

Deciphering benthic ecosystem functioning and resilience in a major port and marine protected area via the multi-trait approach.

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Abstract

The preservation of ecosystem functioning of coastal zones, in face of increasing environmental stressors and species extinctions, relies on the functional redundancy and inherent resilience of its inhabitants. To compare the benthic functioning and resilience of a disturbed area with a relatively less impacted area, a study was conducted in Mumbai Port and Malvan Marine Protected Area (MPA), which exhibited contrasting characteristics. The hypothesis posited that the anthropogenically influenced Mumbai port would exhibit lower functional parameters and resilience compared to Malvan. Overall, the MPA presented higher species richness and functional diversity with a greater presence of sensitive species, while Mumbai was dominated by the presence of opportunistic species, as anticipated. However, our findings demonstrated that despite varied trends in species diversity metrics, in both the coastal areas, the resemblance in benthic functioning was high due to similarity in dominant trait profiles. Surprisingly, Functional Richness was higher at Mumbai, while Functional Evenness, Divergence and Dispersion were comparable at both sites. The resilience, as quantified by Functional Redundancy, was also comparable at both areas attributable to the presence of clusters of species with similar traits and a low occurrence of rare traits. The combination of traits observed in both areas was influenced by the extant environmental conditions, as revealed by RLQ analyses. This study underscores the valuable insights provided by the application of Biological Trait Analysis (BTA) tool in deciphering the relationship between species diversity and ecosystem functioning, as well as the resilience capabilities of ecosystems subjected to varying levels of perturbation. Moreover, the incorporation of functional diversity indices yielded valuable inferences regarding ecosystems resilience, which can aid future ecosystem management strategies.

Keywords: Macroinvertebrates, biological trait analysis, functional diversity, resilience, ecosystem functioning, coastal .

1. Introduction

Unprecedented changes in marine ecosystems caused by several anthropogenic stressors can leave an irreversible impact on biodiversity and ecosystem services. Abrupt changes in the environment often lead to the loss of ecosystem functions and can significantly reduce the resilience of the ecosystem (Cardinale et al., 2012; Alestra and Schiel, 2015). Given this, keeping track of the benthic ecosystem and its resilience is essential to protect the marine ecosystem and conduct appropriate environmental management (D'Alessandro et al., 2020; Festjens et al., 2023). The macroinvertebrates are described as essential bio-indicators as they respond to differential sources of stressors, perform various forms of feeding at different trophic levels, and have tube-building and bioturbation activities thereby mediating exchanges between sediment and water column (Mestdagh et al., 2018; Kim et al., 2019; Bhowmick and Mandal, 2020). Indeed, the traditional taxonomy-based approach of monitoring has been widely implemented with the focus being on the composition of communities (Llanos et al., 2020).

The limitation of structural measurements is that they are simply based on taxonomic identities that provide inadequate information on the ecosystem functioning. Recently, a steady increase in the incorporation of functional metrics in environmental monitoring, that infer the ecosystem processes and provide an in-depth understanding of the species communities' responses to ecosystem alterations, is observed (D'Alessandro et al., 2020). The macrofaunal functional information is a crucial determinant factor of ecosystem functioning that indicate the species relationship to specific benthic processes rather than species composition as such (Rodil et al., 2020). It provides a direct link to functions related to life history, morphological and behavioural traits via biological trait analysis (BTA) which could help in predicting the impact of stressors on the ecosystem functioning (Tsikopoulou et al., 2022). BTA is based on the multi-trait approach that combines the taxonomic species data with their functional traits (Tonroos and Bonsdorff, 2012). The functional trait approach also determines the stability and ecosystems' resilience against inimical environmental stressors (Darr et al., 2014).

An alternate method to measure the ecological importance of species in a benthic community is the use of functional diversity metrics (D'Alessandro et al., 2020). These indices can be further assessed to point out the different aspects of the functional matrix. For instance, when the species assemblages differ largely in their functional roles, higher functional diversity indices are to be expected (Llanos et al., 2020; Paganelli et al., 2012). As proposed by Mason et al. (2005), functional diversity comprises three independent components that describe the species distribution in terms of their biological roles in the functional space (Pedelacq et al., 2022): functional richness, functional

evenness and functional divergence (Villéger et al., 2008). Also, an additional metric, functional dispersion was proposed by Laliberté and Legendre (2010), which is a multidimensional index based on trait dispersion.

Functional redundancy is the ability of an ecosystem to stabilize and maintain its functions under stress (Bates, 2019; Wang et al., 2023). This concept is based on the fact that the resilience of ecosystems is dictated by the similarity in the functional roles of the existing species rather than the species composition per se (Oliver et al., 2015). Depending on the functional characteristics of the species, the ratio of functional diversity to species diversity can fluctuate to give varying trends of low or high functional redundancy (van der Linden et al., 2012, Dias et al., 2022). For instance, low redundancy indicates that the extant species have unique functional roles leading to the loss of functions upon species loss (Calapez et al., 2018). High functional redundancy implies that several species perform similar biological roles in the environment which maintain the ecosystem functioning, even in the absence of some species (Kokarev et al., 2017). This concept provides information on the systems resilience, wherein functional redundancy epitomizes the stability in maintaining the ecosystem functions against multiple stressors. Therefore, species with the best-suited traits are expected to be favoured under certain environmental conditions that mostly pass through the environmental filters indicating the stability in any ecosystem (Grime, 2006; Breton et al., 2017). That functional redundancy indeed engendered superior ecosystem resilience and stability has been established by Biggs et al. (2020).

Undisturbed areas are expected to have more species occupying similar functional space leading to trait overlap and higher redundancies whereas functional redundancy tends to diminish in areas of stress (Wang et al., 2023). Marine protected areas (MPAs) are a biodiversity conservation measure to stall the accelerating rates of marine biodiversity losses. These specialised areas provide protection against various disturbances by fostering ecosystem resilience and stability of resident biotic communities (Mellin et al., 2016). Biological assemblages of MPAs that function as specialized spatial refugia, are assumed to be highly diverse and resilient to external perturbations (Bates, 2019). In such areas, the functional redundancy is expected to be high due to subdued interspecific competition and higher species diversities than functional diversities. This expectation is rooted in the fact that highly diverse communities may have several common functions rendering them highly redundant, thus providing a buffer against possible species loss (Peterson et al., 1998). Conversely, in stressed areas like major Ports, lower species diversities than functional metrics may drive lower functional redundancy of communities (Wang et al., 2023).

The tropical Indian coast is subjected to multifarious anthropogenic stressors resulting in disturbance of benthic communities and ecosystem functioning (Dias and Sukumaran, 2023). Conversely, this geographical zone also supports immense biodiversity and has well-demarcated marine protected areas. Thus, the coastal zone presented divergent scenarios, wherein it was possible to gauge how the benthic functional responses in terms of resilience to stressors would vary in communities of an impacted area versus a protected zone. Considering the paucity of available literature on benthic functioning and functional redundancy in the Indian coastal waters, a study was undertaken wherein two areas with contrasting characteristics along the Northwest coast of India were chosen: Mumbai Port and Malvan Marine Protected Area (MPA). A previous work carried out in these study areas was related to the ecological quality status using taxonomy-based and genomic-based benthic biotic indices (Dias and Sukumaran, 2023). This work concluded that Mumbai was in the ‘Good to Moderate’ Ecological Quality Status (EcoQS) and was marked by the presence of both opportunistic and sensitive species, while Malvan fell in the ‘High to Good’ EcoQS with more representation of sensitive species. As biotic indices are based on species identity and their ecological sensitivity covers only one aspect of the ecosystem functioning, functional studies were considered essential for enhancing environmental management decisions. Keeping this in mind, the objectives of the current study were to: (1) examine in detail the species and functional metrics of an anthropogenically impacted area (Mumbai) vis-a-vis a marine protected area (Malvan), (2) determine how the diverse environmental settings of both study areas influenced the functional traits using biological trait approach (BTA) and (3) compare the ecosystem resilience in a perturbed area and a relatively undisturbed area. It was hypothesised that (i) The functional trait profile of organisms inhabiting an anthropogenically affected zone will consist more of opportunistic traits due to a higher number of r-selected species as compared to an MPA which will have abundant k-selected types and sensitive traits (ii) the modified region will have lower species diversity than functional diversity resulting in low functional redundancy and ecosystem resilience. Conversely, a less impacted area will have high functional redundancy and ecosystem resilience as a consequence of higher species diversity as compared to functional diversity (Fig. 1). The results of the study are expected to improve the understanding of how the biodiversity-ecosystem functioning relationships of tropical coastal zones would vary under altering degrees of anthropogenic stress. The study further evaluated ecosystem resilience and stability, properties that are pivotal to the sustenance of coastal systems against a rapid decline in species diversity occurring due to increasing natural and anthropogenic perturbations.

2. Materials and methods

2.1 Study site

Maharashtra covers a coastal stretch of about 720 km along the North West Indian coast, where Mumbai and Malvan were selected as the two study locations (Fig. 2). Mumbai (18°52' 26.32" N 72°51' 31.03" E) region has two major ports, the Mumbai Port being the busiest port contributing largely to the country's trade (Mandal and Harkantra, 2013). The Mumbai port is a semi-enclosed basin that opens to the Arabian sea with a width of 15km at the mouth narrowing upwards with a length of 27 km (NIO, 2018). The main navigational channel is maintained at 11 m. The circulation in the port region is influenced by the tides that are mainly semi diurnal. Mumbai port receives loads of industrial wastes, sewage and other effluents and many anthropogenic activities take place in these waters. Malvan (16°02' 48.48" N 73° 27' 24.16" E) is a marine protected area (MPA) known to have relatively healthy marine conditions and is characterised by coralline patches with high biodiversity. The total area of the sanctuary is 29.122 km² that includes the core zone and buffer zone with an area of 3.182 km² and 25.94 km² respectively. A popular Sindhudurg Fort is located on the south side of the entrance of the Malvan MPA. The surrounding region of Malvan is an open coast ecosystem dominated by rocky shoals with intermittent sandy beach (NIO, 2018). There is no industrial effluent release or any point source discharges in this region. During recent years, the Malvan coast has been exposed to the ongoing anthropogenic activities such as fisheries, urbanisation and tourism activities (Vijapure et al., 2019; Dias et al., 2023). Both the study locations experience typical tropical weather marked by three different seasons: pre-monsoon, monsoon and post-monsoon that occur from March to May, June to September and October to February respectively.

2.2 Study survey design and processing

Sampling was carried out during three consecutive seasons during pre-monsoon, monsoon and post-monsoon at both locations in the year 2017-2018. During each season, a total of 18 stations were covered: 12 stations at Mumbai and 6 stations at Malvan. For measurement of the physico-chemical parameters, bottom water was collected in duplicates using a Niskin sampler. After collection, dissolved oxygen (DO) in water was first fixed immediately with Winkler's A and Winkler's B reagents and were estimated by adopting the Winkler's titrimetric method according to the procedure given by Grasshoff et al. (1999). Salinity was measured using AUTOSAL salinometer (GUILDLINE Instruments Ltd., Canada) and was calibrated with International Association for the Physical Sciences of the Oceans (IAPSO) standard seawater with salinity of 34.995 (Ocean Scientific International Ltd., UK). For the analysis of SS, a known volume of water was filtered through a pre-

weighted 0.45 µm millipore membrane filter paper, later was dried and weighed again for post weight. Rest of the water samples were stored in ice post collection and analysed immediately in the laboratory for nutrients such as nitrates (NO₃⁻-N), nitrites (NO₂⁻-N) and ammonia (NH₄⁺-N) following the standard procedures described by Grasshoff et al. (1999). Additionally, sediments were sampled for the analyses of total organic carbon (TOC) and sediment grain size using a van Veen grab (0.04m²). These samples were further dried in the oven at 85°C for TOC analysis, homogenized with the aid of agate mortar and pestle, and measured through a TOC analyser (make of SHIMADZU SSM-5000A series). Grain size analysis was carried out following the method of wet-sieving pipette for sand, silt and silt composition (Buchanan, 1984). Collection of sediment samples for macrobenthos were made in triplicates using a van Veen grab wherein, 216 grabs in total were obtained from 18 stations during the three sampling surveys. The sediment samples were sieved immediately using a sieve with mesh size of 0.5 mm, preserved in 5% formalin after staining with rose bengal for taxonomic identification. The stored macrobenthic samples were further sorted, enumerated and identified up to species level with the aid of available literature.

2.3 Biological Trait analysis (BTA)

To determine the ecosystem functioning of the macrofaunal assemblages at both Mumbai and Malvan areas, a suite of 10 biological traits classified in to 42 modalities were chosen (Table 1) with emphasis on characteristics such as behavioral - motility, feeding mode, living habitat, bioturbation, position in sediments; morphological - body size and morphology; and life-history life span and mode of reproduction. Additionally, the ecological sensitivity of the species was also taken into account under trait AMBI ecological group to provide explicit details on their sensitivity to stress. The trait information was acquired via observation results for species trait 'size' and other various sources of literature such as research articles (Macdonald et al., 2010, van der Linden et al., 2012; Queiros et al., 2013; Darr et al., 2014; Jumars et al., 2015), online information from various functional trait databases: Biological Traits Information Catalogue (BIOTIC, MarLIN, 2006), Encyclopaedia of life (EOL, <http://eol.org>), Polytraits (a database on biological traits of polychaetes (lifewatchgreece.eu); (Faulwetter et al., 2014), and AZTI Marine Biotic Index - AMBI program v.5.0 (<http://www.azti.es>); (Borja et al., 2000). In case information on traits of species were missing, the functional trait attributes of the similar genus or closest phylogenetic related species information were considered (Dias et al., 2022). An approach based on fuzzy codes was adopted wherein a score range of 0 to 3 was employed to each species; 0 implying absence of affinity and 3 indicating high affinity to the trait (Chevenet et al., 1994; Statzner and Bêche, 2010). When information on a

particular trait for any species was lacking, fuzzy coding score zero was assigned to all the modalities under that particular trait.

2.4 Data Analyses

Firstly, univariate analyses were carried out on the macrobenthic species abundance data to measure the S - number of species; d - Margalef richness index; J' - Pielou's evenness index and H' - Shannon-Weiner Index. The univariate indices and multivariate analyses such as non-metric multidimensional scaling (nMDS) which was based on Bray-Curtis similarity matrix were carried out using the macrobenthic species abundance dataset on the PRIMER v.7 software (Clarke and Gorley, 2015). Physico-chemical variables, univariate and functional metrics were tested for normality to assess differences between Malvan and Mumbai. Non-parametric data were $\log_{10}(x+1)$ transformed. When transformation failed to normalise the data, the non-parametric Wilcoxon signed rank test ($P>0.05$) was applied. Unpaired t-test was performed for normally distributed ($P>0.05$) data set. All analyses were conducted using Statistica 7. Functional diversity (FD) was also measured at each station as the expression of different functions exhibited by the macrobenthic species (Petchey and Gaston, 2002). The following FD indices were also computed using the FDiversity software (Casanoves, 2011) from the trait by station matrices for both Mumbai and Malvan areas separately in the open source software R v. 3.6.3 (R Core Team, 2020) for which the "FD" package was used (Laliberté and Legendre, 2010; Casanoves et al., 2011).

(i) Functional Richness (FRic) - is the volume occupied by a given species community within the functional space

(ii) Functional Evenness (FEve) - is the regularity of the species abundance distribution within the functional trait space

(iii) Functional Divergence (FDiv) - is the distribution of the species abundances along the functional axis within the trait space

(iv) Functional Dispersion (FDisp) - is the distance between the individual species and the centre of the functional trait space.

The ratio between FD and H' (FD/H') was calculated to assess the resilience of the ecosystem (FR-functional redundancy) (van der Linden et al., 2012). Furthermore, a regression analysis of FD and H' was plotted for both the areas to determine the relationship between the two parameters (Kokarev et al., 2017; Dias et al., 2022). Thus, the slope close to 1 signified strong relationship or low redundancy, indicating that each species played a unique functional role, whereas slope close to zero

suggested weak relationship or high redundancy conveying those multiple species performed similar functional roles (Kokarev et al., 2017).

We employed RLQ to investigate the links between macrobenthos abundance, functional traits and physico-chemical variables following Doledec et al. (1996). RLQ ordination was useful to explore the information in three tables: R table (physico-chemical parameters); L table (species abundance) and Q table (functional traits) (Dray et al., 2014). Correspondence ordination analysis (CA) was employed on the table L and a principal component analysis (PCA) was applied to the Q table, while Hill-Smith analysis was used on the R table (Dray and Dufour, 2007; Dray et al., 2014). The RLQ analyses were carried out on all the tables simultaneously to estimate the correlations between the functional traits and abiotic variables by computing a crossed arrangement matrix of species abundances. The RLQ analyses were performed using the R software version 3.5.1 (R Development Core Team, 2018) with “ade4” package (Dray and Dufour, 2007).

3. Results

3.1 Physico-chemical variables and macrobenthic taxonomic structure

The physico-chemical variables for the two sampled areas are listed in Table 2. The average salinity was 31.9 ± 4.3 at Mumbai and 32.6 ± 1.8 at Malvan. Decreasing trend of salinity was observed from outer to the inner stations of Mumbai, whereas spatial variations in salinity at Malvan were minimal. Mumbai had significantly higher concentrations of nutrients and suspended solids as compared to Malvan (Table 2). On the other hand, Malvan registered significantly higher values of dissolved oxygen (av 5.6 ± 1.7 mg l⁻¹) than in Mumbai (4.3 ± 1.1 mg l⁻¹). The sediment granulometry was composed of mostly silt in Mumbai (av 73.3 ± 21.8) whereas sand was the predominant constituent of sediments at Malvan ($77.6 \pm 35.5\%$). The TOC content was variable in both the areas highest being in Mumbai (2.0 ± 0.5 %) as compared to Malvan ($1.6 \pm 0.9\%$). Station 4, which was located in the offshore region, had higher nitrites, clay, TOC as compared to other stations of Malvan (Table A.1). Nearshore stations of Malvan (1, 2,5,6) had higher DO with sandy bottoms. The sediments in the Mumbai Port were constituted mostly by silt. Stations located in the inner Mumbai Port (1-9) had higher nitrites and nitrates. Lower DO values were observed in stations 1-5 located at inner zone of the Port.

A total of 62,923 individuals belonging to 84 taxa in Mumbai and 115 taxa in Malvan were recorded during all three seasons. Overall, the polychaetes largely dominated the macrobenthic community in both the areas. The most dominant species that dominated Mumbai were the polychaetes, *Paraprionospio patiens* (18.2%) and *Cossura coasta* (10.9%), whereas Malvan had the

dominant presence of *Cossura coasta* (9.1 %) and *Mediomastus* sp. (8.7%). The other predominant group, Amphipoda, was represented by *Cheiriphotis megacheles* (5.1%) at Mumbai. The cumacean, *Iphinoe* sp. - 8.6 % was the next prevailing group at Malvan. As per Table 3, all the univariate indices (N, S, d and J') presented significantly higher values at Malvan than Mumbai. The average species diversity index (H') was a little higher at Malvan though not significantly. The nMDS plot, based on species similarities, portrayed that there was considerable overlap of stations belonging to all three seasons in both the areas indicating no clear seasonal trends (Fig. 3).

3.2 Macrobenthic functional structure and redundancy

The functional composition of 10 traits sub-divided into 42 modalities varied considerably among the stations in both Mumbai (Fig. A.1) and Malvan (Fig. A.2). While most of the species were non-motile/semi-motile forms at Mumbai, Malvan had a good proportion of all types of motility trait. Deposit feeders followed by suspension feeders dominated the macrobenthic communities at both study areas. Mumbai was characterised by the presence of burrow-dwellers followed by tube-dwellers. Conversely, Malvan had more tube-dwellers followed by burrow-dwellers and free-living forms. The macrobenthic assemblages of both the areas were commonly dominated by large to small sized, soft-bodied, surface depositors, gonochoristic, infaunal species with medium lifespan. The ecological sensitivity indicated that most species belonged to second-order opportunistic group in Mumbai with sensitive and indifferent species occurring at some stations, while Malvan was dominated by sensitive species at most of the stations followed by second-order opportunistic species.

The functional diversity indices showed variable trends in Mumbai and Malvan (Table 3). The mean FD value in Malvan was slightly higher (2.1 ± 0.2) as compared to Mumbai (1.9 ± 0.4), though this increment was insignificant (Table 3). The other functional indices (FEve, FDiv and FDisp) displayed similar values at Mumbai and Malvan. FRic was higher at Mumbai and nil at Malvan, though the locational differences were not statistically significant. The higher FRic values at Mumbai were mostly observed at stations 5 and 8 (Table A.2). The functional ratios produced a mean value of 0.8 for both Mumbai and Malvan. In view of this, a linear relationship between H' and FD was obtained (Figs. 4a and b) with a slope value of 0.28 in Malvan and 0.43 at Mumbai.

3.3 RLQ analyses

For Mumbai (Fig. 5), the first two RLQ axes explained a total inertia of about 85.9 % of all the tables where, the first axis of RLQ contributed about 75.3% and second RLQ axis contributed about 10.8% of the total variance (Table A.3). The left of the first RLQ axis indicated that the

modalities such as swimmers, crawlers, burrowers, surface depositors, free-living and sensitive to disturbance (Fig. 5a), mostly corresponded to species like *Neanthes glandicincta*, *Syllis* sp. and few pelecypod species (Fig. 5b) that were associated with an environment having higher salinity, DO and $\text{NH}_4^+\text{-N}$ (Fig. 5c). The positive part on the right of the first RLQ axis disclosed that certain traits (non-motile/semi-motile, large size, upward conveyors, deposit feeders, soft-bodied, infaunal, second-order opportunistic and tolerant to disturbance) belonging to *Cossura coasta*, *Lagis koreni*, *Isolda pulchella*, *Polycirrus swakopianus*, *Prionospio cirrifera*, *Prionospio* sp., *Paraprionospio patiens* and *Paraprionospio* sp were largely correlated with high nitrates in the inner stations. The bottom (negative) part of the second RLQ axis indicated that the traits like diffusive mixers, medium size, scavengers, herbivores, sequential hermaphrodite, asexual reproduction, first order opportunistic and indifferent to disturbance belonging to *Sigalion capensis* and *Cirratulus* sp were favoured by predominantly clay/sand substrata and high SS. Furthermore, the top (positive) part of the second RLQ axis showed that species that were characterised by gonochoristic reproduction, tube dwellers and suspension feeders had an affinity for silty substratum.

The RLQ analyses for Malvan portrayed that the first two axes contributed to 97.1% of the total inertia, with 84.7% explained by the first axis and 12.5 % by the second axis as shown in Table A.3. On the negative side (left) of the first RLQ axis (Fig. 6), species with trait modalities such as burrowers, sensitive to disturbance, detritivores, epifaunal and very small size (Fig. 6a) were seen to be strongly associated with higher sand and DO of the nearshore stations (Fig. 6c). The right (positive) side of the first RLQ axis indicated that higher nitrite, salinity, TOC and clay corresponded to the outer stations that were populated by the polychaete species (*Mediomastus* sp., *Parheteromastus tenuis*, *Heterospio* sp., *Sternaspis scutata*, *Cossura coasta* and *Paraprionospio patiens*) that shared trait modalities such as non-motile/semi-motile, short lifespan, upward conveyors, sequential hermaphrodite, tolerant and second order opportunistic. Furthermore, the top (positive) part of the second RLQ axis indicated that trait modalities (long lifespan, asexual reproduction, diffusive mixers and indifferent to disturbance) showed higher affinity towards SS, nitrate and ammonia which were represented by species such as *Cirratulus* sp., *Lumbrineris* sp., *Lumbrineris meteorana* and *Eunice* sp. (Fig. 6b).

4 Discussion

The inclusion of functional diversity metrics provided in-depth insights into ecosystem functioning of the Mumbai port and the Malvan Marine Protected Area. It is largely expected for areas with different levels of perturbations to show varying resilience capacities depending on the species composition and their ecological sensitivities. In view of this, the present study explored the

trends in functional traits and resilience of Mumbai and Malvan coastal areas. Overall, the results highlighted the influence of different environmental settings on the ecosystem functioning by filtering the biological traits that confer resilience in the two differently modified areas.

4.1 Environmental scene: abiotic and biotic

The previous study conducted by Dias et al. (2023) has shown that Mumbai was more polluted than Malvan owing to the fact that the former had more anthropogenic inputs and the latter had relatively less human interference. The significantly elevated concentrations of nutrients and SS at Mumbai can be attributed largely to various sources (Pradhan et al., 2021; Dias et al., 2023). In Malvan, the considerably low concentrations of nutrients and high DO levels confirmed its good ecological health (Dias et al., 2023). The higher species richness and abundance of macroinvertebrates at Malvan were expected due to its MPA status, heterogeneous substrata and absence of point source discharges (Vijapur et al., 2019). The macrobenthic community structure in Mumbai had a higher presence of opportunistic species such as polychaetes (*Paraprionospio patiens*) which is a scenario typical of areas exposed to anthropogenic sources (Sukumaran and Saraladevi, 2009). Although Malvan had a dominance of *Cossura coasta* (opportunistic species), the area also had substantial presence of sensitive species whose combined composition was much higher, thereby elevating the diversity indices. Also, *C. coasta* was present in large numbers only at the predominantly silty station 4, which contrasted with other Malvan stations that were sandy in nature.

4.2 Functional profile: diversity metrics and resilience

The functional matrix provided an overview of the spatial distribution of trait modalities in Mumbai and Malvan, wherein compositions of traits differed depending on the sampling area at both places. Thus, though the taxonomical indices were superior at Malvan, the functional indices between both areas were comparable. Despite the diverse species assemblages in both the areas, the dominant trait profiles were almost similar with a few exceptions. However, the relative composition of traits varied between the two places. For instance, though both areas displayed all types of motilities, Malvan had better representation of traits associated with k-selected species, such as swimmers, crawlers, epifauna, and free-living organisms with high sensitivity to pollution. The exception at Malvan was station 4, characterised by silty substrate and high C_{org} content. This station was predominantly occupied by *C. coasta*, exhibiting opportunistic characteristics like semi-motile, burrow dwellers, small sized tolerant/opportunistic soft bodied infauna. The stations of Mumbai (stations 1-9) were colonized by mostly sedentary, deposit feeders, burrow/tube dwellers, infaunal, soft bodied, upward and downward conveyors which are categorised as opportunistic traits.

Interestingly, the three outermost Mumbai Port stations, relatively less impacted and having high amphipod populations, displayed predominantly sensitive traits i.e. motile, surface depositors, epifauna with exoskeleton sensitive to organic enrichment. Malvan, being an MPA, had better ecological health (as explained in Section 4.1) and predominantly sandy substrata that aided the establishment of sensitive traits. Conversely, Mumbai's anthropogenic stress probably led to a prevalence of opportunistic species and their associated traits, likely conferring better resistance to stressors (Edegbene et al., 2021). However, even at Mumbai, the outer stations that were well flushed by tidal variations, displayed more sensitive traits. This supports our initial hypothesis that anthropogenically affected zones would have more opportunistic traits due to the abundance of r-selected species, unlike low-impact zones. This highlights how individual species perform an array of functions within their habitat, and only those with traits adapted to the stressors survive, following the concept of environmental filtering (van der Linden et al., 2016). Similarly, in affected areas, zones which are relatively free of impacts may regain some sensitive traits as demonstrated in Mumbai's outer stations.

Functional diversity metrics provide an important measure to document ecosystem alterations by examining benthic community mechanisms and systems resilience against disturbances (Rincón-Díaz et al., 2018). In this study, the Functional Diversity (FD) was only marginally higher at Malvan, contrary to the expectation that an MPA would yield superior functional values. This was probably because, though Mumbai had a surfeit of opportunistic species and Malvan had more sensitive species, both locations harboured individuals subscribing to all trait modalities. Functional Richness (FRic) is an indicator of the extent of functional space occupied by the species and is generally a good predictor of disturbance, diminishing with increasing perturbations (Mason et al., 2005; Mouillot et al., 2013). However, the study surprisingly found higher FRic values in Mumbai and zero values in Malvan. The FRic values did not indicate any relation with species richness which was distinctly higher at Malvan. FRic of both the areas was probably dictated by the multiple ecological preferences of the constituent species rather than the species richness itself. For instance, in Mumbai, the dominant *P. patiens* occupied multiple modalities of each trait expanding its ecological niche space. Conversely, in Malvan, the dominant species *C. coasta* subscribed to only specific trait modalities. Thus, FRic is dependent on the extent of niche coverage, whether opportunistic or sensitive, rather than the trait's sensitivity. As suggested by van der Linden et al. (2016), FRic performed similarly to the taxonomic species richness indicating that with the addition or loss of species, rare or unique traits are also added or lost to the system. Consequently, species with rare

functional traits tend to occupy larger functional space which inflates FRic leading to overestimation (Schuldt et al., 2014; Llanos et al., 2020).

Both areas demonstrated moderate yet comparable Functional Evenness (FEve), since specific modalities of each trait were heavily subscribed by individuals in both locations. Preferred modalities included non-motile/semi-motile (motility), tube-dwelling (habitat), deposit feeders (feeding mode), infauna (position in sediment). The modest FEve values indicated moderate resource utilisation by the species (Mouillot et al., 2013). This concurs with the conclusions of D'Alessandro et al. (2020) in the polluted Syracuse port in the Mediterranean Sea, wherein high FEve values were presented, signifying high stability of the area to the pollutants. High Functional Divergence (FDiv) in both zones suggested reduced competition for resources due to high level of niche differentiation, which aligned with Mason et al. (2005). Similar high FDiv occurred in both the impacted port and protected areas, as both harboured abundant species with varying trait combinations (van der Linden et al., 2016). For instance, in Mumbai, the most dominant species *P. patiens* showed affinity for tube-dwelling, large size, upward and downward conveyors, while the second dominant species *C. coasta* preferred burrow dwelling, small size and surface depositors. In Malvan, the second most abundant species *Iphinoe* subscribed to motile, free-living, having exoskeleton, epifauna with sensitivity as opposed to the primarily dominant *C. coasta* (non-motile, burrow dwelling, soft bodied infauna with opportunistic trait). High FDiv signifies stronger niche separation, lowered competition and efficient utilization of resources (Mason et al., 2005). Functional Dispersion (FDisp) encompassing both FDiv and FRic, measures the distance between the species individually and the centre of the functional trait matrix (Laliberté and Legendre, 2010; Mason et al., 2013). FDisp values in both areas were quite similar and notably high, reflecting wide variation in the modalities employed by different species. High FDisp, according to Llanos et al. (2020), signified improved ecosystem functioning with more efficient resource utilization, indicating rich functional diversity.

The incorporation of functional diversity metrics demonstrated its utility for gaining significant insights into the ecosystem functioning of Mumbai and Malvan. At Mumbai port, the selected functional metrics, excluding FRic, displayed values comparable to those of Malvan. Malvan exhibited evidently good ecological conditions which accounted for the fair values of FD, FEve, FDiv, and FDisp. The analysis of functional metrics unveiled that while Mumbai's functioning was influenced by the stress gradient (inner vs outer zone), the functional parameters closely resembled those of the less stressed Malvan. The ratio between species diversity and functional diversity demonstrated a linear relationship, with a slope value closer to zero, indicating high functional redundancy (FR) for both the areas. High FR implies that multiple species performed

analogous roles, maintaining ecosystem functions (van der Linden et al., 2016). Prior studies have indicated that areas with lower environmental stress tend to exhibit higher functional redundancy due to reduced interspecific competition (Helmus et al., 2010; Wang et al., 2023). It was expected that the Mumbai port, being subjected to high perturbations, would display higher slope value (low FR) as the taxonomic diversity was lower. However, Mumbai had several functionally similar taxa indicating higher FR. Such a scenario may occur wherein, species with similar functions maintain functional stability even with declines in taxonomic diversity, as proposed by Biggs et al. (2020). A study conducted by Darr et al. (2014) in the Baltic Sea highlighted dominant benthic communities sharing numerous trait modalities, resulting in comprehensive coverage of functional space and consequently, high FR. The resilience of a system relies on key species performing similar functions, enabling them to withstand stressors even after loss of species with rare traits. High FR was observed in both areas since many species subscribed to analogous traits, irrespective of sensitivity. As van der Linden et al. (2016) pointed out, FR can increase when rare species disappear, reducing the number of rare traits, and the remaining dominant species undertake similar functions, yielding high FR. The low proportion of rare traits subscribed by individuals in both areas likely contributed to high FR, even in Mumbai. For instance, traits such as carnivory (1 sp.), herbivory (1 sp.), hermaphroditism (5 sp.) at Mumbai and carnivory (1 sp.), hermaphroditism (2 sp.) at Malvan were subscribed only by a few individuals, comprising only a small proportion (5-7%) of the total traits (39) considered for both places in this study. Consequently, Mumbai exhibited higher resilience closer to that of Malvan, indicating the stability and maintenance of the ecosystem functions in both regions despite exposure to stressors. This finding contradicts our hypothesis that Mumbai, with higher anthropogenic stress would display lower resilience than Malvan, an area with MPA status. It is important to note that while higher FR implies enhanced stability in extant benthic functioning, it does not necessarily denote superior functioning overall. This is because an ecosystem could potentially overlook several crucial functions when numerous species excessively associate with a limited number of traits (Mouillot et al., 2014). Therefore, both FR and FD hold equal significance for the sustenance of estuarine ecological processes, along with other functional parameters like FEve, FRic, FDiv and FDisp.

4.3 Link between abiotic variables and macrobenthic functional traits

It is a well known fact that the benthic organisms interact with their surrounding environment depending on their characteristics and ecological preferences (Bremner et al., 2006). This study delves into the influence of abiotic variables on functional traits particularly in areas exposed to different levels of perturbations. The projection on the RLQ plots was efficacious in segregating the

functional traits and the associated species that correlate with abiotic variables. In Mumbai, the RLQ analyses distinctly depicted the variance in functional traits across the axes, elucidating clusters of ecological preferences in the face of stressors. Traits of certain species, such as sensitive, swimmers, crawlers, burrowers, surface depositors, free-living were confined to outer stations, opportunistic traits (non-motile/semi-motile, upward conveyors, deposit feeders, soft-bodied, infaunal) were clustered at the inner stations indicating that the distribution of traits were influenced by abiotic conditions. The inner stations displayed higher nutrient concentrations compared to the outer stations, indicating moderate stress, consistent with earlier findings Dias et al. (2023). Within the inner zone of Mumbai port, higher nitrate levels, lower DO conditions along with silty substratum aided the establishment of opportunistic traits. Notably, the RLQ figures clearly portrayed the shift from opportunistic to sensitive traits in the relatively less impacted outer stations, which featured higher DO, salinity and sand percentages. Although predominantly opportunistic species inhabited Mumbai, certain taxa shared functional attributes similar to sensitive species, contributing to substantial redundancy (Hu et al., 2019). Middle stations favored species with r-strategist traits due to favorable sand, clay and SS. SS along with the finer sediments can have possible influence on the organisms due to smothering and clogging effects (Dias et al., 2022) favouring only those species that possess robust survival ecological preferences. In contrast, in Malvan, RLQ plots indicated that the coastal stations primarily associated with sand and DO harboured more sensitive traits. However, the outermost station 4 favoured opportunistic traits driven primarily by sediment texture. Substrate composition is known to influence the choice of functional role (Bremner et al., 2006; Greenfield et al., 2016) and our study underscores this by illustrating how finer sediments promoted opportunistic traits, while sandy substrates corresponded to sensitive traits. Disparities in trait functions is resultant of factors such as sediment type, nutrients, alongside other possibly unmeasured factors. However, the identity of each species and their ecological preferences are crucial as it makes a remarkable difference while interpreting the link between ecosystem functioning and abiotic variables.

The inferences drawn from this study underscores the critical role of biological trait analysis and functional diversity metrics in comprehending the ecosystem functioning and its resilience. Benthic ecosystem functioning cannot be predicted on the basis of a single trait or few traits, but requires numerous traits to gain an in-depth information on the resistance of species to a stressor. The choice of traits in this study, gave valuable information in both the areas and indicated the influence of abiotic parameters, signifying the environmental filtering concept. Hence, these traits were deemed suitable for future studies in other geographical areas. Furthermore, these results augment existing research conducted in the same geographical areas, which has up till now,

predominantly focused on evaluating ecological quality status, taxonomic diversity and functional structure with a limited range of traits. This research work presents a benchmark for forthcoming surveys that could prove invaluable across diverse habitats, facilitating a comprehensive evaluation of benthic ecosystem functioning and its resilience against diverse stressors. Moreover, conducting additional in-depth investigations in other milieu would be beneficial to proactively detect functional imbalances within an ecosystem, allowing for timely anticipatory measures and adaptations.

Conclusion

The present study highlighted the important trends in ecosystem functioning of differently perturbed areas (Mumbai and Malvan) through biological trait analysis and functional diversity metrics. It was anticipated that the Mumbai port, exposed to higher anthropogenic stress, would exhibit a prevalence of opportunistic functional traits, lower functional parameters and reduced resilience compared to the Malvan Marine Protected Area. The results of the study indicated that Malvan demonstrated higher species richness and functional trait diversity with more representation of sensitive species, aligning with our expectations of a less disturbed area. However, the various functional diversity metrics revealed that the ecosystem functioning in Mumbai was almost as stable as that of Malvan, despite the differential stress gradient. Additionally, both areas presented high and similar levels of resilience, as measured by Functional Redundancy. This resilience was attributed to the fact that many dominant species shared similar functional traits in both the areas, regardless of the stress gradient. Furthermore, the presence of rare species was minimal, reducing the influence of uncommon traits. This resulted in strong resilience against the stressors, signifying high stability and maintenance of ecosystem functions by the benthic assemblages. These results also indicate that the distinction between sensitive and opportunistic traits was irrelevant while estimating functional redundancy, which conferred similar resilience to both areas. However, due to a higher proportion of sensitive in Malvan, this area had the advantage of the functions associated with these traits. Environmental variables were perceptively observed to have wielded influences on the combination of traits adopted by the constituent species at both areas. Overall, this study demonstrated that inclusion of multiple functional traits and functional diversity indices can elucidate the mechanisms of ecosystem functioning, its relationship with species diversity and benthic resilience. The study also indicated that the mere evaluation of species diversity may be insufficient and incorporating measurements of ecological functioning and resilience are crucial to have an overall holistic view for future ecosystem management. Further improvement in the understanding of coastal benthic functioning can be obtained by extending similar studies to other less studied tropical coastal zones as well.

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Figure captions

Fig. 1 Anthropogenic activities in Mumbai and Malvan areas. Hypothesis I: Opportunistic traits will increase in anthropogenically stressed zone. Hypothesis II: Lower species and functional diversity will result in low functional redundancy.

Fig. 2 Study area map showing the locations in Mumbai and Malvan coastal waters.

Fig. 3 nMDS ordination based on the macrobenthic species abundance data for Mumbai and Malvan.

Fig. 4 Relationship between the functional diversity (FD) and Shannon-Weiner diversity (H') based on macrobenthic abundance data in (a) Mumbai and (b) Malvan.

Fig. 5 RLQ analysis represented by first and second axis in Mumbai Port (a) trait modalities, (b) score of species, (c) coefficients of abiotic variables, and (d) projection of sampling stations. Refer Tables 1 for the trait modality labels and Table 2 for abiotic variable abbreviations.

Fig. 6 RLQ analysis represented by first and second axis in Malvan MPA (a) trait modalities, (b) score of species, (c) coefficients of abiotic variables, and (d) projection of sampling stations. Refer Table 1 for the trait modality labels and Table 2 for abiotic variable abbreviations.

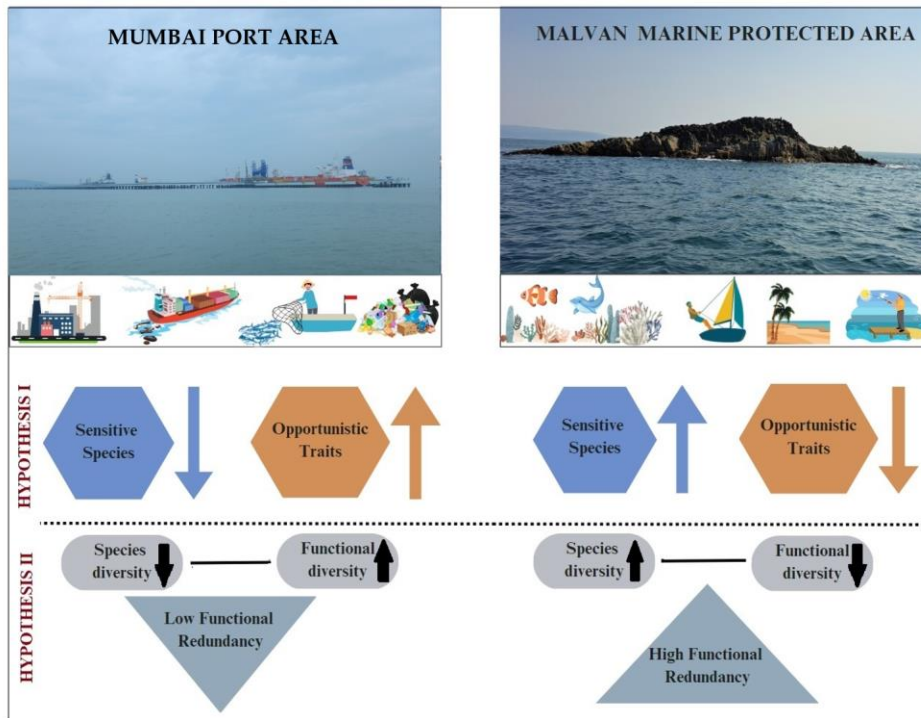


Fig. 1

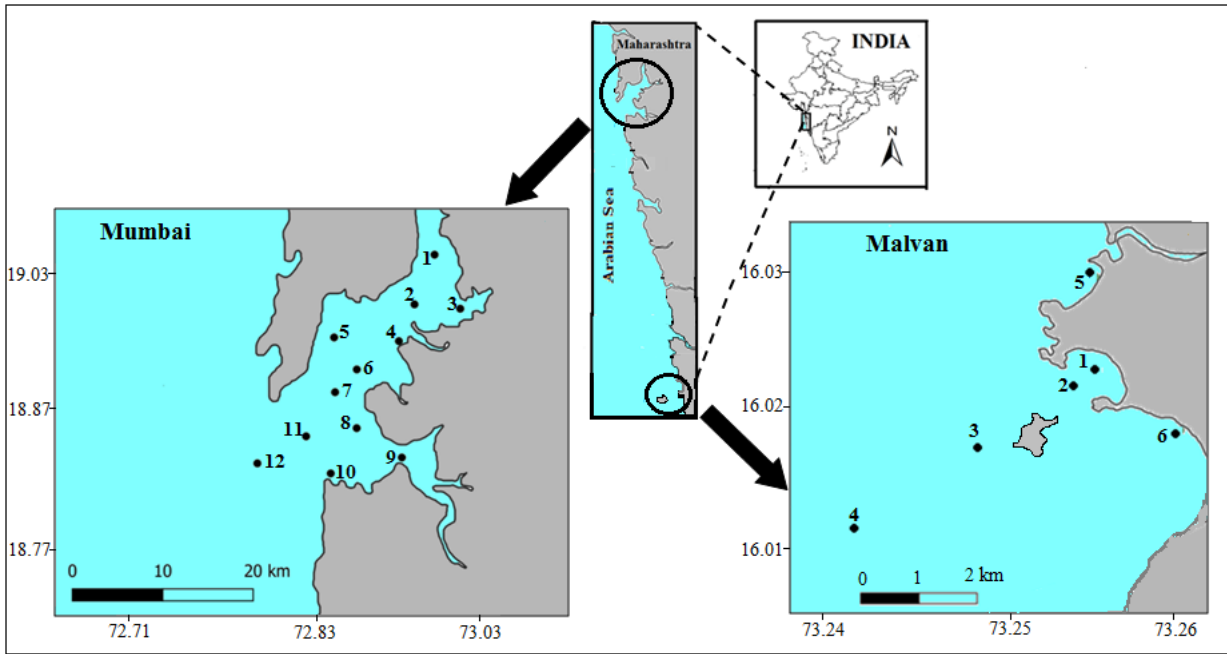


Fig. 2

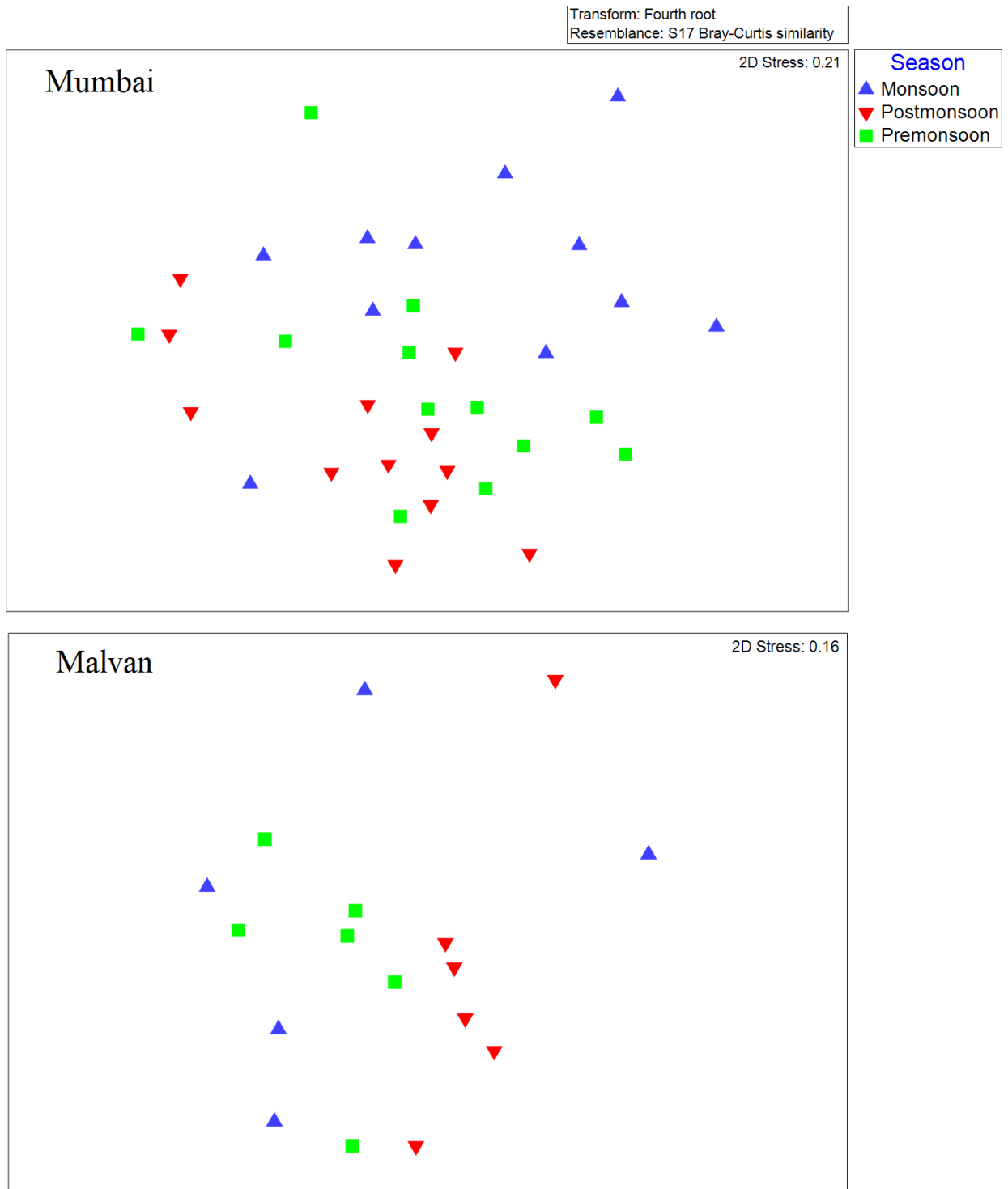


Fig. 3

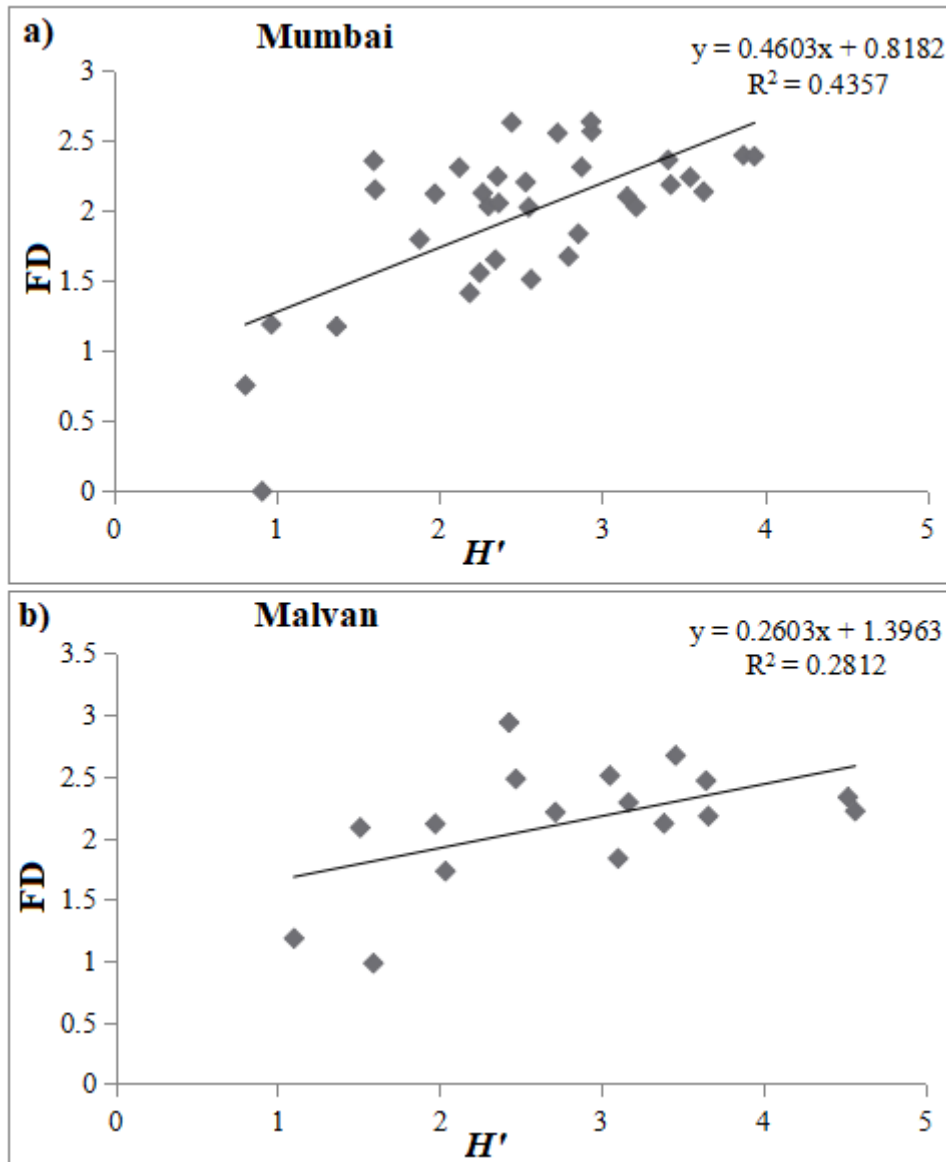


Fig. 4

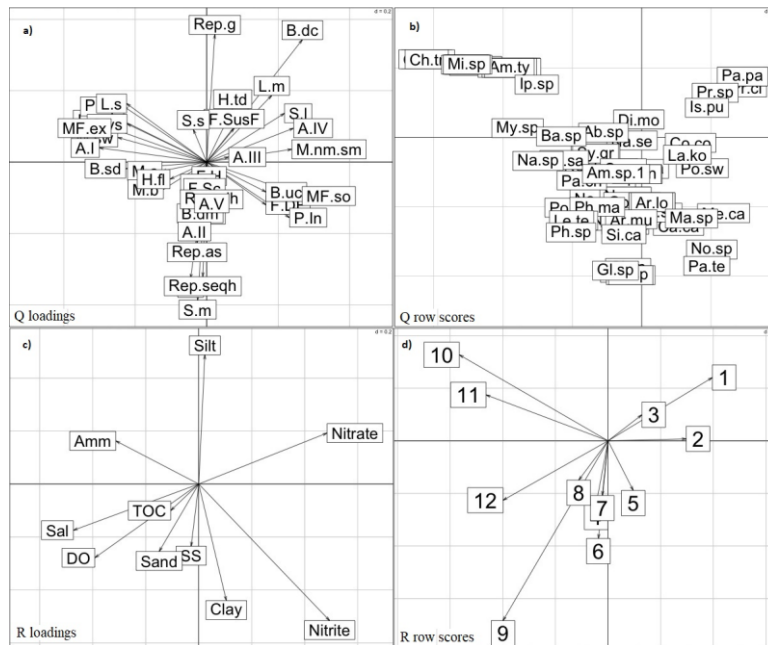


Fig. 5

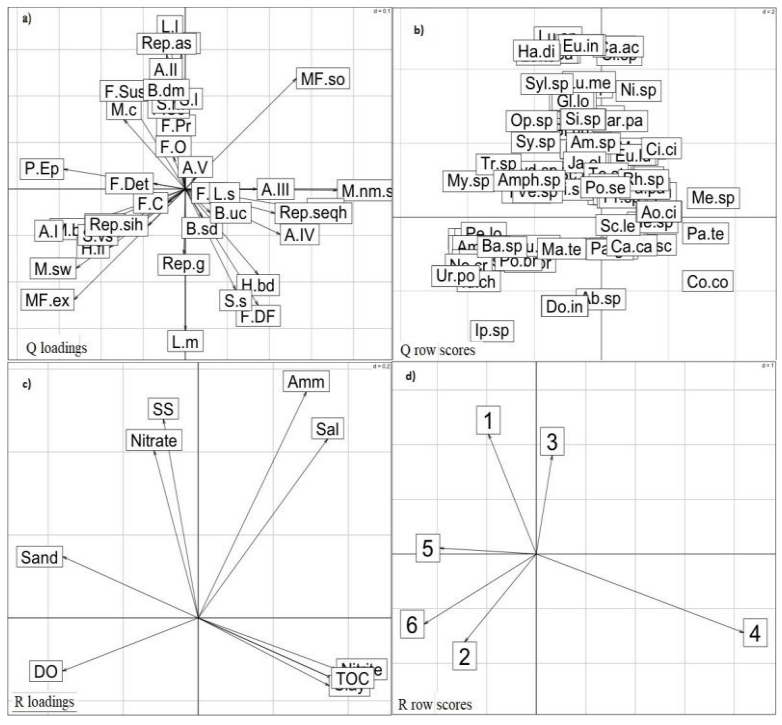


Fig. 6

Fig. A.1 Functional trait composition for macrobenthic species in Mumbai. See Table 1 for trait modality labels.

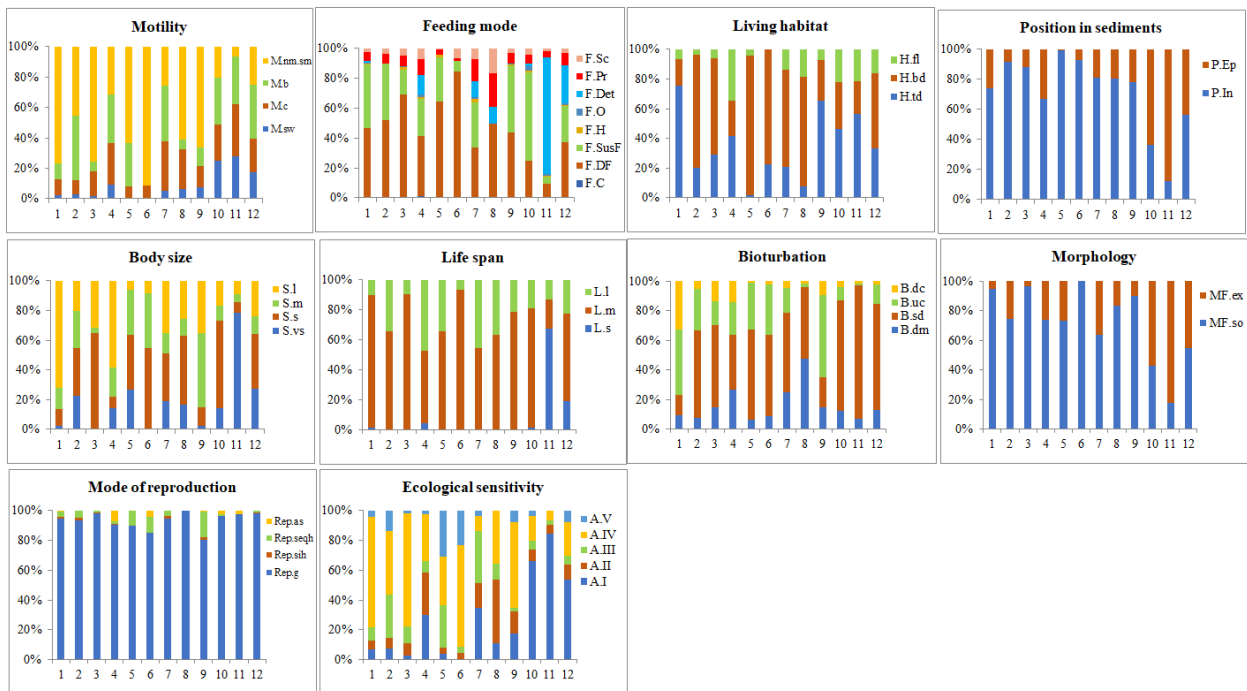


Fig. A.2 Functional trait composition for macrobenthic species in Malvan. See Table 1 for trait modality labels.

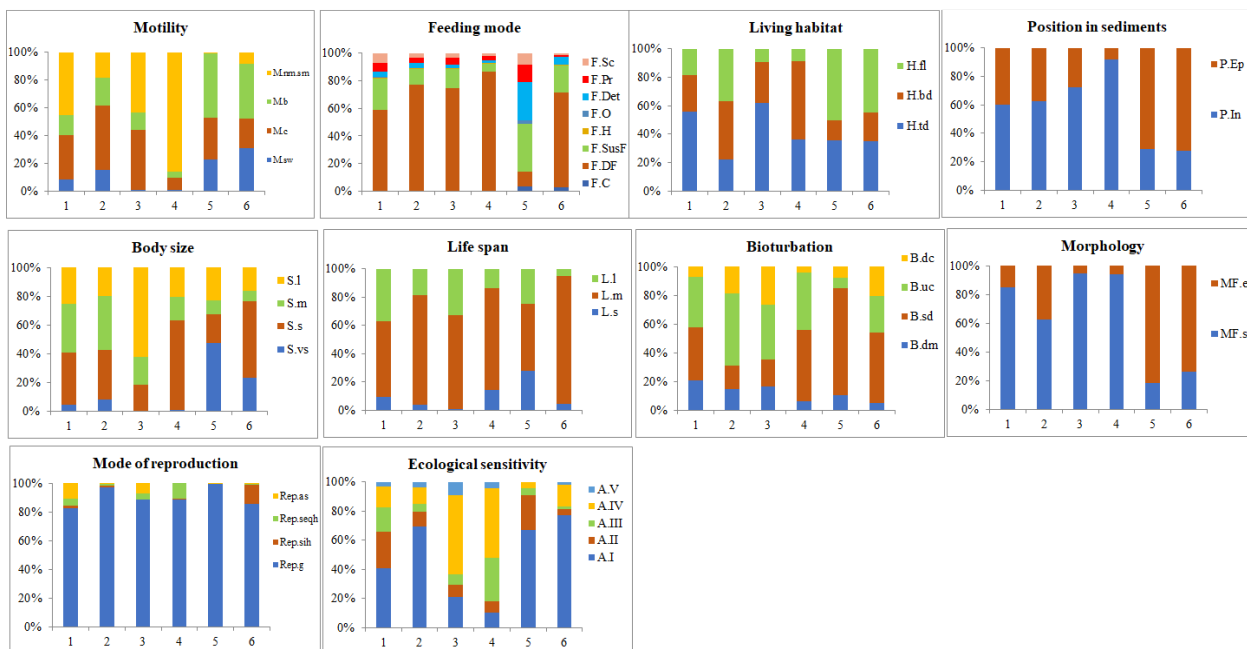


Table 1 List of the 10 biological traits and modalities used in Mumbai and Malvan.

Traits	Modalities	Labels
Motility	swimmer	M.sw
	crawler	M.c
	burrower	M.b
	non-motile/semi-motile	M.nm.sm
Feeding mode	carnivore	F.C
	deposit feeder	F.DF
	suspension feeder	F.SusF
	herbivore	F.H
	omnivore	F.O
	detritivore	F.Det
	predator	F.Pr
	scavenger	F.Sc
Living habitat	tube-dwelling	H.td
	burrow-dwelling	H.bd
	free living	H.fl
Position in sediments	infauna	P.In
	epifauna	P.Ep
Body size	very small (<1cm)	S.vs
	small (1-3cm)	S.s
	medium (3.1-6cm)	S.m
	large (6.1-10cm)	S.l
Lifespan	<1 yr	L.s
	1-3 yrs	L.m
	3-10 yrs	L.l
Bioturbation	diffusive mixing	B.dm
	surface deposition	B.sd
	upward conveyor	B.uc
	downward conveyor	B.dc
Morphology	soft-bodied	MF.so
	exoskeleton	MF.ex
Mode of reproduction	gonochoristic	Rep.g
	simultaneous hermaphrodite	Rep.sih
	sequential hermaphrodite	Rep.seqh
	asexual reproduction	Rep.as
Ecological sensitivity	sensitive	A.I
	indifferent	A.II
	tolerant	A.III
	2nd order opportunistic	A.IV
	1st order opportunistic	A.V