



Beta diversity of demersal fish and implications for conservation in a subtropical environment

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ABSTRACT. The present study aimed to evaluate the variation in the composition and diversity of the fish assemblages (beta diversity) along the east-west axis of the Paranaguá Estuarine Complex and the Adjacent Continental Shelf. To this end, seasonal collections were carried out between 2014 and 2016 at 12 sampling sites, totaling 144 collections. These sites were distributed in 4 sectors (External, Lower, Middle, and Upper) on an axis from the continental shelf to the interior of the estuary. Beta diversity (β SOR), calculated by the Sørensen index, was divided into the components turnover (β SIM) and nestedness (β SNE) and evaluated the contributions of each to the total heterogeneity. β ratio, the ratio of β SNE to β SOR, was estimated to identify the components with the greatest contribution to the total beta diversity. To corroborate the results, nestedness estimates were made using the NODF (Nestedness metric based on Overlap and Decreasing Filling), compared to the null model. For the Upper, Lower, and External sectors, β ratio values were lower than 0.5, indicating that the turnover was predominant for variations in total beta diversity, as expected for these environments. Unlike the other sectors, in the Middle sector, β ratio values were greater than 0.5, indicating that nestedness was predominant for variations in total beta diversity, which may reflect possible natural or human stressors since innumerable disturbances have already been detected in this environment.

Keywords: turnover; nestedness; fish assemblage; Paranaguá estuarine complex.

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Introduction

Human activities have grown in recent decades and impacted coastal and oceanic ecosystems, especially marine pollution, causing disturbances in these environments and altering the habitats and the structure of biological assemblages (Kennish, 2002; Lotze et al., 2006). The increase in port activities, as well as their maintenance through dredging, alters the geomorphology, hydrography, and physiography of estuarine regions, changing the dynamics of fish fauna and causing a rapid decline in biodiversity (Cardinale et al., 2012; Cattani & Lamour, 2016). In this way, the joint action of natural and anthropic factors can control the abundance, behavior, and habitat selection of estuarine organisms, and from there, it is necessary to have a thorough analysis of the impacts caused by human action on these ecosystems.

Estuaries are ecologically important areas, used by fish as nursery areas, overwintering areas, migration routes, feeding grounds, and refuge areas (Elliott & Hemingway, 2002; Barletta & Blaber, 2007; Franco et al., 2008). Therefore, knowing and measuring the diversity of organisms allows us to understand the processes that govern the functioning of these ecosystems (Loreau, 2010).

Beta diversity (β) can be defined as the variation in species composition between sites, making it possible to infer ecological and ecosystem patterns (Legendre et al., 2005; Barros et al., 2014). Anderson et al. (2011) expanded the concept of diversity and defined beta diversity as any variation in species composition, thus it can be partitioned into two essential components: turnover and variation (nestedness). Turnover is defined as a change in the structure of a given community between its sampling units, always in response to a certain gradient, which may be temporal, spatial, or environmental. The variation component is defined as changes in the community structure within a set of sampling units without the influence of a certain gradient, given a spatial or temporal extension (Anderson et al., 2011). On the other hand, Ulrich and Gotelli (2007a) defined

variation as the situation in which the species of a sampling unit represent a subset of a sampling unit with higher species richness.

Thus, turnover and variation can explain distinctions between communities, since the processes responsible for these differences are only the replacement of species and/or the gain or loss of species (Baselga, 2010). The partitioning of β diversity into its components replacement (turnover) and nestedness, and the linking of these patterns to metacommunity factors, can provide important insights into the organization of biodiversity on spatial scales (Gianuca et al., 2017). The alignment of the results of beta diversity with the knowledge of ecosystems allows us to infer and recognize the fundamental ecological processes in the understanding of spatial, environmental, or temporal changes and their influence on fish assemblages (Baselga, 2013).

The objective of this study was to understand the patterns of beta diversity in demersal fish assemblages over time and space. This analysis considered spatio-temporal variations across three sampling years (2014 to 2016) and a spatial gradient that includes the Paranaguá Estuarine Complex (PEC) and the adjacent continental shelf at a bathymetric depth of 20 meters. Additionally, the study examined the turnover and nestedness components of beta diversity.

Material and methods

Study area

The coast of the state of Paraná, southern Brazil, has an important estuarine system, the PEC, on the northern coast of the state. It is a system with an area of 612 km², composed of four main bodies of water, the bays of Antonina, Paranaguá, Laranjeiras, and Pinheiros (Lana et al., 2001) (Figure 1).

The PEC is divided into two main axes, the East-West axis, with approximately 56 km in length, and the North-South axis, with approximately 30 km in length. This region is inhabited by many fishermen, who have fishing as the basis of their livelihood (Mendonça et al., 2017). Thus, the PEC has great economic importance in the fishing, industrial, and tourism sectors, associated with the intense activities of two ports located in the complex: the port of Paranaguá, the second largest grain port in Latin America, and the port of Antonina (Andriguetto Filho et al., 1998).

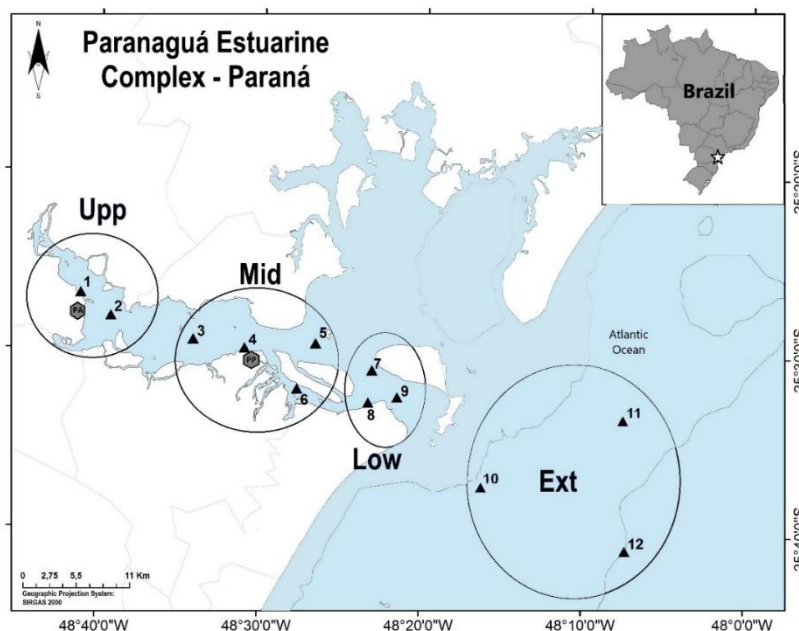


Figure 1. Location of the 12 sampling sites in the Paranaguá Estuarine Complex and on the adjacent continental shelf in the state of Paraná. The ports of Antonina (PA) and Paranaguá (PP) and the four (4) separate sectors of the East-West axis are highlighted: External (Ext), Lower (Low), Middle (Mid), and Upper (Upp) sectors.

The focus of the present study is the East-West axis of the PEC, which includes the waterway channel that leads the ships to the berths of the ports of Paranaguá and Antonina. This axis is more than 50 km in length and 7 km maximum width, besides encompassing the bays of Antonina and Paranaguá.

Data collection

Collections were carried out quarterly at 12 sampling sites between 2014 and 2016, totaling 144 collections, distributed in 4 sectors (External, Lower, Middle, and Upper) (Figure 1). The first nine sites are along the East-West axis of the Paranaguá Estuarine Complex (PEC) and the last three are in the open sea area (20 m bathymetry). For sampling, two simultaneous double tows were performed with a trawling vessel using an otter trawl; the mouth was 10 m wide in the lead and float line, with a mesh size of 3 cm in the top and bottom panel, and a mesh size of 2 cm in the cod end.

Data analysis

All individuals were identified to the lowest possible taxonomic level, according to specialized literature (Barletta & Corrêa, 1992; Figueiredo, 1978; Figueiredo & Menezes, 1978, 1980a, 1980b, 2000). Data were analyzed using the general dissimilarity estimates between multiple samplings, with the calculation of total beta diversity through the Sørensen index (β SOR), and its partitioning into two components: turnover (β SIM), through the Simpson index, and resulting nestedness (β SNE), by subtracting the turnover from the total beta diversity (β SNE = β SOR - β SIM) (Baselga, 2010). Such estimates, which use indices of comparison between multiple samplings, prevent the loss of information shared between three or more samplings, as well as the dependence on pairwise similarities (Diserud & Ødegaard, 2007).

For the comparison of dissimilarity between sectors with a different number of sampling sites (Baselga, 2010) (Upper: 24 sites; Middle: 48 sites; Lower: 36 sites; External: 36 sites), we utilized resampling techniques. This involved taking 100 random samples from a total of 23 sites, resulting in calculated mean dissimilarity values for β SOR, β SIM, and β SNE. The proportion of the contribution of the resulting nestedness (β ratio) to total dissimilarity (β SOR) was calculated according to Si et al. (2015), which presents the ratio: β ratio = β SNE/ β SOR. Values for β ratio < 0.5 indicate that turnover is the dominant component for total beta diversity, while values for β ratio > 0.5 indicate that nestedness is the dominant component (Dobrovolski et al., 2012).

These analyses were performed in the computer environment R (R Core Team, 2019), using the `beta.multi` and `beta.samp` functions of the `betapart` package (Baselga et al., 2013). Boxplots for each sector were built with the 100 values obtained at random from the three dissimilarity indices between multiple sampling (β SOR, β SIM, and β SNE), as previously described. An ANOVA was applied, followed by Fisher's post-hoc test to identify differences in the dissimilarity measures (β SOR, β SIM, and β SNE) within each sector. Such analyses were performed using the `boxplot` function of the `graphics` package (R Core Team, 2019), the `AoV` function of the `stats` package (R Core Team, 2019), and the `PostHocTest` function of the `DescTools` package (Signorell et al., 2020). All assumptions were checked and met (Normality, Independence, and Homoscedasticity).

In addition, dissimilarity values estimated by the nestedness component were calculated using the NODF (nestedness based on the overlap and decreasing fill) metric (Almeida-Neto et al., 2008). The NODF results avoid overestimation of the nestedness pattern (type I error), as well as the independent contributions of the rows (NODFr) and columns (NODFc) (Almeida-Neto et al., 2008; Matthews et al., 2015). Such analyses were performed by the NODF program, version 2.0, which generated 1,000 randomly simulated matrices based on the row-proportional and column-proportional (PP) algorithms, through the null model approach (Gotelli, 2000, 2001; Ulrich & Gotelli 2007a, 2007b). For all estimates described above, presence/absence matrices were used.

Results and discussion

The collected demersal fish totaled 15,040 specimens, distributed in 21 orders, 33 families, and 77 species. The families with the highest number of taxa were Sciaenidae (16 species), Paralichthyidae (6 species), Haemulidae and Tetraodontidae (5 species each), Achiridae (4 species), Ariidae, Gerreidae and Gobiidae (3 species each), Batrachoididae, Diodontidae, Mullidae, Ophidiidae, Trygonorhinidae, Serranidae and Synodontidae (2 species each). The other families had only one taxon.

The latest surveys carried out in the PEC, including all vertical habitats, recorded an average of 180 species (Contente et al., 2011; Passos et al., 2013). So far, there has been no record of a study comparing the beta diversity of demersal fish, covering the adjacent continental shelf (20 m bathymetry) to the Upper sector of the Paranaguá Estuarine Complex on its East-West axis, in environments with salinity ranging from 5 to 25 ‰ (Netto & Lana, 1997; Lana et al., 2001; Passos et al., 2013).

Studies have already shown that variations in salinity and other physical-chemical factors in this environment are directly driven by patterns influenced by the estuarine ecocline (Barletta et al., 2017).

Consequently, these patterns alter the structural diversity of fish in the spatio-temporal use of habitats (Possatto et al., 2016; Carvalho & Spach, 2015; Passos et al., 2013). Therefore, the ecocline is the strongest structuring force of fish communities within any estuarine ecosystem Barletta et al. (2008), acting directly on fish diversity along the East-West axis of the PEC.

Mean values of Sørensen dissimilarity for multiple samplings (β SOR) showed no large variations between the Upper, Middle, and Lower sectors (0.883 vs 8.875 vs 0.889, respectively), highlighting the highest estimate for the External Sector (0.911). However, the resulting turnover (β SIM) and nestedness (β SNE) varied more noticeably between sectors. The highest mean value of β SIM was presented by the External Sector (0.874), in contrast to the Middle Sector (0.381), responsible for the lowest mean estimate. The Upper and Lower sectors, on the other hand, exhibited intermediate mean values for the β SIM component (0.817 vs 0.848, respectively). When analyzing the resulting nestedness (β SNE), the Middle Sector had the highest mean value (0.494), followed by the Upper (0.065), Lower (0.04), and External (0.036) sectors, respectively (Figure 2).

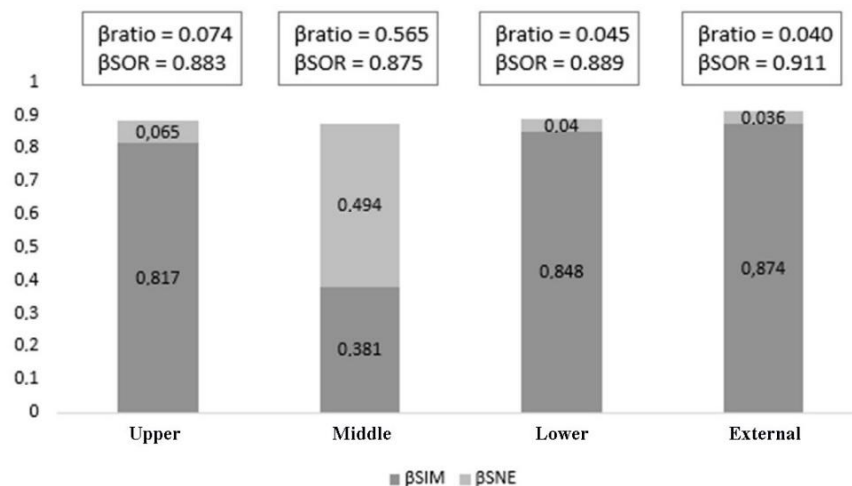


Figure 2. Sørensen dissimilarity for multiple samplings (β SOR) and its components Turnover (β SIM) and resulting Nestedness (β SNE) for the sampled sectors. β ratio indicates the ratio of β SNE to β SOR.

The Upper, Lower, and External sectors presented β ratio values below 0.5 (0.074 vs 0.045 vs 0.040 respectively), justified by their high β SIM values. However, the Middle Sector was the only presenting β ratio value greater than 0.5 (0.565), thus indicating that the nestedness pattern operates predominantly in variations in the fish fauna composition in this sector, differently from the other sectors, where the predominant response pattern is turnover.

Figure 3 illustrates the values obtained from 100 random samples for total dissimilarity (β SOR) and its components turnover (β SIM) and resulting nestedness (β SNE). The ANOVA results evidenced significant differences between sectors for each of the dissimilarity estimates, β SOR (F-value = 725.6; p-value < 0.001), β SIM (F-value = 2686; p-value < 0.001), and β SNE (F-value = 3081; p-value < 0.001). The Post-hoc test (Table 1) indicated significant differences between all sectors for total dissimilarity (β SOR) and its components turnover (β SIM) and resulting nestedness (β SNE), except for the comparison between the Lower and External sectors for β SNE.

Table 1. Results of Fisher's LSD post-hoc test used to compare the means between sectors for Total Dissimilarity (β SOR), Turnover (β SIM), and the resulting Nestedness (β SNE).

Sectors	β SOR p-value	β SIM p-value	β SNE p-value
Lower - External	< 0.001	< 0.001	0.5340
Middle - External	< 0.001	< 0.001	< 0.001
Upper - External	< 0.001	< 0.001	< 0.001
Middle - Lower	< 0.001	< 0.001	< 0.001
Upper - Lower	< 0.001	< 0.001	< 0.001
Upper - Middle	< 0.001	< 0.001	< 0.001

β SOR: total dissimilarity; β SIM: turnover dissimilarity; β SNE: resulting nestedness dissimilarity.

The Middle Sector presented the greatest variability for the estimates of β SOR, β SIM, and β SNE, compared to the other sectors. The Lower and External sectors, after the Middle Sector, presented the greatest variability for the β SOR estimates, with no expressive variation in the Upper sector. This low variability also occurred for the Upper, Lower, and External sectors for the estimates of β SIM and β SNE.

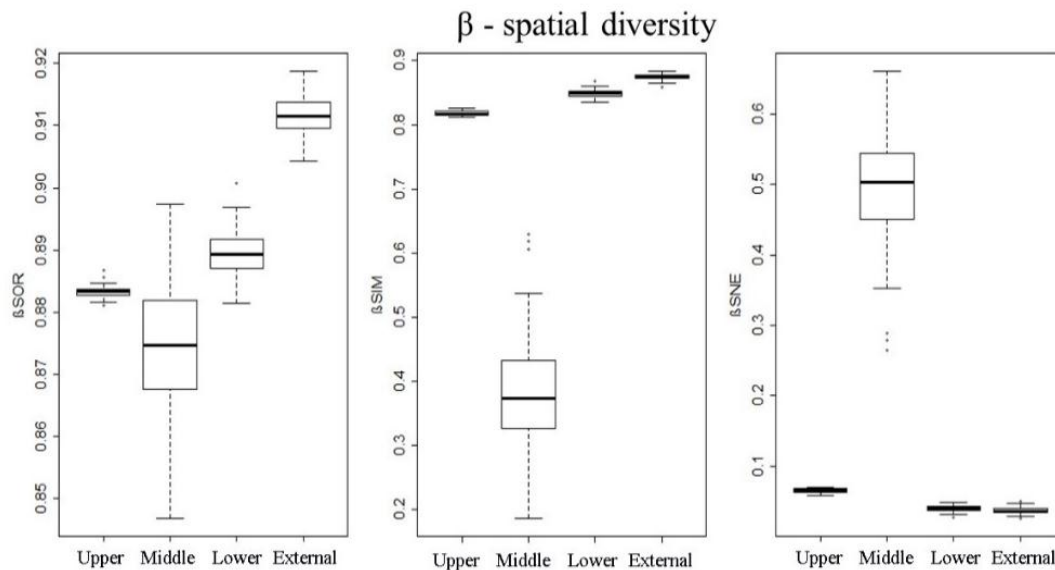


Figure 3. Median Total Dissimilarity values between multiple samplings (β SOR) and their components Turnover (β SIM) and Resulting Nestedness (β SNE) for the sampled sectors.

For the NODF metric, nestedness values observed in the Upper, Lower and External sectors were not significantly different from those expected by the null model (Upper: Nobs = 44; Nesp = 43.6; Z-value = 0.16; $p = 0.424$; Lower: Nobs = 35.45; Nesp = 37.35; Z-value = -1.49; $p = 0.058$; External: Nobs = 27.75; Nesp = 27.95; Z-value = -0.18; $p = 0.449$) (Table 2). Nevertheless, for the Middle Sector, the observed value (Nobs = 72.33) was significantly lower than expected by the null model (Nesp = 82.64; Z-value = -16.89; $p = 0.001$). These results indicate, therefore, that the demersal fish fauna of the Upper, Lower, and External sectors do not show significantly more nestedness than expected by random patterns, while for the Middle Sector, the nestedness value of the fish community was significantly lower than expected by null models.

Table 2. Results of the nestedness analysis in the NODF program for fish fauna species sampled in the Upper, Middle, Lower, and External sectors.

Sector	Number of species	Number of sampling sites	Nobs	Nexp (SD)	Filling	Z-value	p-value
Upper	29	2 (24)	44	43.6 (2.45)	21.1%	0.16	0.424
Middle	47	4 (48)	72.33	82.64 (0.61)	41.3%	-16.89	0.001*
Lower	53	3 (36)	35.45	37.35 (1.28)	21.1%	-1.49	0.058
External	57	3 (36)	27.75	27.95 (1.14)	14.7%	-0.18	0.449

Nobs: NODF observed for each sector; Nesp (SD): NODF expected for each sector with the respective standard deviation; Filling: matrix filling.

Concerning the total dissimilarity (β SOR) between the sectors, very close values were found, from 0.87 (Middle) to 0.91 (External). This is due to the number of species identified in the sectors, considered normal values related to the estuarine ecocline of this environment. Importantly, the greater the difference in species between habitats, the higher the value of this variable (Magurran, 2012). Using this simple metric, it was possible to demonstrate that the sectors are very similar environments. However, when total dissimilarity is partitioned into its components, the different values of turnover (β SIM) and resulting nestedness (β SNE) suggest the influence of possible stressors of natural or anthropic origin (Gutiérrez Cánovas et al., 2013).

As for the β ratio for all sectors, a marked difference was identified for the Middle Sector. The high value (above 0.5) only for the Middle Sector is given by the predominance of the resulting nestedness, unlike the other sectors (Upper, Lower, and External sectors), where β ratio values below 0.5 represent a predominance of turnover in the environments analyzed. According to Gianuca et al. (2017), the species' characteristics and behavior in biological communities reflect environmental heterogeneity. In this sense, regarding expected or

ideal relationships in species behavior within communities, the nestedness component will likely decrease with the expansion in the species dispersal area, while the turnover component will increase.

Except for the Middle Sector, the components of beta diversity separated for each sector indicate a decline in nestedness with increasing dispersal area: in the Upper Sector, the value was 0.065, in the Lower sector, 0.04, and in the External sector, 0.036. The same pattern was found for the replacement component (turnover) for the three sectors. In contrast to the nestedness component, there was an increase in values with an expanding dispersal area (Upper Sector = 0.817, Lower Sector = 0.848, and External Sector = 0.874). Thus, except for the Middle sector, the results corroborate what was expected at random, in which the nestedness component is likely to decrease with the expansion in the species dispersal area, while the turnover component increases (Gianuca et al., 2017).

The values obtained for the nestedness and replacement components indicate the predominance of turnover in the Upper, Lower, and External sectors. Both estuaries and the continental shelf are ecosystems shaped by large environmental gradients. Estuaries, due to their position at the interface between the marine and inland water environments, are strongly influenced by salinity and organic matter (Teichert et al., 2018) while the continental shelf is influenced by gradients of depth, temperature, hydrodynamic energy, among others (Damalas et al., 2010). In this sense, high turnover rates are expected in these environments, due to changes in species composition along these gradients (Basset et al., 2013).

Unlike the other sectors, the Middle Sector showed great differences in turnover and nestedness, directly affecting the β ratio value (0.565). The results observed in this sector were inverse to the others, with a predominance of nestedness (0.494) over the replacement component (0.381). Previous studies have shown that this sector suffers, in different proportions, environmental disturbances including the presence of contaminants like fecal steroids, coprostanol, and even metalloids arsenic, from human activities and sewage near the port and the city of Paranaguá (Anjos et al., 2012; Martins et al., 2011), which may justify the results found herein. Human activities modify habitats and their characteristics, as well as the abundance of species and their physiological tolerance to abiotic factors, which may explain the emergence of nestedness in metacommunities (Higgins et al., 2006). In this way, and with a smaller number of species that support habitat changes, the replacement of species becomes smaller.

In the Middle Sector, the presence of the largest bulk port in Latin America (Andriguetto Filho et al., 1998) directly influences the distribution and diversity of the fish fauna. According to Possatto et al. (2017), the PEC is considered one of the most preserved estuaries in Brazil, except for the East-West axis and the Middle Sector, in which the anthropogenic effects become apparent. Dredging operations for maintaining the navigation channel are also highlighted in this sector, intensified in this location due to the proximity to the port, resulting in changes in fish communities and directly altering the local geomorphology (Barletta et al., 2016). These same authors also highlighted the decrease of some species and even the disappearance of Sciaenidae species associated with the influence of the dredging process.

As the results showed changes in values of both components of beta diversity for the Middle Sector of the estuary, in comparison to the other sectors, it was decided to use a metric that estimates the nestedness pattern, in a more appropriate and reliable way—NODF (Wang et al., 2013). For this metric, nestedness values observed for the Upper, Lower, and External sectors were not significantly different from those expected by the null model. However, the Middle Sector of the estuary showed a value significantly lower than expected by the null model. Despite this underestimation, the NODF analysis indicated no type I error, that is, the overestimation of the nestedness pattern for all sectors. There is a clear difference between the observed and expected values for the Middle Sector compared to the other sectors (Table 2), thus indicating that this was the sector with the highest nestedness pattern, despite still having an underestimated value. These facts corroborate previous analyses and discussions.

Conclusion

Beta diversity is an important tool for planning environmental conservation. Based on the results obtained, it is possible to state that human activities have adversely impacted the demersal fish community in the Middle Sector of the PEC. This sector has been identified as the most vulnerable, which justifies enhanced strategic planning for environmental protection and maintenance by competent bodies. Unlike the other sectors, the Middle Sector has demonstrated a greater sensitivity to within the PEC and the adjacent continental shelf.

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