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Bruno Damasceno Cordeiro

Applying beta diversity indexes and estuarine use functional guilds to test the ecocline theory for fish assemblages of a tropical bay

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Dissertação submetida como requisito para obtenção do grau de Mestre em Ciências Biológicas, no Curso de Pós-Graduação em Ciências Biológicas, área de concentração: Biodiversidade Neotropical

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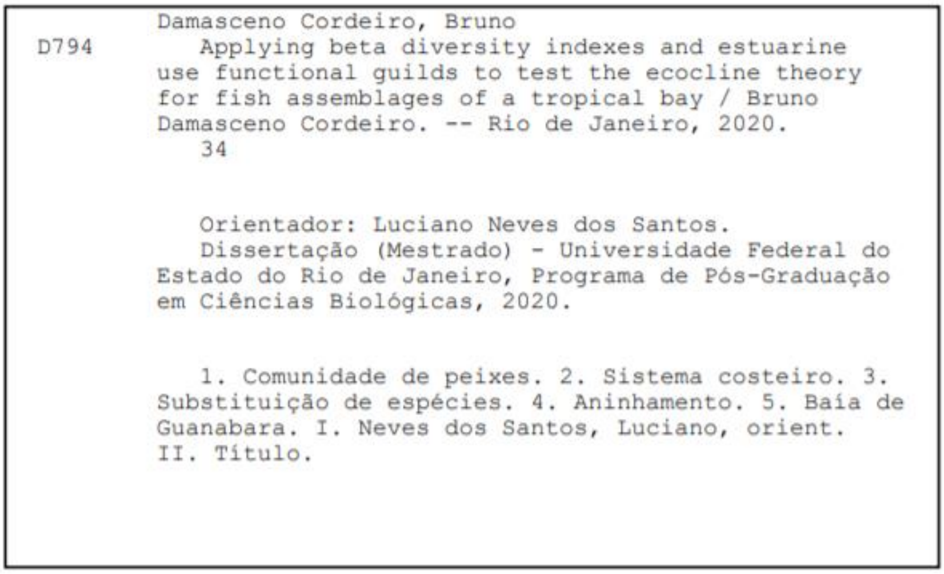

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Abstract

Estuaries are transitional ecosystems where gradual changes in community attributes may occur along environmental gradients (i.e. ecoclines), such as from freshwater zone to mid-estuary and from mid-estuary to the ocean. The use of functional guilds of estuary use is a novel and interesting approach to improve the knowledge on the contribution of fish species to the spatial turnover within estuaries worldwide, but barely tested for tropical systems. Using the turnover and nestedness components of beta diversity and their analogous from abundance-based method (balanced variation in abundance and abundance gradient, respectively) can reveal the contribution of species and individuals replacement (turnover) and losses (nestedness) to changes in fish assemblages along environmental gradients. The purpose of this study is to test three main hypotheses for fish assemblages distributed in a marine-estuarine ecocline within a tropical bay: (1) higher beta diversities are expected for distant rather than adjacent zones, as well as for species and individual loss from the mixing (mid-estuary) zone in relation to the other zones; (2) higher abundance-based values compared to incidence-based beta diversities are predicted; (3) the contribution of species (grouped in guilds) to species and individual replacement will support the ecocline pattern, driven mainly by salinity, with increased contributions of estuarine and diadromous guilds and decreased contributions of marine ones towards the brackish zone. Our findings reveal that the beta diversities between adjacent zones were lower than those more distanced (lower and upper zones) confirming our expectations, but only individual losses, not species, were detected from the upper zone (estuarine section) to the middle zone (transitional section). Species and individual replacements (turnover and balanced variation in abundance) were the major components from the pair-wise beta diversities of the bay zones. The values of abundance-based beta diversities were considerably higher than the ones calculated by species presence and absence, as predicted. These two approaches for beta diversity displayed different community facets and their concomitant use facilitates outcome interpretation. Species contributions to turnover and balanced variations in abundance indicated the affinity of marine species without estuarine dependency with the lower zone. In addition, the analyses revealed that broad salinity variations in the upper zone may have rendered species with distinct environmental affinities to inhabit this zone in different conditions. Therefore, an estuarine use functional diversity gradient driven by the extent of salinity variation was recorded, stressing the role of this variable as a structuring factor of estuarine communities.

Keywords: Community; coastal system; turnover; nestedness; environmental affinity; Guanabara Bay

Resumo

Estuários são ecossistemas transicionais nos quais graduais mudanças na comunidade podem ocorrer ao longo de gradientes ambientais (i.e., ecoclina), como da água doce ao médio-estuário e do médio-estuário ao oceano. O uso de guildas funcionais de uso de estuário é uma abordagem recente e interessante para aprimorar o conhecimento acerca da contribuição das espécies de peixes para a substituição de espécie ao longo do espaço em estuários do mundo todo. Usar os componentes da beta diversidade, substituição de espécies e aninhamento, juntamente com seus análogos provenientes do método baseado na abundância (variação balanceada de abundância e gradiente de abundância, respectivamente), pode revelar a contribuição da substituição e perda (aninhamento) de espécies e indivíduos para as mudanças na comunidade de peixes ao longo de gradientes ambientais. O objetivo deste estudo é testar três principais hipóteses das comunidades de peixes distribuídas em uma ecoclina marinha-estuarina de uma baía tropical: (1) são esperadas maiores beta diversidades entre zonas separadas do que em zonas adjacentes, além da perda de espécies e indivíduos da zona salobra (médio-estuário) em relação às outras zonas; (2) são previstos maiores valores de beta diversidade baseada na abundância em comparação a baseada na incidência; (3) as contribuições das espécies (agrupadas em guildas) para a substituição de espécies e indivíduos sustentarão o padrão da ecoclina, governado principalmente pela salinidade, com contribuições mais altas das guildas estuarinas e diádromas e mais baixas das guildas marinhas em direção à zona estuarina. Nossos resultados revelaram que as beta diversidades entre zonas adjacentes foram mais baixas do que das duas zonas separadas (zonas alta e baixa) confirmando nossas expectativas, mas apenas perda de indivíduos (não perda de espécies) foram detectadas da zona alta (setor estuarino) para a zona central (setor transicional). Substituições de espécies e indivíduos (substituição de espécies e variação balanceada de abundância) foram os componentes majoritários da beta diversidade par-a-par entre as zonas da baía. Os valores da beta diversidade baseada na abundância foram consideravelmente mais altos do que os calculados através da presença e ausência de espécies, como previsto. Essas duas abordagens exibiram facetas distintas da comunidade e o usá-los concomitantemente facilita a interpretação dos resultados. As contribuições das espécies para a substituição de espécies e variação balanceada de abundância demonstrou a afinidade de espécies marinhas sem dependência estuarina com a zona baixa. Além disso, revelou que as amplas variações de salinidade da zona alta podem ter permitido espécies com afinidades ambientais distintas habitarem esta zona em diferentes condições. Portanto, um gradiente de diversidade funcional de uso estuarino conduzido pela extensão da variação de salinidade foi registrado, reforçando o papel desta variável na estruturação de comunidades estuarinas.

Palavras-chave: Comunidade; sistema costeiro; substituição de espécies; aninhamento; afinidade ambiental; baía de Guanabara

Summary

1. Introduction

Estuaries are transitional ecosystems with variable contributions of marine and fresh waters. They are generally defined as partially enclosed coastal environments connected to the ocean that receives inland runoffs at least periodically (Fairbridge, 1980; Potter et al. 2010). Estuarine systems are composed by a particular biota, able to succeed in harsh environmental conditions and to shift in composition and structure along the freshwater-marine gradient, mainly dictated by salinity (Elliott and Whitfield, 2011; Whitfield et al., 2012). This freshwater-marine gradient is commonly sectorized in three main zones: a marine zone, displaying environmental features similar to the ocean; a mixing zone, dominated by brackish water and subject to strong salinity fluctuations; and a freshwater zone, comprising oligohaline waters cyclically influenced by the tidal regime (Fairbridge, 1980). The composition and structure in these transitional ecosystems of aquatic assemblages may shift rapidly, lying in a narrow boundary between different communities (ecotone), or gradually, showing gradational changes in ecological attributes (ecocline) (van der Maarel, 1990).

The concept of ecocline has been increasingly tested for aquatic communities in estuarine systems, in which three major premises have been predicted (Attrill and Rundle, 2002; Cortelezzi et al., 2007; Greenwood, 2007; Quinlan and Philips, 2007; Muylaert et al. 2009; Chaves et al., 2018). . First, gradual biotic changes, in response to a major abiotic gradient, and an environmentally harsh zone (brackish zone, in the case of estuaries) with lower richness and abundance, are intrinsic patterns to ecoclinal ecosystems (van der Maarel, 1990; Attrill and Rundle, 2002). Secondly, some fish species are capable of inhabit several salinity conditions and migrate between marine, freshwater and estuarine systems (McDowall, 1988; Riede, 2004; Elliott et al., 2007). Finally, fish are susceptible to tidal transport and freshwater discharges, especially in early life stages (Norcross and Shaw, 1984; Ré, 1990; Neira and Potter, 1992; McDowall, 2008). Therefore, some species might be found in low abundances within zones to which they have little or no affinity and in high abundances in zones of greater affinity. Attrill and Rundle (2002) reported two overlapping ecoclines for a northern temperate estuary, one from the freshwater zone to mid-estuary, and another from the mid-estuary to the ocean. This mid-estuary, typically dominated by brackish conditions, was defined as a maximum stressful zone for freshwater and marine organisms to survive in. This approach was, however, performed specifically for macroinvertebrates, and tested only for typical marine and freshwater species, excluding many migratory and diadromous species with the ability to deal with salinity changes and transit within both systems (McDowall, 1988; Riede, 2004).

The use of functional guilds of estuary use, such as those proposed by Elliot et al. (2007) and Potter et al. (2015), may be an interesting alternative to address the complexity of estuarine fish assemblage composition and structure. This approach appear to be particularly useful for fish assemblages of temperate (Harrison and Whitfield, 2008; Ramos et al., 2012; Moreno-Valcárcel et al., 2013) and tropical systems (Araújo et al., 2016; Silva et al., 2016; Chaves et al., 2018). A single study (Henriques et al., 2017) calculated the contributions of four functional guilds (e.g. marine, estuarine, freshwater, and diadromous) to species turnover, and verified, by comparing several estuaries from different biogeographical regions worldwide, that the contributions of each guild are related to species-specific variations in abundance and dispersal capacity within the assemblages of each ecosystem. Therefore, fish species from fragmentated environments (freshwater and estuarine) contributed significantly to the beta diversity, as defined as the extent of change in community composition by Whittaker (1960), even accounting for only a small proportion of the total species richness in estuarine fish assemblages (Henriques et al., 2017).

Turnover and nestedness are two antithetic components of beta diversity (Harrison et al., 1992; Baselga, 2010). Turnover is the replacement of species from one site to another (Qian et al., 2005), while nestedness is the loss of species from a richer area to a poorer one (Wright and Reeves, 1992). Baselga (2010) provided the way to calculate each component contribution for incidence-based (presence-absence of species) assemblages, whereas Baselga (2013) proposed two components analogous to turnover and nestedness for species abundance, thus, considering individual replacement (balanced variation in abundance) and loss (abundance gradient). Since these two beta diversity measures are sensitive to different assemblage features, such as composition (presence-absence) and structure (abundance), they display an interesting potential for the unveiling of the spatial distribution of fish assemblages in estuarine systems.

This study tested for ecocline predictions using fish beta diversities between three zones (upper, middle and lower) at Guanabara Bay, where a marine-estuarine gradient has been recorded (Chaves et al., 2018). Differing from previous studies, the ecocline premises were innovatively addressed through beta diversity spatial patterns using fish species occurrence and abundance within functional guilds of estuary use. Accordingly, three main hypotheses were tested herein: (1) fish assemblage composition will display lower beta diversities between adjacent zones in comparison to more distanced zones, and species and individuals losses (nestedness and abundance gradient) will be higher in the brackish zone; (2) fish beta diversities will be higher for abundance-based values compared to incidence-based ones; and (3) the contribution of species (grouped in guilds) to species and individual replacement will support the ecocline pattern, driven, mainly, by salinity, with increased contributions of estuarine and diadromous guilds (tolerant to salt content variations) and decreased contributions of marine ones towards the brackish zone.

2. Material and methods

2.1 Study site

This study took place in Guanabara Bay, the second largest bay on the Brazilian coast, comprising ~380 km^2, displaying a rainy tropical climate and intense ocean influence. Guanabara Bay is located in the Rio de Janeiro metropolitan region, an intense urbanized area that harbours circa 16 million people. This bay plays an essential role regarding ecosystem services, being both economic and ecologically important for the society located in surrounding regions. Despite this, several negative impacts (e.g., vast daily sewage discharges) threaten its ecosystems functioning and processes (Fistarol et al., 2015; Soares-Gomes et al., 2016). The bay is characterized by an ecocline with a marine-estuarine gradient from the entrance (marine influence) to the inner area (a mixed influence of marine tides and rivers/continental inputs), wherein salinity ranges from 13 to 36 (Paranhos and Mayr, 1993; Chaves et al., 2018). The tidal regime is mainly semidiurnal with a mean tidal range of 0.7 m and 50 % water renewal time of 11.4 days, with a significantly longer inner area renewal time. Guanabara Bay has a central channel 30 m deep, but overall, this system is mostly shallow, with an average water depth of 5.7 m (Kjerfve et al., 1997), raising the importance of the shallow portions to the ecosystem functioning.

2.2 Data sampling

Fish and water abiotic variables were sampled (during the day - 08 to 15 h) bimonthly between September 2017 and July 2019, totalling 12 campaigns. Samplings were conducted in three zones - three beaches per zone - at Guanabara Bay: the upper bay (1. Piedade; 2.

Suruí; 3. Mauá); middle bay (4. Zumbi; 5. Ribeira; 6. Bica); and lower bay (7. Flamengo; 8. Urca; 9. Dentro) (Fig. 1). Fish were caught with a beach seine (20 m width x 2 m height – 7 mm mesh size with a codend of 3 mm mesh size) attached to 20 m ropes that were dragged perpendicularly towards the shoreline for ~10 minutes, totalling approximately 200 m² of sampled area. Water temperature and salinity were measured through a multiparameter HANNA HI 9829 probe placed on the middle of the beach depth and water transparency determined using a Secchi disk. Both fish and abiotic variables were sampled in triplicate, without overlapping samplings.

Captured fishes were preserved on ice and transported to the Laboratory of Theoretical and Applied Ichthyology (LICTA) for identification at the species level, according to Figueiredo and Menezes (1978, 1980, 2000) and Menezes and Figueiredo (1980, 1985) guides. All taxonomic classifications were updated according to Nelson et al. (2016). Following Elliot et al. (2007) and improvements by Potter et al. (2015), all fish species were allocated in estuarine use functional guilds. To assess if individuals belonging to specific guilds (amphidromous and marine estuarine-dependent) were juvenile or adult, total lengths were measured and compared to data of first maturity length available at the FishBase database (Froese and Pauly, 2019).

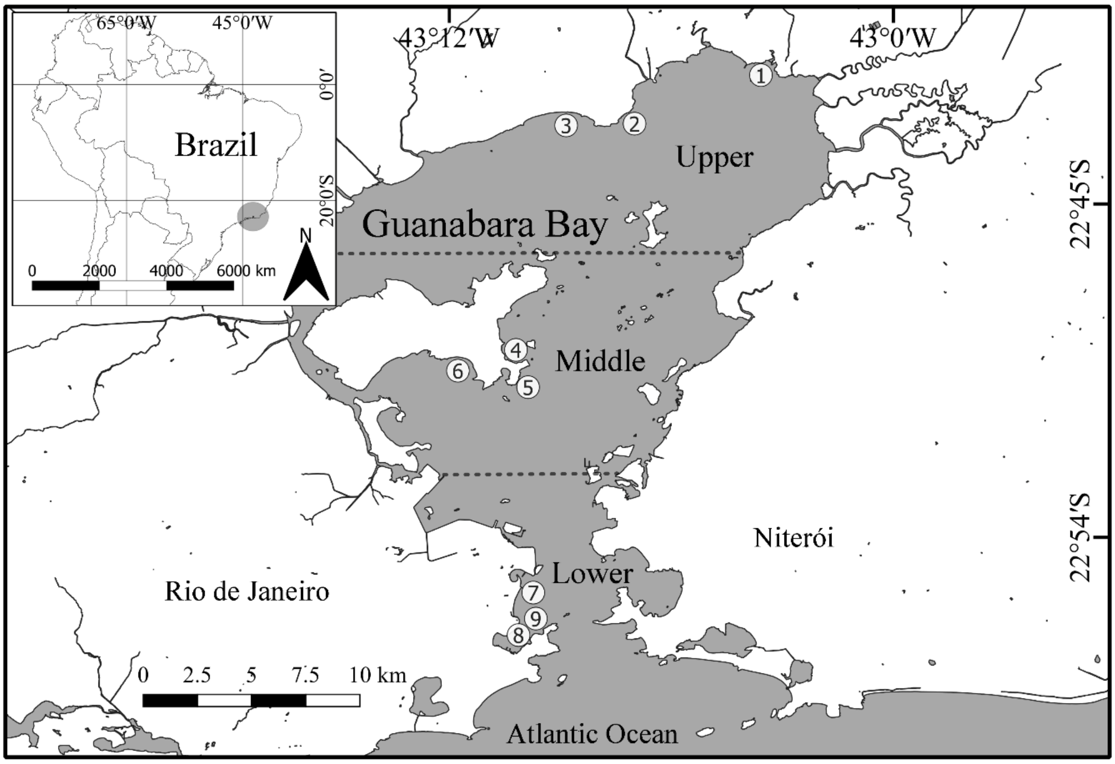

Fig. 1. Guanabara Bay sample design map, showing three zones (upper, middle and lower) and nine beaches (1. Piedade; 2. Suruí; 3. Mauá; 4. Zumbi; 5. Ribeira; 6. Bica; 7. Flamengo; 8. Urca; 9. Dentro) across the bay.

2.3 Data analysis

A principal component analysis (PCA) was applied to the standardize environmental data matrix to evaluate how the abiotic variables behave along the bay zones. A broken stick model estimated the statistically significance of PCA axes. Then, two-way factorial analyses of variance (ANOVA) were applied to the abiotic variable matrix (Box-Cox transformed salinity, $\lambda = 4$, and transparency, $\lambda = 0$, to achieve homoscedasticity) to test for significant differences ($p < 0.05$) between the three bay zones. Both the ANOVA and PCA (and subsequent broken stick) analyses were performed using the R software (R Development Core Team, 2008).

A non-metric multidimensional scaling (NMDS) was applied to the species abundance matrix ($\log_{10}$ transformed; Bray-Curtis distance) to assess how the composition and structure of fish assemblages behave along the bay zones and to test whether the zones could exhibit differences between their communities. Pairwise beta diversities between the fish communities from the three bay zones were calculated through two indices: incidence (Sorensen) and abundance (Bray-Curtis) of species. Incidence-based beta diversities were partitioned into turnover (TO) and nestedness (NE) beta diversity components (Baselga, 2010), while abundance-based beta diversities were decomposed in balanced variation in abundance (BVA) and abundance gradients (AG) (Baselga, 2013). Beta diversities and their components were calculated using the *betapart* package available in the R software.

In order to calculate each species contribution to pairwise turnover, the equation developed by Henriques et al. (2017) was adapted concerning the incidence-based method, the first step divides the turnover equally for each zone:

$$C_{za} = \frac{TO}{2}; \, C_{zb} = \frac{TO}{2}$$

where C_z is the contribution of each zone (*a* and *b*) to the calculated turnover. Leading to the second step:

$$C_{sp} = \frac{C_{za}}{E_{za}}$$

where C_{sp} is the contribution of each species exclusive to the given zone *a* and E_{za} is the number of exclusive species within zone *a*, both in a pairwise comparison.

Regarding the abundance-based method, we developed a novel formula to calculate each species contribution to pairwise balanced variation in abundance as follows:

$$C_{spi} = \frac{HAb_{spi} - LAb_{spi}}{\sum HAb_{sp} - \sum LAb_{sp}} \times BVA$$

where C_{spi} is the contribution of a certain species (*spi*) to balanced variation in abundance (*BVA*), *HAb* is the highest abundance, *LAb* is the lowest abundance of species *i* and of all species (*sp*). These equations provide the contribution of each exclusive species to a zone (in the case of incidence) and in the zone with the highest abundance of a determined species (in the case of abundance) through pairwise comparisons. The two contributions (because each zone is compared separately to the two other zones) of a species to that zone, in both methods, are summed, resulting in the contribution of each species to each zone. Finally, the contribution of functional guilds of estuary use for the TO and BVA in each zone was determined through summing the contributions of all species belonging to each guild.

To detect significant interactions ($p < 0.05$) between guild abundance and abiotic variables, guild abundance versus bay zones, and guild abundance versus abiotic variables along with bay zones, a multivariate permutational analysis of variance (PERMANOVA; 999 permutations) was applied to guild abundance and the abiotic variables (using the same transformations from ANOVA analyses), with the zones as random factor. This analysis was performed using the "adonis" function available in the *vegan* package in the R software (Oksanen et al., 2016). To check the possibility of a significant dispersion effect ($p < 0.05$) leading to incorrect inferences regarding PERMANOVA results, a test for homogeneity of multivariate dispersions (PERMDISP) was applied to guild abundance grouped by zones, using the "betadisper" function, also available in the *vegan* package (Oksanen et al., 2016).

Finally, two distance-based redundancy analysis (dbRDA) were applied to address how the abiotic variables (standardized) influence fish guild incidences (Jaccard) and abundances ($\log_{10}$ transformed; Bray-Curtis). To test for the significance ($p < 0.05$) of the two ordinations generated by dbRDA, two analysis of variance (ANOVA) were applied to the dbRDA results. Samples were coded by bay zone and dbRDA were performed in the R software through the "capscale" function available in the *vegan* package (Oksanen et al., 2016).

3. Results

3.1 Abiotic variables

The PCA results demonstrated that the first axis (eigenvalue = 1.83) explained 60.8% of the data variance, whereas only 22.3% was explained by the second axis (eigenvalue = 0.67) (Fig. 2). Salinity and transparency were mostly related with PC1 (0.59 and 0.60, respectively), while temperature was highly associated with PC2 (0.84), but also negatively with PC1 (-0.54). The broken stick criteria (PC1 = 1.83) selected only PC1 as significant, where most of the points from the lower zone have positive values and from the upper zone, negative values; values from the middle zone are homogeneously split into positive and negative values. These features indicate a salinity and transparency gradient increasing from the upper to lower bay zones, with the middle acting as a transition zone. The ANOVA confirmed the trend indicated by the PCA ordination, with the three bay zones differing significantly regarding salinity (p-values < 0.001; F range = 12.46 – 64.11) and transparency (p-values < 0.001; F range = 25.18 – 177.2) in all pairwise comparisons. Concerning temperature, only the lower zone differed significantly from the middle and upper zones (p-values < 0.001; F = 12.89 and 13.2, respectively), while the middle/upper zones were not significantly different (p = 0.998; F = 0) (Table 1).

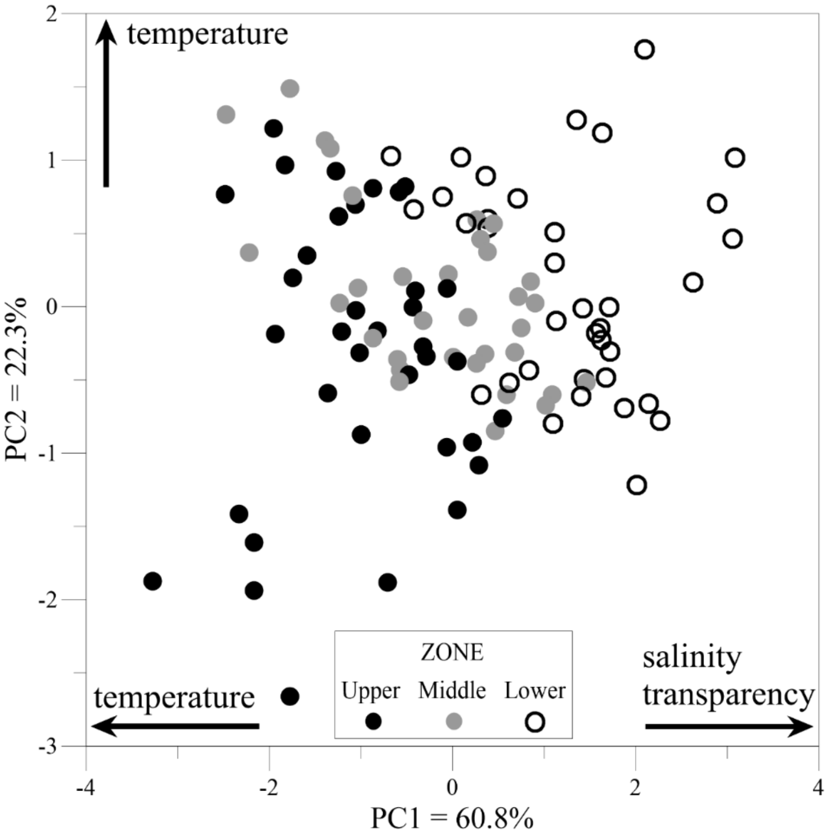

Fig. 2. Ordination diagram of the first two axes from the principal component analysis (PCA) applied to the abiotic variables coded by the three bay zones (upper, middle and lower).

Table 1 Abiotic variables means (range) per zone of the bay. A (*) indicates significant differences (p<0.001) in comparison to the other two zones by an ANOVA analysis.

Abiotic variables	Upper	Middle	Lower
Salinity	26.72* (6.94 - 33.82)	30.66* (20.96 - 34.6)	33.25* (29.45 - 37)
Temperature °C	27.31 (22.47 - 33.16)	27.30 (22.41 - 34.44)	24.76* (19.42 - 30.69)
Transparency cm	45.46* (15 - 110)	79.38* (20 - 150)	180.02* (52 - 370)

3.2 Community features

A total of 73 fish species, belonging to 37 families and 22 orders were sampled, being assigned to eight functional guilds of estuary use: freshwater estuarine-opportunist; amphidromous; semi-anadromous; estuarine-freshwater; estuarine-marine; marine estuarine-dependent; marine estuarine-opportunist; and marine straggler. The number of species was similar in the three bay zones (ranging from 46 to 47) (Table S1; supplementary material). Despite total species richness resemblance, NMDS (Stress value = 0.2) (Fig. 3) verified that fish assemblages were quite dissimilar among zones, mainly between the upper and lower zones, while displaying similarities to the adjacent middle zone. These results follow the same ecocline gradient as noted by the abiotic variables in the PCA ordination.

Confirming the NMDS results, the calculated beta diversities for fish assemblages between zones were low for the incidence-based method: upper × middle = 0.298 (TO = 0.298); middle × lower = 0.312 (TO = 0.304); and upper × lower = 0.398 (TO = 0.391). However, beta diversity was higher for the abundance-based method: upper × middle = 0.627 (BVA = 0.477); middle × lower = 0.768 (BVA = 0.748); and upper × lower = 0.82 (BVA = 0.772). Both beta diversities were composed mainly by replacement of species and individuals (TO and BVA) in all pairwise comparisons between zones, while only the upper × middle comparison displayed a considerable AG.

The calculated guild contributions to TO by zone demonstrated high contributions from marine straggler and marine estuarine-opportunist species in the lower zone, decreasing towards the upper zone, while the opposite trend was noted for marine estuarine-dependent and estuarine-marine guilds. Low contributions of estuarine-freshwater, and semi-anadromous species were observed for the upper and middle zones and no contribution for the lower zone. The amphidromous and freshwater estuarine-opportunist species only contributed to the upper zone, presenting moderate and high values, respectively (Fig. 4A). In contrast, species contributions to BVA by zone, only showed high values for marine estuarine-opportunist species in the lower zone and estuarine-marine ones in the middle zone. Semi-anadromous and estuarine-marine presented moderate contributions for the middle and upper zones, respectively. In the upper zone, marine estuarine-dependent and semi-anadromous species contributed moderately, while the contribution of marine estuarine-dependent were higher than the other zones. All other contributions were low (< 0.047) (Fig. 4B). Considering the number of guilds that contributed to TO and BVA by zone, a decreasing trend towards the ocean is verified. The upper zone was the only zone with contributions from all guilds, presenting two exclusive guilds, amphidromous and freshwater estuarine-opportunist. In the middle zone, six guilds contributed to TO, but all guilds contributed less than in the other two zones. The lower zone only displayed contributions to TO from three guilds, estuarine-marine, marine estuarine-opportunist and marine straggler, but with the higher contributions from marine guilds. Concerning contributions to BVA, marine estuarine-dependent guild species contributed with very low values (Fig. 4).

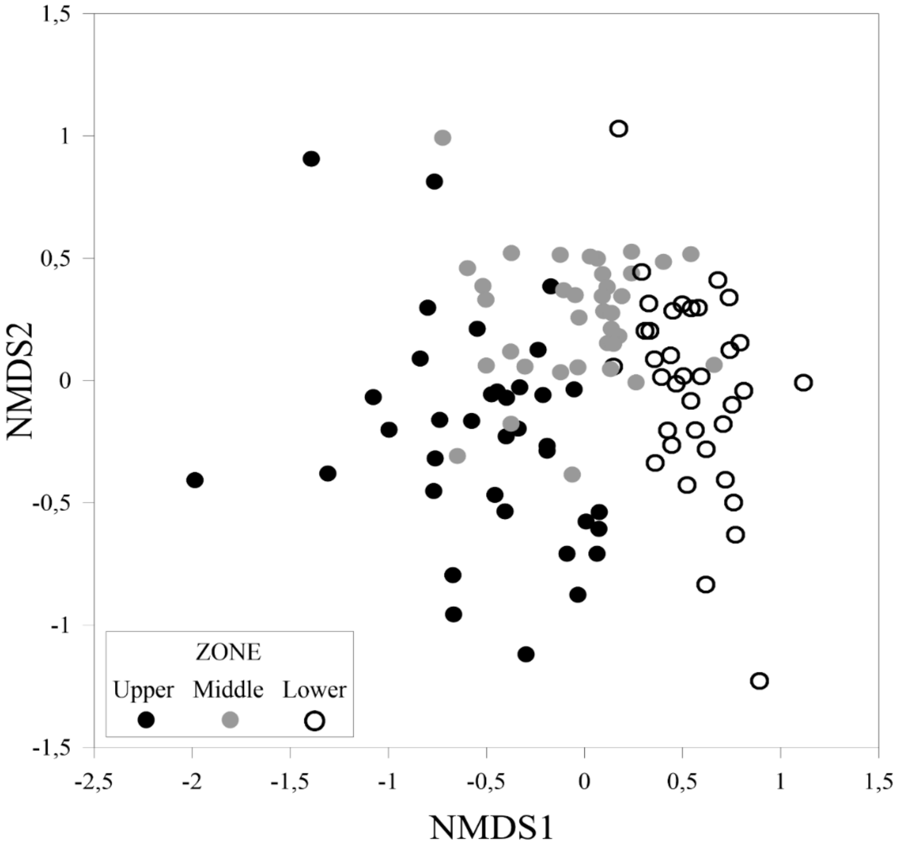

Fig. 3. Ordination diagram of the non-metric multidimensional scaling (NMDS) applied to species abundance ($\log_{10}$ transformed) coded by the three bay zones.

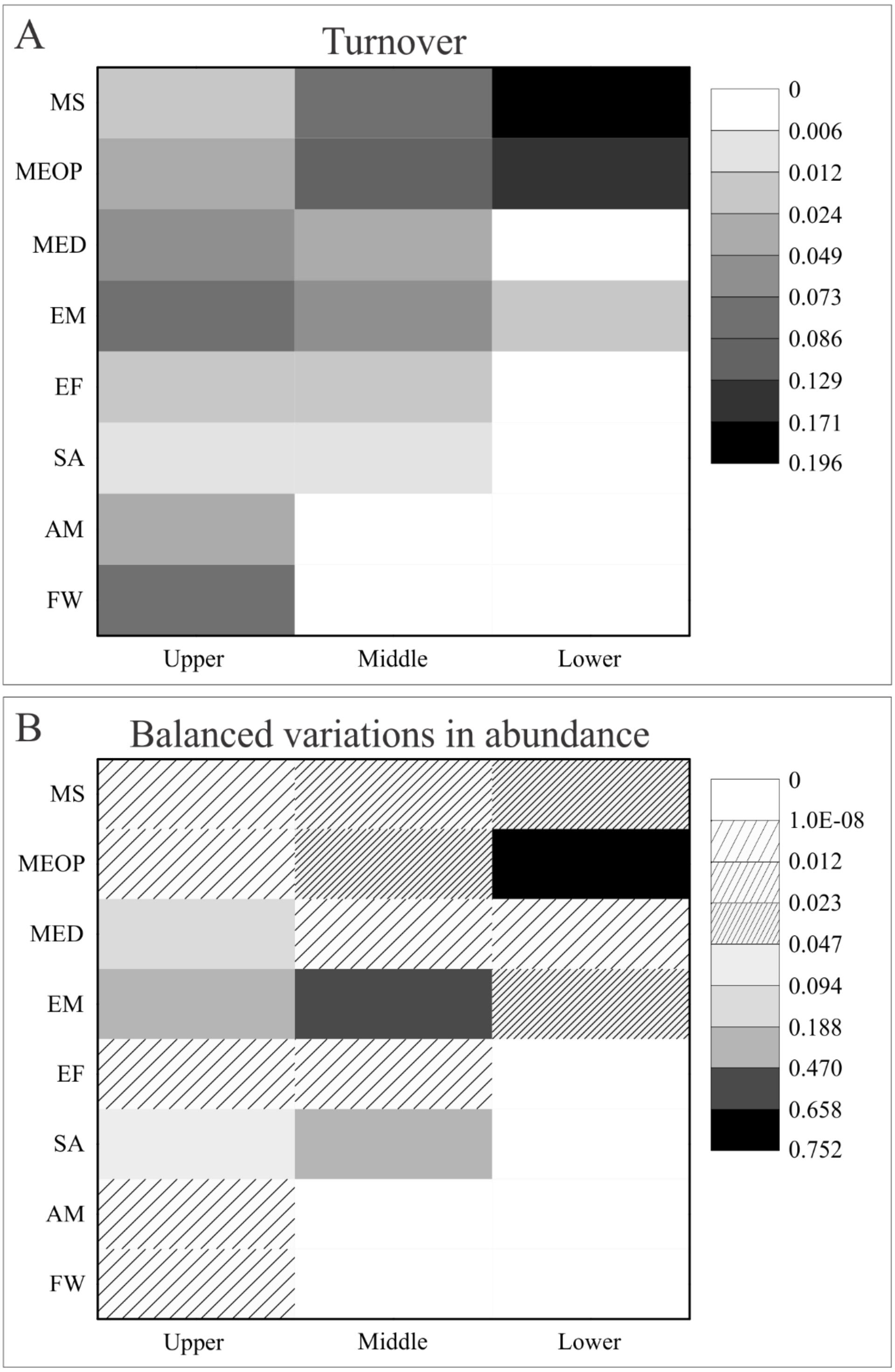

Fig. 4. Estuarine use guild contribution to turnover (TO) in incidence-based beta diversities (A) and to balanced variations in abundance (BVA) in abundance-based beta diversities (B) by bay zone. Estuarine use guilds code: FW = Freshwater estuarine-opportunist; AM = Amphidromous; SA = Semi-anadromous; EF = Estuarine-freshwater; Estuarine-marine; MED = Marine estuarine-dependent; MEOP = Marine estuarine-opportunist; MS = Marine straggler.

3.3 Abiotic variables and fish guild relationships

The PERMANOVA detected significant interactions between guild abundance and salinity (F = 2.54; p = 0.016), transparency (F = 3.19; p = 0.003), zone (F = 3.73; p = 0.002) and salinity by zone (F = 2.57; p = 0.014). Showing the role of salinity in driving the guilds distributions along the bay zones. As for the temperature, no significant relations were revealed. Further, the PERMDISP showed no significant dispersion effect regarding fish guild abundance grouped by zone (F = 2.86; p = 0.065), validating thus PERMANOVA results.

According to the dbRDA analysis, the two ordinations demonstrated a similar gradient for the number of guilds that contributed to TO and BVA, with samples from the upper zone widely scattered, indicating great estuarine-use functional diversity. Samples from the middle zone were less dispersed and those from lower zone were closer to each other, revealing poor estuarine-use functional diversity. Regarding the abiotic variables, salinity and transparency were more associated with the first axis in both incidence (0.70 and 0.84, respectively) and abundance (0.69 and 0.94, respectively) analysis. In relation to temperature, only weak associations were recorded for the two main axes in both dbRDA (< 0.27) comprising 91.7% (CAP1 = 76.6% and CAP2 = 15.1%) of incidence ordination and 89.4% (CAP1 = 73.6% and CAP2 = 15.8%) of abundance ordination. An ANOVA confirmed significant ordinations for incidence (F = 9.97; p = 0.001) and abundance (F = 7.12; p = 0.001). dbRDA displayed apparent relations between guild incidence and abundance with salinity and transparency, while temperature did not appear to be related (Fig. 5). The patterns for each guild associations with abiotic variables were similar in both incidence and abundance ordinations. Two marine guilds (marine straggler and marine estuarine-opportunist) were associated with the highest salinity and transparency values from the lower zone, while the other marine guild (marine estuarine-dependent) was related to the more turbid brackish waters from the upper zone. The two estuarine guilds (estuarine-marine and estuarine-freshwater) were correlated with the intermediate water variables values found at the middle zone. The freshwater-dependent guilds (freshwater estuarine-opportunist and amphidromous) were associated with the oligohaline and intermediate water transparency of the upper zone. The semi-anadromous guild was related to more turbid and intermediate salinity waters occasionally found in the upper and middle zones.

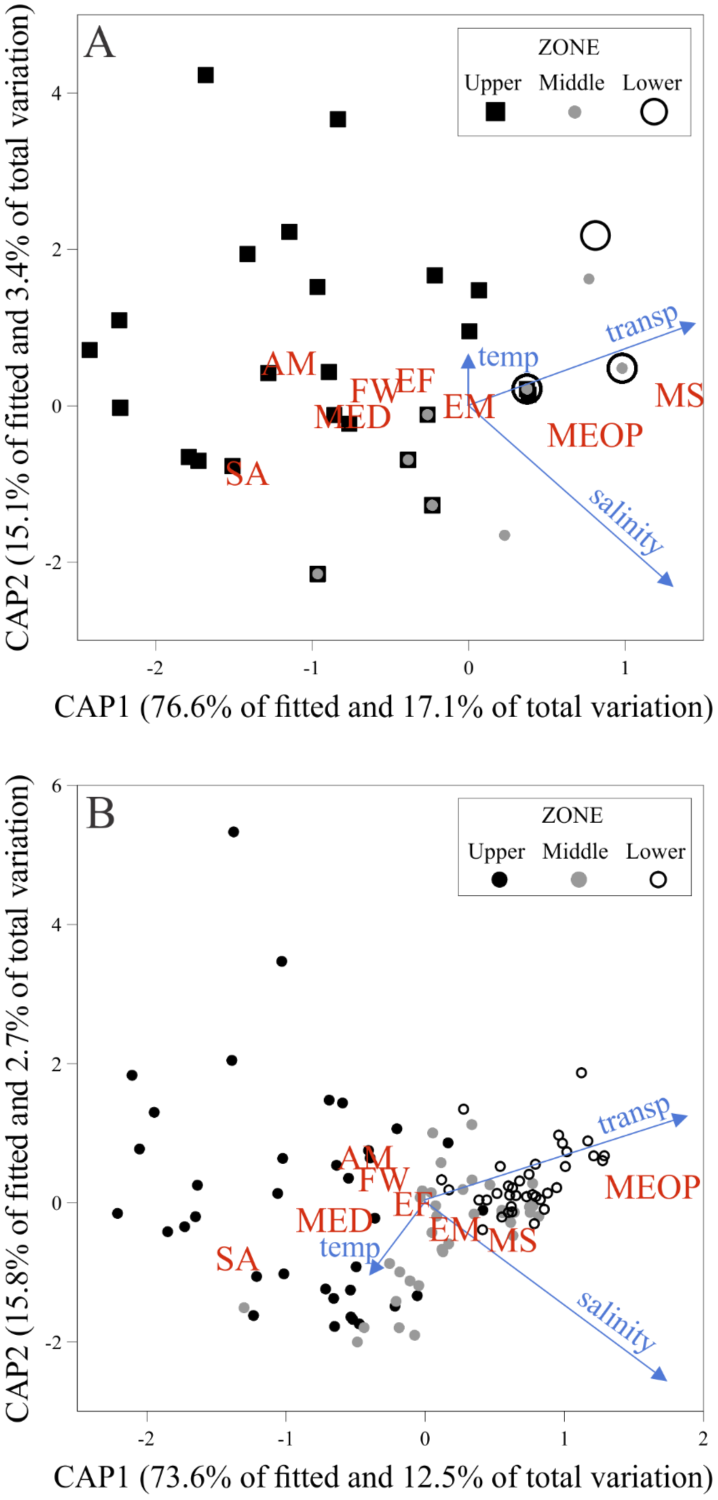

Fig. 5. Ordination diagrams of distance-based redundancy analysis (dbRDA) displaying the relations between guild incidence (A) and abundance (B) with abiotic variables, coded by the three bay zones (upper, middle and lower). Estuarine use guilds code: FW = Freshwater estuarine-opportunist; AM = Amphidromous; SA = Semi-anadromous; EF = Estuarine-freshwater; Estuarine-marine; MED = Marine estuarine-dependent; MEOP = Marine estuarine-opportunist; MS = Marine straggler.

4. Discussion

Our results support a previous study suggesting the existence of an estuarine-marine ecocline in Guanabara Bay waters (Chaves et al., 2018). In agreement with this previous study applied to fish associated with rock shores, we also found a salinity and transparency gradient that gradually increases towards its connection with the ocean, and a smooth variation of fish fauna composition and structure that follow the environmental gradient were found using fish assemblages associated with sandy beaches. Several studies have stressed that unstable turbid brackish water as those found in the estuarine upper zone of Guanabara Bay might act as an environmental filter or stressor (harsh condition) to several fish species and play an important role as nursery and growth habitat to other species (Attrill and Rundle, 2002; Castro et al., 2005; Elliot et al., 2007; Chaves et al., 2018). Otherwise, a more stable and clear marine water is found in the lower zone, where only exclusive marine and estuarine fishes were recorded (Table S1, supplementary material). The middle zone may function as intermedia transitional interface between the two former zones, regarding stability, environmental conditions and community features. In addition, our study agrees with the dominance of marine fish species inside estuarine systems (Elliot et al., 2007). Corroborated by the extensive number of marine species sampled in this study (Table S1, supplementary material) and other studies performed in Guanabara Bay (da Silva et al., 2016; Soares-Gomes et al., 2016; Chaves et al., 2018). However, only the estuarine-marine portion of Guanabara Bay was comprised in our study, since the estuarine-freshwater segments from the rivers that drain into the bay (Paranhos and Mayr, 1993; Costa et al., 2018) were not addressed.

The first hypothesis of our study was partially confirmed by the results, since the beta diversities between adjacent zones were, indeed, lower than in direct comparison between upper and lower zones, for both approaches (i.e. species incidence and abundance). Such findings agree with expected ecoclinal ecosystems pattern, where gradual community changes were observed in response to a major environmental variable (in our case salinity) (van der Maarel, 1990; Attrill and Rundle, 2002). However, diverging from the incidence-based method, the lower zone was more dissimilar than the two other zones in the abundance-based beta diversity. This can be explained by the higher abundance of marine estuarine-opportunist species in the lower zone and the higher abundance of the only semi-anadromous species (*Anchoa januaria*), estuarine-freshwater and estuarine-marine species in upper and middle zones, according to the species contributions to balanced variations in abundance (BVA) (Fig. 4B). These community features show that, despite the abiotic differences between upper and middle zones, other forces (e.g. food availability) might influence the level of association of these tolerant species (estuarine and semi-anadromous) to the less haline and transparent waters of these zones. However, they also show the high affinity of marine estuarine-opportunist species to the upper zone marine waters, with dominant schooling species recruiting in these sheltered shallow waters, like clupeids *Harengula clupeola* and *Sardinella brasiliensis* and the bluefish *Pomatomus saltatrix* (Juanes et al., 1996; Pessanha et al., 2003; Jablonski and Legey, 2004).

Another issue addressed in our first hypothesis is that nestedness (NE) and abundance gradient (AG), i.e. species or individual losses, were expected between the upper zone and the other two zones. Due to the richness similarity between the bay zones, only insignificant NE values were detected, contradicting our expectations. Hence, the great majority of incidence differences between the zones are assigned to species replacement, i.e. turnover (TO). Therefore, there were no poorer zones acting as subsets of richer zones in Guanabara Bay. Considering the abundance-based beta diversity, the upper-middle and the upper-lower comparison presented moderate (0.15) and low (0.05) values of AG, reflecting total abundance differences between these zones, respectively (Table S1, supplementary material).

The lower abundance and similar richness found for the upper zone show that, for non-tolerant species, strong salinity fluctuations might result in small populations or even only few transient individuals. This result is probably related to occasional inward movements carried by river discharges (freshwater species) and marine currents (marine species) (Kjerfve et al., 1997) or intentional dispersion when favorable conditions occurs. Movements outside this zone and high mortality rates whenever stressful conditions take place might also occur. These unintentional movements due to hydrodynamic influences might be high in the case of young juvenile fish that recruit in the shallow waters from beaches (Olds et al., 2017), as their swimming capabilities are expected to be lower than adults. Additionally, the increase gradient of functional diversity towards the upper zone appears to be related to the extent of salinity variation, that demonstrated a similar gradient (Table 1). Broad salinity variations allow species with different affinities (e.g. marine and freshwater species) to inhabit the upper zone in different periods, enhancing the number of guilds found within its waters, while the stable marine salinities from the lower zone only supported marine and estuarine species (Fig. 4 and Table S1, supplementary material). Further studies dealing with seasonal or temporal shift on fish assemblage composition and structure in the upper zone would be important to better understand the role of salinity fluctuations in driving these movements of non-tolerant species. Other studies have shown how these seasonal fluctuations in the community are driven by environmental filtering (Barletta et al. 2008; Lebrija-Trejos et al. 2010; Passos et al., 2016).

Confirming our second hypothesis, the abundance-based approach provided higher beta diversity values between zones than incidence-based ones, showing that not only the community composition but also the structure are dissimilar in each Guanabara Bay zone. In transitional ecosystems that behave as an ecocline, where gradual changes of community structure and composition are intrinsic (van der Mareel, 1990; Attrill and Rundle, 2002), spatial differences in species abundance are expected to exist combined with species incidence. For species that occurred in all bay zones, these gradual or abrupt changes in their abundances are not considered by the incidence-based beta diversity. This can be a valuable information since inwards and outwards movements among zones influences the occurrence of few individuals outside its optimal habitat (zones with low/any affinities), while high abundances of species are found in zones with great affinities. Despite the fact that every incidence of species divergences can be accounted by the abundance-based, with rare species (when abundance differences between zones are probably quite low) this type of analysis may underestimate these divergences, while the incidence-based method apparently does not (all species have the same weight) (Legendre and Legendre, 2012). Therefore, using these two methods to calculate beta diversity between communities can emphasize different biotic features, such as rare and abundant species. Similarly, using species contribution (grouped in estuarine use guilds) to TO and BVA were useful to show the number of exclusive species by guilds in each zone and the extent of species abundance differences between zones by guilds, respectively.

Contrasting with our expectations, our third hypothesis was partially corroborated. The marine guilds that enter estuaries only occasionally (marine estuarine-opportunist and marine straggler) (Potter et al. 2015) were associated with the marine portion of the bay (lower zone), with a higher number of exclusive species and abundance of these guilds as expected. However, the other marine guild, marine estuarine-dependent, demonstrated higher affinity to the estuarine sector (upper zone). This is probably explained by the dependence of this guild's juveniles on sheltered estuarine areas to survive and grow (Potter et al. 2015) and most of the sampled specimens from this guild were young juveniles.

The patterns of the two estuarine guilds (estuarine-marine and estuarine-freshwater) were quite different. First, the estuarine-marine guild was richer (in comparison with the estuarine-freshwater guild) and more abundant, dominated by the Brazilian silversides *Atherinella brasiliensis* (Table S1, supplementary material), stressing similar findings for Australian estuaries (Potter and Hyndes, 1999). Secondly, the estuarine-marine number of exclusive species were higher in the estuarine area (upper zone) and species abundances were greater in the transitional one (middle zone). This pattern indicates that probable wide variations in salinity of the mixing zone may have weakened the dominance of some species (mostly Brazilian silversides), enabling the occurrence of other more tolerant estuarine-marine species and enhancing this guild richness.

The two guilds from diadromous category (semi-anadromous and amphidromous) also exhibited distinct contributions. These guilds were similar concerning the low number of species, with only one semi-anadromous and two amphidromous species recorded in this study. Regarding the abundance-based approach, the semi-anadromous species was abundant in the upper and middle zones but not found in the lower zone, showing the affinity of tolerant species (particularly Rio anchovy *Anchoa januaria*) to highly unstable environments, mainly regarding salinity. The amphidromous species (Fat snook *Centropomus paralellus* and Common snook *C. undecimalis*) were less abundant and exclusive to the estuarine zone. Furthermore, all specimens sampled from this guild were small juveniles, apparently growing and migrating towards the ocean, as part of amphidromous species route (Riede, 2004; Fortes et al., 2014; Potter et al. 2015; Daros et al., 2016). The freshwater estuarine-opportunist was another exclusive guild found in the upper zone and the species from this guild are capable of opportunistically inhabit estuarine waters in moderate abundances (Potter et al. 2015), as supported by our results.

The second component from our third hypothesis was that salinity is the environmental driver of species and individual replacement. PERMANOVA results confirmed that salinity accounted for most differences in guilds abundances between bay zones. However, this analysis also showed the relation between transparency and guilds abundances, irrespectively of spatial differences. Therefore, water transparency is probably driving the variations among season and beaches (within each zone). As for our dbRDA results, salinity and transparency were responsible for most of guild incidence and abundance variations. They also, confirmed the estuarine use functional diversity gradient that occurred in Guanabara Bay marine-estuarine ecocline, with increasing functionality towards the estuarine zone, exhibiting further evidence that this gradient is driven by the strength of environmental variations (mainly salinity), a previously discussed inference.

These ordinations also corroborated the relation between environmental affinity and guild incidence and abundance, demonstrating that fish species and individuals (grouped in guilds) replacement along the bay zones are driven by water salinity and transparency. Thus, the highest number of exclusive species and species abundances in each guild were found, generally, in the system segment that gathers the most suitable habitat conditions. Even species tolerant to salinity variations are susceptible to the energy cost that osmoregulation requires and have an optimal salinity range to achieve higher growth rates (Boeuf and Payan, 2001; Tseng and Hwang, 2008). Again, using incidence and abundance to generate two dbRDA ordinations was an important approach to elucidate the relations between guilds and environmental variables. In the case of low abundances and frequent guilds, the incidence-based ordination was able to indicate each environmental affinity through their higher occurrence rates in a specific abiotic condition, e.g. marine straggler guild relations with marine waters (higher transparency and salinity). Conversely, the abundance-based analysis was able to detect each guild environmental affinity (mainly for abundant guilds) through higher abundances in a set of abiotic conditions, even for guilds sampled in all replicates (e.g. estuarine-marine).

In conclusion, our study was robust enough in elucidating four main outcomes: (1) species and individual replacements were the major components from pair-wise beta diversities between zones along an marine-estuarine ecocline; (2) abundance and incidence analyses explained distinct facets of the community beta diversity along Guanabara Bay waters; (3) each species (grouped in guilds) contributions to species and individual replacements were able to infer the environmental affinity of each guild and reveal the functional diversity gradient that increases towards the estuarine zone; (4) salinity was the major driver of fish assemblages, influencing the functional diversity over the environmental gradient and the guilds abundance and incidence differences between the bay zones. Furthermore, the main components from beta diversity between zones, TO and BVA, were lower between adjacent zones than those more separated zones. This pattern agrees with the smoothness of community variation (in response to a major environmental variable) along an ecocline system (van der Maarel, 1990; Attrill and Rundle, 2002). Abundance and incidence analyses can demonstrate different features of each functional guild or species. For communities with different species/guild characteristics regarding abundance and frequency, the concomitant use of these two types of analyses may be very useful to unveil underlying complementary patterns. Although some predictions can be made about the environmental affinity of species and its guilds, some particularities may be found depending on the features of each transitional system and each guild. From guild characteristics, we believe that fish life cycle and individuals size structure are the most determinant to access their environmental affinity. In addition, strong fluctuations in salinity can enhance fish functional diversity by enabling species and guilds with specific (exclusively marine or freshwater species) or broad (estuarine and diadromous ones) environmental preference (Elliott et al., 2007; Potter et al., 2015) to inhabit the mixing zone of estuaries and in different circumstances.

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Supplementary Material

Table S1: List of sampled species and their guilds, abundance by zone (upper, middle and lower) and total abundance. Estuarine use guilds codes: FW = Freshwater estuarine-opportunist; AM = Amphidromous; SA = Semi-anadromous; EF = Estuarine & freshwater; Estuarine & marine; MED = Marine estuarine-dependent; MEOP = Marine estuarine-opportunist; MS = Marine straggler.

Species	Guild	Zone			Total
		Upper	Middle	Lower	
Elops saurus	MED	171	5	8	184
Albula Vulpes	MS	8	52	129	189
Anchoa januaria	SA	6021	13478		19509
Anchoa lyolepis	MS	145	1422	1182	2749
Anchoa tricolor	MED	10	117	14	131
Cetengraulis edentulus	EM	1466	1718	1	3185
Brevoortia aurea	MED	2908	19		2927
Harengula clupeola	MEOP	12	747	14181	14940
Opisthonema oglinum	MEOP		1676	31	1707
Sardinella brasiliensis	MEOP	18	43	18535	18596
Genidens genidens	EM	2713	2		2715
Synodus foetens	MS			5	5
Opsanus beta	EM		1		1
Bathygobius soporator	MEOP		2		2
Ctenogobius boleosoma	EM	7	48		55
Gobionellus oceanicus	EF	20			20
Mugil curema	MED	21	103	179	303
Mugil liza	MED		14		14
Geophagus brasiliensis	FW	1			1
Oreochromis niloticus	FW	11			11
Dactyloscopus crossotus	MEOP			35	35
Atherinella brasiliensis	EM	6338	29381	8725	44444
Strongylura marina	MEOP	25	15	6	46
Strongylura timucu	MEOP			3	3
Hemiramphus brasiliensis	MS	15	105	3	123
Hyporhamphus unifasciatus	MS	8	1	2	11
Jenynsia multidentata	FW	13			13
Poecilia vivipara	FW	219			219
Caranx latus	MEOP	1	7	15	23
Chloroscombrus chrysurus	MED	28			28
Oligoplites saliens	MEOP	34	51	2	87
Oligoplites saurus	MEOP	135	340	13	488
Selene vomer	MS	2	4		6
Trachinotus carolinus	MS		81	207	288
Trachinotus falcatus	MS	3	54	26	83
Trachinotus goodei	MS		1	9	10
Trachurus lathami	MS			1	1
Sphyraena tome	MEOP		3		3
Citharichthys arenaceus	MEOP			1	1

Achirus lineatus	EM	11		1	12
Trinectes paulistanus	EM	2			2
Symphurus tesselatus	EM	3			3
Hippocampus reidi	MEOP		1		1
Microphis lineatus	EF		2		2
Syngnathus scovelli	EM		39	8	47
Fistularia petimba	MEOP			5	5
Dactylopterus volitans	MS		84	6	90
Centropomus parallelus	AM	121			121
Centropomus undecimalis	AM	11			11
Diapterus rhombeus	EM	7148	1213		8361
Eucinostomus argenteus	EM	327	3412	508	4247
Eucinostomus gula	EM	1	4	6	11
Kyphosus sp.	MS			1	1
Diplectrum radiale	MS		2		2
Pomatomus saltatrix	MEOP		12	2106	2118
Conodon nobilis	MS			1	1
Orthopristis ruber	MS	2	197	85	284
Polydactylus virginicus	MS			1	1
Chaetodipiterus faber	MEOP	38	10	3	51
Cynoscion acoupa	MED	26			26
Larimus breviceps	MEOP	4			4
Menticirrhus americanus	MEOP	18	12	7	37
Menticirrhus littoralis	MS	1		14	15
Micropogonias furnieri	MED	2266	55	1	2322
Pogonias cromis	MED	94	6	2	102
Stellifer sp.	MEOP			1	1
Umbrina coroides	MS			333	333
Archosargus rhomboidalis	MEOP	2	70		72
Diplodus argenteus	MS			332	332
Stephanolepis hispidus	MS	1	6	1	8
Sphoeroides greeleyi	EM	6	218	83	307
Sphoeroides testudineus	EM	2	21	29	52
Chilomycterus spinosus	MS		3		3
Total abundance		30437	54857	46847	132141
Number of species		47	47	46	73