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Simplified fish larval supply in coastal areas after a dam burst in Brazil

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ABSTRACT

Coastal and estuarine systems play an important role in the maintenance of marine biodiversity, providing nursery, feeding, developmental and reproductive areas for terrestrial and aquatic species. The Fundão dam collapse is considered one of the biggest environmental disasters in Brazil, causing great social, economic and ecological damage in the affected areas. In our study, we used beta diversity and its components as a tool to monitor the spatio-temporal variation of fish larvae in four marine areas adjacent to the Doce River. The results show that the four areas undergo different spatio-temporal dynamics, with the composition of fish larvae in the Doce being simplified in the last years after the dam burst, compared to the other adjacent marine areas. In addition, turbidity is an important factor that has caused the homogenization of the larval composition of the Doce, demonstrating that mud resuspension events can cause a decrease in diversity and also suggesting the toxicity of the mud composition. The change from negative to positive additive and colonizing components in recent years suggests a slight recovery of diversity in the Doce compared to other marine areas. Finally, we have shown that some species may be tolerant to the impact, but with probable behavioral, energetic and physiological costs, which justifies the constant monitoring of these areas.

1. Introduction

Coastal and estuarine ecosystems play significant roles in supporting marine biodiversity and providing multiple benefits to human society. These ecosystems serve as natural nurseries, feeding grounds, and migratory routes for various aquatic and terrestrial species (Elliot and Quintino, 2007; Kelleway et al., 2017). The complexity and dynamical nature of coastal and esturine habitats promote coexistence of specialized and generalist species, contributing to the maintenance of marine biodiversity worldwide (Barrilli et al., 2021). Despite their global importance, however, these ecosystems are facing severe degradation, primarily due to excessive human activities and resource overexploitations associated with inadequate governance (Wingard and Lorenz, 2014; Zou et al., 2020).

Poor governance of natural resource utilization led to the rupture of the Fundão tailings dam in 2015 — one of Brazil's largest environmental accident in history. This environmental disaster released an estimated quantity of 60 × 106 m^3 of waste from iron ore extractions, causing catastrophic environmental and socioeconomic damages (de Lucena, 2015). The waste flew into the Doce river and to the Atlantic Ocean (Marta-Almeida et al., 2016). Accumulations of the waste on continental shelves caused marked reductions in water and sediment quality, killing tons of fish and posing long-lasting deleterious impacts on the estuarine of the Doce river and surrounding coasts (Fernandes et al., 2016).

Among the concerns associated with impacts, community restructuring is the subject of study by many ecologists. In this context, the importance of environmental factors in the processes of larval supply (e.g. fish larvae) (Félix-Hackradt et al., 2013a) and post-settlement processes for the establishment of fish assemblages (Félix-Hackradt et al., 2013b) and the health of the environment is emphasized (Brown et al.,

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2004; Nickols et al., 2013). Therefore, quantitative monitoring is critical in assessing the impact of environmental disasters on biodiversity. Beta diversity, which measures the variation in species composition between locations, is often used in post-disaster biodiversity assessments. (Legendre 2019; Tatsumi et al., 2020). Previous research has detected significant alterations in species composition caused by human-induced heat stress, salinization, and resource limitation (Lunt and Smee, 2020; Whitfield, 2021). Assessments of such anthropogenic alterations and subsequent recovery of ecological communities are essential for ecosystem restoration and conservation in the face of global change (Heino et al., 2015).

Previous environmental assessments based on beta diversity have mostly used snapshot data at a single point in time. Recent analytical advances, however, have provided a way to analyze beta diversity over time. Specifically, the temporal beta diversity index (TBI) proposed by Legendre (2019) measures the difference in species composition between two time points at a given site. A partitioning method developed by Tatsumi et al. (2021a, 2022) quantifies the extinction-colonization dynamics and changes in species richness that underlie temporal decreases and increases in spatial beta diversity (i.e., biotic homogenization and heterogenization). These new methods allow inferences to be made about community assembly and disassembly processes, such as dispersal among habitats and local population growth. In assessing the impacts of environmental disasters, understanding these processes can provide deeper insights into changing biodiversity.

Here, we quantified fish assemblage beta diversity as a function of spatial and temporal variation in post-larval supply following the Fundão dam rupture. Using a spatially and temporally replicated monitoring dataset collected near the Doce River estuary and three other adjacent estuaries along the southeastern and northeastern Brazilian tropical coasts, we specifically aimed to: (1) reveal community structure and the existence of spatio-temporal dissimilarity in species composition; (2) characterize the different marine areas studied; and (3) evaluate beta-diversity components influencing community change over time. Based on our results, we discussed effective restoration and conservation of coastal and estuarine ecosystems in one of the world's biodiversity hotspots.

2. Material and methods

2.1. Study sites

We conducted this study on the Brazilian coast between the states of Bahia (14° 45′18.8″ S and 39°05′54.47″ W) and Espírito Santo (20°37′10.56″S and 40°22′8.39 W) (Fig. 1). Our study sites consisted of four marine areas adjacent to the Doce, Piraquê-Açu, São Mateus and Mucuri rivers. These rivers are characterized by multiple types of ecosystems such as mangroves, sandbanks, dunes and beaches. They are of great ecological and socioeconomic importance to local populations, providing subsistence services such as tourism and fishing do (Vale and Ross, 2011; Gomes et al., 2014; Lourdes et al., 2021). In our study, the area called Doce was directly affected by the dam collapse, while the areas of Mucuri, São Mateus and Piraquê-Açu were indirectly affected by a partial dispersion of the sediment plume. For this reason, they were used as control areas.

2.2. Fish monitoring data

We sampled fish in post-larval stages during the summers of 2018 to 2022 in the four marine sites using CARE light traps (ECOCEAN). At the new moon period each summer, the light traps were distributed at nine points in each site for two consecutive nights. The total sample size was thus $n = 180$ (5 years × 4 sites × 9 sampling points). After approximately 12 h of fishing per night, the fish samples from the light traps

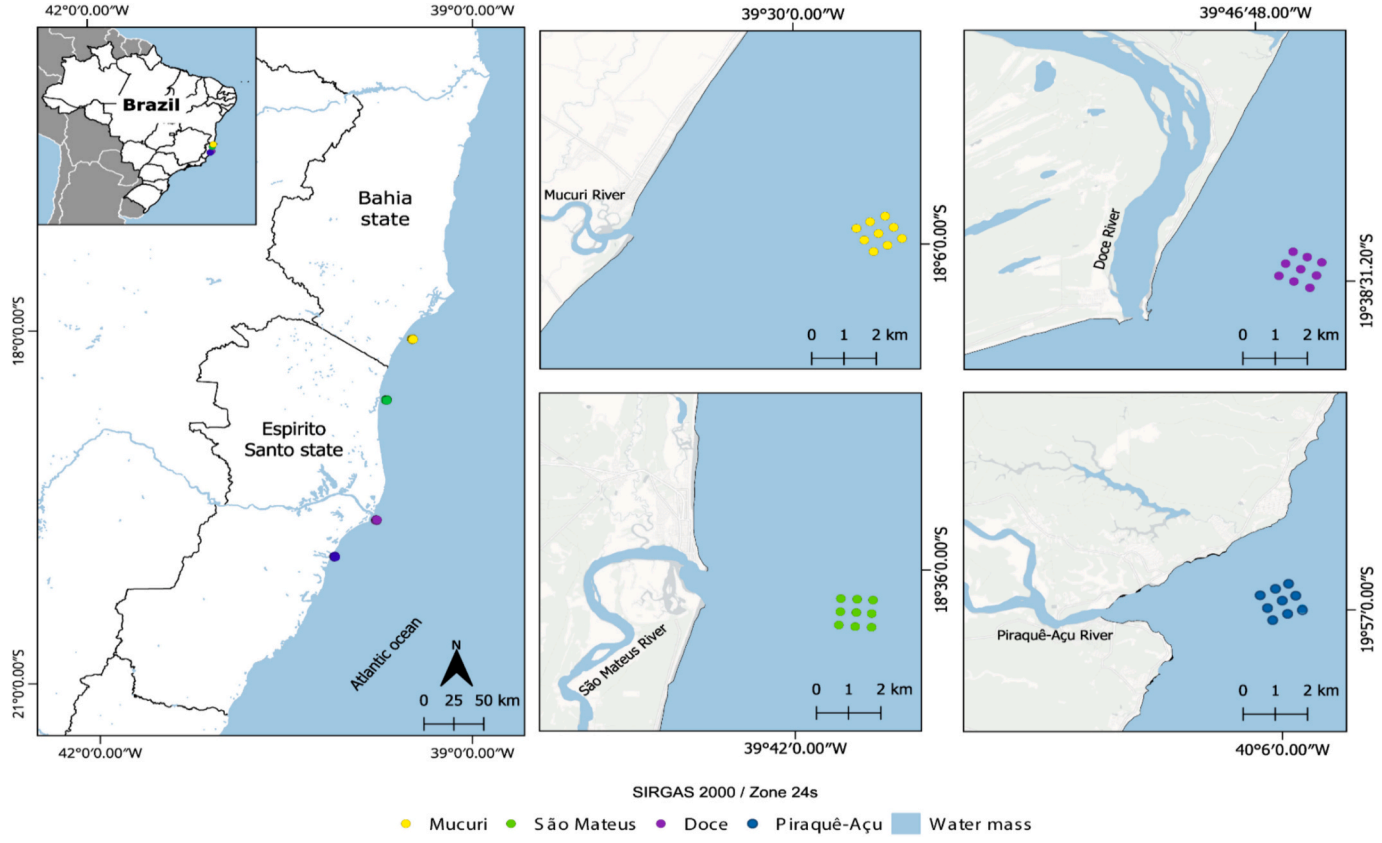

Fig. 1. Study area and the light traps layout in the marine área of the Mucuri (yellow dots), São Mateus (green dots), Doce (purple dots) and Piraquê - Açu (Blue dots) rivers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were collected and preserved in 70 % ethanol. In the laboratory, post-larval fish were identified based on available bibliography (Richards 2005; Bonecker et al. 2014). For each species, the number of fish individuals was used as a measure of abundance.

In sampling point, we measured physico-chemical variables, namely temperature, salinity, pH, dissolved oxygen, and turbidity, using a Horiba multi-parameter probe (Table A.1). We measured the water depth of each site using the vessel's sonar and the intensity of the current using a flow meter. Meteoceanographic variables, specifically wave height and wind intensity, were obtained through direct visualization or extracted from the portal of the Center for Weather Forecasting and Climate Studies (CPTEC: www.cptec.inpe.br) and Surfguru (www.surfguru.com.br).

2.3. Data analysis

We visualized the temporal changes in species composition using the Non-Metric Multidimensional Scaling (NMDS) using the Bray-Curtis index after transforming the abundance data based on the Hellinger transformation. Standardized environmental variables (*Z*-score) and species identities were correlated to the ordering dimensions using the envfit function from the vegan package. The vectors of continuous variables were adjusted for ordering. The two-way multivariate permutation analysis of variance (PERMANOVA; Anderson, 2001) and pairwise tests were performed between sampling years in each site to test the temporal changes in species composition.

To quantify the temporal changes in fish species composition, we calculated the Temporal Beta Diversity Indices (TBI, Legendre, 2019) in each site based on species incidence (Sørensen index) and abundances (Bray–Curtis index). This index measures dissimilarity in species composition between two time points at a given location (Legendre, 2019). The value ranges from 0, when communities at two time points are identical in species composition, to 1, when they do not share any species. This index can also be partitioned into components that represent the contributions of species gains and losses to total temporal dissimilarity, demonstrating which component contributes most to temporal beta diversity (Legendre, 2019).

In this study, we calculated the TBIs and its components between pairs of separate years: 2018 and 2019, 2019 and 2020, 2020 and 2021, and 2021 and 2022. We then associated the values with water depth, current intensity, physico-chemical variables, and meteoceanographic variables (Table A.1) between pairs of years. To achieve this, we calculated the variation in each environmental variable by subtracting its value in the most recent year from the preceding year (for example, 2019–2018). These data were standardized and transformed into non-negative values, as described by Lindholm et al. (2021). Then, we used beta regression to identify how the effect of environment variables contributed to local composition variation of post larval fishes within shallow marine ecosystems. Beta regression is the most appropriate analysis because it incorporates heteroskedasticity or skewness which are often observed in response variables taking values from 0 to 1 (Cribari-Neto and Zeleis 2010).

To quantify the temporal changes in spatial beta diversity, we employed a partitioning method developed by Tatsumi et al. (2021a, 2022). This method partitions temporal decreases and increases in beta diversity (i.e., biotic homogenization and heterogenization) into components that represent species extinctions and colonizations (for incidence data) or losses and gains in local species abundances (for abundance data) as well as species-level contributions to each component. In this study, we defined spatial beta diversity as the variation in species composition among sampling points within a site.

Species Abundance Distributions (SAD) were adjusted to analyze the fish larval supply structure over time in different locations, and subsequently evaluated and compared with the following theoretical models: Broken-Stick, Preemption, Lognormal, Zipf and Zipf-Mandelbrot (Magurran, 2004; McGill et al., 2007). The best fit was defined by estimating the maximum probability, which compares the models using the Akaike (AIC), Bayesian (BIC) and Deviance information criteria (model fit residuals), with the lowest values of the criteria indicate the best fitted ecological model.

We used the packages 'vegan' for NMDS, envfit and SAD analyses (Oksanen et al., 2022), 'adespatial' for temporal beta diversity index (Dray et al. 2022), and 'ecopart' for beta diversity partitioning (Tatsumi et al. 2022) in R v4.3.1 (R Core Team, 2023).

3. Results

From 2018 to 2022, a total of 6291 individuals distributed across 48 families and 126 species were identified (Table A.2). The Doce had the highest species richness, ranging from 13 to 30 species during the sampling period, totaling 83 species. In contrast, Mucuri (5 to 13 species) and Piraquê-Açu (8 to 18 species) had the lowest richness compared to the other environments in the study, with 43 species each. São Mateus ranged from 12 to 18 species, totaling 48 species sampled during the study period.

Spatio-temporal differences were observed in the species composition of the sample sites recorded by NMDS (Fig. 2) and confirmed by permanova analysis (Table 1). In addition, NMDS combined with envfit analysis (Fig. 2) showed significant contributions from the salinity, pH, turbidity, tidal variation and wave height to the environmental differences. Considering the internal variation in each site (Table A.3), except for São Mateus, the pairwise comparison between all years was significant. On the other hand, significant differences were found only between the pairs of years 2018–2019, 2018–2020 and 2018–2021. When analyzing the species composition between marine sites (Table A.4), only pairwise comparisons between Doce and São Mateus in 2019 and 2021, and Mucuri and Piraquê-Açu in 2021 and 2022 showed no significant differences.

The TBI showed consistently high values (above 0.80) in the Mucuri (Fig. 3a and e), Doce (Fig. 3c and g) and Piraquê-Açu (Fig – 3d and 3 h) sites throughout all periods due to fluctuations in gains and losses of both species incidence and abundance. However, in São Mateus (Fig. 3b and f), there was a significant decrease in beta diversity between 2020 and 2021, with resulting values of 0.48 ± 0.18 and 0.39 ± 0.16 for data based on species incidence and abundance, respectively. Nonetheless, a recovery trend was observed in the subsequent period (0.60 ± 0.15 and 0.70 ± 0.14).

The beta regression models (Table A.5) that best explained the TBI were those generated for the Doce site. Thus, based on the species incidence, turbidity (Estimate = 3.834; Z = 2.599; $p = 0.009$) was the predictor that best explained the temporal changes in species composition (Estimate = −5.474; Z = −2.138; $p = 0.033$). On the other hand, in addition to turbidity (Estimate = 3.254; Z = 2.295; $p = 0.021$), salinity (Estimate = 0.999; Z = 2.041; $p = 0.041$) and dissolved oxygen (Estimate = 2.890; Z = 2.986; $p = 0.002$) were the predictors associated with changes in TBI, based on species abundances (Estimate = −3.019; Z = −2.24; $p = 0.042$).

Regarding the temporal changes in spatial beta diversity and its components (Fig. 4), Piraquê-Açu showed the prevalence of positive additive (Fig. 4d) and colonizing (Fig. 4h) components in all periods. Mucuri (Fig. 4a and e) and São Mateus (Fig. 4b and f) showed positive additive and colonization components in all years, except for the period 2019–2020. For Doce, there was a predominant shift from negative to positive additive (Fig. 4c) and colonization (Fig. 4g) components between the 2018–2020 and 2020–2022 periods, respectively.

Based on the incidence (Fig. A.1), species-level impacts on beta diversity om the Doce site showed that the negative colonization component had the largest contributions from the taxa *Ulaema lefroyi*, Clupeidae spp., *Anchoa* sp., *Anchoviella* and *Abudefduf saxatilis*, in the period 2018–2019, *Symphurus plagusia*, *Ancanthostracion* sp., Clupeidae spp., *Gymnthorax* sp. and Engraulidae spp., in 2019–2020. In the following period (2020−2021), the taxa *Acanthostracion* sp., Clupeidae

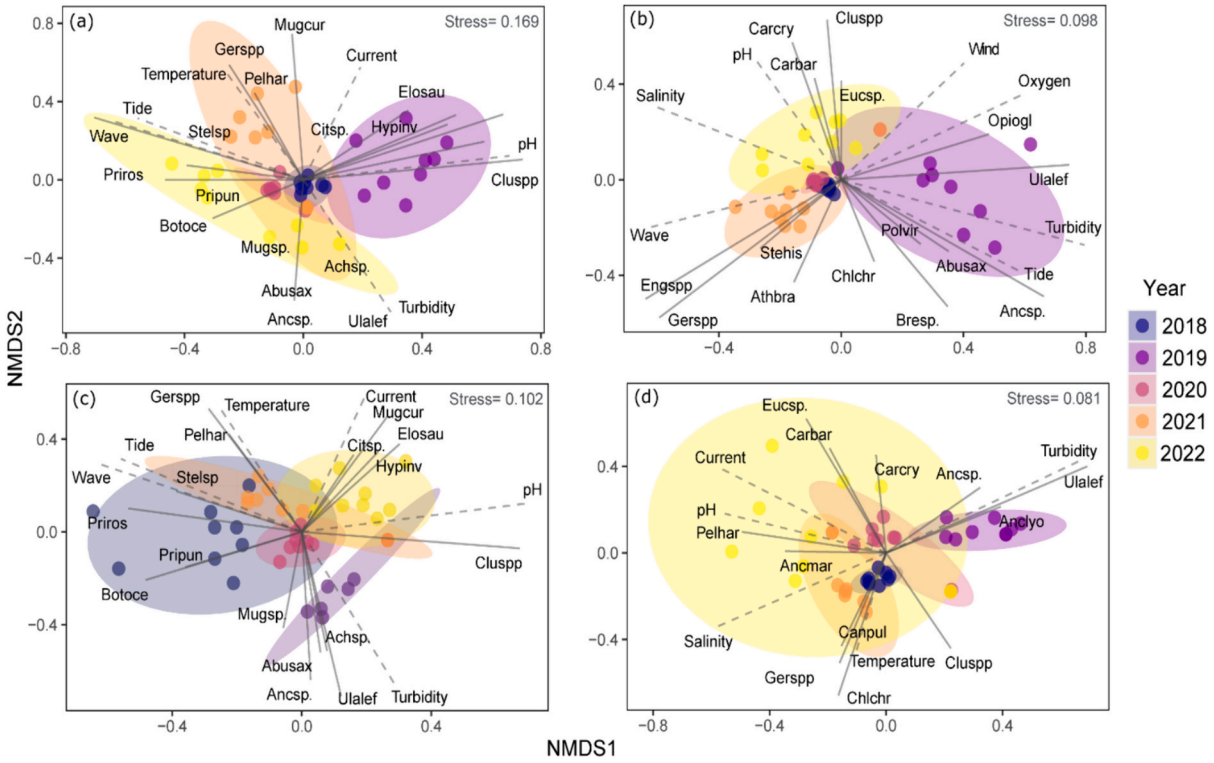

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of the composition and abundance of fish post-larvae species based on the Bray-Curtis similarity matrix, with significant correlations of environmental variables (dotted line) and species (solid line) (envfit, $p < 0.01$). Legends: Marine areas – Mucuri (a), São Mateus (b), Doce (c) and Piraquê-Açu. Species codes: Abusax = *Abudefduf saxatilis*, Anclyo = *Anchoa lyoleps*, Ancmar = *Anchoa marinii*, Ancsp = *Anchoa* sp., Achsp = *Anchoviella* sp., Athbra = *Atherinella brasiliensis*, Botoce = *Bothus ocellatus*, Bresp = *Brevoortia* sp., Canpul = *Cantherhines pullus*, Carbar = *Caranx bartholomaei*, Chlcry = *Chloroscombrus chysurus*, Cluspp = Clupeidae spp., Citsp. = *Citharichthys* sp., Elosau = *Elops saurus*, Engspp = Engraulidae spp., Eucsp = *Eucinostomus* sp., Gerspp = Gerreidae spp., Hypinv = *Hypsoblennius invemar*, Mugcur = *Mugil curema*, Mugisp = *Mugil* sp., Opogl = *Opisthonema oglinum*, Pelhar = *Pellona harroweri*, Polvir = *Polydactilus virginicus*, Priros = *Prionotus roseus*, Pripun = *Prionotus punctatus*, Stehis = *Stephanolepis hispida*, Stelsp = *Stellifer* sp., Ulalef = *Ulaema lefroyi*. The length of the arrow proportional to the correlation obtained. In the graphs, only the variables that exhibited significant correlation ($P < 0.01$) were presented.

Table 1
Results of the analysis of fish post-larvae species composition using Permutational Analysis of Variance (PERMANOVA) in the marine areas of Mucuri, São Mateus, Doce, and Piraquê-Açu rivers from 2018 to 2022.

Source	df	SS	Pseudo-F	P(perm)
Time	4	1.34E+05	22.840	0.001
Areas	3	5.16E+04	11.754	0.001
Time x Areas	12	1.10E+05	6.265	0.001
Residual	160	2.34E+05		
Total	179	5.30E+05		

spp., *Gymnothorax* sp. and *S. plagusia* contributed positively to the extinction component, while Labrisomus nuchpinnis contributed positively to the colonization component. In 2021–2022, the taxa Engraulidae spp., Gerreidae spp., *Chloroscombrus chrysurus*, *Pellona harroweri* stood out in the positive contribution to the extinction component.

For the Mucuri site, the greatest highlights for the positive extinction component were observed by the taxa Clupeidae spp. Gerreidae spp. and *Lycengraulis grossidens* (2018–2019); *Anchoa* sp. and *Atherinella* sp. (2019–2020); *Astropogon puncticulatus*, Clupeidae spp. and Engraulidae spp. (2020–2021). Colonization components showed larger positive contributions from the species *Anchoa lyolepis* and *Lagocephalus lagocephalus* (2018–2019); *Halichoeres poeyi*, *Hyppocampus reide* and *Lutjanus jocu* (2019–2020); *Membras dissimilis* (2020–2021); *Archosargus probatocephalus*, *Caranx crysos*, *L. nuchpinnis*, *Lutjanus analis* and *Megalops atlanticus* (2021−2022) and negatively by Gerreidae spp. (2020–2021).

The colonization component in the São Mateus site had a positive contribution from the species *Lutjanus* sp., *Pomacanthus* sp. and *Cosmocampus elucens* (2018–2019); *Pellona harroweri* and *Stellifer* sp. (2020–2021); *Diapterus rhombeus*, *Lutjanus* sp., *Sardinella aurita* and *Synodus foetens* (2021–2022); and a negative contribution from the taxa Clupeidae spp. On the other hand, *Chromis flavicauda* and *Scomberomorus regalis* (2019–2020); and *Caranx bartholomaei* and *Hypleurochilus* sp. (2020–2021) contributed negatively to the extinction component, while Engraulidae spp. and Gerreidae spp. (2018–2019, 2021–2022); and Clupeidae (2020–2021) contributed positively to this component.

The Piraquê-Açu site showed greater positive contributions to the colonization component by the species *A. saxatilis*, *Halichoeres poeyi*, and *Ocyurus chrysurus* (2018–2019); *Halichoeres poeyi*, and *Ocyurus chrysurus* (2018–2019); *Astropogon puncticulatus*, *Caranx hippos*, *Hyppocampus reide*, and *Lutjanus* sp. (2019–2020); *Lutjanus alexandrei* and *C. elucens* (2020–2021); and *Caranx bartholomaei* and *H. poey* (2021–2022). The species *C. chrysurus* and *Stephanolepis hispidus* (2018–2019); *Ulaema lefroyi* (2019–2020), *C. crysos*, Clupeidae spp. and *Stellifer* sp. (2020–2021); and *Cantherhines pullus*, *C. chrysurus* and Engraulidae spp. contributed positively to the extinction component.

The species-level impacts on changes in beta diversity based on abundances (Fig. A.2) indicates that the additive component was negatively influenced by the species Anchoa sp., Anchoviella sp. and *U. lefroyi* (2018–2019); *Acanthostracion* sp. and *Symphurus plagusia* (2019–2020); and positively by the taxa *Citharichtys* sp. and Scianidae spp. (2020–2021) and *Ahlia eggmontis*, *Atherinella brasiliensis*, *Bothus* sp. and *Halichoeres* sp. (2021–2022), in the Doce site. As for the subtractive component, the main positive contributions came from the species *Prionotus punctatus* (2018–2019), *Acanthostracion* sp., Clupeidae spp. and *Symphurus plagusia* (2020–2021); and Engraulidae spp. and Gerreidae spp. (2021–2022).

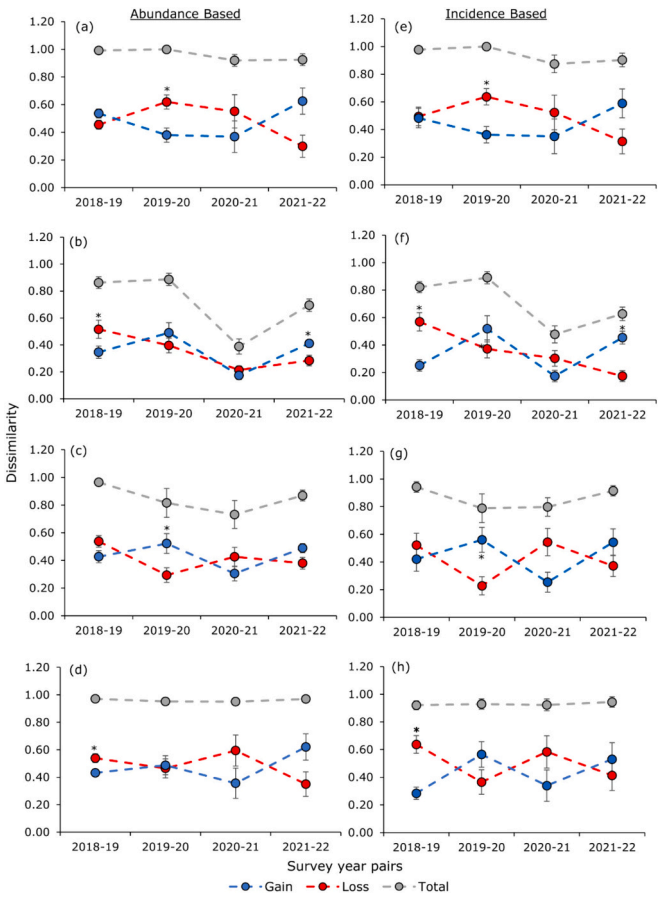

Fig. 3. Temporal beta diversity (Total) and its gain (Gain) and loss (Loss) components, based on the incidences (a - d) and abundances (e - h) of the species sampled in the Mucuri ("a" and "e"), São Mateus ("b" and "f"), Doce ("c" and "g") and Piraquê-Açu ("d" and "h") marine areas. Asterisk indicates significant difference between gain and loss components. (one-sample *t*-test; $p < 0.05$).

In the Mucuri site, the main species that positively contributed to the additive component were *A. lyolepis*, *C. chrysurus*, *Sarda sarda* and *Stellifer* sp. (2018–2019); *C. chrysurus*, Gerreidae spp. and *M. dissimilis* (2020–2021); *Anchoa marinii*, *A. brasiliensis*, *C. crysos* and *M. atlanticus* (2021–2022), while Clupeidae spp. and Engraulidae spp. negatively contributed to this component in 2019–2020. On the other hand, the subtractive component showed positive contributions from the taxa Clupeidae spp. (2018–2019), Clupeidae and Engraulidae (2020–2021), and Gerreidae spp. (2021–2022).

In the São Mateus site, the additive component was represented positively by the species *Anchoa* sp., *Brevoortia* sp. and *Opisthonema oglinum* (2018–2019); *A. brasiliensis* and *P. harroweri* (2020–2021); and *C. crysos*, *D. rhombeus* and *Sardinella aurita* (2021–2022). The taxa Clupeidae spp., Engraulidae spp. and Gerreidae spp. contributed negatively to additive component in 2019–2020. As for the subtractive component, the taxa Clupeidae, Gerreidae spp. (2018–2019, 2020–2021 and 2021–2022), and Engraulidae spp. (2021–2022) contributed positively to this component.

Finally, the Piraquê-Açu site showed positive contributions to the additive component from the taxa *A. saxatilis*, *H. poeyi* and *S. hispidus* (2018–2019); *Albula vulpes*, *Dacapterus macarellus* and Engraulidae spp. (2019–2020); Gerreidae (2020–2021); *Anchoa tricolor*, Engraulidae spp. and *H. poeyi* (2021–2022). The taxas Gerreidae (2018–2019); *U. lefroyi* (2019–2020); *C. crysos*, *Cluepeidae* spp. and *S. hispidus* (2020–2021); *C. pullus* and *C. chrysurus* (2021–2022) contributed positively to the subtractive component.

Based on AIC, the models with the best explanatory power for species distribution in marine sites varied between Zipf – Mandelbrot, preemption, and null (Fig. 5). Mucuri alternated between the Zipf (Muc 2018 and 2020) and null (Muc 2019,2021 and 2022) models during the sampling years. Doce remained under the Zipf model for the first four years (2018–2021), switching to the null model in the last year (2022). Meanwhile, São Mateus switched between the Preemption (SM 2018, 2020), Zipf (SM 2019) and Mandelbroat (SM 2021 and 2022) models. Finally, Piraque-Açu exhibited the Mandelbroat (PA 2018 and 2020), Zipf (PA 2019 and 2021) models for the first four years, switching to the preemption model (PA 2022) in the last year.

4. Discussion

The fish larval supply in each site seem to have different spatio-temporal dynamics, as shown by the NMDS ordination analysis. In this context, the Doce marine site showed a high dispersion of samples in the first year, while all three other areas showed a lower dispersion, but increased in the following years. These patterns can be explained by the intrinsic characteristics of each estuary, which are related to different factors such as complex hydrodynamics, habitat quality and heterogeneity, and anthropogenic impacts specific to each estuary (Elliot and Whitfield, 2011; Queirós et al., 2016; Monteiro et al., 2021; Barrilli et al., 2024).

The TBIs showed similar patterns for Doce, Mucuri and Piraquê-Açu, where the high values occurred due to oscillations between the gain and loss components between periods. Although this result was also recorded for São Mateus in 2018–2021, the sharp decrease of TBI in 2020–2021 suggests a homogenization of the composition of the fish larval supply during this period, followed by a recovery in the following years. However, beta-diversity relationships with environmental variables were only significant in the Doce, where TBI showed an inverse relationship with turbidity and a direct relationship with salinity. Species associated with estuarine zones have different tolerance limits to variables such as salinity, turbidity, and temperature (Hoeksema et al. 2006; Whitfield, 2021), which may explain the differentiation of composition in the area over time. In addition, turbidity can be beneficial in the early life stages of fishes by reducing the visual acuity of predators, but when caused by anthropogenic activities, it can cause high fish mortality and negatively alter trophic interactions, homogenizing the environment (Lunt and Smee, 2020; Whitfield, 2021).

Biotic homogenization and biotic differentiation represent decreases and increases in spatial beta diversity, respectively, which are responses to complex processes of population dynamics and can generally be associated with local colonization and extinction events (Socolar et al., 2016; Rosenblad and Sax, 2017; Tatsumi et al., 2020, 2021a). In this context, the positive additive components observed almost consistently in the Mucuri, São Mateus, and Piraquê-açu may indicate that species adapted to specific locations within each estuary have increased their population sizes, which may reflect relatively stable (less disturbed) environments. In other words, within each of the three sites, local species have become more diverse in composition, probably as a result of deterministic clustering processes (species adapted to the local environment becoming more abundant) rather than dispersal processes (internal dispersal between sites within each area), which would reduce beta diversity (Catano et al. 2017, Tatsumi et al., 2020, 2021a). However, it is also possible to observe the predominance of positive colonization components in these areas, suggesting that beta diversity was driven by external dispersal (colonization of species that did not occur in a given area).

In the Doce marine site, there was a shift from negative to positive additive components (Fig. 4a). This could indicate that during the first years of the study (2018–2020), the local site composition became more homogeneous, possibly due to internal dispersal. In other words, species that managed to survive (escape) the dam collapse at some sites (refugia) were redistributed to other sites within the area itself, resulting

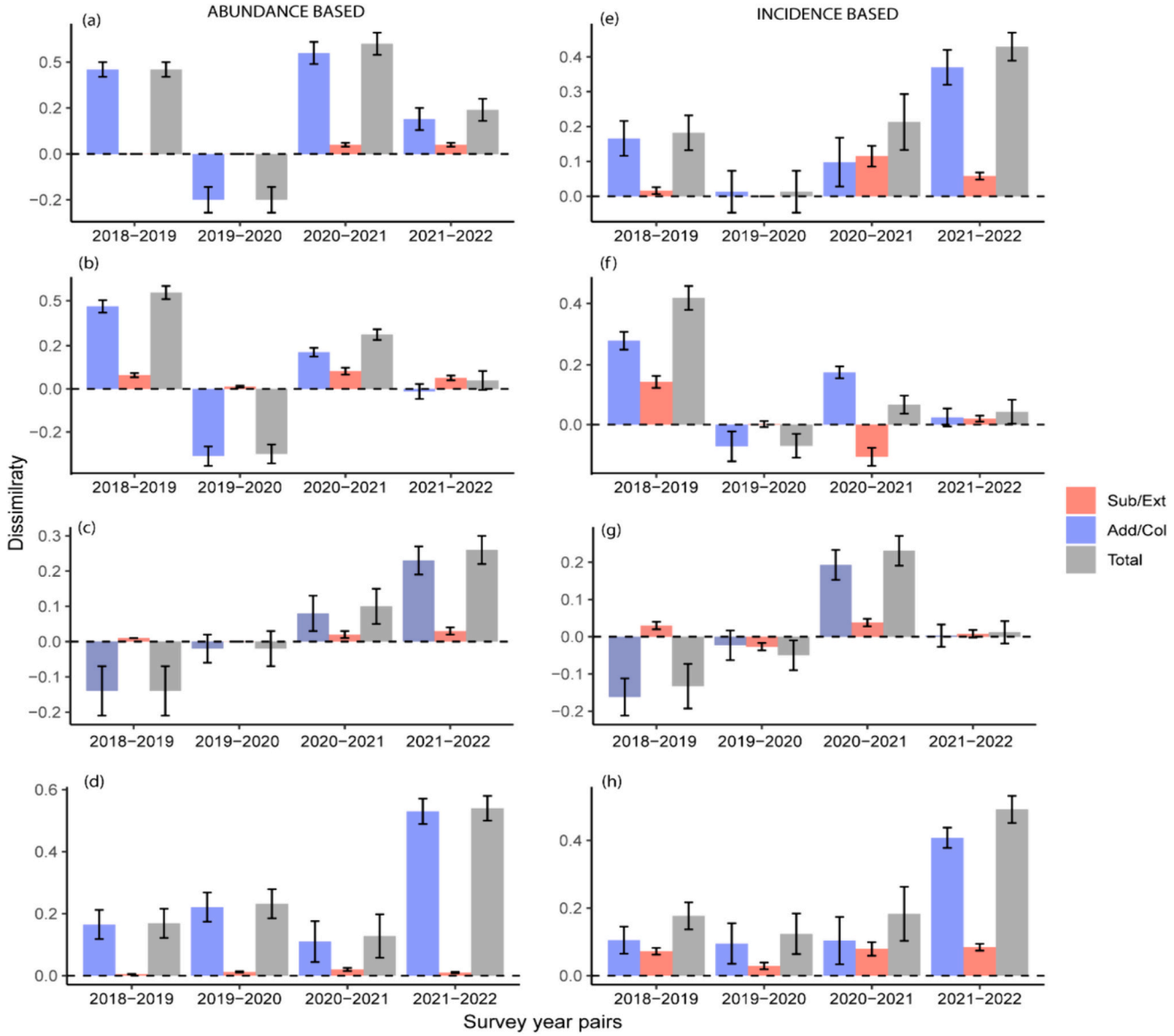

Fig. 4. Temporal change in beta diversity and its components in the marine areas of Mucuri River ("a" and "e"), São Mateus ("b" and "f"), Doce ("c" and "g") and Piraquê-açu ("d" and "h") from 2018 to 2022, based on species abundances ("a" - "d") and incidences ("e" - "h"). Incidence data is represented by the temporal change in beta diversity ("Total" - gray bar) and its components of extinction (red bar) and colonization (blue bar). Abundance data is represented by the temporal change in beta diversity ("Total" - gray bar) and its subtractive (red bar) and additive (blue bar) components. Bars represent means with standard errors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in homogenization. The relationship between increased dispersal leading to community homogenization has already been consistently addressed in several studies (Grainger and Gilbert, 2016; Catano et al., 2017; Tatsumi et al., 2020, 2021a). After the redistribution phase, the communities shifted towards positive additive components (Fig. 4a), possibly for the same reason as in the other sites, such as an increase in the size of the populations of species adapted to each site. In 2020–2021, the incidence-based index was largely positive. This could mean that there were colonizations of species that were not present in the DOCE site before 2020. Each of the new species may have sporadically colonized a few sites within this area, thus increasing the incidence-based beta diversity. By 2021–2022, the abundance-based index was positive, while the incidence-based index was close to zero. These patterns indicate increasing population sizes of the adapted species at this site (Tatsumi et al., 2022).

Considering the species contribution to the changes in beta diversity, a general pattern of homogenization was observed, with an increase in the occurrence and abundance of the families Clupeidae, Engraulidae and Gerreidae for all marine areas. Species in these families have high reproductive potential, wide distribution and tolerance to a range of environmental conditions (de Paiva et al., 2009). However, the main taxa influencing the change in beta-diversity of the Doce contributed more to homogenization than to environmental differentiation, suggesting that the species are highly adapted to local conditions and thus dominate this environment. On the other hand, when these dominant species decrease their occurrence and abundance, they positively favor beta diversity due to niche vacancy, making the composition more heterogeneous (Lu et al. 2019).

Although similar groups negatively influenced the change in temporal beta diversity, the species L. *nuchipinnis* contributed to the heterogeneous colonization in the four areas. The species L. *nuchipinnis* is very common and abundant along the Brazilian coast, with larvae that behave pelagically (Gibran et al., 2004), which may explain its presence as a colonizer in different types of environments. On the other hand,

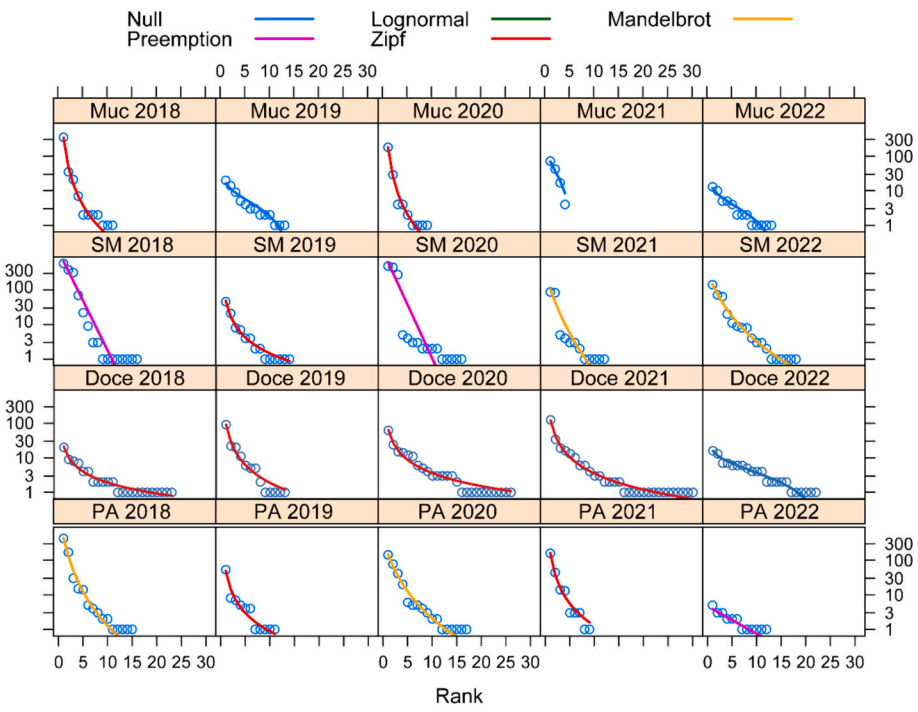

Fig. 5. Abundance distribution models of the species sampled from 2018 to 2022 in the Mucuri (Muc), São Mateus (SM), Doce and Piraquê-Açu (PA) marine areas. Values for the Akaike criteria are shown in the supplementary material (Table A.6).

with the exception of Doce, the species *Lutjanus* sp. and *Halichoeres poeyi* were commonly observed in the other areas, acting as heterogeneous colonizers. These species are associated with environments of greater environmental complexity, using reef areas for feeding and refuge, but also estuarine zones for reproduction and development (Wells et al., 2008; Nunes et al., 2013).

The species *A. lyolepis*, *M. dissimilis*, *A. probatocephalus*, *C. crysos* and *M. atlanticus* had a fundamental role in the heterogeneous colonization of the Mucuri marine area, while *Pomacanthus* sp., *C. elucens*, *Pellona harroweri* and *Stellifer* sp. contributed to this component in the São Mateus. In addition, the species *Acantrostracion* sp., *C. bartholomaei*, *C. hippos* and *H.reide* were differentially colonized in Piraquê-açu. In general, the main species that contributed to the colonization of these areas have a preference for brackish, oxygenated waters with high hydrodynamics (Wade et al., 1962; Nelson et al., 2016).

The Zipf and Null species distribution models recorded for the Doce and Mucuri marine areas showed that specialized late-successional species have already colonized these areas and are in the early stages of maturity (Gray, 1987; Tatsumi et al., 2020, 2021b). In this type of distribution, late colonization species have the greatest need for a specialized niche and are therefore rarer than early colonization species, preferring more stable environments (Favero et al., 2015). On the other hand, São Mateus and Piraquê-Açu, although also regularly followed late successional models (Zipf-Mandelbroat), exhibited the preemption model in at least one of the periods. This type of distribution is often found in the early stages and is generally associated with less stable, simplified or frequently disturbed environments, as has been recorded for different taxa, including fungi (Tatsumi et al., 2021b), plants (Fávero et al., 2015) and some groups of invertebrates (Caruso and Migliorini, 2006).

Our results suggest that, for the time being, fish communities are well adapted to the environmental stresses that occur in the study area. However, it is important to highlight that the results also showed a negative interaction between turbidity and species composition in the Doce, suggesting that mud resuspension events may affect the diversity of the larval fish supply. Studies have documented the impacts of the mud from Fundão tailings dam failure on the aquatic biota, such as plankton, tadpoles, shrimps and fish communities (Bonecker et al., 2019; Girotto et al., 2020; Marques et al., 2022; Maraschi et al., 2022; Condini et al., 2022; De Biasi et al., 2023). In general, some estuarine species are well adapted to dealing with environmental stresses and some fish are considered to be resilient to this variability (Whitfield, 2021). This ability to absorb stress without apparent adverse effects has been previously discussed by Elliott and Quintino (2007), who termed it 'environmental homeostasis'. As such, species in these locations are able to capitalize on these conditions for their own benefit, but at an energetic and physiological cost that can be damaging in the long term (Elliott and Quintino, 2007; Whitfield, 2021). In this context, a study conducted in the same area by Bonecker et al. (2019), recorded fish larvae with damaged digestive tracts as a result of bioaccumulation resulting from exposure to contaminants from the Doce mud plume. This result suggests that the permanence of species in areas under the influence of the mud plume can have negative effects on organisms.

Despite the limitations raised about the efficiency of light traps as a sampling method for some fish species (Sponaugle and Cowen, 1996; Lecaillon, 2004; Lecaillon and Lourie, 2007), it is important to note that our study showed a high representation of the same families (e.g. Carangidae, Clupeidae, Engraulidae, Gerreidae, Labridae, Labrisomidae) that were captured by the bongo net and neustonic net methods, as demonstrated by a previous study carried out in the same region (Bonecker et al., 2019), but with a higher number of species. Furthermore, although the efficiency of light traps can be influenced by environmental variables such as turbidity (Lindquist and Shaw, 2005), it is important to note that turbidity is a condition established in the Doce River after the dam breach, making it a relevant and representative environmental characteristic of the context in which the study was carried out, and that even so, the Doce still has the most representative composition in the study region.

5. Conclusion

The positive contribution of beta diversity recorded in recent years indicates that the species composition has become more unique over time, suggesting a certain resilience of fish species to the impacts

occurring there. In addition, mud resuspension events, especially in Doce, promote the homogenization of species composition, simplifying fish larval supply. However, studies aimed at understanding the adaptive potential of species in the face of anthropogenic impacts are extremely important for the assessment of environmental quality and resident stocks, thus improving the contribution of ecosystem services in these areas. Furthermore, we highlight the importance of constant monitoring of areas, especially in mud resuspension events that can simplify communities in areas affected by the dam collapse.

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CRediT authorship contribution statement

Germano Henrique Costa Barrilli: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Shinichi Tatsumi:** Writing – review & editing, Visualization, Software. **Juliana Beltramin De Biasi:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation. **Ana Rosângela Santos Cruz:** Data curation. **Thais Christina Torres de Oliveira:** Data curation. **Mauricio Hostim-Silva:** Resources, Project administration. **Carlos Werner Hackradt:** Writing – review & editing, Supervision, Investigation. **Fabiana Cézar Félix-Hackradt:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation.

Declaration of competing interest

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

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Data availability

I have shared de data information in supplementary material.

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Appendix A. Supplementary data

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