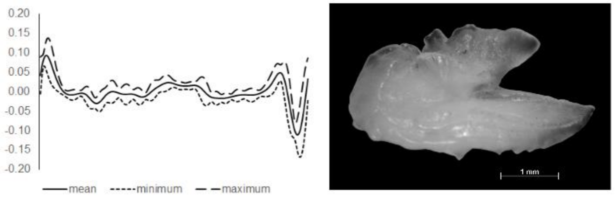
Selene vomer **(Family Carangidae)**



Hemiramphus brasiliensis **(Family Hemiramphidae)**



Harengula clupeola **(Family Clupeidae)**



Hyporhamphus unifasciatus **(Family Hemiramphidae)**

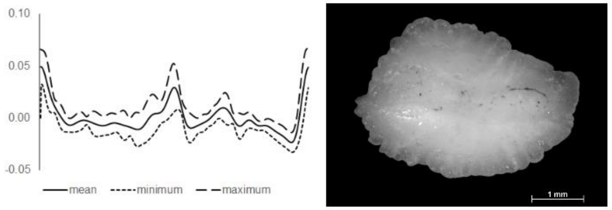
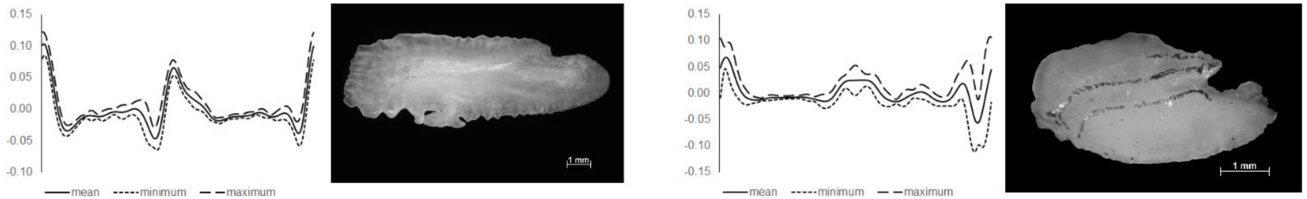
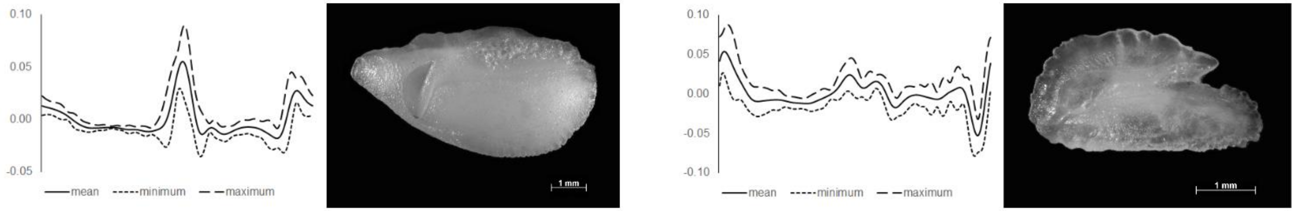


Figure 23. Plate 1 - Mean, minimum and maximum wavelet 5 representation from left otoliths of pelagic fishes (Family's name in navy blue colour).



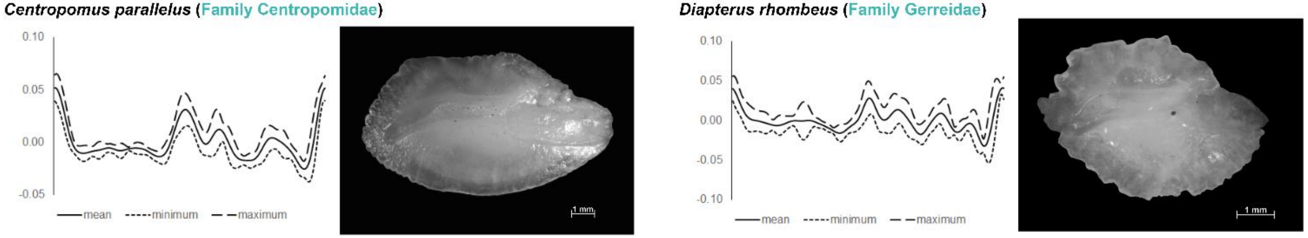
Pomatomus saltatrix **(Family Pomatomidae)**

Chaetodon striatus **(Family Chaetodontidae)**



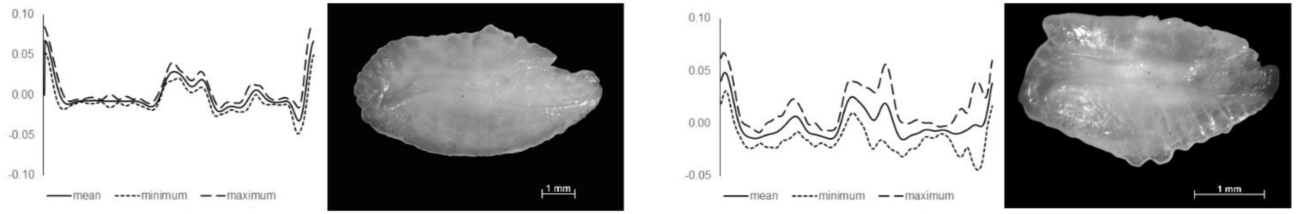
Albula vulpes **(Family Albulidae)**

Chaetodipterus faber **(Família Ephippidae)**



Centropomus parallelus **(Family Centropomidae)**

Diapterus rhombeus **(Family Gerreidae)**

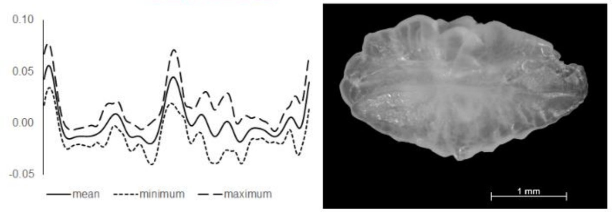


Centropomus undecimalis **(Family Centropomidae)**

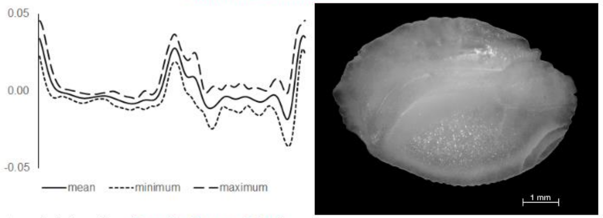
Eucinostomus argenteus **(Family Gerreidae)**

Figure 23. Plate 2 - Mean, minimum and maximum wavelet 5 representation from left otoliths of pelagic (Family's name in navy blue colour) and benthopelagic fishes (Family's name in cyan blue colour).

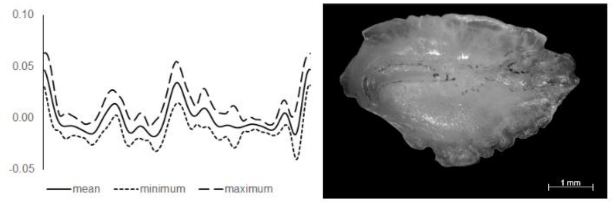
***Eucinostomus gula* (Family Gerreidae)**



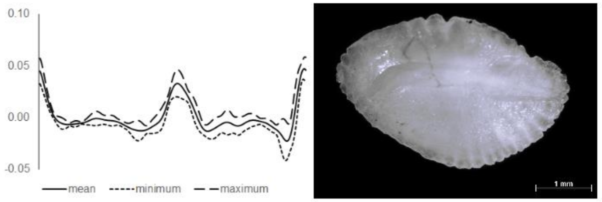
***Haemulon steindachneri* (Família Haemulidae)**



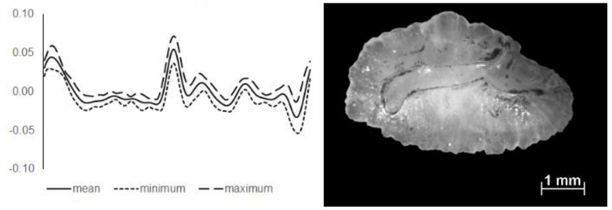
***Eucinostomus melanopterus* (Family Gerreidae)**



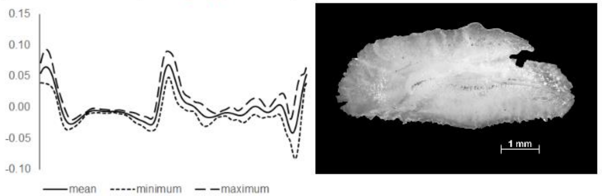
***Ortopristhis ruber* (Family Haemulidae)**



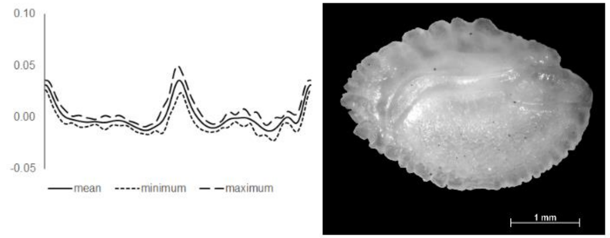
***Eugerres brasilianus* (Family Gerreidae)**



***Kyphosus sectatrix* (Family Kyphosidae)**



***Haemulopsis corvinaeformis* (Family Haemulidae)**



***Lutjanus analis* (Family Lutjanidae)**

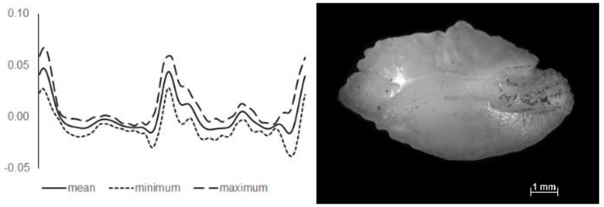
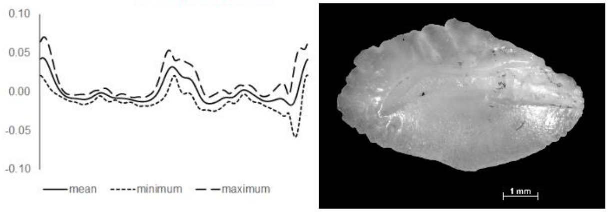
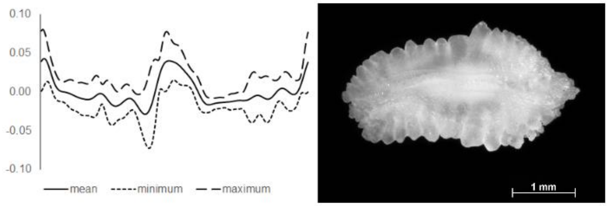


Figure 23. Plate 3 - Mean, minimum and maximum wavelet 5 representation from left otoliths of benthopelagic fishes (Family's name in cyan blue colour).

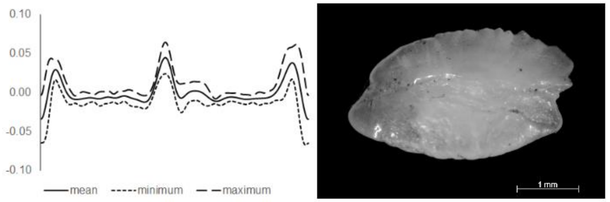
Lutjanus synagris **(Family Lutjanidae)**



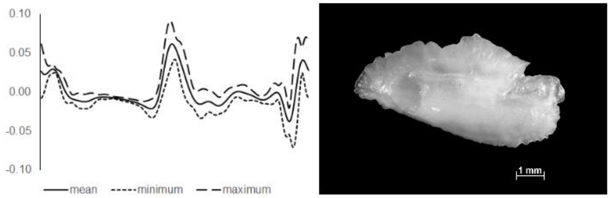
Mugil curema **(Family Mugilidae)**



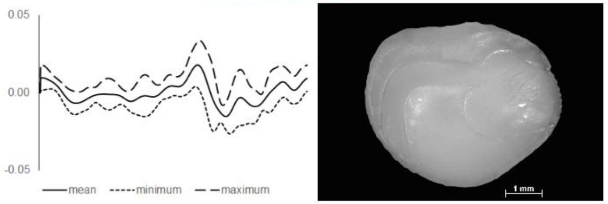
Gymnothorax ocellatus **(Family Muraenidae)**



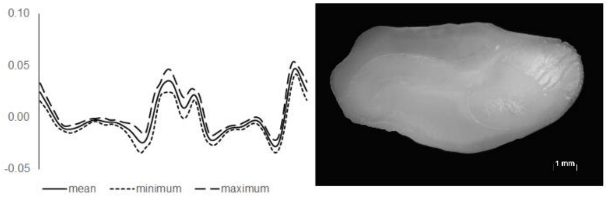
Polydactylus virginicus **(Family Polynemidae)**



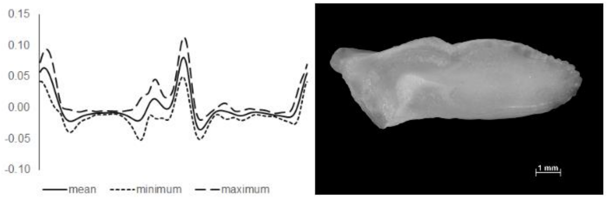
Ctenosciaena gracilicirrhus **(Familia Sciaenidae)**



Cynoscion jamaicensis **(Family Sciaenidae)**



Menticirrhus americanus **(Family Sciaenidae)**



Micropogonias furnieri **(Family Sciaenidae)**

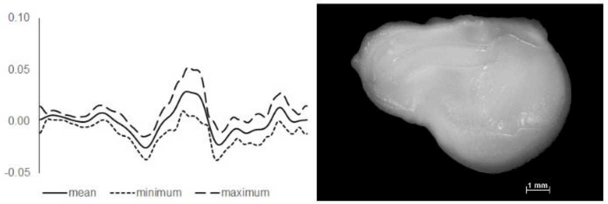
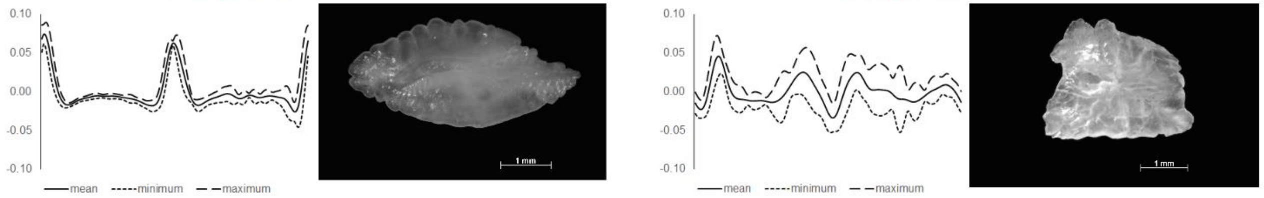
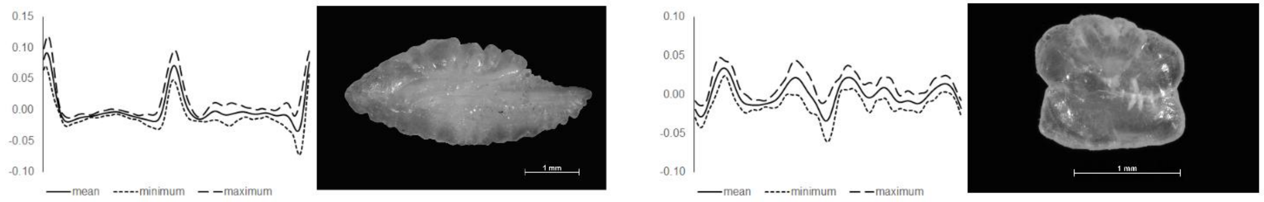


Figure 23. Plate 4 - Mean, minimum and maximum wavelet 5 representation from left otoliths of benthopelagic fishes (Family’s name in cyan blue colour).



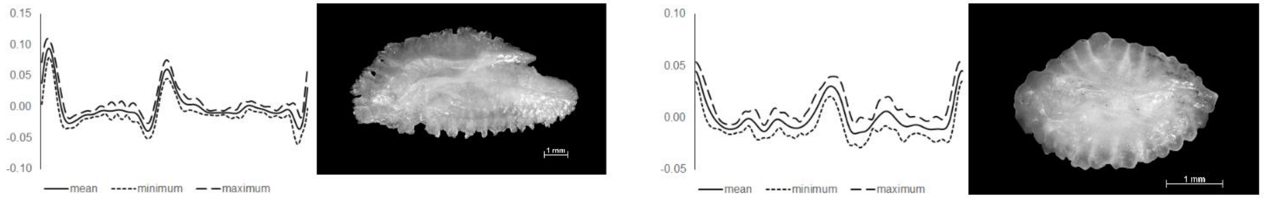
Diplectrum formosum **(Family Serranidae)**

Bathygobius soporator **(Familia Gobiidae)**



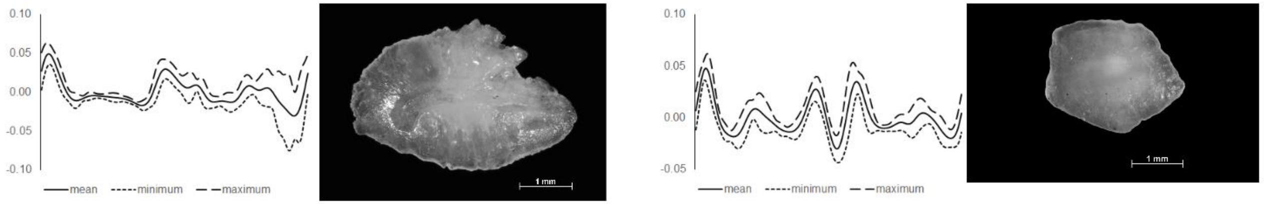
Diplectrum radiale **(Family Serranidae)**

Ctenogobius boleosoma **(Family Gobiidae)**



Epinephelus marginatus **(Family Serranidae)**

Prionotus punctatus **(Family Triglidae)**

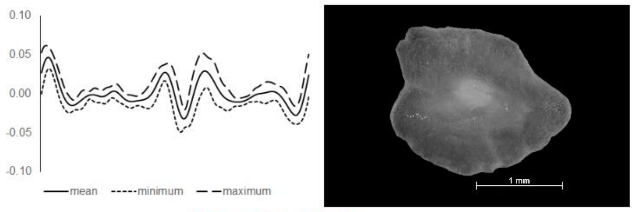


Archosargus rhomboidalis **(Family Sparidae)**

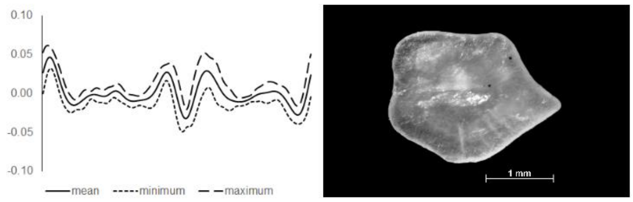
Etropus crossotus **(Family Paralichthydae)**

Figure 23. Plate 5 - Mean, minimum and maximum wavelet 5 representation from left otoliths of benthopelagic (Family's name in cyan blue colour), epibenthic (Family's name in red colour) and endobenthic fishes (Family's name in orange colour).

Citharichthys macrops **(Family Paralichthydae)**



Citharichthys spilopterus **(Family Paralichthydae)**



Synodus foetens **(Family Synodontidae)**

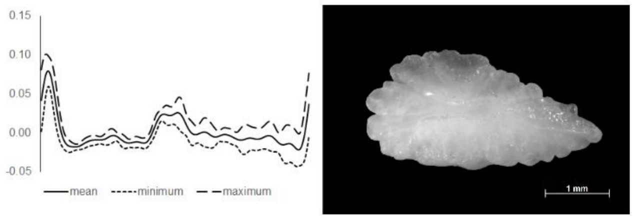


Figure 23. Plate 6 - Mean, minimum and maximum wavelet 5 representation from left otoliths endobenthic fishes (Family's name in orange colour).

Table 15. Results from the multivariate permutational analysis (Two-way PERMANOVA) performed for variables derived of distinct methods analysis of otoliths by species and habits (SS: sum of squares, df: degrees of freedom).

Source	**Aspect ratios**				**Shape Indices**			
	SS	df	F	p-value	SS	df	F	p-value
Species	25906	42	0.67	0.0001	11026	42	0.29	0.0001
Habit	7678.3	3	27.91	0.0001	1601.8	3	0.59	0.0169
Interaction	-1.97	126	-17.05	1	-1.90	126	-1.65	0.98
Residual	2.37	258			2.35	258		
Total	73232	429			58108	429		

Source	**Landmarks**				**Wavelets 5**			
	SS	df	F	p-value	SS	df	F	p-value
Species	12.27	42	4.02	0.0001	41.97	42	15	0.0001
Habit	3.48	3	16	0.0001	10.99	3	56	0.0001
Interaction	-18.48	126	-2	1	-145.17	126	-18	1
Residual	18.75	258			167.73	258		
Total	16.02	429			76	429		

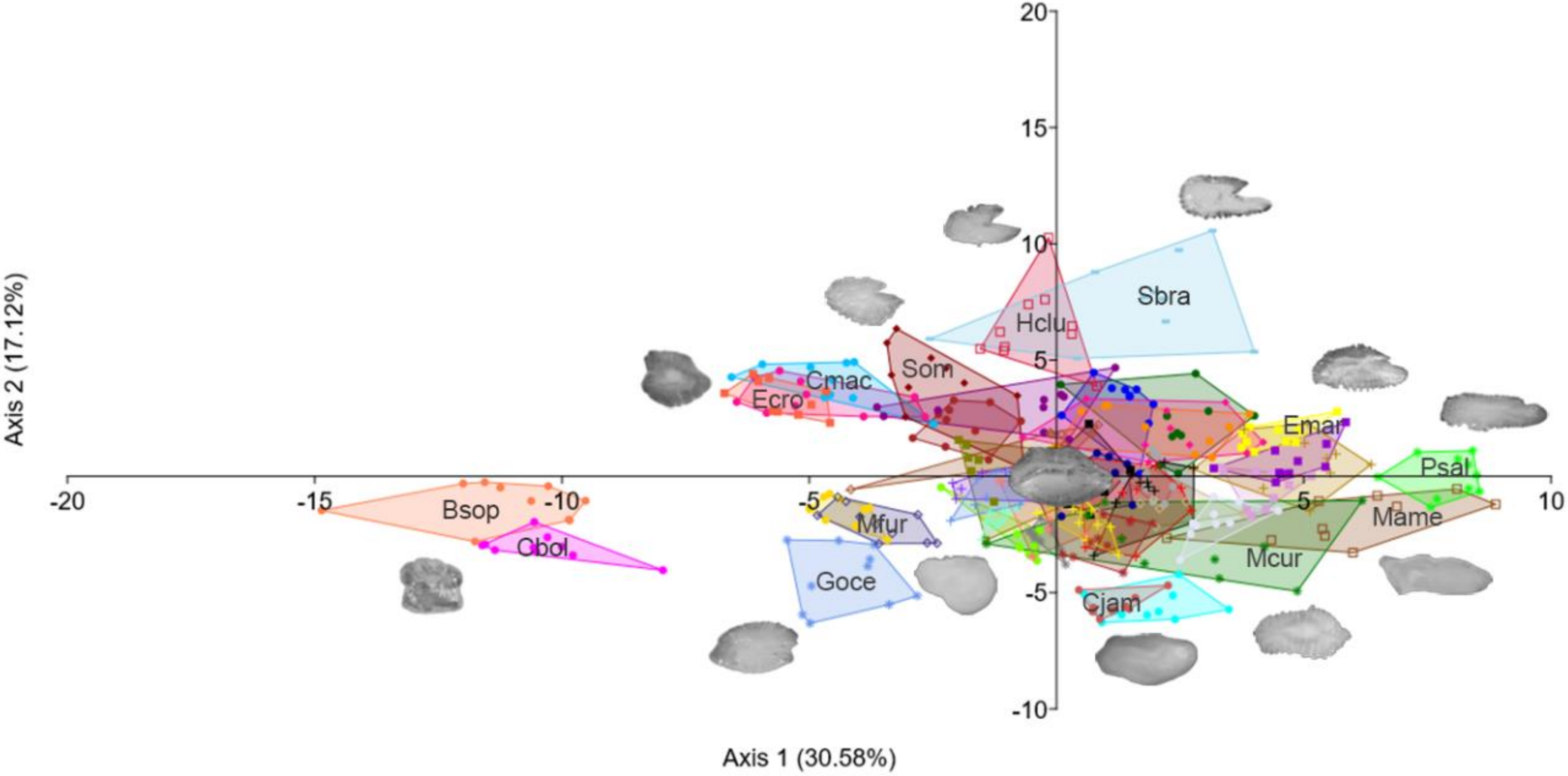


Figure 24. First and second axis obtained in Linear Discriminant Analysis for the wavelets transform 5. Acronyms are presented in Supplementary Material 1 (SM 1).

3.6. Morphological correspondence between otolith and fish body shapes

The morphological correspondence between fish body shape and otolith shape was positive for the morphological distances obtained by the landmark method (Mantel test p-value = 0.0002, r = 0.3814), and for the wavelets representation (Mantel test p-value = 0.0064, r = 0.2987). However, otolith shape indices did not present correlation with fish bodies shapes (Mantel test p-value = 0.7458, r = -0.0798).

The body and otolith morphospaces were built for 43 species, by means of geometric morphometric analysis. In the fish body morphospace, the first eight warps explained 89.37% of the interspecific variability of fish bodies (Figure 25). The first axis represented 35.61% of the total variance and was related to the position of the first dorsal fin and body shape; elongated for negative values, and higher bodies, laterally compressed for positive values. The second axis revealed 25.86% of the fish morphological variability and defined elongated fish shapes with the first dorsal fin distant to the head (positive values), and benthic fishes with dorsal-ventral flattened shapes or elongated dorsal and anal fins (negative values). The third axis expressed 8.07%, being the pelvic fin position and gave positive values when anterior and near to the scapular girdle or negative values when the pelvic fin was posterior or modified.

The landmarks analysis linked to the otolith relative weight (ARwe) was the best to classify species showing a lower percentage of average error (14.65%), followed by wavelet 5 also linked to the otolith relative weight (ARwe) (16.51%). Moreover, landmark method aggregated ecological value to the analysis indicating different fish life styles. On the opposite way, the use of shape indices is controversial since it showed high average error (55.58 %) even after incorporating the *sulcus acusticus* information (ARsa and ARsh) (46.51%) and the otolith relative weight (ARwe) (25.21%). The average error for classification of species by otolith analysing methods are showed in Table 15.

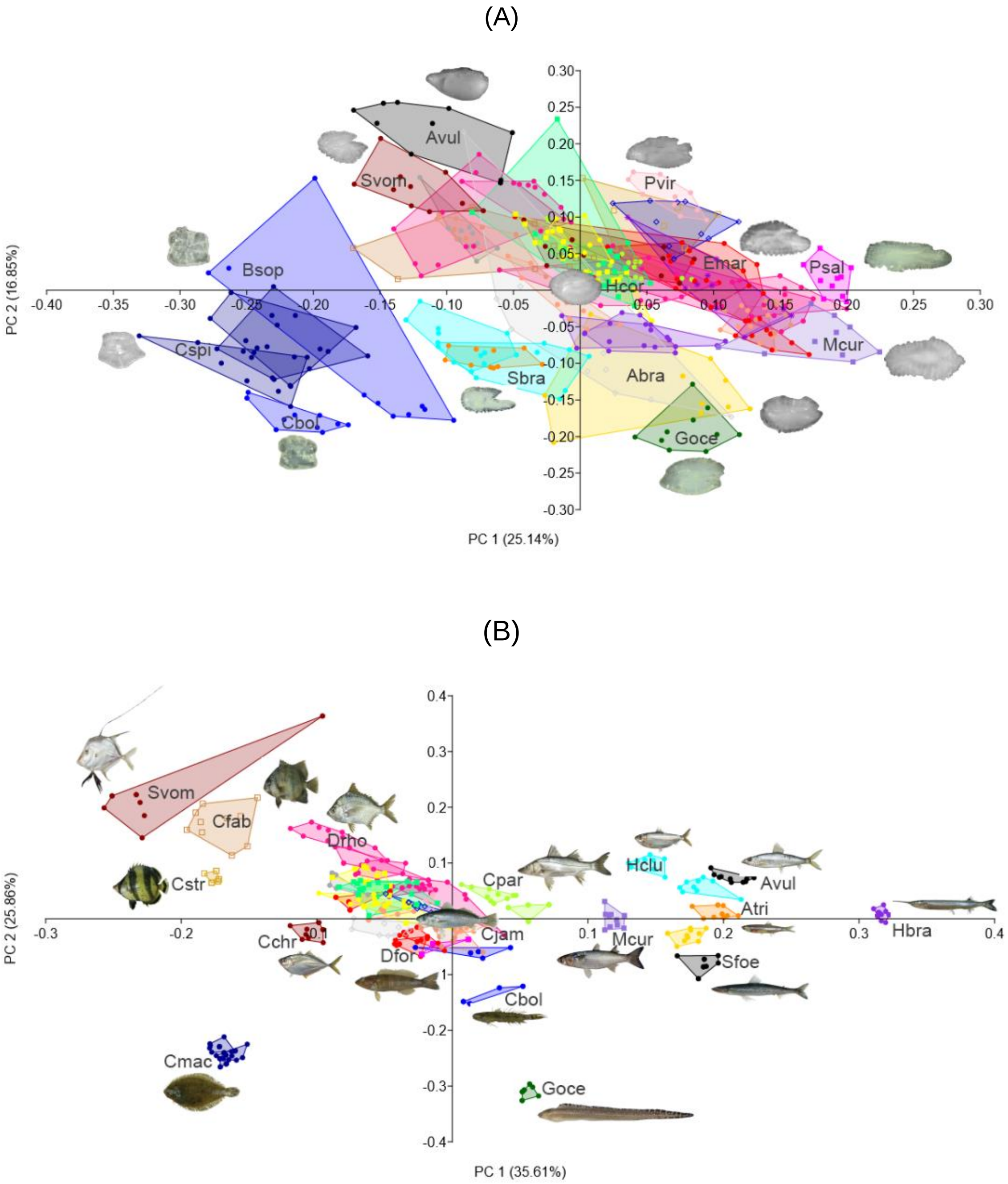


Figure 25. First and second principal components explaining the morphological variability of otolith shape (A) and fish body shape (B). Acronyms are in Supplementary Material 1 (SM 1).

Table 16. Average error of classification of species by otolith analysis methods (ARwe = OW/OL, ARsa = SA/OA, ARsh = SH/SL).

Method of Analysis	**Number of Trees**	**Number of Predictors**	**Average error (%)**
Shape Indices	999	2	55.58
Shape Indices + ARsa + ARsh	999	2	46.51
Shape Indices + ARwe	999	2	25.21
Wavelets 5	999	5	25.58
Wavelets 5 + ARsa + ARsh	999	5	22.70
Wavelets 5 + ARwe	999	5	16.51
Landmarks	999	2	33.49
Landmarks + ARwe	999	2	14.65

4. Discussion

Our study shows that otolith shapes and fish bodies shapes are correspondent, and both reveal the diversity and ecology of fish assemblages. Otolith shapes present high interspecific variability and have been a powerful taxonomic feature to discriminate fish species and families. Otolith measurements also provide useful information for fish size back-calculations, supporting paleontological and trophodynamic studies.

We found significant correlation between fish length and otolith morphometries among 41 species. Only two species, *Archosargus rhomboidalis* and *Chaetodon striatus*, did not show significant relationships due to the extreme variation in their otolith shapes related to different patterns in their growth axis, as mentioned by Lombarte et al. (1993) and Monteiro et al. (2004). Relationships between fish length and otolith length (OL) or weight (OW) are mentioned in previous studies (HARVEY et al., 2000; BATTAGLIA et al., 2010; JAWAD et al., 2011; KUMAR et al., 2015; AGUILAR-PEREIRA; QUIJANO-PUERTO, 2016; DEHGHANI et al., 2016). Here we provide additional information by considering other otolith measurements (otolith height, otolith area, otolith perimeter), and *sulcus acusticus* metrics (*sulcus* length, *sulcus* height, *sulcus* area), and relating them to habit, swimming type, sound production and fish diet.

Fishes of benthopelagic habit (e.g. Albulidae, Centropomidae) show elongated and thick *sagittae*, different of the pelagic (e.g. Atheriniidae, Clupeidae) and benthic ones (e.g. Gobiidae, Paralychthidae), which possess thin and small structures. Such variability in shapes can provide the ability of sound production, which is normally present in swim-bladder fishes. Among the swimming types, only the balistiforms (Chaetodontidae) and carangiforms (Carangidae, Clupeidae) swimmers showed similarities in otolith shape, since they are species with small and taller *sagittae*, following the dorsoventral skull development. Ecological factors are clearly reflected in otolith shape, including the diet type, which vary according the items anteriorly mentioned, but the use only of morphometric data was enough to identify, in detail, related influences.

Shapes indices clustered species according to their similar formats, also reflecting their distinct ecological strategies. Most *sagittae* of pelagic fishes were characteristically elliptic, long, with a prolonged rostrum; benthopelagic species showed elongated fusiform or oval otoliths, with a very developed ventral area and, a short rostrum; benthic fishes had rounded or squared shapes. Alone, otolith shape indices were inefficient to classify species. In turn, aspect ratios highlighted two important features: the relative *sulcus acusticus* area (ARsa) and the relative otolith weight (ARwe). These features serve as proxys to otolith sizes, shapes and in the macula format (LOMBARTE, 1992), implying in diversified functional specializations among species and sensory thresholds to receive different sound frequencies (GAULDIE, 1988; TORRES; LOMBARTE; MORALES-NIN, 2000). According to Gauldie (1988), Paxton (2000), Lychakov and Rebane (2000, 2002), and Cruz and Lombarte (2004), such variabilities determine fish hearing capabilities related to sound acuity.

Hearing generalists were identified in the Araçá bay, such as Centropomidae, Gerreidae, Gobiidae, Haemulidae and Sparidae, capable to detect low frequency sounds (<1 kHz) and relative high sound intensities (POPPER; SADLER; FRY, 2003; LADICH; POPPER, 2004; AMOSER; LADICH, 2005). Clupeidae and Sciaenidae were among the hearing specialists, which identify the pressure component of sounds over a broader frequency range (up to several kHz) and much lower sound intensities (POPPER; SADLER; FRY, 2003; LADICH; POPPER, 2004).

Fish hearing abilities involve modification of the swim bladder that acts as an acoustic amplifier (BRAUN; GRANDE, 2008; SCHULZ-MIRBACH; METSCHER; LADICH, 2012). Oscillations in volume and wall pulsations cause fluctuations in pressure owing to sound waves (RADFORD et al., 2013) which are converted into displacements being transmitted to the inner ear (YAN et al., 2000; PARMENTIER; MANN; MANN, 2011). The presence of specialized structures connecting swim bladder extensions to the internal ear are related to the threshold and bandwidth of sound sensitivity (PLATT; POPPER, 1981; CRUZ; LOMBARTE, 2004). This acoustic complex, named by Bregman (1990) as “auditory scene”, provides the perception of the environment that extends far beyond other senses, thereby increasing fish survival chances (POPPER; SCHILT, 2008; POPPER, 2008).

Usually, specialist fishes present accessory hearing structures (AMOSER; LADICH, 2005) such as are Clupeids (i.e. *Sardinella brasiliensis*), which possess a quite different specialization, the *auditory bullae* connection. They have a large prootic bullae formed by the anterior swim bladder extension, in which the gas is separated only by a membrane from the inner ear fluid (LADICH; SCHULZ-MIRBACH, 2016). In contact with the lateral line, the *bullae* form the *acoustico lateralis* system (BLAXTER; DENTON; GRAY, 1981), designed to favour ultrasounds detection, enabling the echolocation of predators (i.e. dolphins) and the fish orientation inside the shoal (MANN et al., 1997).

The benthopelagics Sciaenids (i.e. *Micropogonias furnieri, Menticirrhus* americanus) are highly specialized. They have an extensive diversity in inner ear structure as well as in the relationship between the swim bladder and the inner ear (RAMCHARITAR; GANNON; POPPER, 2006; POPPER, 2008). According to Ramcharitar, Gannon and Popper (2006) inside this family there are many differences associated to sound production mechanisms, variety of sounds produced, sound acuity (ability to discriminate between different frequencies) and sound sensitivity (range of frequencies that a species can hear). Sciaenids produce reproductive and disturbance calls, most commonly during the spawning season (CONNAUGHTON et al., 2002; RAMCHARITAR; GANNON; POPPER, 2006).

Some sparids (i.e. *Chaetodon striatus*) also have the *acoustic lateralis sensory system* but they are not real hearing specialists, just being capable to produce low frequency hydrodynamic pulses for territory defence (TRICAS; KAJIURA; KOSAKI, 2006). Similarly, Centropomids present this system and produce sounds, but well detecting only low frequencies. Webb, Montgomery and Mogdans, (2008) mention that Centropomids sensory performance have not yet been confirmed by behavioural or physiological studies.

Tavolga (1958) described to Gobiids males (i.e. *Bathygobius soporator*) the emiction of low pitched grunts to attract females, as a communicatory signal associated to their pre-spawning behaviour. Webb, Smith and Ketten (2006) showed that

Chaetodontids (i.e. *Chaetodon striatus*) possess a highly specialized swim bladder, producing sounds during social interactions. Cruz and Lombarte (2004) refer to Haemulids (i.e. *Haemulon steindachneri*) as hearing generalists but specialists in acoustic communication.

Swim bladder adaptations/extensions do not necessarily produce communication sounds (PARMENTIER; MANN; MANN, 2011). Gerreids (i.e. *Eucinostomus argenteus*) presents two specializations, being its anterior part divided into two horns connected to the *auditory bullae* through a fenestra (opening between two bones), and posteriorly projected into the interhemal bone (an integral part of the anal fin) (GREEN, 1971; PARMENTIER; MANN; MANN, 2011). This adaptation of an inclined swim bladder position facilitates the catching of preys (PARMENTIER; MANN; MANN, 2011).

Our results show that the shape descriptors wavelets and landmarks analysis differentiate adequately species and families. Wavelets were suited to verify the variability related to curvatures, posterior and anterior region configurations, *rostrum* and *antirostrum* development. This method has been applied to differentiate shapes of individuals pertaining to the same species, stocks and populations (PARISI-BARADAD et al., 2005; LIBUNGAN; ÓSKARSSON; PÁLSSON, 2013; LIBUNGAN; PÁLSSON, 2015). Here, the average success rate achieved was high (> 75%) in differentiating fish at species level. Our results also show that wavelets transform is a useful tool to detect shape differences, even in a numerous and diverse sample. In this sense, we agree with Sadighzadeh et al. (2014) and Libungan and Pálsson (2015) which reported that, in shape analysis, wavelets transform provides a powerful alternative than the more commonly applied Fourier transform, being more accurate to explain shape differences (AGÜERA; BROPHY, 2011).

Among the methods applied in the present study, landmarks coordinates were powerful, allowing less biased estimates of average otolith shapes, and better evidencing the interspecific variability of the Araçá fish assemblage. The analysis in details of the *sulcus acusticus* proved good results on detecting intraspecific variabilities. In other words, the landmarks method gathered the results obtained by shape indices, aspect ratios (except ARwe), and wavelets transform. Therefore, the general contour (shape, dorsal–ventral curvature, type of posterior zone and the presence and type of *rostrum*) further the *sulcus acusticus* morphology (opening, *ostium* relative size and *cauda* type and curvature) provided relevant specific functional information. In addition, the variability in the relative size of the *ostium* and the *cauda*, showed by the warps, would be correlated to the proportion of sensory hair cells, as proposed by Popper and Fay (2011).

Landmarks partitioned fish groups according their similar otolith morphologies: a) small, lanceolate shape, with prominent rostrum, wider *ostium* and concave *cauda*; b) large, elliptic and rectangular shapes with prominent anterior edge, wider *ostium* and convex *cauda*; c) squared shape with poorly defined *rostrum*, mesial opened *ostium* and concave *cauda*, being the correspondence between otolith shape and fish habit as follows: pelagic, benthopelagic, epibenthic/endobenthic, respectively. Several studies on otolith shape have also found ecomorphological patterns (VOLPEDO; ECHEVERRÍA, 2003; VOLPEDO; TOMBARI; ECHEVERRÍA, 2008; LOMBARTE; CRUZ, 2007; TEIMORI et al., 2012; TUSET et al., 2016). However, Tuset et al. (2016) affirm that this is not consistent in some cases because these patterns can be biased by morpho-functional aspects. Some authors report that the species packing seems to coincide with the best-adapted morphologies in order to an efficient exploitation of ecosystem resources (SCHOENER, 1974; GATZ, 1979; WAINWRIGHT; RICHARD, 1995; RICKLEFS, 2010; TUSET et al., 2016).

The correspondence between otolith morphospace and the trophic niche of fish has been reported in previous studies (LOMBARTE et al., 2010; TUSET et al., 2015). In the present study, flatfishes (i.e. *Citharichthys spinosus*) and ells (i.e. *Gymnothorax ocellatus*) form similar species packings/groups both in otolith and body morphospaces. The same occurs with sardines (i.e. *Sardinella brasiliensis, Harengula clupeola*) and anchovies (i.e. *Anchoa tricolor*), although they had a different spatial variability in otolith morphospace. On the other hand, at the otolith morphospace, gobies (i.e. *Bathygobius soporator*) and flatfishes (i.e. *Citharichthys macrops*) constitute a same packing and shared the same trophic niche. We believe that the otolith species overlap in the morphospace is due to the great variability of fish with invertivore diets present at Araçá bay.

We found clear differences in the potential application of the otolith general outline, the *sulcus acusticus* information and the relative weight *versus* the classification through shape indices. These indices (compactness, form-factor, rectangularity) did not depict the correspondence between otolith and fish body shapes, and presented more than 50% average error in otoliths classification. Often, shape indices have been employed linked to Elliptical Fourier descriptors to separate fish stocks (CAMPANA; CASSELMAN, 1993; FRIEDLAND; REDDIN, 1994; BEGG; BROWN 2000; CARDINALE et al., 2004; AGUËRA; BROPHY, 2011; FERGUSON; WARD; GILLANDERS, 2011; KEATING et al., 2014; HÜSSY et al., 2016; DUNCAN; BROPHY; ARRIZABALAGA, 2018). In these cases, we suggest the inclusion of raw morphometric data analysis or landmark coordinates to improve and detail those studies.

Several authors have shown that otolith weight is a powerful variable to enhance species classification/identification (SADIGHZADEH et al., 2012; TUSET; PARISI-BARADAD; LOMBARTE 2013) and to predict fish age (CARDINALE; ARRHENIUS; JOHNSSON, 2000; STEWARD; DEMARIA; SHENKER, 2009; BERMEJO, 2014; MAPP et al., 2017). Our results support these findings and reinforce that when AR*we* (otolith relative weight aspect ratio) is included, the average error in classification diminish substantially. We consider that *ARwe* joined with *landmarks* is the better method to species discrimination and a relevant result to be applied in future studies.

It is known that landmarks method permits a richer source of information for biological studies than the structures contours or outlines (MONTEIRO et al., 2004). Based in our findings, it could be considered the best method concerning ecological significances, since it contains biological relevant information in each reference point (operationally homologous) among the specimens analysed.

Given the morphological correspondence between otoliths shape and fish bodies shape, our results support the hypothesis that *sagittae* morphologic features represent an important element to be used revealing fish strategies.

Taking in consideration the three methods applied, the originality of this study was to quantify, for the first time, the otolith capacity in representing body morphology and, to calculate the average error involved in each one in order to species classification.

5.

FINAL CONSIDERATIONS

Final Considerations

Along the Science History, despite many methods to measure or quantify species shape have been developed, the morphology remained as the major player in this field. More possibilities emerged with the advent of computing, and the science passed from traditionally descriptive to measurable and quantitative.

Initially, the shape of species was assessed underpinned on linear measurements methods through morphometrics, and for a while it was sufficient to evaluate the existent morphological variability. Neverthless, these traditional morphometrics studies presented biases due to allometry and size effects (STRAUSS; BOOKSTEIN, 1982; WINEMILLER, 1991; ROHLF; MARCUS 1993).

In the late 1980’s, the geometric morphometry (GM) was created, consisting of the analysis of Cartesian geometric coordinates to describe complex morphological structures in more detail (BOOKSTEIN, 1991; ROHLF; MARCUS, 1993). Currently, the landmarks-based GM method, supported by powerful statistical analysis, is the most appropriate and fast methodology to quantify shape variations between structures (ADAMS et al., 2004; ADAMS; OTAROLA-CASTILLO, 2013), and had been presenting potential to be applied in biodiversity studies. Due to its complexity, biodiversity cannot be explained by simple indexes (MAGURRAN, 2013; LOISEAU; GAERTNER, 2015). As a multidimensional concept, biodiversity includes genetic and phenotypic variability, species richness, their functional properties and phylogenetic relationships (PURVIS; HECTOR, 2000). In this sense, ecological, taxonomical, phylogenetical, morphological and functional measures are recommended (LYASHEVSKA; FARNSWORTH, 2012). Among them, the morpho-functional approach is the most effective in providing the community structure and organization (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012). Especially when the information at the studied area is scarce or absent, even the qualitative application presents good results.

In the beginning of this study, we intended to verify the capacity of the geometric morphology methodology in describing the variability of fish bodies, in a highly diverse ecosystem, the Araçá bay.

The landmarks analysis was able to explain more than 95% of the morphological variability of the fish assemblages present at that area, exceeding the expectations. The advantage of the method is to be low cost effective only requiring images from which outlines are extracted and analysed with statistical software. The homologue points (landmarks) previously defined in the analysis showed to influence in the species distribution inside the morphospace. Moreover, the semilandmarks were necessary and important to differentiate species concerning their fin adaptations or sensory organs presence, given the ecological value associated to these features.

The qualitative application of geometric morphology allowed defining the best samplers to represent the morphological composition of the fish assemblages, giving an overview of how they were spatially distributed inside the tidal plain. The catch effectiveness was differentiated according to the gear type employed.

Such methodology permitted the acquisition of indices of morphological diversity (MD, MR and EMI) which complemented the information about the shape variability inferring functions, roles and strategies of the fishes inhabiting the bay. It also was useful to predict the habitats of major richness. Indices of morphological diversity are independent of each other, being significantly correlated with other components of biodiversity (MD is linked to taxonomic diversity, EMI defines the structural and taxonomic complexity of the community, and MR is correlated to measures of specific richness and functional diversity) reinforcing their capacity as a complementary tool in biodiversity studies (FARRÉ et al. 2016).

The qualitative perspective will make possible to monitor the evolution of the Araçá fish assemblages along large temporal scales from a list of fish presence/absence. On the other side, the quantitative application of the geometric morphology enriched the knowledge about how fish assemblages use different habitats. The inclusion of fish density data in the morpho and functional spaces demonstrated the structure related to the functioning of the fish assemblages. Differences of abundancies reinforced the hypothesis that fish morphology is related to the complexity of the Araçá habitats: communities that have greater structural complexity (mixture of types of substrates) contain a greater number of body forms since they allow to support a greater variability of ecological strategies.

The habitat complexity affects significantly the ecological composition of the fish assemblages. Fishes living in habitats comprising different substrates, and close to mangrove zones or rocks presented more rich composition and density, whereas simple bottoms were ecologically simpler and less populated. Although the pattern of species distribution in the morphological and functional spaces was similar between the two most diverse habitats (IH and IOS), they presented differences related to dominant species, number of functional groups, functional redundancy and availability of resources.

The functional diversity increased with the habitat complexity, which cause an impoverishment of the functionality at less complex habitats. In the IH, due to the high availability of resources, fish species showed higher degrees of specialization and the differentiation of the niche, thus reducing interspecific competition. In this way, less complex habitats showed enlarged morphological and functional redundancies. Since functional redundancy acts as biological insurance against diversity loss, IH must be a priority protected area, and has to be monitored.

As a multifunctional tool, the landmarks analysis was adequate to quantify the correspondence among otoliths shapes and fish body shapes. Landmarks analysis together with the aspect ratio of the otolith weight were the best methods for species discrimination and for recognizing ecological aspects of the fishes at the Araçá bay. Details of the sulcus acusticus clarified the intraspecific variabilities, rendering the landmarks analysis of otoliths a richer source of information for biological studies, more than the structures contours or outlines.

The results of this thesis reinforce the idea that fish morphology is a valid tool to investigate their ecological and functional roles within ecosystems. The landmarks analysis of fish body shape allows inferring the main aspects of the habitats functioning, such as the species distribution, habitat influences, resources use, coexistence, competition and dominance.

Additionally, landmarks analysis of otoliths emphasized fish ecological patterns, detailing the intraspecific variability embedded in the sulcus acusticus morphology and size. Therefore, the morphology remains an active tool and can help to improve studies on fish assemblages structure, organization and functioning in ecosystems with high diversity.

SUPPLEMENTARY MATERIALS

SM 1. Fish species captured in Araçá bay and fishing gears employed. Active gears: beach seine (BS), otter trawl (OT), inner encircling gillnet (IEG), marginal encircling gillnet (MEG), and cast net (CN). Passive gears: large gillnet (LG), small gillnet (SG), hook and line (HL), and fish trap (FT) (*Continue…*).

Order	**Family**	**Genus and Species**	**Acronym**	**Fishing Gears**
Albuliformes	Albulidae	*Albula vulpes* (Linnaeus, 1758)	AlVul	OT, BS, CN
Anguiliformes	Muraenidae	*Gymnothorax ocellatus* Agassiz, 1831	GyOce	OT
Anguiliformes	Ophichthidae	*Myrophis punctatus* Lutken 1852	MyPun	BS
Anguiliformes	Ophichthidae	*Ophichthus gomesii* (Castelnau 1855)	OpGom	BS
Atheriniformes	Atherinopsidae	*Atherinella brasiliensis* (Quoy & Gaimard, 1825)	AtBra	BS, CN
Aulopiformes	Synodontidae	*Synodus foetens* (Linnaeus, 1758)	SyFoe	OT, BS, MEG, SG
Aulopiformes	Synodontidae	*Trachinocephalus myops* (Forster, 1801)	TrMyo	BS
Beloniformes	Belonidae	*Strongylura marina* (Walbaum, 1792)	StMar	BS
Beloniformes	Belonidae	*Tylosurus acus* (Lacepède 1803)	TyAcu	LG
Beloniformes	Hemiramphidae	*Hemiramphus brasiliensis* (Linnaeus, 1758)	HeBra	BS
Beloniformes	Hemiramphidae	*Hyporhamphus roberti* (Valenciennes, 1847)	HyRob	BS
Beloniformes	Hemiramphidae	*Hyporhamphus unifasciatus* (Ranzani, 1841)	HyUni	OT, BS, CN
Clupeiformes	Clupeidae	*Harengula clupeola* (Cuvier, 1829)	HaClu	OT, IEG, BS, MEG, SG, CN
Clupeiformes	Clupeidae	*Opisthonema oglinum* (Lesueur, 1818)	OpOgl	BS
Clupeiformes	Clupeidae	*Sardinella brasiliensis* (Steindachner, 1879)	SaBra	BS, SG, CN
Clupeiformes	Engraulidae	*Anchoa lyolepis* (Evermann & Marsh, 1900)	AnLyo	BS
Clupeiformes	Engraulidae	*Anchoa tricolor* (Spix & Agassiz, 1829)	AnTri	IEG, BS, SG, CN
Clupeiformes	Engraulidae	*Anchovia clupeoides* (Swainson, 1839)	AnClu	CN
Clupeiformes	Engraulidae	*Anchoviella lepidentostole* (Fowler, 1911)	AnLep	LG
Clupeiformes	Pristigasteridae	*Lycengraulis grossidens* (Spix & Agassiz, 1829)	LyGro	SG
Clupeiformes	Pristigasteridae	*Pellona harroweri* (Fowler, 1917)	PeHar	IEG
Elopiformes	Elopidae	*Elops saurus* Linnaeus, 1766	ElSau	HL, BS
Mugiliformes	Mugilidae	*Mugil curema* Valenciennes, 1836	MuCur	OT, IEG, LG, BS, MEG, SG, CN
Mugiliformes	Mugilidae	*Mugil brevirostris* (Ribeiro 1915)	MuBre	CN
Mugiliformes	Mugilidae	*Mugil incilis* Hancock, 1830	MuInc	SG
Mugiliformes	Mugilidae	*Mugil liza* Valenciennes, 1836	MuLiz	IEG, LG, BS, MEG, CN
Perciformes	Blenniidae	*Scartella cristata* (Linnaeus, 1758)	ScCri	HL, BS

SM 1. Fish species captured in Araçá bay and fishing gears employed. Active gears: beach seine (BS), otter trawl (OT), inner encircling gillnet (IEG), marginal encircling gillnet (MEG), and cast net (CN). Passive gears: large gillnet (LG), small gillnet (SG), hook and line (HL), and fish trap (FT) (*Continue…*).

Order	Family	Genus and Species	Acronym	Fishing Gears
Perciformes	Carangidae	*Caranx latus* Agassiz, 1831	CaLat	IEG, LG, BS, MEG
Perciformes	Carangidae	*Chloroscombrus chrysurus* (Linnaeus, 1766)	ChChr	OT, IEG, MEG
Perciformes	Carangidae	*Hemicaranx amblyrhynchus* (Cuvier, 1833)	HeAmb	OT
Perciformes	Carangidae	*Oligoplites saliens* (Bloch, 1793)	OlSal	OT, LG, BS, MEG, CN
Perciformes	Carangidae	*Oligoplites saurus* (Bloch & Schneider, 1801)	OlSau	OT, IEG, BS, MEG, CN
Perciformes	Carangidae	*Selene setapinnis* (Mitchill, 1815)	SeSet	OT, MEG, SG
Perciformes	Carangidae	*Selene vomer* (Linnaeus, 1758)	SeVom	OT, IEG, BS, MEG, SG, CN
Perciformes	Carangidae	*Trachinotus carolinus* (Linnaeus, 1766)	TrCar	LG, BS, MEG, CN
Perciformes	Carangidae	*Trachinotus falcatus* (Linnaeus, 1758)	TrFal	BS
Perciformes	Carangidae	*Trachinotus goodei* Jordan & Evermann, 1896	TrGoo	BS
Perciformes	Centropomidae	*Centropomus parallelus* Poey, 1860	CePar	OT, IEG, LG, HL, MEG, SG
Perciformes	Centropomidae	*Centropomus undecimalis* (Bloch, 1792)	CeUnd	BS, MEG
Perciformes	Chaetodontidae	*Chaetodon striatus* Linnaeus, 1758	ChStr	FT
Perciformes	Ephippidae	*Chaetodipterus faber* (Broussonet, 1782)	ChFab	OT, LG, BS, MEG, SG, FT
Perciformes	Gerreidae	*Diapterus rhombeus* (Cuvier, 1829)	DiRho	OT, IEG, LG, BS, MEG, SG, CN
Perciformes	Gerreidae	*Eucinostomus argenteus* Baird & Girard, 1855	EuArg	OT, IEG, BS, MEG, SG, CN, FT
Perciformes	Gerreidae	*Eucinostomus gula* (Quoy & Gaimard, 1824)	EuGul	OT, IEG, BS, MEG, CN
Perciformes	Gerreidae	*Eucinostomus melanopterus* (Bleeker, 1863)	EuMel	OT, IEG, BS, MEG, CN
Perciformes	Gerreidae	*Eugerres brasilianus* (Cuvier, 1830)	EuBra	LG, MEG
Perciformes	Gobiidae	*Bathygobius soporator* (Valenciennes, 1837)	BaSop	BS, CN
Perciformes	Gobiidae	*Ctenogobius boleosoma* (Jordan & Gilbert, 1882)	CtBol	BS
Perciformes	Haemulidae	*Anisotremus surinamensis* (Bloch, 1791)	AnSur	LG, MEG
Perciformes	Haemulidae	*Anisotremus virginicus* (Linnaeus, 1758)	AnVir	LG, FT
Perciformes	Haemulidae	*Conodon nobilis* (Linnaeus, 1758)	CoNob	BS
Perciformes	Haemulidae	*Haemulon steindachneri* (Jordan & Gilbert, 1882)	HaSte	OT, LG, HL, MEG, FT
Perciformes	Haemulidae	*Haemulopsis corvinaeformis* (Steindachner, 1868)	HaCor	OT, BS, MEG, SG, CN
Perciformes	Haemulidae	*Orthopristis ruber* (Cuvier, 1830)	OrRub	OT, BS, MEG, SG, CN

SM 1. Fish species captured in Araçá bay and fishing gears employed. Active gears: beach seine (BS), otter trawl (OT), inner encircling gillnet (IEG), marginal encircling gillnet (MEG), and cast net (CN). Passive gears: large gillnet (LG), small gillnet (SG), hook and line (HL), and fish trap (FT) (*Continue…*).

Order	Family	Genus and Species	Acronym	Fishing Gears
Perciformes	Kyphosidae	*Kyphosus incisor* (Cuvier, 1831)	KyInc	MEG
Perciformes	Kyphosidae	*Kyphosus sectatrix* (Linnaeus, 1758)	KySec	LG, HL, BS, CN
Perciformes	Labrisomidae	*Labrisomus nuchipinnis* (Quoy & Gaimard, 1824)	LaNuc	HL
Perciformes	Labrisomidae	*Malacoctenus delalandii* (Valenciennes, 1836)	MaDel	BS
Perciformes	Lutjanidae	*Lutjanus analis* (Cuvier, 1828)	LuAna	OT, IEG, LG, HL, BS, MEG, SG
Perciformes	Lutjanidae	*Lutjanus cyanopterus* (Cuvier, 1828)	LuCya	MEG
Perciformes	Lutjanidae	*Lutjanus synagris* (Linnaeus, 1758)	LuSyn	OT, CN, FT
Perciformes	Mullidae	*Upeneus parvus* Poey 1852	UpPar	OT
Perciformes	Polynemidae	*Polydactylus virginicus* (Linnaeus, 1758)	PoVir	IEG, LG, MEG, SG
Perciformes	Pomacentridae	*Abudefduf saxatilis* (Linnaeus, 1758)	AbSax	FT
Perciformes	Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)	PoSal	BS, MEG, SG
Perciformes	Scaridae	*Nicholsina usta usta* (Valenciennes, 1840)	NiUst	FT
Perciformes	Sciaenidae	*Ctenosciaena gracilicirrhus* (Metzelaar, 1919)	CtGra	OT, IEG
Perciformes	Sciaenidae	*Cynoscion jamaicensis* (Vaillant & Bocourt, 1883)	CyJam	OT, IEG, LG, MEG, SG
Perciformes	Sciaenidae	*Cynoscion leiarchus* (Cuvier, 1830)	CyLei	IEG, LG
Perciformes	Sciaenidae	*Larimus breviceps* Cuvier, 1830	LaBre	OT
Perciformes	Sciaenidae	*Menticirrhus americanus* (Linnaeus, 1758)	MeAme	OT, IEG, LG, BS, SG
Perciformes	Sciaenidae	*Micropogonias furnieri* (Desmarest, 1823)	MiFur	OT, LG, SG, CN
Perciformes	Sciaenidae	*Odontoscion dentex* (Cuvier 1830)	OdDen	HL
Perciformes	Sciaenidae	*Umbrina coroides* Cuvier, 1830	UmCor	OT, BS
Perciformes	Scombridae	*Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, 1978	ScoBra	LG
Perciformes	Serranidae	*Diplectrum formosum* (Linnaeus, 1766)	DiFor	OT, HL
Perciformes	Serranidae	*Diplectrum radiale* (Quoy & Gaimard, 1824)	DiRad	OT, HL, BS, CN
Perciformes	Serranidae	*Epinephelus marginatus* (Lowe, 1834)	EpMar	HL, FT
Perciformes	Serranidae	*Mycteroperca acutirostris* (Valenciennes, 1828)	MyAcu	HL, FT
Perciformes	Sparidae	*Archosargus rhomboidalis* (Linnaeus, 1758)	ArRho	LG, BS
Perciformes	Sparidae	*Calamus penna* (Valenciennes, 1830)	CaPen	OT

SM 1. Fish species captured in Araçá bay and fishing gears employed. Active gears: beach seine (BS), otter trawl (OT), inner encircling gillnet (IEG), marginal encircling gillnet (MEG), and cast net (CN). Passive gears: large gillnet (LG), small gillnet (SG), hook and line (HL), and fish trap (FT).

Order	**Family**	**Genus and Species**	**Acronym**	**Fishing Gears**
Perciformes	Sparidae	*Diplodus argenteus* (Valenciennes, 1830)	DiArg	FT
Perciformes	Sphyraenidae	*Sphyraena tome* Fowler, 1903	SpTom	OT
Perciformes	Trichiuridae	*Trichiurus lepturus* Linnaeus, 1758	TrLep	OT, IEG, LG, SG
Perciformes	Uranoscopidae	*Astroscopus y-graecum* (Cuvier, 1829)	AsYgr	OT
Pleuronectiformes	Achiridae	*Achirus lineatus* (Linnaeus, 1758)	AcLin	OT
Pleuronectiformes	Bothidae	*Bothus ocellatus* (Agassiz 1831)	BoOce	OT
Pleuronectiformes	Cynoglossidae	*Symphurus tessellatus* (Quoy & Gaimard, 1824)	SyTes	OT
Pleuronectiformes	Paralichthyidae	*Citharichthys arenaceus* Evermann & Marsh, 1900	CiAre	OT
Pleuronectiformes	Paralichthyidae	*Citharichthys macrops* Dresel, 1885	CiMac	OT
Pleuronectiformes	Paralichthyidae	*Citharichthys spilopterus* Günther, 1862	CiSpi	OT, BS, SG, CN
Pleuronectiformes	Paralichthyidae	*Etropus crossotus* Jordan & Gilbert, 1882	EtCro	OT, IEG, BS, CN
Pleuronectiformes	Paralichthyidae	*Etropus longimanus* Norman 1933	EtLon	OT
Pleuronectiformes	Paralichthyidae	*Syacium papillosum* (Linnaeus, 1758)	SyPap	OT
Scorpaeniformes	Dactylopteridae	*Dactylopterus volitans* (Linnaeus, 1758)	DaVol	OT
Scorpaeniformes	Scorpaenidae	*Scorpaena brasiliensis* Cuvier 1829	ScBra	OT
Scorpaeniformes	Scorpaenidae	*Scorpaena plumieri* Bloch, 1789	ScPlu	LG
Scorpaeniformes	Triglidae	*Prionotus punctatus* (Bloch, 1793)	PrPun	OT, BS, CN
Siluriformes	Ariidae	*Genidens genidens* (Cuvier, 1829)	GeGen	SG
Syngnathiformes	Syngnathidae	*Hippocampus reidi* Ginsburg, 1933	HiRei	BS
Tetraodontiformes	Diodontidae	*Chilomycterus spinosus* (Linnaeus, 1758)	ChSpi	BS
Tetraodontiformes	Monacanthidae	*Stephanolepis hispidus* (Linnaeus, 1766)	StHis	OT, CN, FT
Tetraodontiformes	Tetraodontidae	*Lagocephalus laevigatus* (Linnaeus, 1766)	LaLae	OT
Tetraodontiformes	Tetraodontidae	*Sphoeroides greeleyi* Gilbert, 1900	SpGre	OT, BS, CN, FT
Tetraodontiformes	Tetraodontidae	*Sphoeroides spengleri* (Bloch 1785)	SpSpe	OT
Tetraodontiformes	Tetraodontidae	*Sphoeroides testudineus* (Linnaeus, 1758)	SpTes	OT, BS

SM 2. Taxonomical classification of species and functional-trait matrix. Functional codes available in Table 3 (*Continue…*).

Class	***Order***	***Family***	***Genus and Species***	***Acronym***	***Body shape***	***Swiming***	***Motility***	***Burying***	***Diet***	***Size***	***Vertical distribution***	***Environment***
Actinopterygii	Albuliformes	Albulidae	*Albula vulpes*	Avul	Fu	Car	H	N	MINV	M	BP	Oe
Actinopterygii	Anguiliformes	Muraenidae	*Gymnothorax ocellatus*	Goce	Ang	Ang	S	N	MAC	L	BP	Oe
Actinopterygii	Anguiliformes	Ophichthidae	*Myrophis punctatus*	Mpun	Ang	Bal	S	Y	SAND	M	ENDB	Oe
Actinopterygii	Anguiliformes	Ophichthidae	*Ophichthus gomesii*	Ogom	Ang	Bal	S	Y	SAND	M	ENDB	Oe
Actinopterygii	Atheriniformes	Atherinopsidae	*Atherinella brasiliensis*	Abra	El	Car	R	N	OMNI	SM	P	Oe
Actinopterygii	Aulopiformes	Synodontidae	*Synodus foetens*	Sfoe	El	Sub	S	Y	PIS	M	ENDB	Oe
Actinopterygii	Aulopiformes	Synodontidae	*Trachinocephalus myops*	Tmyo	El	Sub	S	Y	PIS	SM	ENDB	Oe
Actinopterygii	Beloniformes	Belonidae	*Strongylura marina*	Smar	El	Sub	R	N	MAC	ML	P	Oe
Actinopterygii	Beloniformes	Hemiramphidae	*Hemiramphus brasiliensis*	Hbra	El	Sub	R	N	MALG	SM	P	Em
Actinopterygii	Beloniformes	Hemiramphidae	*Hyporhamphus roberti*	Hrob	El	Sub	R	N	OMNI	SM	P	Oe
Actinopterygii	Beloniformes	Hemiramphidae	*Hyporhamphus unifasciatus*	Huni	El	Sub	R	N	OMNI	ML	P	Oe
Actinopterygii	Clupeiformes	Clupeidae	*Harengula clupeola*	Hclu	Fu	Car	H	N	NPLA	M	P	Oe
Actinopterygii	Clupeiformes	Clupeidae	*Opisthonema oglinum*	Oogl	Fu	Car	H	N	NPLA	S	P	Oe
Actinopterygii	Clupeiformes	Clupeidae	*Sardinella brasiliensis*	Sbra	Fu	Car	H	N	NPLA	S	P	Oe
Actinopterygii	Clupeiformes	Engraulidae	*Anchoa lyolepis*	Alyo	Fu	Car	H	N	DPLA	S	P	Oe
Actinopterygii	Clupeiformes	Engraulidae	*Anchoa tricolor*	Atri	Fu	Car	H	N	DPLA	S	P	Oe
Actinopterygii	Elopiformes	Elopidae	*Elops saurus*	Esau	El	Sub	H	N	MAC	SM	P	Oe
Actinopterygii	Perciformes	Blenniidae	*Scartella cristata*	Scri	Ob	Sub	S	N	SCRP	S	EPIB	Em
Actinopterygii	Perciformes	Carangidae	*Caranx latus*	Clat	Fu	Car	H	N	MAC	M	P	Oe
Actinopterygii	Perciformes	Carangidae	*Chloroscombrus chrysurus*	Cchr	Ov	Car	H	N	DPLA	SM	P	Oe
Actinopterygii	Perciformes	Carangidae	*Hemicaranx amblyrhynchus*	Hamb	Fu	Car	H	N	SAND	S	P	Oe
Actinopterygii	Perciformes	Carangidae	*Oligoplites saliens*	Osal	Fu	Car	H	N	DPLA	SM	P	Oe
Actinopterygii	Perciformes	Carangidae	*Oligoplites saurus*	Osau	Fu	Car	H	N	DPLA	SM	P	Oe
Actinopterygii	Perciformes	Carangidae	*Selene setapinnis*	Sset	Ov	Car	H	N	MAC	SM	P	Oe
Actinopterygii	Perciformes	Carangidae	*Selene vomer*	Svom	Ov	Car	H	N	MAC	M	P	Oe
Actinopterygii	Perciformes	Carangidae	*Trachinotus carolinus*	Tcar	Fu	Car	H	N	MINV	SM	P	Oe
Actinopterygii	Perciformes	Carangidae	*Trachinotus falcatus*	Tfal	Fu	Car	H	N	MINV	S	P	Oe
Actinopterygii	Perciformes	Carangidae	*Trachinotus goodei*	Tgoo	Fu	Car	H	N	MINV	S	P	Oe
Actinopterygii	Perciformes	Centropomidae	*Centropomus parallelus*	Cpar	Fu	Sub	H	N	MAC	ML	BP	Oe
Actinopterygii	Perciformes	Centropomidae	*Centropomus undecimalis*	Cund	Fu	Sub	H	N	MAC	ML	BP	Oe
Actinopterygii	Perciformes	Ephippidae	*Chaetodipterus faber*	Cfab	Ov	Car	R	N	SINV	SM	BP	Oe
Actinopterygii	Perciformes	Gerreidae	*Diapterus rhombeus*	Drho	Ov	Car	R	N	OMNI	M	BP	Oe
Actinopterygii	Perciformes	Gerreidae	*Eucinostomus argenteus*	Earg	Fu	Car	R	N	SAND	SM	BP	Oe
Actinopterygii	Perciformes	Gerreidae	*Eucinostomus gula*	Egul	Fu	Car	R	N	SAND	SM	BP	Oe
Actinopterygii	Perciformes	Gerreidae	*Eucinostomus melanopterus*	Emel	Fu	Car	R	N	SAND	M	BP	Oe
Actinopterygii	Perciformes	Gerreidae	*Eugerres brasilianus*	Ebra	Ov	Car	R	N	SAND	M	BP	Oe
Actinopterygii	Perciformes	Gobiidae	*Bathygobius soporator*	Bsop	Ob	Dio	S	N	MINV	S	EPIB	Oe
Actinopterygii	Perciformes	Gobiidae	*Ctenogobius boleosoma*	Cbol	Ob	Dio	S	N	MINV	S	EPIB	Oe

SM 2. Taxonomical classification of species and functional-trait matrix. Functional codes available in Table 3 (*Continue …*).

Class	***Order***	***Family***	***Genus and Species***	***Acronym***	***Body shape***	***Swiming***	***Motility***	***Burying***	***Diet***	***Size***	***Vertical distribution***	***Environment***
Actinopterygii	Perciformes	Haemulidae	*Anisotremus surinamensis*	Asur	Fu	Sub	R	N	MINV	SM	BP	Em
Actinopterygii	Perciformes	Haemulidae	*Conodon nobilis*	Cnob	Fu	Sub	R	N	SAND	S	BP	Em
Actinopterygii	Perciformes	Haemulidae	*Haemulon steindachneri*	Hste	Fu	Sub	R	N	MINV	M	BP	Oe
Actinopterygii	Perciformes	Haemulidae	*Haemulopsis corvinaeformis*	Hcor	Fu	Sub	R	N	MINV	SM	BP	OE
Actinopterygii	Perciformes	Haemulidae	*Orthopristis ruber*	Orub	Fu	Sub	R	N	SAND	S	BP	Oe
Actinopterygii	Perciformes	Kyphosidae	*Kyphosus incisor*	Kinc	Fu	Car	R	N	MALG	ML	BP	Em
Actinopterygii	Perciformes	Kyphosidae	*Kyphosus sectatrix*	Ksec	Fu	Car	R	N	MALG	S	BP	Em
Actinopterygii	Perciformes	Labrisomidae	*Malacoctenus delalandii*	Mdel	Ob	Sub	S	N	MINV	S	EPIB	Em
Actinopterygii	Perciformes	Lutjanidae	*Lutjanus analis*	Lana	Fu	Sub	R	N	MAC	M	BP	Oe
Actinopterygii	Perciformes	Lutjanidae	*Lutjanus cyanopterus*	Lcya	Fu	Sub	R	N	MAC	M	BP	Oe
Actinopterygii	Perciformes	Lutjanidae	*Lutjanus synagris*	Lsyn	Fu	Sub	R	N	MAC	ML	BP	Oe
Actinopterygii	Perciformes	Mugilidae	*Mugil curema*	Mcur	Fu	Sub	R	N	OMNI	L	BP	Oe
Actinopterygii	Perciformes	Mugilidae	*Mugil liza*	Mliz	Fu	Sub	R	N	OMNI	L	BP	Oe
Actinopterygii	Perciformes	Mullidae	*Upeneus parvus*	Upar	Ob	Sub	R	N	SAND	S	BP	Em
Actinopterygii	Perciformes	Polynemidae	*Polydactylus virginicus*	Pvir	Fu	Sub	R	N	MINV	ML	BP	Oe
Actinopterygii	Perciformes	Pomatomidae	*Pomatomus saltatrix*	Psal	Fu	Car	R	N	MAC	SM	P	Oe
Actinopterygii	Perciformes	Sciaenidae	*Ctenosciaena gracilicirrhus*	Cgra	Fu	Sub	R	N	MAC	SM	BP	Oe
Actinopterygii	Perciformes	Sciaenidae	*Cynoscion jamaicensis*	Cjam	Fu	Sub	R	N	MAC	M	BP	Oe
Actinopterygii	Perciformes	Sciaenidae	*Larimus breviceps*	Lbre	Fu	Sub	R	N	MAC	SM	BP	Oe
Actinopterygii	Perciformes	Sciaenidae	*Menticirrhus americanus*	Mame	Fu	Sub	R	N	MAC	ML	BP	Oe
Actinopterygii	Perciformes	Sciaenidae	*Micropogonias furnieri*	Mfur	Fu	Sub	R	N	MAC	SM	BP	Oe
Actinopterygii	Perciformes	Sciaenidae	*Umbrina coroides*	Ucor	Fu	Sub	R	N	MINV	SM	BP	Oe
Actinopterygii	Perciformes	Serranidae	*Diplectrum formosum*	Dfor	Fu	Sub	R	N	MAC	SM	BP	Oe
Actinopterygii	Perciformes	Serranidae	*Diplectrum radiale*	Drad	Fu	Sub	R	N	MAC	M	BP	Oe
Actinopterygii	Perciformes	Sparidae	*Archosargus rhomboidalis*	Arho	Ov	Car	R	N	DPLA	S	BP	Oe
Actinopterygii	Perciformes	Sparidae	*Calamus penna*	Cpen	Ov	Car	R	N	SAND	SM	BP	Oe
Actinopterygii	Perciformes	Sparidae	*Diplodus argenteus*	Darg	Ov	Car	R	N	OMNI	SM	BP	Em
Actinopterygii	Perciformes	Sphyraenidae	*Sphyraena tome*	Stom	El	Sub	H	N	MAC	M	P	Em
Actinopterygii	Perciformes	Trichiuridae	*Trichiurus lepturus*	Tlep	Ang	Ang	H	N	MAC	L	P	Oe
Actinopterygii	Perciformes	Uranoscopidae	*Astroscopus y-graecum*	Aygr	Ob	Sub	S	Y	PIS	S	ENDB	Em
Actinopterygii	Pleuronectiformes	Achiridae	*Achirus lineatus*	Alin	As	Ang	S	Y	SINV	SM	ENDB	Oe
Actinopterygii	Pleuronectiformes	Bothidae	*Bothus ocellatus*	Boce	As	Ang	S	Y	SAND	S	ENDB	Oe
Actinopterygii	Pleuronectiformes	Cynoglossidae	*Symphurus tessellatus*	Stes	As	Ang	S	Y	SAND	M	ENDB	Oe
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Citharichthys arenaceus*	Care	As	Ang	S	Y	SAND	SM	ENDB	Oe
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Citharichthys macrops*	Cmac	As	Ang	S	Y	SAND	SM	ENDB	Em
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Citharichthys spilopterus*	Cspi	As	Ang	S	Y	SAND	SM	ENDB	Oe

SM 2. Taxonomical classification of species and functional-trait matrix. Functional codes available in Table 3.

Class	***Order***	***Family***	***Genus and Species***	***Acronym***	***Body shape***	***Swiming***	***Motility***	***Burying***	***Diet***	***Size***	***Vertical distribution***	***Environment***
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Etropus crossotus*	Ecro	As	Ang	S	Y	SAND	SM	ENDB	Oe
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Etropus longimanus*	Elon	As	Ang	S	Y	SAND	S	ENDB	Oe
Actinopterygii	Pleuronectiformes	Paralichthyidae	*Syacium papillosum*	Spap	As	Ang	S	Y	SAND	SM	ENDB	Em
Actinopterygii	Scorpaeniformes	Dactylopteridae	*Dactylopterus volitans*	Dvol	Ob	Sub	R	N	MINV	S	EPIB	Oe
Actinopterygii	Scorpaeniformes	Scorpaenidae	*Scorpaena brasiliensis*	Scbra	Ob	Sub	S	N	MINV	S	EPIB	Em
Actinopterygii	Scorpaeniformes	Triglidae	*Prionotus punctatus*	Ppun	Ob	Sub	R	N	MAC	M	EPIB	Oe
Actinopterygii	Syngnathiformes	Syngnathidae	*Hippocampus reidi*	Hrei	Hor	Ami	S	N	MINV	S	EPIB	Oe
Actinopterygii	Tetraodontiformes	Diodontidae	*Chilomycterus spinosus*	Cispi	Ov	Dio	R	N	SINV	S	BP	Oe
Actinopterygii	Tetraodontiformes	Monacanthidae	*Stephanolepis hispidus*	Shis	Ov	Bal	R	N	OMNI	S	BP	Em
Actinopterygii	Tetraodontiformes	Tetraodontidae	*Lagocephalus laevigatus*	Llae	Ob	Tet	H	N	MINV	M	BP	Oe
Actinopterygii	Tetraodontiformes	Tetraodontidae	*Sphoeroides greeleyi*	Sgre	Ob	Tet	R	N	SINV	SM	BP	Oe
Actinopterygii	Tetraodontiformes	Tetraodontidae	*Sphoeroides spengleri*	Sspe	Ob	Tet	R	N	SINV	S	BP	Oe
Actinopterygii	Tetraodontiformes	Tetraodontidae	*Sphoeroides testudineus*	Stest	Ob	Tet	R	N	SINV	M	BP	Oe

SM 3. Results of PCA (Principal Component Analysis) routine. Eigenvalues of the variance-covariance matrix and correspondent percentages of the variances for each relative warp (RW). IH, Intertidal habitat; IOS, Inner/outer sublittoral habitat; MSS, marginal shallow sublittoral habitat.

RW's	**IH**		**IOS**		**MEG**	
	Eigenvalues	Variance (%)	Eigenvalues	Variance (%)	Eigenvalues	Variance (%)
1	0.0237	42.80	0.0254	49.85	0.0134	53.95
2	0.0148	26.79	0.0140	27.41	0.0058	23.31
3	0.0070	12.56	0.0043	8.52	0.0023	9.07
4	0.0028	5.13	0.0022	4.41	0.0014	5.43
5	0.0024	4.32	0.0018	3.54	0.0008	3.20
6	0.0019	3.41	0.0016	3.16	0.0006	2.50
7	0.0017	2.99	0.0008	1.64	0.0003	1.46
8	0.0011	2.00	0.0007	1.48	0.0002	1.11

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