Seasonal upwelling and depth-driven gradients foster functional overdispersion in Southwestern Atlantic annelid assemblages

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Abstract

Marine communities on continental shelves form through a combination of environmental filtering, biotic interaction, and dispersal-based processes. These shelves present depth-related environmental gradients from nearshore and seasonal upwelling systems, which periodically supply cold, dispersal-enhancing, nutrient-rich waters, providing an ideal setting to explore spatiotemporal trait-based assembly patterns and underlying mechanisms. Although eastern boundary upwelling ecosystems are well-studied, the role of upwelling in southwestern Atlantic benthic assembly remains less understood, especially from a functional perspective. Here, we integrated the morphological, size, reproductive, and behavioral traits of annelids with environmental variables. We found that deeper, low-dynamic, coarser, poorly sorted sediments with moderate nutrient amounts and quality on the outer shelf maintained overdispersed annelid assemblages. Nevertheless, particularly in the Austral summer, cold bottom water from South Atlantic Central Water (SACW) on the northern São Paulo inner shelf promoted functional overdispersion, a pattern generally assumed to occur over evolutionary timescales. Immediately after SACW retraction, we observed trait clustering, typical of environmental filtering likely by intensifying hydrodynamics and lower-quality organic inputs expected for the area. RLQ analysis revealed the predominance of sedentarian Scolecida and Sabellida traits on the inner shelf, whereas outer shelf traits were broader but dominated by errant, larger, mobile carnivorous annelids. However, high environmental heterogeneity, likely modulated by spatial contingency results in random assemblages on the inner shelf overall. Our study highlights how long-established spatial gradients and short-term events can temporarily alter community assembly processes, underscoring the need for more nuanced temporal and functional approaches to marine biodiversity assessments and conservation strategies in upwelling-impacted shelf systems.

KEY WORDS: Functional Diversity, Benthic Macrofauna, Eastern South Atlantic Central Water (ESACW), Polychaete, MNTD, MPD.

1. INTRODUCTION

Comprehending the fundamental rules for the assembly of biological communities and the mechanisms behind them has long been a central goal in community ecology. Early concepts envisioned a “filtering” metaphor whereby local communities form through spatially and temporally mediated processes that select or exclude species based on their traits (Diamond 1975, Southwood 1977, Weiher & Keddy 1995, Kraft et al. 2015). Two major deterministic processes were postulated to govern these filters and hence species coexistence: (i) competition, which enforces limiting similarity among coexisting species (MacArthur & Levins 1967, Weiher & Keddy 1995, Chesson 2000, HilleRisLambers et al. 2012), and (ii) abiotic filtering, related to physiological constraints that favors specific trait configurations in particular environments (Southwood 1977, Weiher & Keddy 1995, Kraft et al. 2015).

Functional traits generally encompass morphological, physiological, or behavioral characteristics affecting fitness and provide a mechanistic link between form and function (Violle et al. 2007). Within these, response traits define how species cope with environmental conditions (e.g., mechanical support structures), while effect traits capture the ways species modify ecological processes (e.g., bioturbation) (Lavorel & Garnier 2002; Beauchard et al. 2017). Examining trait distributions in a community can thus reveal the processes driving observed assembly patterns (Cornwell et al. 2006, Violle et al. 2007, HilleRisLambers et al. 2012, Münkemüller et al. 2020).

Traditionally, environmental filtering has been linked to reduced trait differentiation, with communities exhibiting stronger similarity than expected by chance, leading to trait clustering (Weiher & Keddy 1995, Cavender-Bares et al. 2009, HilleRisLambers et al. 2012, Coyle et al. 2014, Swenson & Weiser 2014). However, this clustering occurs only if the measured traits reflect keyways in which species cope with environmental discontinuity (Münkemüller et al. 2020). For instance, small, short-lived, r-strategist annelids might dominate in unstable or severe habitats (Flach 2001, Quintana et al. 2015, Clinton et al. 2024). By contrast, trait overdispersion arises when species are more functionally dissimilar than expected by chance (Cavender-Bares et al. 2009, HilleRisLambers et al. 2012). This has been explained as a response to symmetric competition, evolutionarily forcing species to diverge in their traits and specialize in exploring a resource niche optimum, commonly taking place in milder environmental fluctuations (MacArthur & Levins 1967, Mayfield & Levine 2010, Pavoine & Bonsall 2011). Yet a key question remains: can short-scale ecological processes also generate functional overdispersion patterns?

Recent work on marine macroinvertebrate communities indicates that dispersal-based processes (e.g., adult or larval immigration) often account for the bulk of species richness in a community, overshadowing niche-based mechanisms (Loke & Chisholm 2023). When increased immigration and resource availability coincide, especially in stable low dynamics habitats, communities can reach higher species richness, which often correlates with greater functional trait differences (Petchey & Gaston 2006). In marine systems, a trait overdispersion pattern is likely to emerge in low-dynamic, physically stable, and productive habitats, where milder dynamics constraints allow for the maintenance of traits associated with distinct life strategies (Beauchard et al. 2022).

Continental shelves present excellent opportunities to investigate these community assembly dynamics. Despite being relatively connected through both the water column and the seabed, shelves exhibit strong spatial gradients such as depth, salinity, hydrodynamics, sediment texture, resource availability and quality, and temporal changes (e.g., seasonal upwelling events) that can directly shape marine biodiversity (Pires 1992, Paiva 1993, Morais et al. 2019). Upwelling systems combine geomorphological complexity, Earth rotation, and wind-driven seasonal variation of water mass movement. As cold, nutrient-rich waters reach sub- and surface layers, productivity is enhanced (García-Reyes 2015), as well as species immigration through larval dispersion, as the planktonic organisms living within these water masses are dislocated inshore (García-Reyes 2015, Bashevkin et al. 2020, Brandão et al. 2020). The interplay of these space-time dynamics can favor distinct life strategies. Yet, few studies have examined how upwelling influences soft-bottom communities from an explicit functional trait perspective, with most focusing on eastern boundary upwelling systems (EBUEs) (Fréon et al. 2009, Pacheco et al. 2011, Soto et al. 2017, Bon et al. 2021, Sivadas et al. 2021). Assessing these processes over relevant spatial and temporal scales, supported by appropriate trait-based frameworks, could deepen the understanding of the mechanisms shaping soft-bottom community assembly.

On the Brazilian coast, the Ubatuba region lies in the Santos Basin off northern São Paulo State, encompassing a large segment of the Brazilian southwestern continental shelf and hosting a notable upwelling system (Pires 1992, Paiva 1993, Pires-Vanin et al. 1993, Alves et al. 2014, Moura et al. 2023). Owing to oceanographic and taxonomic distinctiveness, this shelf area is typically divided into an inner shelf sector, which is shallower, subject to anthropogenic stressors, wave action, bottom shear stress, and strong hydrodynamic changes (including upwelling of South Atlantic Central Water, SACW), and an outer shelf sector, deeper and less affected by waves, featuring a more stable hydrodynamic regime (Pires 1992 Paiva 1993, Pires-Vanin et al. 1993, Dos Santos & Pires-Vanin 1999, Santos & Pires-Vanin 2004, Sumida et al. 2006, Alves et al. 2014, Quintana et al. 2015, Melo Júnior et al. 2016, Figueiredo Jr et al. 2020, Moura et al. 2023).

Although both sectors lie within the same sedimentary province, they exhibit differences in total organic carbon with lower values down to the 25 m isobath, higher values between 25 and 50 m, and more moderate, similar values down to 100 m; the quality of the organic content follows a similar pattern (Figueiredo Jr et al. 2020, Carreira et al. 2023). During non-upwelling months, a high dynamic environment with wind-driven sediment resuspension in the inner shelf promotes lower-quality phytoflagellate blooms, reflecting high community densities dominated by opportunistic annelid species (Quintana et al. 2015). In contrast, the outer sector remains under SACW influence year-round, supporting a more stable, higher-quality resource supply for benthic macrofauna (Sumida et al. 2007, Paiva 1993, Pires-Vanin et al. 1993) (Fig. 1a). When SACW upwells at austral summer, environmental stability increases in the inner shelf, and cold, resource-rich water sustaining diatom blooms and depositing fresh organic matter that fosters a richer benthic community, dominated by larger, more mobile, and carnivorous annelids (Paiva 1993, Sumida et al. 2007; Quintana et al. 2015) (Fig. 1b).

Although annelid taxonomic diversity patterns for this region have been examined, revealing differences between shelf sectors and the effects of SACW upwelling, few inferences about the spatiotemporal assembly mechanisms have emerged from a functional trait perspective (Paiva 1993, Quintana et al. 2015, Shimabukuro et al. 2016). In a broader spatial study of annelid community diversity, Paiva (1993) documented a marked distinction between the two shelf sectors, with taxonomic diversity values consistently lower on the outer shelf during summer and higher in winter. In contrast, the inner platform exhibited more complex diversity patterns, with seasonal fluctuations at shallower depths. The highest diversity values in shallow stations were attributed to a greater number of species, whereas in deeper stations, they resulted from higher evenness.

Macrofaunal annelids are among the most diverse and abundant groups in marine benthic systems, with their members playing central roles in maintaining ecosystem processes, such as energy flow and nutrient cycling (Rouse et al. 2022). The group displays a plethora of morphological, behavioral, and reproductive traits, occupying soft and hard bottoms from shallow to abyssal ecosystems (Rouse et al. 2022). For this reason, annelids have been used as models or present in general macrofauna to understand the assembly process of marine and estuarine communities, revealing interesting patterns of trait dissimilarity in response to environmental gradients based on an array of trait combinations, often including morphological ones (Otegui et al. 2016, Breine et al. 2018, Wouters et al. 2018, Morais et al. 2019, Nogueira et al. 2023, Medeiros et al. 2021). In an era marked by extensive human-induced alterations and accelerating effects of climate change, building upon previous studies to address new scientific questions is imperative. Doing so not only advances ecological science but also provides a vital baseline for biodiversity impact assessments, management, and conservation.

With these goals, we developed a functional trait database that includes all annelids recorded by Paiva (1993) from 1985 to 1996. We aim to examine the spatiotemporal dynamics of assembly processes in soft-bottom habitats, grounded in the known regional patterns of annelid and macrofauna diversity (Paiva 1993, Quintana et al. 2015, Shimabukuro et al. 2016) and contemporary community assembly theory. Specifically, we propose two functional trait-based hypotheses related to the depth–stability gradient and the seasonal SACW upwelling. First, we expect that the inner shelf, under stronger environmental filtering – harsh hydrodynamics, generally labile low-quality organic matter, strong selected muddy sediments – will exhibit functional clustering, dominated by sedentary opportunistic smaller species, with infaunal or tube-dweller behavior, r-selected reproductive strategies, and microphagous feeding traits. Conversely, in the outer shelf – more stable hydrodynamically, with higher organic matter quality and mixed sediment, we anticipate a wider array of traits such as errant and sedentarian body plans, micro and macrophagous strategies with varied feeding apparatus, r and K-selected reproductive strategies, culminating in a predominant trait overdispersion pattern. Second, we hypothesize that SACW upwelling provides sufficient environmental stability and additional high-quality resource input to weaken filtering in the inner sector and sustain the arrival of new species due to stimulated dispersal inshore, triggering a temporary shift toward trait overdispersion (Fig. 1b).

2. MATERIAL AND METHODS

2.1 Macrofauna sampling

The surveys were conducted at 54 oceanographic stations along two sectors of the northern continental shelf of São Paulo (Fig. 1c-d). The inner (shallow) shelf, with depths ranging from 15 to 50 meters, was surveyed in October 1985, January (Austral Summer), April, and July 1986. The Samples were taken in three transects perpendicular to the shoreline, in each transect, samples were taken at three depths: 20, 35, and 45 meters (Fig. 1d). The outer shelf (deeper) was sampled in late December 1986 (Austral Summer) and July 1986 (Austral Winter) at nine stations extending from the inner shelf, reaching depths of approximately 50, 75, and 117 meters (Fig. 1d). Sampling in the inner shelf was conducted aboard the research vessel "Veliger II," while in the outer sector, samples were collected aboard the "Prof. W. Besnard," both vessels operated by the Oceanographic Institute of the University of São Paulo (IO-USP). For more details, refer to Paiva (1993).

Biological material was collected using a Van Veen grab with a sampling area of 0.1 m^2. The sediment from each grab was sieved for the macrofauna. The material retained on the sieves was preserved in 4% formaldehyde and sorted under a stereomicroscope into major taxonomic groups (phyla, classes, or orders), then identified to species level and counted. Annelid worm density was estimated as the number of individuals per 0.1 m^2, forming the sample-by-species abundance matrix. All analyses performed in this study were carried out using taxa at the genus level to overcome the challenges imposed by the Raunkiæran shortfall (Hortal et al. 2015), and literature inconsistencies in the assignment of fuzzy weights to species trait modalities.

2.2 Environmental variables measurements

At each sampling station, bottom-water samples were collected using Nansen bottles, with temperature recorded by reversing thermometers attached to the bottles. Water samples were analysed for salinity using an inductive salinometer, and dissolved oxygen content was determined by Winkler's titration method (Strickland & Parsons 1968). Hydrographic analyses were carried out both onboard and in the laboratories of the Department of Physical Oceanography at IOUSP. A sediment sample was collected from the material retrieved with the Van Veen grab for sedimentological analysis. Granulometric analyses were conducted using sieving and pipette methods (Suguio 1973), with statistical parameters calculated according to Folk & Ward (1957). Additionally, the relative frequencies of four granulometric classes were determined: mud (clay + silt), fine sand, medium sand, and coarse sand (%). The sand was divided into these fractions due to the selectivity of certain species for specific grain sizes (Van Tomme 2013). The biogenic carbonate content in the sediment was measured through hydrochloric acid digestion (10%), and the organic matter content (%) was analyzed using the H_2O_2 oxidation method (Gross 1971). These sedimentological analyses were performed in the Sedimentology Laboratory at IOUSP.

2.3 Annelid functional traits

A total of 22 functional traits were measured ("Functional Trait dataset" in Online Supplementary material). All traits were quantified using a fuzzy coding approach (Chevenet et al. 1994). In this coding system, species traits are dummy variables and receive assigned scores ranging from 0 to 3 for each modality regarding their adult life stage. A score of 0 indicates no affinity, 1 indicates low affinity, 2 indicates high affinity, and 3 indicates absolute affinity (Oug et al. 2012). As some taxa from the abundances per sampling unit matrix were not assigned to the species level, for the sake of comparisons, all functional traits were coded at the generic level. In some cases, the information about a trait was absent from the generic resolution, we then inferred the scores from family-level literature (Rouse et al. 2022).

Traits were organized into four categories: morphology, reproduction, size, and behavior. The behavior category was then divided into three traits: feeding strategy, habitat occupation strategy, and motility. The size, motility, feeding, and habitat occupation strategy trait modalities were obtained from Jumars et al. (2015). Finally, the morphology and reproductive traits and their respective modalities were modified from Otegui et al. (2016) and Wilson et al. (1991), respectively.

The morphological traits measured can be summarised in four groups: i) support structures (Otegui et al. 2016), ii) sensorial structures (Bartolomaeus & Purshcke 2005, Otegui et al. 2016), iii) respiratory structures (Otegui et al. 2016), and iv) auxiliary foraging structures (Bartolomaeus & Purshcke 2005, Jumars et al. 2015, Otegui et al. 2016). The support structures are related to or facilitate in different degrees the following biological aspects: locomotion, body mechanical support, and defence against natural enemies. The traits are body surface (smooth, intermediate, or heavily covered), parapodial lobes or lamellae (present or absent), parapodial rami (uni, sub or bi-rami), parapodial appendages (absent, dorsal cirri, ventral cirri, elytra, crests or plates) and chaetae (chitin shield, pectinate, harpoon, forked, aciculae, capillary, hooks, uncini, compound, lyrate, spines, paleae, see Rouse et al. (2022) for detailed definitions).

The sensorial structures relate to how the specimen perceives and explores its environment, thus affecting its biology and life habits. They are: prostomial or head appendages (absent, present as a single structure or multiple structures), palps (absent or present as a radiolar crown, a single pair, or multiple pairs), body appendages (present or absent), and sense organs (absent, nuchal organs, segmental or interramal photoreceptors, peristomial photoreceptors, radiolar or opercular photoreceptors, pygidial photoreceptors, prostomial photoreceptors, lateral sense organs, cirri, statocysts). The respiratory structures can be absent or present as a radiolar crown, regionalized or not-regionalized branchiae. Finally, the foraging structures help species to capture and process food. The traits are pharynx complexity (simple tube, ventral, axial muscular, axial non-muscular) and pharynx feeding apparatus (armoured or unarmoured pharynx). All these traits were obtained from the respective generic diagnosis, species descriptions, and family-level literature.

The reproductive traits are considered herein due to their relevance in the assessment of coupling mechanisms of species with local environmental conditions, especially colonization, recruitment, and dispersal success (Beauchard et al. 2017). So, we adapted the reproduction category and divided it into three traits: larval development (direct, indirect with planktotrophic larvae or indirect with lecithotrophic larvae), the fate of ova (free spawning, internal brooding, external brooding, brooding inside the tube, brooding within gelatinous egg masses, or brooding within egg capsules), asexual reproduction (present or absent), and body reproductive transformations (absent, epigamy, schizogamy). Larval development of annelids was reviewed by Wilson et al. (1991) and Rouse (2000). The fate of ova was reviewed by Wilson (1991), but Rouse et al. (2022) present updated family-level information. The presence of asexual reproduction and body reproductive transformation traits can be assessed through Rouse et al (2022) and further family-level information (e.g. Aguado et al. (2012) for Syllidae Grube, 1850, and Rouse & Fitzhugh (1994) for Sabellidae Latreille, 1825).

The body size category was divided into two traits: body length (Jumars et al. 2015) and segment number (Otegui et al. 2016, Wouters et al. 2018). Jumars et al. (2015) divided the body length into three modalities: small (0.05 to 20 mm), medium (up to 200 mm), and large (more than 200mm). Subsequently, Otegui et al. (2016) and Wouters et al. (2018) divided the segment number into two modalities: small (less than 100 segments) and large (more than 100 segments). In the behavior trait category, feeding strategy, motility, and habitat occupation strategy traits were obtained from Jumars et al. (2015). The feeding strategy trait was assigned to the following modalities: predator, herbivore, scavenger/opportunistic, deposit feeder, and suspension feeder. The motility trait was assigned to sessile, low motility, medium motility, and high motility modalities. Moreover, the habitat exploration strategy trait was assigned to epifaunal, interface, and infaunal modalities.

2.5 Data analysis

The discrimination of shelf sectors and sampling months based on their environmental characteristics was assessed using a Permutational Multivariate Analysis of Variance (PERMANOVA), followed by pairwise PERMANOVA for individual comparisons. Two fixed factors were used, shelf sector (two levels) and survey (four levels). In addition, all continuous environmental variables were scaled. A Principal Component Analysis (PCA) and Pearson correlation matrix were conducted to explore the collinearity among them (Figure S1), yielding the detection of high collinearity among sediment variables (Fig. S1a,b). For this reason, two principal components, Sediment PC1 and Sediment PC2, were extracted as latent variables (Figure S1b) from a PCA performed with only the sediment variables. Sediment PC1 explained most of the variation in CaCO3, fine, medium, and coarse sand content, while Sediment PC2 captured variations in the sorting coefficient, mud, and organic matter content. These two latent variables, along with site depth, bottom-water temperature, and salinity, formed the environmental variables matrix.

To address our study question and hypothesis, we employed two distinct approaches. First, we examined the overall pattern of trait dispersion by looking for evidence of trait clustering or overdispersion across shelf sectors and surveyed months, as well as the influence of environmental gradients. Subsequently, we search for a multivariate non-random pattern in trait-environment correlation and specific trait modalities associated with environmental variables by evaluating individual trait-environment correlations. All analyses performed herein considered an $\alpha = 0.05$.

2.5.1 Trait dispersion modelling

A distance matrix based on species functional traits was constructed to assess functional dispersion, employing Gower’s coefficients calculated using the *dist.ktab* function from the ade4 R package (Dray & Dufour 2007). From this matrix, along with the sample-by-species matrix, two key metrics were derived from a functional dendrogram to investigate trait dispersion in each assemblage: the mean pairwise distance (MPD) and the mean nearest-taxon distance (MNTD) (Webb et al. 2002, Kembel et al. 2010, Tucker et al. 2016, Gross et al. 2022). Ecologically, MPD calculation represent the average of the trait distances between all pairs of species found within a given assemblage, while MNTD capture the average minimum distance between species pairs for a given assemblage, thus both indices reflect two-ways to inform the degree of functional dissimilarity (Webb et al. 2002, de Bello et al. 2016, Tucker et al. 2016). These metrics have been used to test functional and phylogenetic hypotheses regarding the relative influence of abiotic environmental filtering versus biotic interactions in community assembly processes in other study areas (de Bello et al. 2016, Tucker et al. 2016, Sessa et al. 2018, Gross et al. 2022, Macheriotou et al. 2023). Although MPD and MNTD differ in their mathematical formulations, both metrics are less sensitive to species richness differences than other functional diversity indices (de Bello et al. 2016, Tucker et al. 2016), and are complementary to each other (Webb et al. 2002, Tucker et al. 2016).

The calculation of MPD and MNTD for the same assemblages enhances sensitivity for detecting distinct ecological patterns, as they differ in how they capture structural changes in each assemblage functional dendrogram (Webb et al. 2002, Tucker et al. 2016, Sessa et al. 2018, Gross et al. 2022, Macheriotou et al. 2023). Specifically, MPD is more sensitive to basal changes in the functional dendrogram internal nodes, reflecting broader shifts in functional dispersion, while MNTD is more responsive to changes in the branching pattern at its tips (Tucker et al. 2016, Gross et al. 2022, Macheriotou et al. 2023). As we hypothesized a functional difference between inner and outer shelves driven by the long-established spatial pattern, it should be strongly captured in a metric sensitive to changes toward the bases of the annelid assemblages dendrograms. In contrast, the seasonal upwelling process affecting annelids' incidence, increasing richness and functional dispersion (as hypothesised) is expected to influence changes towards their tips. Thus, the combined use of MPD and MNTD will allow us to test for these patterns and assess how annelid traits are dispersed between sectors and across months properly.

To assess whether the observed species traits in each community differed from random expectations, we calculated the standard effect sizes (SES) of MPD and MNTD. This was performed by comparing the observed values with a null distribution of 999 randomized communities generated using an independent swap algorithm, which randomly reassembles the sample-by-species assemblage matrix while maintaining the species richness and incidence (Kembel et al. 2010). These calculations were performed using the *picante* R package (Kembel et al. 2010). One sample, two tailed student's *t* tests were performed to explore if SES values from both indices were significantly different from zero mean (random pattern) for each survey in the inner and outer shelves, together and separately, allowing us to check if assemblages were significantly clustered (negative SES values) or overdispersed (positive SES values) in relation to the null expectation.

Two linear models were fitted using ses.MPD and ses.MNTD as the response variable. The models incorporated the interaction between spatial variation, fixed factor with two levels: inner and outer shelves, and temporal variation, fixed factor with four levels: October 1985, December 1985/January 1986, April 1986, and July 1986. Subsequently, a model selection procedure, based on the AICc – Akaike Information Criterion corrected for small sample sizes, dAICc – differences from the AICc score of the best model, considering value < 2, and AICw – Akaike weights, was applied using the MuMIn R package (Bartón 2024). For this step, sediment principal components (Fig S1b), depth, salinity, and bottom-water temperature were implemented in ses.MPD and ses.MNTD modelling. The environmental variables identified in the best models were considered as the most relevant in explaining trait dispersion variation (Symonds & Moussalli 2011).

2.5.2 Assessing individual trait-environment relationships

RLQ and fourthcorner analyses were performed using the R package ade4 to explore possible correlations between traits and environmental variables. RLQ analysis integrates three datasets: R (scaled environmental variables), L (genera abundances), and Q (fuzzy coded functional traits), to identify multivariate relationships between environmental gradients and functional traits mediated by genera abundances (Dray et al. 2014). The fourthcorner analysis complements this by testing the significance of bivariate relationships between traits and environmental variables (Dray et al. 2014). This analysis is not sensitive to the number of variables and handles to some extent with their collinearity (Dray et al. 2014, Beauchard et al. 2022), and for this reason, we used all sediment fractions.

Before performing RLQ, each dataset – species-by-traits (Q-table), environmental variables (R-table), and species abundances (L-table) – was processed using a proper multivariate analysis. A Fuzzy Correspondence Analysis (FCA) was implemented to process the Q matrix. In contrast, a Principal Component Analysis (PCA) and a Correspondence Analysis (CA) were implemented to process the R and L matrices, respectively. These results were then incorporated into the RLQ analysis. The significance of the multivariate associations from the RLQ was assessed with a Monte Carlo test based on the total coinertia of the RLQ output, using randtest.rlq function with 49.999 repetitions within model 6. For the fourthcorner analysis, the *fourthcorner* function was applied with 49.999 permutations, also within model 6. The p-values for both RLQ and fourthcorner analyses were adjusted for multiple comparisons using the False Discovery Rate (FDR) method (Benjamini & Hochberg 1995, Dray et al. 2014). All analyses of the present study were performed in R Studio (R Core Team 2024).

3. Results

3.1 Environmental characterization of the inner and outer shelf sectors

Overall, the PCA incorporating all environmental variables revealed moderate ecological variability, but with some degree of environmental distinction between the inner and outer shelves (pseudo-$F_{1,47}$ = 5.31, p = 0.001; Table S1, Fig. S1). The outer shelf sites formed a more cohesive cluster, while the inner shelf exhibited greater environmental heterogeneity among sampled sites (Fig. S1a). The ordination suggests some site groupings: (1) most inner shelf sites, along with some from the outer shelf, characterized by high organic matter, mud content, well-sorted sediments, moderately higher bottom-water temperature, and dissolved oxygen; (2) another cluster, also primarily from the inner shelf, distinguished by high fine-sand content; (3) a group of five inner shelf sites, independent of sampling period, associated with the highest concentrations of coarse and medium sand, as well as $CaCO_3$; and (4) the majority of outer shelf sites, which share characteristics with the coarse/medium sand sites, are distinct for having the greatest depths, lowest mud and organic matter content, and reduced bottom-water temperature and dissolved oxygen (Fig. S1a). Environmental conditions varied significantly throughout the study period (pseudo-$F_{3,47}$ = 2.64, p = 0.002; Table S2). However, the spring-summer sampling period (December-January) was the most distinct (Fig. S1a, Fig. S2), showing significant differences compared to April (pseudo-$F_{1,25}$ = 3.861, adj. p = 0.024; Table S2) and July (pseudo-$F_{1,33}$ = 6.42, adj. p = 0.006; Table S3; Fig. S2). It is important to highlight that during that spring-summer period (December-January), both shelves were quite homogeneous concerning the low temperature and salinity, mostly below 16ºC and 35.6, respectively (Fig. S2), typical of the SACW water mass.

3.2 Spatio-temporal patterns of functional trait dispersion

In the inner shelf, the mean ses.MPD (T-test mean = -0.08) and ses.MNTD (T-test mean = -0.21) of annelid assemblages across all sampling periods were negative but did not significantly differ from zero, indicating no overarching year-round trend toward clustering or overdispersion (Table S3; Fig. 2a, c). Nonetheless, inner shelf temporal variability was evident: during December–January, ses.MPD was positive and approached significance (T-test mean =

0.33, p = 0.059) and ses.MNTD was significantly positive (T-test mean = 0.60, p = 0.0097), indicating overdispersion (Table S3; Fig. 2a, c). In contrast, April showed significantly negative ses.MNTD values (T-test mean = -0.87, p = 0.0082), reflecting a shift toward trait clustering (Table S3; Fig. 2c). Meanwhile, the October and July samples displayed negative mean values that were not statistically different from zero (Table S3; Fig. 2a, c). In the outer shelf, both overall ses.MPD (T-test mean = 0.67, p = 0.0018) and ses.MNTD (T-test mean = 0.42, p = 0.0368) were significantly greater than zero, indicating a consistent pattern of overdispersion throughout the study period (Table S3; Fig. 2b, d). Further, the summer months (December–January) showed consistently high and often significant positive values for both metrics, reflecting a pronounced functional overdispersion (Table S3; Fig. 2b, d).

Bottom water temperature emerged as the most important environmental variable influencing ses.MNTD variation (Selected model: df = 3, AICc = 146.7, w = 0.71; Table S4), with a negative relationship, thus low bottom water temperatures – typical of SACW– were associated with more overdispersed assemblages (Table S4; Fig. 3a). The ses.MPD was primarily influenced by the depth and Sediment PC2 (Selected model: df = 4, AICc = 122.7, w = 0.66; Table S4), which accounted for the gradients in sediment selection coefficient, organic matter, and mud content (Fig. S1b). As depth increased, assemblages tended to be functionally overdispersed (Table S4; Fig. 3b), whereas higher values of sediment PC2, which likely reflects finer sediments and organic matter, were related to slight trait clustering (Fig. 3c, Fig. S1b).

3.3. Trait–Environment correlations

The randomization test for the RLQ analysis, based on total inertia, was significant (Monte Carlo permutation test FDR-adjusted $p < 0.05$ for both models 2 and 4), indicating a non-random multivariate relationship between traits and environmental gradients (Figs. 4, 5). Overall, the RLQ showed a partial separation between the inner and outer shelves, with the outer shelf forming a more cohesive cluster, while the inner shelf displayed greater variability among sampling stations (Fig. 4a). The first axis of the RLQ accounted for 95% of the variation (L correlation = 0.60). On the left side, higher percentages of $CaCO_3$, medium, and coarse sand contents influenced sessile, suspension-feeding annelids bearing radiolar crowns, uncini, and simple tube pharynges (Figs. 4a-c; 5a, b, e, h). These traits were the only ones significantly correlated with RLQ axis 1 (Table S5), suggesting that a set of inner shelf sites (regardless of sampling period) favours a sedentary “Sabellida-like” assemblage (sensu Rouse & Pleijel 2001).

Also, in the shallower inner shelf sites, partially distributed along both RLQ axis 1 and axis 2 (3.21% of the variance, L correlation = 0.21), sediment with higher organic matter, mud content, selection coefficient, along with moderately higher dissolved oxygen and bottom temperatures, are related to another group of sedentary annelid – those with simple chaetae, deposit-feeding strategies, infaunal behavior, and small body length (Fig. 4a-c). Such traits are typical of "Scolecida-like" annelids (sensu Rouse & Pleijel 2001), especially Paraonidae Cerruti, 1909 and Capitellidae Grube, 1862 (Fig. 3). By contrast, most outer shelf and some inner shelf sites (mainly from December-January) exhibited higher densities of errant genera. These genera were mainly associated with deeper, colder bottom waters (fig. 4a-c). Their most closely linked traits included pectinate and compound chaetae, parapodia with cirri, body-bearing appendages, prostomium bearing multiple structures, an armored axial muscular pharynx, macrophagous feeding (herbivory to omnivory), regionalized branchiae, a single pair of palps, high motility, occupation of sediment interface, external brooding of eggs, and large body size (Figs. 4c; 5). Although some trait modalities correlated significantly with axis 1 (Table S5; Fig. 4), the fourth-corner analysis did not detect any significant bivariate relationships between these annelid traits and the measured environmental variables (FDR-adjusted $p > 0.05$).

4. Discussion

In this study, we employed a functional dispersion framework to investigate the assembly process in a soft-bottom continental shelf system, using annelid assemblages as models along a depth gradient, relying on their seasonal upwelling shifts, and the effects of the most influential environmental variables. Our results demonstrate spatial and temporal variability in environmental conditions along the northern portion of the São Paulo continental shelf, with the outer shelf forming a more cohesive and generally colder and dynamically stable cluster, while the inner shelf exhibited marked heterogeneity. In turn, these differences shape different patterns of trait dispersion: the inner shelf assemblages fluctuate between clustering and overdispersion, particularly marked by a summertime shift toward overdispersion associated with colder, resource-rich bottom waters (SACW upwelling), whereas the outer shelf shows a consistent overdispersion of traits. This also aligns with the revealed distinct multivariate trait-environment correlations.

4.1. On the functional trait dispersion patterns

We hypothesized that severe environmental filtering would lead annelid assemblages to a more clustered functional dispersion pattern in the inner shelf, whereas the outer shelf assemblages would exhibit an overdispersed pattern. Indeed, the observed environmental variability between both inner and outer shelves was in line with previous findings for the whole studied shelf area (Pires 1992, Pires-Vanin et al. 1993, Paiva 1993, Dos Santos & Pires-Vanin 1999, Alves et al. 2014, Melo Júnior et al. 2016, Figueiredo Jr et al. 2020, Carreira et al. 2023, Moura et al. 2023), which would support this broad expectation. Nonetheless, our initial hypothesis was only partially supported: although most of the outer shelf assemblages were overdispersed, the inner shelf showed substantial variation on functional trait dispersion, with some assemblages clustered and others overdispersed, resulting in an overall pattern indistinguishable from a random assembly. Notably, for both ses.MPD and ses.MNTD, few inner shelf assemblages had standardized effect sizes near zero, implying that the apparent randomness or neutrality emerges only when the entire shelf is analysed as a whole. This can be interpreted through the lens of spatial contingency (Peres-Neto et al. 2012, Beauchard et al. 2022), in which habitat heterogeneity across multiple scales produces fluctuating intensities of environmental filtering (Belyea & Lancaster 1999). In such a highly heterogeneous setting, multiple ecological processes may operate simultaneously, potentially opposing each other out when viewed at a broader scale (Helmus et al. 2007).

A recent study in a contrasting dynamic environment in the Dutch sector of the North Sea with similar bathymetry found that strong physical forces in high-dynamics areas that should reflect stronger environmental filtering reduced overall soft-bottom macrofauna functional richness but paradoxically increased functional dispersion (Beauchard et al. 2022). In other words, the harsh conditions might filter out certain traits, yet those that remained spanned a wide range of reproductive strategies modalities, contributing to unexpectedly high trait divergence, implying that the interacting effects of spatial contingencies, hydrodynamic disturbance and habitat heterogeneity create localized pockets of niche availability, allowing multiple trait combinations to coexist (Beauchard et al. 2022). These findings align with our results. For instance, some coarse sediment inner shelf sites with higher calcium carbonate content showed a distinct association with traits that collectively set them apart from other inner shelf sites.

On the other hand, as hypothesized, we observed an overdispersed pattern in the outer shelf annelid assemblages, which are associated with deeper and colder sites, physically more stable conditions, and less severe environmental filters. Biotic interactions, such as competition, can theoretically increase or reduce functional dispersion under similar abiotic tolerances (Mayfield & Levine 2010); their role has been expected in stable soft-bottom habitats (Sanders 1968, Flach 2002). Although the total amount of organic matter (OM) was moderately lower on the outer shelf – potentially supporting competitive effects – competition, if present, did not converge around a single limiting resource that would produce clustering. Instead, species appear to occupy multiple resource niches, consistent with the observed functional overdispersion (MacArthur & Levins 1967, Webb et al. 2002, Cavender-Bares et al. 2009, Pavoine & Bonsall 2011). However, in soft-bottom environments, interspecific competition is generally weak and rarely drives drastic changes in community structure (Peterson 1979, Wilson 1984, 1990, Grant 2000, McClain & Schlacher 2015). Moreover, to assert that competition is a primary driver in macrofaunal community assembly would require a way to directly quantify such biotic interactions (Gross et al. 2022).

Our data indicate that total organic matter (OM) was moderately lower on the outer shelf, which could suggest potential competitive effects. However, our OM measurements may not fully capture resource availability. In the same area, a recent study using more sensitive metrics found that higher resource concentrations on the inner shelf occur only between the 25- and 50-m isobaths (9.6–14 mg g^{-1} of total organic carbon, TOC), whereas shallower depths (<25 m) show TOC ranging from 0.4 to 2.1 mg g^{-1}. In contrast, the 75- and 100-m isobaths – which characterize the outer shelf – present similar higher TOC values (2.1-5 mg g^{-1}; Carreira et al. 2013). The authors further argue that, given the favorable quality at those outer shelf isobaths – moderate to high chlorophyll-a, phaeopigments, and biopolymeric carbon – the available organic matter can support benthic communities (Carreira et al. 2023). Moreover, a literature synthesis indicates that while greater food quantity generally increases benthic abundance, trophic groups respond differently to quality parameters, underscoring the significant influence of food quality on benthic community structure (Campanyà-Llovet et al. 2017). Indeed, enhanced resource quality associated with higher hydrodynamic stability has been linked to shifts in annelid assemblages – from dense, opportunistic species to less dense communities with broader morphological and trophic traits (Quintana et al. 2015). Accordingly, all traits recorded in both shelves were present in the outer shelf.

This pattern on the outer shelf aligns with findings from other continental shelf soft-bottom macrofaunal communities, where deeper, low-dynamic habitats supported diverse trait combinations – including both r- and K-strategists (Beauchard et al. 2022). Facilitative processes, such as sediment mixing and bioirrigation by engineer species (e.g., the larger and more mobile Errantia taxa present on the outer shelf), may broaden the available niche space, promoting the coexistence of functionally distinct taxa (Pearson 2001, Mermillod-Blondin 2011, Beauchard et al. 2022). Consequently, the overdispersion observed in the outer shelf likely reflects multiple coexisting species with multiple trait sets maintained by sufficient resource levels and stable hydrographic conditions.

The spatial - particularly bathymetric – changes in the annelid functional dispersion were significantly influenced by gradients in depth and sediment PC2 – a latent variable composed mainly of gradients of mud and organic matter content, and grain selection coefficient. Those are factors known to drive functional diversity of soft-bottom macrofauna, including annelids (Carvalho et al. 2013, Otegui et al. 2016, Van Der Wal et al. 2017, Breine et al. 2018, Wouters et al. 2018, Morais et al. 2019, Sobczyk et al. 2021, Charrier et al. 2023, Gusmao et al. 2022). Mechanistically, changes in depth-stability-associated hydrodynamics can modify levels of turbulence and bottom shear stress, sedimentation processes, light availability, and nutrient delivery and quality, being recognized as critical physical drivers of soft-bottom communities (Quintana et al. 2015, Shimabukuro et al. 2016, Beauchard et al. 2022, Clinton et al. 2024), including evidence from annelid assemblages in the study area (Paiva 1993, Quintana et al. 2015, Shimabukuro et al. 2016). Accordingly, mud-dominated, strongly selected, and organic-rich sediments seem to constrain the set of traits more strongly than poorly selected and often mixed substrates. For instance, depth, organic matter, and sediment texture were primary drivers of soft-bottom macrofaunal functional diversity along a bathymetric gradient in the Gulf of Mexico (Carvalho et al. 2013), and sediment type strongly influenced the functional and taxonomic composition of subtidal North Sea communities (Breine et al. 2018).

As hypothesized, during the austral summer survey – when SACW upwelling reaches the inner shelf – annelid assemblages displayed functional trait overdispersion on both the inner and outer shelves. Historical data (1985-1986) indicate that during part of the austral spring (October), autumn (April), and winter (July), the inner shelf was mainly influenced by Tropical Water (TW) and Coastal Water (CW), without clear stratification (Paiva 1993, Pires-Vanin et al. 1993). However, from December to January, colder, nutrient-rich South Atlantic Central Water (SACW) intrudes and stratifies the water column on the inner shelf, while the outer shelf remains in contact with SACW year-round (Paiva 1993, Pires-Vanin et al. 1993). We found that bottom water temperature emerged as the primary driver of functional dispersion over time, with higher (overdispersed) ses.MNTD values are associated with colder waters. Thus, the functional overdispersion observed in the austral summer across the northern São Paulo continental shelf can be attributed to SACW upwelling, as detected in both shelf sectors during the December/January survey. These findings underscore upwelling as a key driver of overall functional trait dispersion in annelid assemblages, overriding the spatial gradient between the two shelf sectors, most prominently affecting inner shelf assemblages.

Marine community diversity can be limited by the quality of nutrient inputs and energy flow, both of which are tied to ecosystem productivity (Paine 1966, Birkeland 1987, Worm 2002). Productivity in turn shapes biodiversity by modulating species interactions and community recovery after disturbances (Paine 1996), particularly in systems with seasonal pulses of nutrient input that favor r-selected strategies and produce temporal shifts in community structure (Paine 1966, Birkeland 1987, Abrams 1995, Worm 2002). On the inner shelf, especially in April (austral autumn), wind-driven hydrodynamics promote the resuspension of phytoflagellates, which offer lower-quality food for macrofauna (Sumida et al. 2005, Venturini et al. 2011, Quintana et al. 2014, 2015). Under these conditions, small, sedentary, opportunistic deposit-feeding annelids occur in high densities (Quintana et al. 2015, Shimabukuro et al. 2016), aligning with the observed tendency toward trait clustering in annelid assemblages in April.

Conversely, organic matter from diatom blooms during SACW upwelling months has higher nutritional quality (Sumida et al. 2005, Venturini et al. 2011, Quintana et al. 2014, 2015). Along with enhanced environmental stability, this resource input promotes shifts in community composition, reducing overall densities while broadening trophic and morphological attributes, such as larger, more mobile carnivores replacing previously dominant opportunists (Paiva 1993, Quintana et al. 2015). These findings support the idea that seasonal increases in resource availability and quality within a stable environment can facilitate trait overdispersion in the inner shelf, specifically during the December/January survey.

Dispersal-based processes also contribute to this pattern. Meroplankton distribution along the Southeastern Brazilian Shelf shows abundance peaks near upwelling regions (Brandão et al. 2020). Accordingly, massive recruitment of annelids is expected in the Ubatuba region during SACW intrusions, boosting species numbers in a less restrictive, higher-carrying-capacity environment (Quintana et al. 2015, Brandão et al. 2020). This is consistent with studies indicating higher densities of annelid larvae inshore under cool, upwelled waters (Garland et al. 2002, Brandão et al. 2020, Satterthwaite et al. 2021). SACW upwelling has been linked to shifts in community assembly and population dynamics – benthic (Pires-Vanin et al. 1993, Paiva 1993, De Leo & Pires-Vanin 2006, Alves et al. 2014, Melo Júnior et al. 2016, Shimabukuro et al. 2016) and pelagic (Tovar-Faro et al. 2013) – in southeastern Brazil. It also drives changes in relative species abundances and promotes offshore-to-inshore migration, raising taxonomic diversity in regions like Ubatuba (São Paulo) and Cabo Frio (Rio de Janeiro) (Pires 1992, Dos Santos & Pires-Vanin 1999, De Leo & Pires-Vanin 2006).

Indeed, Paiva (1993) noted higher annelid species richness on the inner shelf during December/January, coinciding with SACW upwelling, than at other sampling times. In general, greater species richness monotonically increases functional trait differences within a community (Petchey & Gaston 2006). Accordingly, under SACW upwelling, we recorded annelid trait overdispersion, based on both ses.MNTD and ses.MPD (only for the outer shelf) in both shelf sectors. Moreover, the influx of SACW elevates resource quantity and quality, diminishing the importance of niche-based assembly mechanisms mediated by direct biotic interactions (e.g., hierarchical competition) in driving trait overdispersion in the inner sector (MacArthur & Levins 1967, Mayfield & Levine 2007, Münkemüller et al. 2020). Instead, a dispersal-mediated assembly process seems to connect annelid assemblages regionally across both shelf sectors, a pattern also reported for other phyla (De Leo et al. 2006, Barshis et al. 2011, Brandão et al. 2020). Such a shift suggests that dispersal-based dynamics become more influential, revealing an assembly pattern consistent with expectations for marine macrofaunal communities (Loke & Chisholm 2023).

According to recent work, the many species in a community result primarily from dispersal-based processes like immigration, so niche diversity often remains low relative to total species richness (Loke & Chisholm 2023). In these dispersal-assembled systems, new arrivals may saturate available niches, causing transient co-occurrence and dependence on continual recruitment (“mass effects”). From this standpoint, community assembly theory – together with the well-documented regional upwelling effects – clarifies the shift toward trait overdispersion through the combination of two primary mechanisms: (i) a “mass-effect” influx of annelid species into the inner shelf during December/January SACW upwelling (Brandão et al. 2020), sustained, at least momentarily, by (ii) the elevated environmental stability plus higher-quality nutrients reaching the benthos (Sumida et al. 2005, Venturini et al. 2011, Quintana et al. 2014, 2015, Shimabukuro et al. 2016).

Investigations of macrofaunal community assembly on soft bottoms from a functional perspective remain incipient, particularly under the influence of upwelling. Nonetheless, some studies on soft-bottom communities in upwelling systems have highlighted changes in nutrient quality and the strength of environmental filtering as key factors shaping benthic diversity (Pacheco et al. 2011, Soto et al. 2017, Bon et al. 2021, Sivadas et al. 2021, Passos et al. 2023). The movement of water masses also plays a crucial role in connecting populations at a regional scale (Barshis et al. 2011). Importantly, most such studies focus on Eastern Boundary Upwelling Ecosystems (EBUEs), where severe hypoxia creates oxygen minimum zones (OMZs) (Sivadas et al. 2021). These OMZs demarcate deeper, seasonally upwelling water masses characterized by high organic matter content and hypoxic conditions that favor smaller, microphagous, and opportunistic infaunal annelid genera (Pacheco et al. 2011, Soto et al. 2017, Bon et al. 2021, Sivadas et al. 2021). Conversely, under milder abiotic filtering in normoxic, shallower sites, annelid assemblages typically exhibit larger body sizes and more diversified life strategies (Pacheco et al. 2011, Soto et al. 2017, Bon et al. 2021, Sivadas et al. 2021). In our study, the annelids' functional assembly showed an inverse relationship with depth, primarily reflecting pronounced differences in oceanographic conditions across the region. As well as the strong environmental filtering that seems to cluster traits toward opportunistic, r-selected strategies the previous upwelling studies were consistent with trait overdispersion in the studied system. This pattern likewise appears in non-upwelling moments, revealing a complex interplay of spatial and temporal contingencies in shaping annelid assemblages.

4.3. On the Trait–Environment correlations

The contrasting body plans of Errantia and Sedentaria within Annelida are evolutionarily linked to distinct life strategies and ecological niches, culminating in marked morphological adaptations (Struck 2011, Struck et al. 2015). At a macroevolutionary scale, these differences likely arose in response to shifts from epifaunal, soft-bodied ancestors to infaunal or heavily armored lineages during the Ediacaran-Paleozoic transition (Sepkoski 1981, Darroch et al. 2018). Key factors, such as favourable changes in soft-bottom physicochemical conditions combined with predation pressure, are hypothesized to have favoured the acquisition of burrowing behavior and its associated morphological modifications (Sepkoski 1981, Struck 2011, Parry et al. 2014, Mangano & Buatois 2017, Darroch et al. 2018). In general, Sedentaria is characterized by less complex parapodia, weakly developed appendages, and feeding structures suited to microphagy, often involving suspension- or deposit-feeding with discretely motile, or sessile tubicolous life strategy (Fauchald 1977, Rouse & Pleijel 2001, Otegui et al. 2016, Rouse et al. 2022). Errant annelids, on the other hand, exhibit well-developed appendages, diverse chaetae, and robust pharynges armed with a plethora of sclerotized structures, reflecting a broader feeding spectrum (macrophagy or microphagy), higher motility, and varied sensory organs (Fauchald 1977, Rouse & Pleijel 2001, Struck 2011, Rouse et al. 2022). These morphological disparities align with ancestral body plans hypothesized for the phylum, where the loss or modification of appendages and new chaetae types emerged alongside life-history shifts (Struck 2011, Parry et al. 2014). Such adaptations are related to annelids' exploitation of interstitial environments likely during or before the Precambrian-Cambrian boundary (Struck 2011, Eibye-Jacobsen & Vinther 2012, Parry et al. 2014, Struck et al. 2015, Rouse et al. 2022). Hence, such morphological disparities might carry fitness implications, enabling annelid lineages to persist and occupy previously inaccessible evolutionary spaces (Simpson 1953) and ultimately shaping the course of their evolutionary trajectories (Losos 2011).

In our RLQ analysis, trait-environment associations in annelids ranged from the typical "Errantia" body plan, predominantly on the outer shelf, to two distinct "Sedentaria" body plans on the inner shelf. Notably, specific morphological trait modalities – along with feeding behavior and sediment occupation strategies – were significantly correlated with the first RLQ axis. This supports the notion that morphologically based attributes, when grounded in sound anatomical justification, can serve as reliable "soft" traits, effectively capturing both biotic and abiotic filtering processes of annelid assemblages (Pagliosa 2005, Otegui et al. 2016, Otegui et al. 2023). Their consistent alignment with environmental gradients further underscores the utility of trait-based approaches, especially for evaluating how communities respond to hydrodynamic and sediment texture variations (Pagliosa 2005, Otegui et al. 2016, Otegui et al. 2023). This is particularly relevant for annelids, major components of soft-bottom macrofauna, given the limited biological information available for most species. Consequently, many studies focusing on annelids' functional traits rely on morphological features that are known or presumed to be indirectly linked to survival. Admittedly, the ideal scenario would be to use functional response traits explicitly and directly connected to species fitness (Beauchard et al. 2017, Beauchard et al. 2022). However, achieving this requires detailed species-level biological knowledge – a significant challenge considering the Raunkiaeran shortfall, the widespread deficit of functional trait information (Hortal et al. 2015).

Environmental influences have long been recognized as key drivers of annelid species evolution (Fauchald 1977, Struck 2011, Struck et al. 2015, Weigert & Bleidorn 2016). Plasticity in morphological traits has also been documented under controlled conditions (Lamon & Gage 2000, Grimes et al. 2020), and environmental filtering by sediment texture, salinity, and hydrodynamics often shapes the functional composition of marine and estuarine macrofauna, including annelid assemblages (Morais et al. 2019, Medeiros et al. 2021, Gusmao et al. 2022, Charrier et al. 2023). Body size and morphological features are known to shift in response to environmental gradients (Pagliosa 2005, Otegui et al. 2016, 2023). Many shallow and estuarine annelids share traits associated with opportunistic, r-selected strategies, including smaller body sizes, microphagy, and low motility – characteristics closely tied to Sedentaria (Llodra 2002, Otegui et al. 2016, Morais et al. 2019, Medeiros et al. 2021, Gusmão et al. 2022, Otegui et al. 2023). Core morphological features such as simpler parapodia and an unarmored pharynx reflect evolutionary trade-offs that optimize growth, survival, and reproduction under variable environmental conditions (Rouse & Pleijel 2001, Struck et al. 2011, Parry et al. 2014, Rouse et al. 2022). Hence, morphological traits of marine annelids can be linked to functioning, as "response traits" (Lavorel & Garnier 2002, Beauchard 2022), and have been used to provide critical insights into how species persist under fluctuating habitats (Rivera-Ingraham & Lignot 2017, Medeiros et al. 2021, Otegui et al. 2016, 2023).

Despite this, few studies have explicitly tested the effect of environmental gradients on annelids' morphological traits in combination with behavioral and reproductive characteristics (Pagliosa 2005, Otegui et al. 2016, Wouters et al. 2019). Following the filtering metaphor, these trait complexes can indeed act as "response traits" directly affected by conditions such as substrate composition, salinity, and temperature (Lamon & Gage 2000, Otegui et al. 2016, Morais et al. 2019, Grimes et al. 2020, Medeiros et al. 2021). For example, the performance of filter-feeding structures (e.g., radiolar or tentacular crowns) can deteriorate in small-sized particle (muddy) sediments, diminishing fitness in turbid environments (Shimeta & Jumars 1991, Clinton et al. 2024). Water temperature, salinity, and oxygen levels also significantly influence morphological variation in filter-feeding sedentarians (Otegui et al. 2023). Opportunistic infaunal species, typically with smaller body sizes, thrive in muddy, organic-rich substrates (Otegui et al. 2016, Morais et al. 2019, Medeiros et al. 2021, Charrier et al. 2023). Conversely, errant morphological traits have been frequently linked to coarser sediments (Pagliosa 2005, Otegui et al. 2016, Charrier et al. 2023).

Our results parallel these observations. Sessile suspension feeders with radiolar or tentacular crowns predominated in coarser sediment patches of the dynamic inner sector, whereas opportunistic infaunal genera dominated muddier substrates – aligning with previous findings (Otegui et al. 2016, Van der Wal et al. 2017, Morais et al. 2019, 2021, Gusmao et al. 2022, Beauchard et al. 2022, Charrier et al. 2023). These patterns arise from the environmental heterogeneity in the region, where patches of varying sediment textures act as "habitat templates" (Southwood 1977) that filter distinct Sedentaria and Errantia dominant trait configurations. Hence, our framework underscores the importance of incorporating morphological traits, especially in combination with reproduction, size, and behavioral traits, into marine benthic community studies to disentangle the process underlying assembly patterns. By capturing how form meets function, the combination of these traits offered valuable insights into the mechanisms driving functional diversity and distribution.

5. Conclusion

Our results offer new insights into the assembly of benthic communities in coastal upwelling systems, underscoring the importance of spatial and temporal variation in shaping trait dispersion. Depth-related hydrodynamic stability and sediment texture emerged as key drivers of spatial (particularly bathymetric) variation in annelids' functional assemblages, with environmental filtering exerting a non-negligible influence modulated by spatial contingency. Most notably, the upwelling of South Atlantic Central Water (SACW) was the primary driver of community assembly in the inner shelf, periodically promoting functional trait overdispersion. This underscores that functional overdispersion can indeed be generated by ecological-scale processes, a dynamic that was especially evident when seasonal shifts in trait dispersion closely tracked SACW upwelling and retraction.

These findings highlight the need to account for upwelling events in biodiversity monitoring and environmental management programs, as communities sampled during these periods can differ markedly from those observed at other times of the year. Moreover, our study demonstrates the value of a functional dispersion framework in exploring community assembly beyond eastern boundary upwelling ecosystems, as well as the usefulness of morphological traits for addressing ecological questions (Otegui et al. 2016). Complementary metrics such as MPD and MNTD were particularly helpful in capturing different facets of functional assembly processes: for instance, the effects of the SACW upwelling approached significance for ses.MPD in the inner shelf, whereas ses.MNTD showed high significance levels for the survey months with SACW upwelling and posterior retraction, in line with the expectation that the arrival and temporary maintenance of new species would be better captured by a metric more sensitive to changes at the tips of the functional dendrogram. Altogether, these approaches provided a comprehensive view of how environmental variation and dispersal dynamics interact across spatial and temporal scales to assemble soft-bottom macrofaunal communities.

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Figures

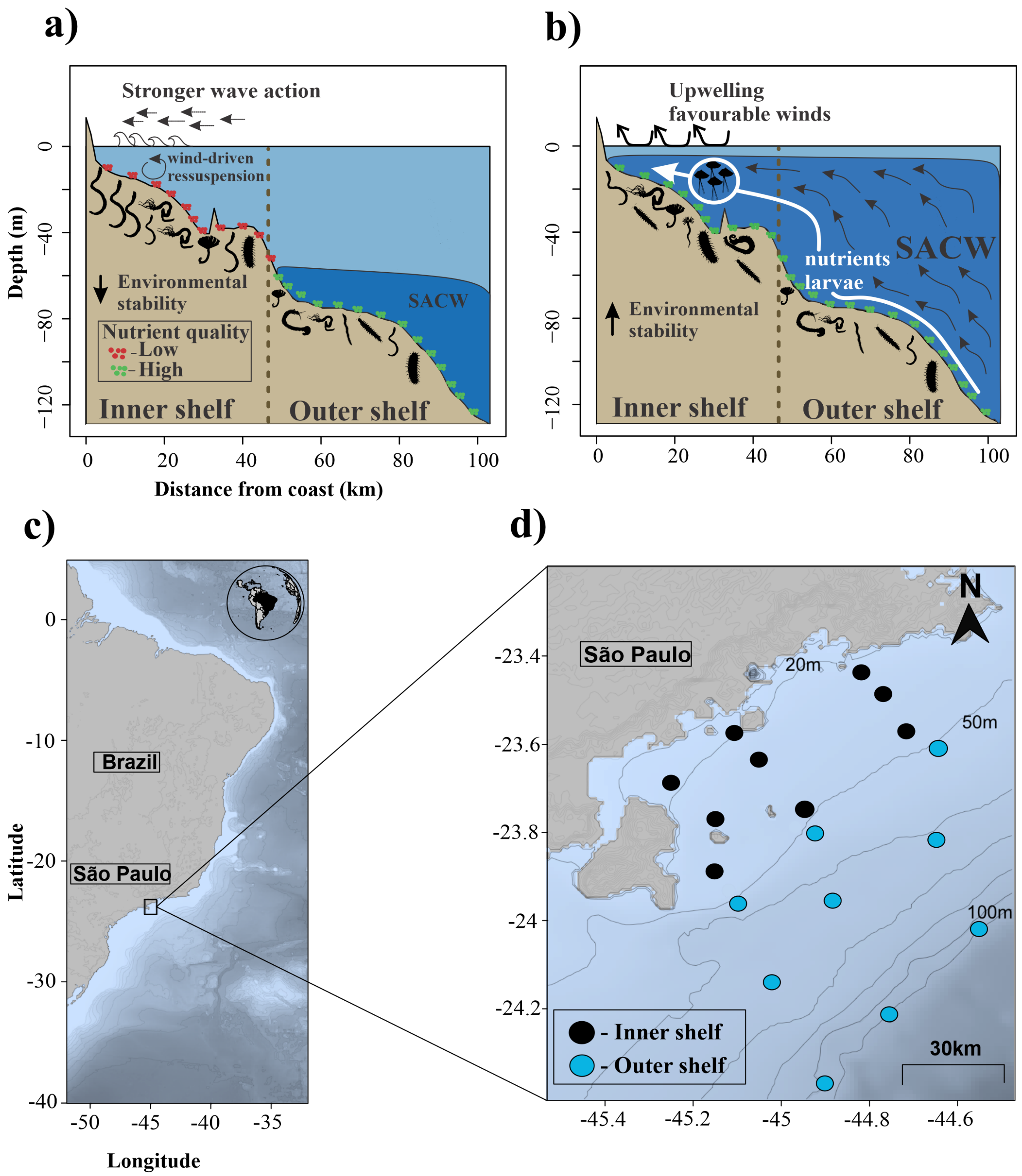

Figure 1. Bathymetric profile of the Ubatuba system (a-b) and sampling area (c-d). We hypothesized that the inner sector would present clustered annelid assemblages due to its environmental instability, in contrast to the hydrographically stable and nutrient-rich outer sector (a). However, with the upwelling of South Atlantic Central Water (SACW), we expected both sectors to present functionally overdispersed annelid assemblages, as its intrusion enhances productivity and favours larval dispersal towards the inner sector, culminating in higher quality nutrient availability, increased recruitment levels, and environmental stability (b). Sampling points were arranged in three parallel transects following a depth gradient, characterizing the internal (black dots) and external (blue dots) shelf sectors (d).

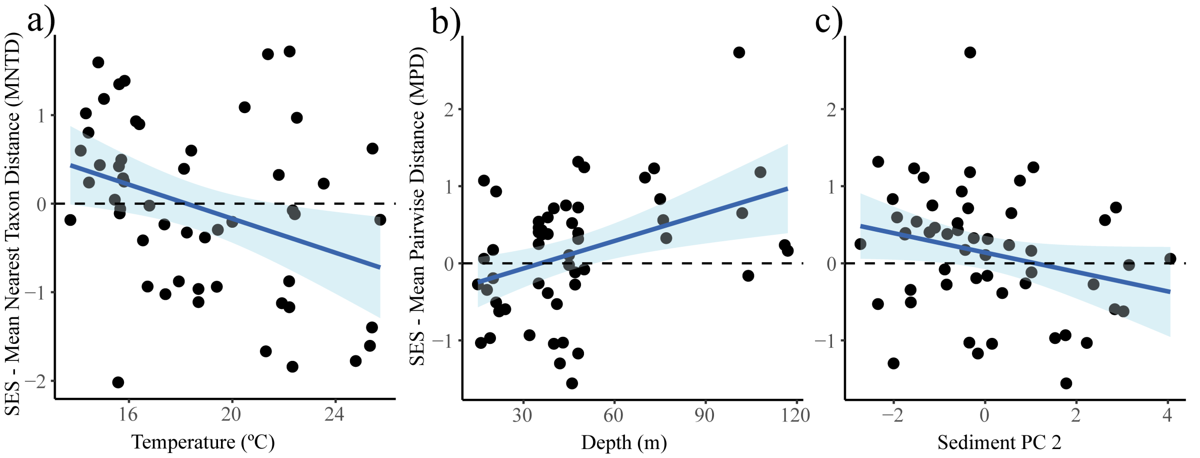

Figure 2. Effects of selected variables on annelid trait dispersion patterns, which are represented by the standardized effect sizes (SES) of the Mean Nearest Taxon Distance (MNTD) and Mean Pairwise Distance (MPD) trait dispersion indexes. The ses.MNTD values decrease as bottom water temperature (°C) increases (a). On the other hand, ses.MPD values increase with site depth (m) (b), and decrease with sediment PC2 (c), which accounted for the most positive variation in sediment selection coefficient, organic matter, and mud content.

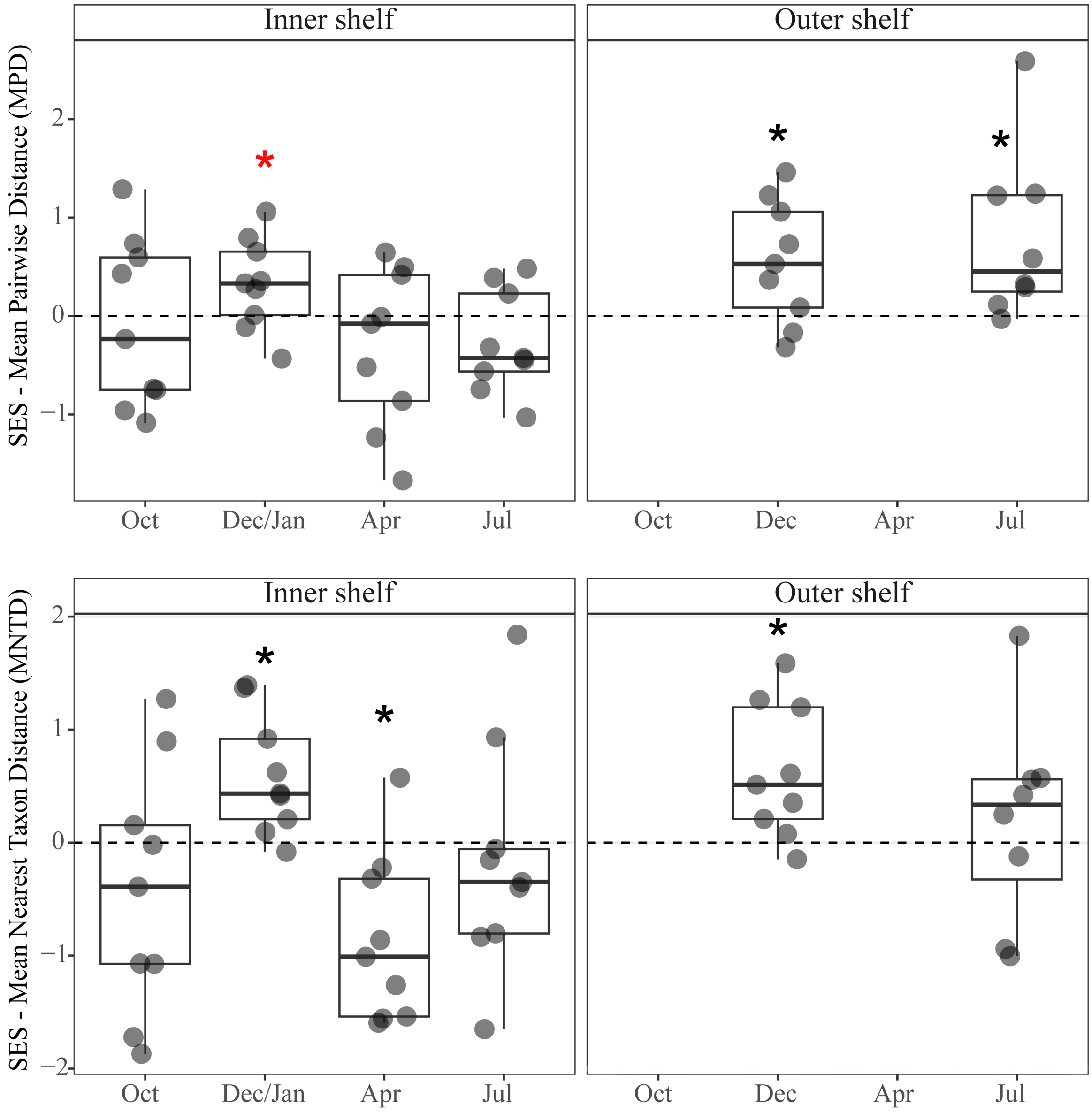

Figure 3. Annelid trait dispersion patterns across shelf sectors and months. The standardized effect sizes (SES) of the Mean Pairwise Distance (MPD) values were significantly overdispersed (positive and different from zero) in December and January within the inner sector (a), whereas in the outer sector, overdispersion persisted throughout the year (b). Similarly, The SES of the Mean Nearest Taxon Distance (MNTD) values were significantly overdispersed in December and January in both the inner (c) and outer sectors (d). However, significant clustering (SES values negative and different from zero) occurred only in the inner shelf during April (c). Abbreviations: Apr = April; Dec = December; Jan = January; Jun = June; Oct = October; * = SES values significantly different from zero. * = SES values approached significance (*p* = .0590)

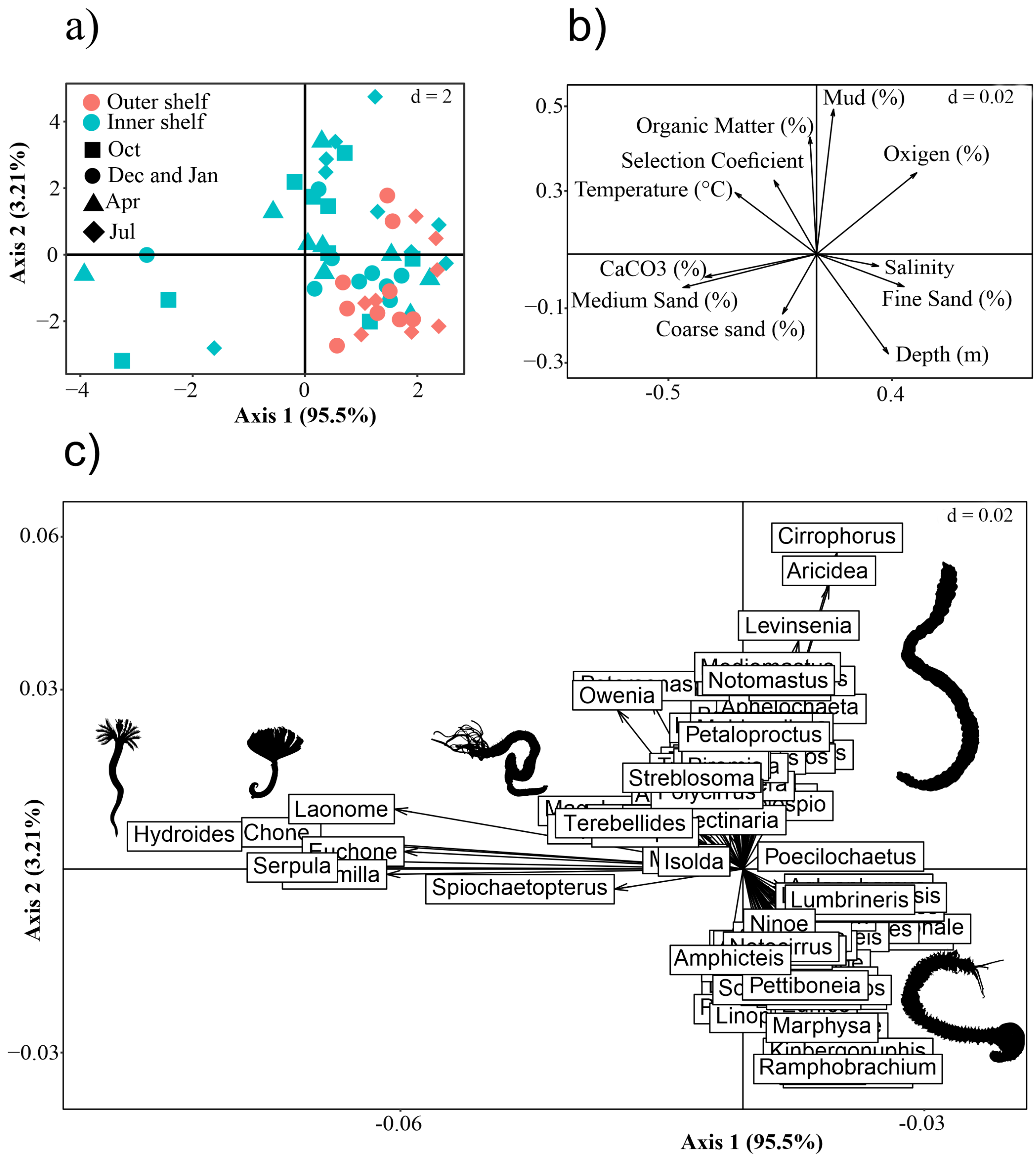

Figure 4. RLQ ordination analysis output shows differences among sectors (a), and the relative influence of environmental variables (b) on the abundance of marine annelid genera (c), The three eco-morphological groups—Errantia, Sedentaria I "Scolecida-like," and Sedentaria II "Sabellida-like"—are shown (c), with their silhouettes obtained under a Creative Commons license (CC0 1.0).

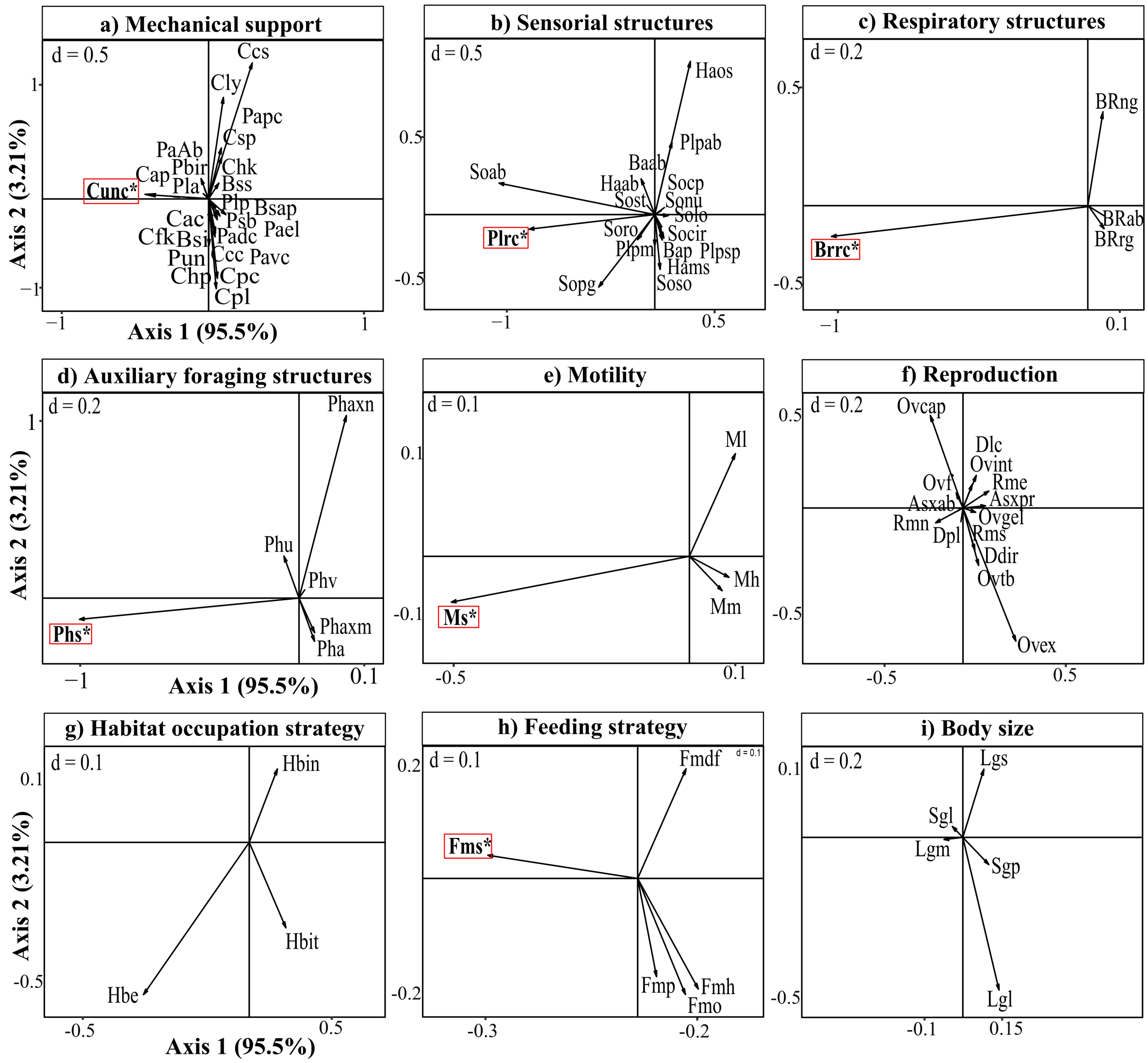

Figure 5. RLQ ordination output for annelid traits. Only the morphology (a-d) and feeding strategy (h) traits presented modalities significantly correlated with the RLQ axis 1, which are highlighted in red. Abbreviations: Asxab = Asexual reproduction absent; Asxpr = Asexual reproduction present; Baab = Body appendages absent; Bap = Body appendages present; Bss = Body surface smooth; Bsi = Body surface intermediate; Bsap = Body surface heavily covered; Brab = Branchiae absent; BRrg = Branchiae regionalized; BRng = Branchiae not-regionalized; BRrc = Radiolar Crown as respiratory structure; Ccs = Chitin Shield chaetae, Cpc = Pectinate chaetae, Chp = Harpoon chaetae; Cfk = Forked chaetae; Cac = Aciculae; Cap = Capillary simple chaetae; Chk = Hooks; Cunc = Uncini; Ccc = Compound chaetae; Cly = Lyrate chaetae; Csp = Spines, Cpl = Paleae; Dpl = Planktotrophic larvae; Dlc = Lecithotrophic larvae; Ddir = Direct development; Fmdf = Deposit-feeder; Fms = Suspension-feeder; Fmo = Omnivorous; Fmh = Herbivorous; Fmp = Predator; Hbe = Epifaunal; Hbit = Interface dweller; Hbin = Infauna; Haab = Head appendages absent, Haos = Head appendages only as a single structure, Hams = Head appendage as a multiple structures; Lgs = Small body length; Lgm = Intermediate body length; Lgl = Large body length; Ms = Sessile; Ml = Low motility; Mm = Medium motility; Mh = High motility; Ovf = Freespawning; Ovex = External brooding; Ovint = Internal brooding; Ovtb = Brooding inside tube; Ovcap = Brood within egg capsules; Ovgel

= Brooding within gelatinous egg masses; Pha = Armoured pharynx; Phu = Unarmoured pharynx; Pun = Unirrami parapodia; Psb = Sub-birrami parapodia; Pbir = Birrami parapodia; PaAb = Parapodial appendages absent; Padc = Dorsal cirri; Pavc = Ventral cirri; Pael = Elytra; Papc = Parapodial crests or plates; Plp = Parapodial lobes or lamellae present; Pla = Parapodial lobes or lamellae absent; Phs = Simple tube pharynx; Phv = Ventral pharynx; Phaxn = Axial non-muscular pharynx; Phaxm = Axial muscular pharynx; Plpab = Palps absent; Plpsp = Single pair of palps; Plpm = multiple palps; Plrc = Radiolar crown as modified palps; Rmn = None reproductive modification; Rme = Epigamy; Rms = Schizogamy; Soab = Sensory organs absent; Sonu = Nuchal organs; Soso = Segmental or interramal photoreceptors; Sope = Peristomial photoreceptors; Soro = Radiolar photoreceptors; Sopg = Pygidial photorecptors; Socp = Cephalic photorecptors; Solo = Lateral organs; Socir = Cirri (Prostomial, Peristomial, Parapodial, Pygidial); Sost = Statocyst; Sgl = less than 100 body segments, Sgp = plus than 100 body segments; * = trait modality significantly correlated with RLQ first axis.