A baseline study of local reef habitat status in the Marine Fisheries Management Area of Kep Archipelago, Cambodia: focus on meiobenthic assemblage structure

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**Keywords:** artificial reefs, bivalve beds, meiofauna, ecosystem functioning, habitat restoration,Cambodia, marine conservation, Kep Archipelago

# Abstract

The Cambodian Sea harbours diverse marine habitats of great ecological significance, but these areas face mounting threats from Illegal, Unreported, and Unregulated fishing, notably trawling. Despite the 2006 ban on trawling in waters shallower than 20 metres, the issue persists, with oyster (bivalve) beds extirpated and vital ecosystem services, like water quality enhancement and shoreline stabilisation, lost. To facilitate ongoing oyster restoration initiatives this study compares extant bivalve beds (BB), Fisheries Production Structures (FPS), and impacted areas by means meiofauna higher taxon diversity as a proxy for sediment health and ecosystem health. The findings indicate that reef structures, both natural and artificial, support significantly higher meiofauna density and diversity, further highlighting the indispensable role of BBs in shaping favourable sediment characteristics decreasing oxygen depletion. FPS offers a viable short-term solution by mitigating illegal fishing and recovering habitat, promoting survival of fish and shellfish stocks. Though the study has unveiled valuable insights, it is subject to limitations, demanding further research and continual monitoring. Addressing these limitations will strengthen future restoration efforts and enable better-informed decisions for conserving and rehabilitating marine ecosystems in the Cambodian Sea.

# 1.Introduction

Cambodia’s marine territory, located within the Gulf of Thailand (GOT), spans an area of approximately 17,791-18,477 km2 (Rivzi & Singer, 2011) with an average depth of 50 m (Sok, 2022). The Cambodian Sea is characterised by the presence of vulnerable and economically important marine habitats, including wetlands, estuaries, mangroves, seagrass meadows, coral reefs, bivalve beds, and barren sand (UNEP, 2007; Strong, et al., 2022; MCC*, unpublished data*). In past decades, Illegal, Unreported, and Unregulated (IUU) fishing has caused significant damage to these ecosystems (Teh et al., 2016; Sala et al., 2018; FAO, 2020), and together with climate change it represents a significant threat (Agnew et. al., 2009; IPCC, 2019; Sumaila and Tai, 2020), particularly illegal beam trawling (Rizvi and Singer, 2011; Song et al., 2020; Widjaja et al., 2020).

Since 2006, the national government has taken measures to protect marine ecosystems, including a trawling ban in waters shallower than 20 metres (The Cambodian Law on Fisheries, Art. 49), the creation of Marine Fisheries Management Areas (MFMA), and Marine Protected Areas (MPA). These efforts are supported by research from NGOs and universities. Marine Conservation Cambodia (MCC) introduced Fisheries Production Structures (FPS) as artificial reefs, which not only restore habitats but also block illegal bottom trawlers. Surveys show FPS significantly increase fish biodiversity (Strong et al., 2022; Reid et al., 2019; Richer, 2020) as they provide hard substrates that support ecological restoration in degraded seascapes (MCC, unpublished data) and aid seagrass recovery, with success rates up to 50% (Reid et al., 2019; MCC, unpublished data).

Targeted restoration efforts have also focused on degraded oyster beds due to their ecosystem benefits (Grabowski & Peterson, 2007; Thayer et al., 1984). As ecosystem engineers, oysters transform bare substrates into biodiverse habitats, stabilizing sediments, reducing erosion, and mitigating eutrophication (Dame et al., 2002; Yahya et al., 2020; Grabowski et al., 2012; Coen & Humphries, 2017). Their filtration improves water quality, preventing harmful algal blooms and benthic hypoxia (Vaughn & Hoellein, 2018; Cressman, 2003), enhancing benthic productivity and food webs (Coen & Humphries, 2017; Newell et al., 2002; van der Schatte et al., 2020). It is therefore crucial to have a baseline assessment of Cambodian oyster beds status and distribution are for effective restoration and resource management in the Cambodian Sea.

Since water column processes are reflected in the sediments, infaunal benthic community structure assessment offers complementary insights into sediment health and ecosystem functioning. Meiofauna—organisms retained on a 38 µm sieve but passing through a 1 mm sieve, including both metazoans and protozoans (Fenchel, 1978) — are a size class of benthic organisms characterised by a predominantly sediment-bound life style, high turnover rates and high sensitivity to changes in water quality and sediment biogeochemistry. Sediments act as ecological archives, capturing processes occurring within the water column (Winterwerp et al., 2004; Schmutz & Sendzimir, 2018), and provide an ecological snapshot of habitat health at any given time. By analysing sediment characteristics alongside infaunal communities, proxies such as organic content, isotopic composition, and meiofaunal community structures help in describing nutrient cycling and identifying broader ecosystem functions (Giere, 2009; Kennedy & Jacoby, 1999; Coull, 1999; Schratzberger & Warwick, 1998). Additionally, this integrated approach allows for the assessment of human-induced environmental impacts, including overfishing, pollution, and climate change (Coull, 1999; Coull & Chandler, 1992; Leasi et al., 2021; Balsamo et al., 2012), offering essential insights into the ecosystem services and resilience of bivalve habitats.

Many meiofaunal taxa recycle organic matter that settles on the sediment surface from the water column, thereby facilitating benthic-pelagic coupling and connecting the sediment microbial loop to higher trophic levels (Ridall & Ingles, 2021; Balsamo et al., 2012; Schmid-Araya, 2002). Their high turnover rates and the predominantly sediment-bound lifestyle make meiofauna ideal for investigating sediment processes as these organisms have evolved to rapidly respond to changes in the interstitial spaces of the sediment matrix (Giere, 2009; Fenchel, 1978). Different meiofauna taxa exhibit varying life strategies and sensitivities to environmental conditions, such as sedimentation rates (Nomaki et al., 2016), organic matter content (Ingles et al., 2009, Danovaro et al., 2002), and hypoxic or anoxic conditions (Moodley et al., 1997), among others (Nomaki et al., 2016). The presence (or absence) of specific taxa (e.g. copepods, foraminifera; Giere, 2009; Kenedy & Jacoby, 1999; Schratzberger & Warwick, 1998; Ridall & Ingles, 2021; Yussal & Rosli, 2019) and the overall meiobenthic abundance are indicative of habitat stability, ecosystem functioning, and overall sediment health (Yussal et al., 2019; Ridall & Ingles, 2021).

Such metrics are particularly valuable given that marine benthic studies in Cambodia are limited (Yahya et al., 2020), leaving substantial gaps in baseline knowledge crucial for coastal ecosystem management. Current challenges, e.g., lack of local expertise and infrastructure, restrict fieldwork capacity and the preservation of sediment samples, which are essential for in-depth meiofauna and bivalve assessments. The remote nature of these environments further complicates access to study sites, underscoring the need for adaptable methodologies that can accommodate preservation limitations whilst delivering reliable data that promotes biomonitoring efforts. Chemical preservatives, such as buffered and diluted formaldehyde as fixative (Palmer et al., 2007; Zacharias & Roff, 2000), can provide a practical alternative to freezing samples (Ogrinc et al., 2005), sustaining low-cost and scalable meiofauna studies.

Despite its ecological significance, meiofauna biodiversity in and around the Cambodian Sea has received little to no attention. Most research in the region has focused on the central Gulf of Thailand (Laongmanee, 2013; Min et al., 2013; Arnupapboon et al., 2019; Yimin et al., 2013), coral reefs (Quan, 2020), or freshwater ecosystems like the Tonle Sap Lake (Ohtaka et al., 2010) and the Mekong River in southern Vietnam (Ngo Xuan Guang et al., 2013; Sinh et al., 2012; Gheerardyn et al., 2010). A comprehensive study of meiofauna in the Cambodian Sea is needed to address this knowledge gap and improve understanding of Cambodia's marine sand ecosystems, especially with the planned expansion of FPS deployments (ADB, 2023).

This study aims at establishing a baseline of the meiofauna benthic assemblage observed across three habitats within the Kep Archipelago of the Cambodian Sea. As part of a broader benthic survey also examining fish and invertebrate interactions (Gorra et al., *in prep*), our primary objective is to provide a snapshot of reef health and status, using simple biodiversity and environmental metrics.Specifically, we identified trawled bare sand (or impacted stations, IS), bivalve beds (BB), and Fisheries Production Structures (FPS). We compared the three habitats in terms of meiofauna diversity and their relationship with various biotic and abiotic variables. The null hypotheses include: (Ho1) benthic meiofauna assemblage characteristics do not differ across the three habitats; (Ho2) sediment characteristics (e.g., grain size, anoxic layer depth, dominant substrate) and other environmental variables (e.g., water temperature, salinity, light availability, depth, visibility) show no variation between habitats; (Ho3) environmental variables do not influence the observed (or unobserved) differences in meiobenthic assemblages across the three habitats.

The anticipated outcomes of this research include: (i) advancing marine research in the Cambodian Sea by providing novel baseline data on meiofauna higher taxon diversity in a previously data-deficient region of the Gulf of Thailand; (ii) establishing a preliminary baseline for conservation objectives; and (iii) evaluating the potential effectiveness of FPS in promoting ecosystem recovery and sediment health.

# 2. Material and Methods

## 2.1 Study Area

Fieldwork was conducted over a four-week period, from 20th January to 24th February 2023, around the island of Koh Ach Seh (10°21'26.5”N, 104°19'12.7’’E) in the Kep Archipelago (Cambodian Sea, see **Fig. 1**), where the average depth is approximately 4.5 metres (MCC, *unpublished data*). Marine Conservation Cambodia (MCC) provided the hosting facility on the island, facilitating this study through their established partnership with the Faculty of Fisheries and Aquaculture at the Royal University of Agriculture in Phnom Penh and the Marine Biology Laboratory of Ghent University (Belgium).

The broader survey was conducted by scuba diving and focused on three subtidal habitats: (i) extant bivalve beds (BB, n=4), (ii) Impacted Stations (IS, n=5), and (iii) Fisheries Production Structures (FPS, n=5). The locations of BB and IS stations were identified through reconnaissance dives, whereas FPS locations were known (GPS coordinates provided by MCC). This study aimed at focusing monitoring efforts on extant oyster beds, however upon reconnaissance, oyster beds were absent or existed in severely scarce/patchy agglomerations. Oysters were found in mixed assemblages alongside other bivalves, predominantly pen shell clams. Based on these observations, we selected bivalve beds characterised by a diverse assemblage of mussels, clams and occasional oysters to represent a filter-feeding community, functioning similarly to oyster beds in terms of ecosystem services.

Survey sites near Koh Ach Seh were prioritised due to (i) their proximity to the Cambodian-Vietnamese border, an area frequently intruded upon by stray illegal fishing vessels; (ii) logistical and weather-related considerations; and (iii) the need to standardise future monitoring efforts in light of upcoming restoration activities (**Fig. 1**). **Table 1** offers descriptions for each survey station and important context for the analyses and findings of the broader study. This current paper focuses on meiofauna and sediment abiotic variables sampled at one FPS, two IS, and two BB stations.

## 2.2 Sampling Strategy

### 2.2.1 Abiotic variables

In situ environmental measurements were collected to support ecological observations and identify potential underlying processes. Divers recorded visibility, depth, temperature, substrate type, and atmospheric conditions at all stations (**Table 2**). Due to constraints in sampling time and logistics, salinity, light availability, and granulometric size distribution were measured only at one selected station representative of each habitat (**Table 3**).

Two divers measured underwater visibility with a meter tape, recording the maximum distance at which they could see each other to the nearest 0.1 m. At all stations, depth and water temperature were estimated using a Suunto Novo dive computer (1° (± 2°C) resolution). Data collection was occasionally limited by boat availability and diving safety conditions. During accessible periods, representative stations were equipped with an Onset HOBO Pendant Temperature/Light 64k Data Logger, which recorded in situ temperatures and light levels every 10 minutes over 24- to 72-hour intervals, with ranges from -20 to 70°C (± 0.53°C) and 0 to 320,000 lux, respectively. Two HOBO data loggers were placed– one at the sediment surface and another one metre above the seabed. A control sensor at MCC provided calibration reference during the study (**Table 2**). These measurements were taken to eliminate potential strong influences of temperature and light variability between the stations.

To estimate the average salinity (in practical salinity units, PSU), two water samples were collected from each station at depth. Salinity was measured using an ATAGO hand refractometer (range: 0 to 53%, ±0.2% at 20℃), calibrated with fresh water before use. Three readings were taken for each sample, and the average was recorded as the final salinity. Duplicate sediment samples were collected using meiofauna perspex push cores (3.6 cm inner diameter) for grain size analysis. Substrate types were recorded at 0.5-m intervals across a 40-m area (Loya, 1978).

### 2.2.2 Meiofauna assemblage

We employed various scuba diving survey methods to assess meiofauna and habitat characteristics across the habitats (BB, FPS, IS) at depths ranging between 2 and 11 m (**Table 1**). Perspex push cores (3.6 cm diameter, total n=28) were randomly collected, spaced at least two metres apart, across each station to represent all ecological habitat types outlined in **Table 1**. The sampling strategy for FPS stations was adapted (**Fig. 2**) to accommodate the three-dimensional structure of the artificial reef and prevailing current direction. The top 0-5 cm of each core was sliced in bulk (Higgins & Thiel, 1988), rinsed with filtered seawater (seawater sieved through a 32-μm mesh three times in situ), and preserved in a 4% formalin-seawater buffer (1:3 vol:vol ratio) for further processing at USTH." Photographic records of each core were taken, and the hypoxic/anoxic layer depth was visually determined using a ruler, based on the average of three measurements per core. The layer was identified by the distinct darkening of the sediment, indicative of organic matter degradation and a drop in interstitial oxygen due to microbial activity.

## 2.3 Sample Processing

Sample processing was conducted partially in the field (initial extraction of meiofauna from sediments, see next sections) and finalised at the University of Science and Technology (USTH) in Hanoi (Vietnam), where the identification of meiofauna higher taxon and grain size analysis took place in the Water-Environment-Oceanography lab.

### 2.3.1 Abiotic variables

Average temperature and light availability data were retrieved from the in-situ loggers using the Onset software (HOBOware v.3.7.25). Additional sediment cores (reserved for grain size analysis) were processed by slicing the top 0-5 cm of the bulk depth profile, followed by sun drying and storage in aluminium foil until further analysis could be conducted. Each sample was analysed using a Mastersizer 3000 laser-diffraction particle-size analyser (Malvern Panalytical, Malvern, Westborough, MA, USA), with approximately 10 g (dry weight) of the sample homogenised in 50 mL of deionised water. Triplicate subsample results were averaged and compared with the Wentworth (1922) grain size classification.

### 2.3.2. Meiofauna assemblage

The initial extraction and preservation of meiofauna from the 0-5 cm bulk sediment samples was conducted in the field using a decantation method (Higgins & Thiel, 1988), where sediment was gently washed with prefiltered (32 µm) rainwater to dislodge the meiofauna (by osmotic shock), which were then collected and preserved in a 4% formalin-seawater buffer. In the lab, the sediment samples were homogenised in a deionised water and underwent repeated decantation procedures to resuspend and separate the organisms from the sediment matrix. The decanted sample was retained on a 40-μm mesh and preserved with Formalin-Acetic-Acid (FAA), then stained with Rose Bengal dye to facilitate accurate counts and identification of meiofauna to higher taxonomic level. Observations and identifications were conducted under a stereomicroscope following guidelines from Higgins & Thiel (1988) and resources such as *The Guide to the Identification of Marine Meiofauna* (Schmidt-Rhaesa, 2020) and *Introduction to the Study of Meiofauna* (Higgins & Thiel, 1988).

## 2.4 Statistical Analyses

All statistical analyses and figures were produced using RStudio [v.2023.3.0.386, Posit team, 2023]. Multivariate data, including relative abundances of meiofauna at higher taxonomic levels, were analysed for differences across factors such as station, habitat (BB, FPS, IS), depth, and habitat characteristics using the permutational multivariate analysis of variance (PERMANOVA). If significant differences were found, the permutation of multivariate dispersion (PERMDISP) analysis was performed to test for homogeneity of dispersions among groups. When PERMDISP wasn’t significant, similarity percentage (SIMPER) analysis was used to identify which taxa contributed to observed assemblage composition differences. To visualise the relationship between factors and community structure, non-metric Multidimensional Scaling (nMDS) was employed. For univariate data (e.g. meiofauna abundances), one-way ANOVA was used, with checking for assumptions for homoscedasticity and unimodal data distribution; where these assumptions failed, alternative tests were employed.

Pairwise analyses were performed only when the main tests (ANOVA or PERMANOVA) were significant and reliable, to identify specific groups' differences. To assess community diversity, we calculated species richness and applied biodiversity indices, comparing these using one-way ANOVA and post-hoc Tukey HSD tests. Statistical procedures were carried out using the tidyverse (v.2.0.0, Wickham et al., 2019), dplyr (v.1.1.4, Wickham et al., 2023), and Vegan (v.2.6, Oksanen et al., 2022) packages in R. Graphical outputs were generated using ggplot2 (v.3.5.1, Wickham, 2016).

### 2.4.1 Abiotic variables

Descriptive statistics were used to summarise the abiotic variables. Comparisons between stations and habitats (BB, FPS, IS) were performed using one-way ANOVAs, assessing variance within each station. Normality of the data was checked using Shapiro-Wilk tests, and homogeneity of variances was tested using Levene’s test.

To examine the relationships between abiotic variables and community structure, Distance-based Redundancy Analysis (DbRDA) was conducted to evaluate how much variation in community structure could be explained by the measured environmental variables. For the DbRDA, the data were transformed to meet normality assumptions where necessary.

Additionally, PERMANOVA was used to assess community dissimilarity across habitats and stations, with PERMDISP following to test for homogeneity of dispersion between groups. This ensured that any significant differences found in PERMANOVA reflected true ecological variation, rather than differences in dispersion.

### 2.4.2 Meiofauna assemblage

All meiofauna density analyses were based on fourth-root density of meiofauna (individuals per 10 cm², then normalised). Total counts (number of individuals per sample) or densities (number of individuals per unit surface) were used to describe both true and relative abundance, as well as diversity indices such as Pielou’s Evenness J (Pielou, 1966), Simpson’s (Simpson, 1949), taxon richness, and Hill’s Index (Hill, 1973). These analyses were univariate, as each index or count was considered separately. Data normality and homoscedasticity were checked using a Shapiro-Wilk test before conducting univariate analyses. The Shannon-Wiener index was applied to the transformed data for diversity analysis, and ANOVA was used specifically for comparing diversity indices (Shannon & Weaver, 1949).

Multivariate analyses were conducted on the higher taxa density data (individuals per 10 cm-2) using PERMANOVA, PERMDISP, nMDS, and SIMPER. These analyses took into account the hierarchical sampling design, with cores as random replicates within stations, and stations as random factors nested within habitat types, to avoid pseudoreplication. One-way PERMANOVA was used to examine differences between habitat types (factor: habitat; levels: BB, IS, FPS), followed by PERMDISP (factor: station, p = 0.001) to test the significance of dispersion differences across groups. Bray-Curtis dissimilarity distances were used for all analyses.

Meiofauna higher taxa were standardised to relative abundances to account for uneven sample counts, especially for dominant taxa like nematodes. These relative abundances were visualised using a nMDS plot, and SIMPER was performed to assess the taxa contributing to significant differences between groups.

# 3. Results

## 3.1. Abiotic surveys

Temperature and salinity ranged from 27 to 34 °C and 30 to 34 PSU, with the lowest levels recorded at BB\_01 and the highest at IS\_05 for both parameters (**Table 2**). Light intensity varied notably across stations: IS\_05 had the lowest values at both 0 m (12.6 ± 28.3 lx) and 1 m (44.4 ± 77.1 lx), while the highest levels were observed at IS\_01 (0 m: 2483.7 ± 4088.9 lx) and BB\_02 (1 m: 6747.6 ± 11312.9 lx). It should be noted that a sensor at IS\_01 was knocked over, potentially skewing the 1 m light data. Detailed measurements for all variables are provided in **Table 2**.

Visual inspection of sediment cores allowed for the assessment of anoxic sediment layer depth across habitats. The shallowest anoxic layer depths were recorded at Impacted Stations (IS), followed by Fisheries Production Structures (FPS), with the deepest anoxic layer horizons starting at 3.71 cm at the Bivalve Beds (BB), BB\_02 (*see* **Table 3**). Average anoxic layer depths were 0 (± 0) cm for IS, 1.51 cm (± 1.13) for FPS, and 3.41 cm (± 0.79) for BB. These measurements revealed significant differences in anoxic layer depth across habitats (ANOVA: factor ‘Habitat’, F = 14.03, p < 0.001).

Sediment profiles and anoxic layer depths also revealed evidence of bioturbation at BB, as inferred by the presence of bivalves in deeper sediment layers (**Table 3**). At FPS, sediment characteristics included distinct pinkish-red clay and gravel, particularly at the central position. High densities of testate amoebas (density = 1,371 ind. cm-² [± 2,374.06], n = 4,115) were observed exclusively at this FPS position as well. Additional data on anoxic sediment depths and median grain sizes are available in **Table 3**.

The 0-5 cm sediment depth profile of BB and FPS was characterised by medium grain sizes (0.25 - 0.5 mm), while IS exhibited coarser grain sizes (0.5 - 1 mm), based on averages where over 90% of each sample was of these grain sizes. ANOVA results showed significant differences in the average anoxic layer between habitats (F = 14.03, p = 0.0089), and the median grain size variation across stations (F = 30.77, p < 0.001; **Table 3**).

Across all 12 stations, sand-silt-pebble (SStPb) was the predominant substrate type, followed by silt (St) and sand-shell (SS), which collectively comprised over 50% of observations (**Table 2**).

## 3.2 Meiofauna assemblage

Across all sampling sites, a total of 24 higher taxon groups were identified. Nematodes dominated the meiofauna assemblages across habitats, comprising up to 60% of the whole assemblage across stations. Copepods and calcareousforaminifera were the second and third most abundant taxa, respectively, with notable peaks at BB\_02 (40.9% for foraminifera) and BB\_01 (13.3% for copepods).

The highest densities of nematodes, copepods, and calcareous foraminifera were recorded at BB\_01 (1,018 ± 465.02 ind. 10 cm-2), BB\_01 (286 ± 189.3 ind. 10 cm-2), and BB\_02 (410 ± 289.05 ind. 10 cm-2), respectively. Conversely, the lowest densities were observed for nematodes at BB\_02 (286 ± 150.13 ind. 10 cm-2), for copepods at IS\_01 (105 ± 44.59 ind. 10 cm-2), and for calcareous foraminifera at BB\_01 (143 ± 172.82 ind. 10 cm-2). A summary of average meiofauna densities across all stations is provided in **Table 4**.

Relative abundances of the meiofauna higher taxa are reported in **Fig. 4**. FPS exhibited the highest relative abundance with 46.88 (± 0.82) ind. cm-2, while IS\_05 had the lowest abundance with 9.08 (± 0.38) ind. cm-2 (pseudo-F = 2.4482, p < 0.01, nperm = 999; PERMDISP = n.s.). Impacted Stations had the highest relative abundance of calcareous foraminifera (342.57 ±264.75 ind. m-2), while BB habitats hosted the greatest relative abundance of nematodes (651.66 ±505.03 ind. m-2) and copepods (201.36 ±166.72 ind. m-2; **Table 4**). FPS ranked second for copepods and third for both nematodes and calcareous foraminifera.

Variability within meiofauna assemblages between stations was significant, as shown by PERMANOVA and nMDS analyses (**Fig. 3**). The nMDS plot (stress = 0.17) captured the primary patterns in meiofaunal community structure, indicating a moderate fit. While some fine-scale relationships may not be fully resolved, the ordination reliably highlights broader ecological trends. Diagnostic metrics, including non-metric R² = 0.97 and linear fit R² = 0.878, support the validity of the analysis for identifying habitat-driven differences. PERMDISP analysis indicated that FPS exhibited the highest within-site variability, likely due to sampling core positions within the semi-enclosed structure.

Distinct patterns emerged in the nMDS plot (**Fig. 3**), with four major groups identified based on taxa filtered using a significance threshold of p = 0.001. SIMPER analysis (n = 36, p < 0.05) identified Tardigrada, Oligochaete, bivalve larvae, and Amphipoda as significant contributors to community dissimilarity. The highest dissimilarity values ranging between 27% to 34% were recorded between BB habitats (**Table 5**).

Both IS and BB habitats displayed variability in meiofauna assemblages, influenced by differences between individual stations (e.g., BB\_01, BB\_02). The highest within-habitat variability was observed at FPS (**Fig. 3**), likely due to differences in core collection positions within the semi-enclosed structure. Distinct dispersion patterns across stations were evident in the nMDS plot (**Fig. 3**), which grouped meiofauna communities into three clusters. These groups were driven by taxa filtered with a significance threshold of p=0.001 (non-metric R2 = 0.97, linear fit R2 = 0.878). Calcareous foraminifera (86.5%), Nemertea (71.5%), and Ostracoda (68.8%) were the main contributors to NMDS1, while proteinaceous foraminifera (70.3%) and Tardigrada (68.6%) were influential along NMDS2 (identified using the envfit function in Vegan). The BB habitats aligned primarily along NMDS2, whereas FPS and IS habitats clustered along NMDS1.

Statistical analyses revealed significant differences in meiofauna taxon richness and Shannon diversity across stations (ANOVA: taxon richness, F = 5.499, p < 0.01; Shannon diversity, F = 7.323, p < 0.001; **Fig. 6, Table 6**). Tukey HSD tests indicated that taxon richness was highest at BB\_02, followed by FPS\_01 and IS\_05, which overlapped significantly. In contrast, BB\_01 exhibited the lowest richness and was statistically distinct from all other stations. Shannon diversity followed a similar trend, with BB\_02 showing the highest mean (2.64) and BB\_01 the lowest (2.08). Intermediate diversity values were observed at IS\_05 (2.48), IS\_01 (2.44), and FPS\_01 (2.34).

In terms of Pielou’s Evenness (J), mean values were greatest at FPS\_01 and lowest at BB\_01, though evenness did not vary significantly across cores within stations (factor “Core ID,” F = 1.144, p = 0.113; **Table 7)**. These results suggest that while certain habitats (e.g., BB\_02) support greater diversity and richness, the relative abundance of taxa within cores at each station remained relatively stable.

For Hill’s Index based on raw count data, the highest average values were observed at BB\_02 for N0 (taxon richness), at IS\_01 for N1 (Shannon Entropy Index), and again at IS\_01 for N2 (Simpson’s Concentration Index), while BB\_01 recorded the lowest values across all indices. ANOVAs revealed significant differences in Hill’s indices among stations (N0: F = 5.088, p = 0.00437; N1: F = 7.301, p = 0.00059; N2: F = 4.534, p = 0.00757). Tukey HSD post-hoc tests indicated that BB\_02 and IS\_01 typically exhibited higher diversity metrics than BB\_01, which was consistently lower across all indices. Additional details, including core replicate variations, are provided in **Table 7**.

The PERMDISP results did not indicate significant variability in data dispersion, suggesting uniformity among groups variances, hence confirming the validity of the Permanova results. DbRDA did not reveal any clear grouping in relation to the environmental variables, indicating that the measured variables did not significantly influence the distribution of meiofauna assemblages. Thus, the null hypothesis was accepted, supporting the idea that ecological processes other than the measured variables may contribute to the observed differences. All results are summarised in **Table 8**.

# 4. Discussion

Historically, oysters and other bivalves were once abundant in the Cambodian Sea, playing a crucial role as ecosystem engineers (Dudgeon et al., 2010). However, over the past few decades, intensive trawling has significantly reduced their populations in the region, disrupting sediment stability, organic matter cycling, and biodiversity (De Silva & Anderson, 2011). This loss underscores the need for habitat restoration strategies. Bivalves, as key habitat engineers, are known to enhance sediment stability and biodiversity (Gosling, 2008). The present study addresses this knowledge gap by investigating the assemblage composition of a key bioindicator benthic size class, the soft sediment meiofauna, in relation to different human impacts. By comparing trawled seabed stations (IS), Fisheries Production Structures (FPS), and local bivalve beds (BB), the research sheds light on how ecosystem engineers influence sediment health, organic matter accumulation, and hypoxic conditions, emphasising the role of bivalves and other restoration efforts in ecosystem recovery.

Meiofauna diversity is influenced by habitat complexity, predator evasion, and the presence of ecological engineers such as bivalves and seagrass. The high diversity observed at BB\_02 can likely be attributed to these factors, with habitat complexity and predator evasion playing a key role (Hicks, 1986; Hosack et al., 2006). Seagrass and bivalves contribute significantly to benthic-pelagic coupling by stimulating bacterial activity through leaf decomposition and enhancing sediment and water column oxidation via bioturbation and filtration (Coen & Humphries, 2017; van der Schatte et al., 2020; Larkum et al., 2006; Lemmens et al., 1996). These ecological services foster diverse meiofauna assemblages, especially in habitats like BB\_02, and to a lesser degree, BB\_01, where shallower depths likely enhance these processes. The combination of habitat structure and the role of filter feeders underscores their importance in maintaining biodiversity in benthic environments.

ARs and natural bivalve-oyster reefs offer ecological benefits, including enhanced biodiversity, bottom relief, and water quality through filtration (Grabowski et al., 2012). However, ARs face challenges, such as degradation of materials like untreated concrete due to salt recrystallization and mechanical wear (Pratiwi et al., 2021; Melchers, 2020). Given reduced water flow, they also accumulate fine sediments and organic matter (Yang et al., 2019), providing meiofauna a constant food source. Increased fish densities associated with FPS (Strong et al., 2022; Reid et al., 2019) likely further stimulate microbial activity, particularly at the structure’s centre, as reflected in shallow average anoxic layers (**Table 3**) and high densities of testate amoebae (**Fig. 4-5**). Proper design and location are key to ARs' ecological success (Yang et al., 2019; Reeds et al., 2018).

High spatial and temporal variation of meiofauna is common in most benthic habitats, particularly in tropical shallow seas, especially during the wet and dry seasons (Pinto & Santos, 2006). Other factors such as station distribution, proximity to the coast, and human activities might also be influential. In our analysis the Distance-based Redundancy Analysis (DbRDA) did not indicate any significant influence of the environmental predictors on the meiofauna assemblage characteristics. Foraminifera, important consumers within the sediment microbial food web (Lipps & Valentine, 1970), have high densities at IS habitats, suggesting the presence of a distinct food web supported by microphytobenthos and microbial biofilms forming the base. Nematodes and foraminifera are also well adapted to low-oxygen conditions, allowing them to sustain high densities in less oxygenated sediments (Gupta & Machain-Castillo, 1993; Kitazume et al., 2018). Further investigation into nematode trophic guilds and functional roles would offer deeper insights into local and microscale trophic dynamics (Snelgrove, 1997).

Meiofauna assemblage composition and abundance serve as valuable indicators of ecosystem health, sediment conditions, trophic interactions, and pollution (Semprucci et al., 2016; Yusal et al., 2017). Copepods typically indicate well-oxygenated environments, while calcareous foraminifera thrive in low-oxygen, high-organic-matter areas (Goldstein, 1999; Phleger & Soutar, 1973). Nematodes are highly adaptable and can thrive in diverse ecological conditions. For example, *Sabatieria*, are adapted to low-oxygen (often hypoxic or anoxic) environments, typically linked to areas with high-organic matter input, where organic enrichment depletes oxygen levels (Gupta & Machain-Castillo, 1993; Kitazume et al., 2018). Other genera, such as *Monhystrella* and *Plectus*, prefer stable, sheltered environments with abundant organic matter, typical of habitats like BB and FPS, where organic material accumulates and disturbances are minimized (Leduc et al., 2001; Vanaverbeke et al., 2016). *IS\_05*, despite being in a relatively open area, may offer a more stable environment due to its depth and accumulation of fine sediment (**Table 1, 3**), reducing exposure to disturbances and creating conditions conducive to stable populations of these genera. In contrast, *Halalaimus* can survive in low-food environments like the deep sea, adapting to low organic matter by efficiently utilizing limited resources (Leduc & Gad, 2010).

Substantial variation was observed in both IS and BB habitats, likely driven by differences between stations (e.g., BB\_01, BB\_02), with the greatest microscale variability evident at FPS (**Fig. 4**). Similar findings of patchiness in meiofaunal abundance and community structure within subtidal sandy sediments have been attributed to distribution of organic matter (OM) and local hydrodynamic conditions (Moccia et al., 2019; Giere, 2009; Reise, 1985). At FPS, variability arose from collecting cores at different locations within the structure. Reduced flow dynamics at the centre of FPS –caused by the semi-enclosed design– likely limit bottom water renewal, promoting OM accumulation and higher meiofauna abundances (**Table 4**; Danovaro et al., 2002). This inference is supported by the shallow depth of the oxic sediment layer (OLSD) in FPS cores, indicating enhanced microbial activity and oxygen consumption, which create favourable conditions for diverse meiofaunal assemblages (Balsamo et al., 2012). The pinkish sediment coloration observed at FPS inner positions further corroborates this, as it may reflect bacterial communities thriving in OM-enriched environments, common in ARs (Cresson et al., 2014). The exceptionally high densities of amoebae within these sediments also highlights their adaptation to OM-rich microhabitats and reliance on bacteria as a food source (Fenchel, 1988; Smirnov & Fenchel, 1996). This spatial heterogeneity in meiofaunal assemblages may stem from the patchy deposition of OM, as seen in studies where localised hydrodynamic processes lead to discrete microzones of nutrient enrichment (Moccia et al., 2019). These findings suggest that FPS may foster conditions beneficial for recolonisation by promoting OM accumulation and microbial activity, which, in turn, support meiofaunal communities integral to sediment nutrient cycling. Higher meiofauna abundances could enhance sediment stability and organic processing, potentially facilitating the recruitment of bivalves and seagrass. However, the extent to which these processes contribute to long-term habitat restoration warrants further investigation. Additionally, spatial variability in meiofaunal communities across FPS highlights the importance of strategic placement, as local hydrodynamics and sediment characteristics may influence their effectiveness. Optimising FPS design to balance OM retention with sufficient water exchange could enhance their role as ecological facilitators in degraded marine environments.

Meiofauna taxa like Nematoda, Foraminifera, Copepoda, and testate amoebas were prevalent (**Fig. 4-5**). SIMPER analysis revealed that tardigrades and bivalves contributed significantly to the observed dissimilarities between BB, with tardigrades particularly abundant at BB\_02. Nematodes, prevalent at FPS, BB\_01, and IS\_05, exhibit diverse feeding behaviours, preying not only on tardigrades, but also nematodes, protists, and microalgae, highlighting their key role in sedimentary trophic dynamics (**Table 5**; Moens & Verhoeven, 2001; Norkko & Norkko, 2006; Vink, 2002). Oligochaetes dominated BB\_01, while amphipods and testate amoebae characterised FPS\_01. The latter were unique to FPS (specifically at the centre position), thriving in extreme conditions, such as low-oxygen and OM-rich environments (Smirnov & Fenchel, 1996; Wu et al., 2023). Testate amoebae likely rely on abundant bacteria sustained by OM accumulation, likely associating from the reduced water circulation within the semi-enclosed centre of the FPS. This raises the question of whether similar patterns occur in larger organisms, such as bivalves, sponges, and crustaceans, which may respond differently to the altered sediment and flow conditions inside FPS compared to surrounding areas. Such reduced flow can limit sediment resuspension and increase OM retention, potentially altering sediment grain size and composition. This pattern was observed in ARs, where reduced water circulation within the enclosed space leads to a finer sediment accumulation at the centre and coarser sediments on the periphery (Dayton et al., 1982). Similarly, *Ambrose and Anderson* (1990) found that the design of ARs caused shifts in sediment grain size distribution, with finer sediments accumulating in areas of low water flow and coarser grains being pushed to the edges. Despite limited replication, this process is consistent with the observed increase in coarse sand at the center of the FPS in our study (**Table 3**), suggesting that the reduced hydrodynamic forces inside these structures may trap larger sediment particles while finer sediments accumulate at the margins (Ambrose & Anderson, 1990). While OM accumulation within FPS fosters microbial productivity and meiofaunal diversity, excessive enrichment could create hypoxic conditions that may not be favourable for larger benthic organisms. Strategies to enhance water exchange, such as modifying FPS design to balance OM retention with sediment transport, could help optimise their function as restoration tools.

Amphipods inhabit diverse environments, depending on feeding habits and low levels of bio-competition (Barnard, 1976), while foraminifera require specific food, depth, and oxygen conditions to thrive. Calcareous foraminifera exhibited a relatively consistent trend across stations with densities less variable than those of proteinaceous foraminifera. Proteinaceous foraminifera were most abundant at BB\_02 nearly double that of IS\_05, followed by IS\_01, and were least abundant or comparable to BB\_01 and FPS habitats (**Fig. 4-5**; **Table 3-4**). These foraminifera are typically found in low-oxygen, organic-rich environments where their food sources, such as microbial biofilms or organic detritus, are abundant (Bernhard & Reimersl, 1991; Levin et al., 2009). In our study, proteinaceous foraminifera were more prominent in areas with low water circulation and presumed higher organic matter content, suggesting a strong association with BB\_02 and IS\_05 habitats.

At IS, taxa like Halacaridae, Tanaidacea, and Cumacea contributed to observed differences (**Table 4-5**). Halacaridae and Tanaidacea were dominant at IS\_01, perhaps given a preference for silty, sandy, and gravel sediments (Blazewicz-Paszkowicz et al., 2012), which are often subjected to high resuspension rates, particularly in trawling areas. Their presence may also be influenced by beam trawl fishing, which can reduce predator populations and increase sediment turnover. Cumacea, on the other hand, were prevalent at IS\_05, perhaps due to less disturbance from anthropogenic activities and more stable environmental conditions. The greater depth at this station could also contribute to reduced disturbance, providing a more stable habitat for *Cumacea* (Gerken, 2016; **Table 2**). This pattern is consistent with previous studies in similar habitats, where deeper, less disturbed environments are more conducive to the presence of *Cumacea* and other sensitive taxa (e.g., Boonyapran, 1991; Chou, 1993).

Bivalve beds are critical ecosystem engineers, enhancing habitat complexity, stabilising sediment, and improving the local sediment characteristics (Grabowski et al., 2012). Our findings confirm that bivalves, including oysters, support ecosystem resilience through nutrient cycling and hypoxia mitigation (Cressman, 2003; Coen & Humphries, 2017). By facilitating benthic-pelagic coupling and oxygenating sediments, oysters contribute to enhanced sediment conditions that benefit secondary production (Coen & Humphries, 2017; Newell et al., 2002). At BB\_02, abundant oysters contributed to deeper anoxic layers and improved water clarity, which we measured as visibility (**Table 2-3**). In contrast, the accumulation of OM at FPS, which was previously linked to BB habitats, suggests that while oyster beds improve sediment conditions and promote water clarity, other factors—such as reduced hydrodynamic flow—may influence organic matter retention differently in the two locations. These contrasting effects raise important considerations for FPS design. While oyster beds improve sediment quality and water clarity through active filtration and bioturbation, FPS may instead promote OM retention due to reduced hydrodynamic flow. Understanding whether one mechanism is more beneficial than the other—and whether FPS could be adapted to better replicate the sediment-enhancing effects of bivalve beds—could help refine their role in habitat restoration.

In shallow habitats, bivalves maximise filtration capacity, particularly during algal blooms, as demonstrated in a 2 m deep estuaries (Gobler et al., 2022; Pomeroy et al., 2006). This filtration ability is reflected at BB stations, which had nearly triple the anoxic layer depth of other stations (**Table 3**). This may explain why BB\_02—a shallow station comprised of a dense oyster and seagrass bed—exhibited the highest water clarity (**Table 2**), deepest anoxic sediment layer (**Table 3**), and highest taxon richness and meiofauna diversity (**Fig. 5**, **Table 6**). In contrast, BB\_01, with a sparser bivalve bed and fewer oysters and seagrass, located near active fishing areas, displayed shallower anoxic layers, lower water clarity, and reduced meiofauna diversity. The proximity to fishing activities, including potential sediment disturbance and reduced filtration capacity due to lower bivalve density, may explain these differences (**Table 3; Fig. 6**). Oysters’ selective filtration, including rejection of particles like pseudofaeces (Hawkins et al., 1998), is essential for sustaining tropical marine ecosystems. Notably, all suspension-feeders collectively enhance ecosystem services in these environments (National Research Council, 2010). The role of bivalve beds in mitigating algal blooms is particularly relevant for Cambodia, where harmful blooms have increased in frequency and severity. A particularly severe event in Kep six to seven years ago resulted in mass fish mortality, beach closures, and the widespread decomposition of marine life. Such events highlight the critical role of bivalve beds in maintaining water quality and underscore the need for their protection.

Conclusions and future directions

The study provides a snapshot of sediment conditions and meiofaunal structures across three habitat types in Kep Archipelago. Fisheries Production Structures (FPS) and Bivalve Beds (BB) play distinct yet complementary roles in enhancing biodiversity, supporting commercially important species, and fostering diverse meiofaunal assemblages. FPS not only deter illegal trawling but also enrich biodiversity through organic matter retention and stable surfaces for the colonisation of bivalves, filter feeders like sponges, and even hard and soft corals, along with algae that attract herbivores. These interactions further enhance the complexity and resilience of the ecosystem, supporting diverse meiofaunal assemblages and contributing to benthic-pelagic coupling (Strong et al., 2022; Reid et al., 2019; Gorra et al., in prep).

Meiofaunal patchiness, shaped by microhabitat variability and anthropogenic impacts, underscores the complexity of community structure and highlights their potential as bioindicators for monitoring habitat health. Future research should incorporate meiofaunal diversity metrics alongside sedimentological and biogeochemical analyses to elucidate benthic ecosystem responses to natural and anthropogenic disturbances. In this context, nematode diversity and maturity indices offer promise as indicators of pollution and ecosystem stress (Wildish et al., 1990; Bongers et al., 1995). Expanding studies across larger temporal and spatial scales will be critical for capturing nuanced habitat-specific influences and establishing robust ecological baselines in data-limited regions like the Cambodian Sea, which can be achieved without the need for sophisticated designs. By adopting proxy metrics, even under constraints, relevant ecosystem data can be gathered to inform conservation efforts. Ultimately, the significant impact of human-driven disturbances, particularly fishing, emerges as a key factor shaping marine benthic communities in the Kep Archipelago, emphasising the urgent need for informed conservation and restoration efforts.

Despite logistic constraints, this study represents a collaborative effort that underscores the feasibility of conducting meaningful ecological research under challenging conditions. Proxy metrics and straightforward methods can provide essential ecosystem data, particularly in regions where access to sophisticated tools is limited. These findings highlight the importance of integrating meiofauna into routine monitoring programs as cost-effective tools for detecting early ecological changes and informing conservation strategies.

However, successful habitat restoration and long-term resilience require more than physical interventions like FPS. The Asian Development Bank's SCFM (Sustainable Coastal and Fisheries Management) project, which includes the addition of 5000 FPS by MCC, represents the first large-scale artificial reef initiative in shallow waters across all four of Cambodia’s coastal provinces (ADB, 2024). This project addresses three primary objectives: curbing illegal fishing activities, restoring critical habitats such as seagrass and bivalve beds, and supporting endangered species like marine mammals by providing free-trawling zones (*pers. comm.* Simon Rétif).

Furthermore, the project underscores the importance of local community engagement, as it is led by Cambodian NGO, MCC, that has successfully scaled a strategy from a small local initiative to a national programme. Empowering local fishing communities through alternative livelihoods, sustainable fishing practices, and capacity-building initiatives is integral to fostering stewardship of marine resources and ensuring long-term sustainability. The socioeconomic benefits of such initiatives are profound, as many coastal families rely entirely on fishing for their livelihoods and face poverty without conservation interventions (FAO, 2020; FAO, 2023).

Finally, cross-border collaboration remains critical, given that many IUU fishing challenges originate from neighbouring countries. Strong governance, robust enforcement, and ecosystem-based management are vital to balancing biodiversity conservation with sustainable resource use, ensuring the recovery and long-term health of the region's marine ecosystems (Lee & Viswanathan, 2020).

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###### 5. Conclusions:

The widespread ecological impacts of trawling are well-documented (Kaiser et al., 1998), and this study highlights the vital roles of bivalve beds and Fisheries Production Structures (FPS) in the Kep Archipelago. Bivalve beds demonstrated strong benthic-pelagic coupling, particularly at BB\_02, where overlapping ecosystems enhanced biodiversity and nutrient cycling, while FPS provided temporary refuge and structural support for biodiversity recovery in degraded areas. While FPS cannot substitute natural habitats like bivalve beds, coral reefs, or seagrass meadows, they serve as interim conservation tools. Long-term solutions require restoring natural habitats, creating alternative livelihoods, building local capacity, and enforcing fishing regulations to mitigate destructive practices. Sustained monitoring of meiofauna communities and other ecological indicators will be crucial for understanding FPS impacts and guiding adaptive management, ensuring resilience and sustainable marine resource use in the Cambodian Sea.

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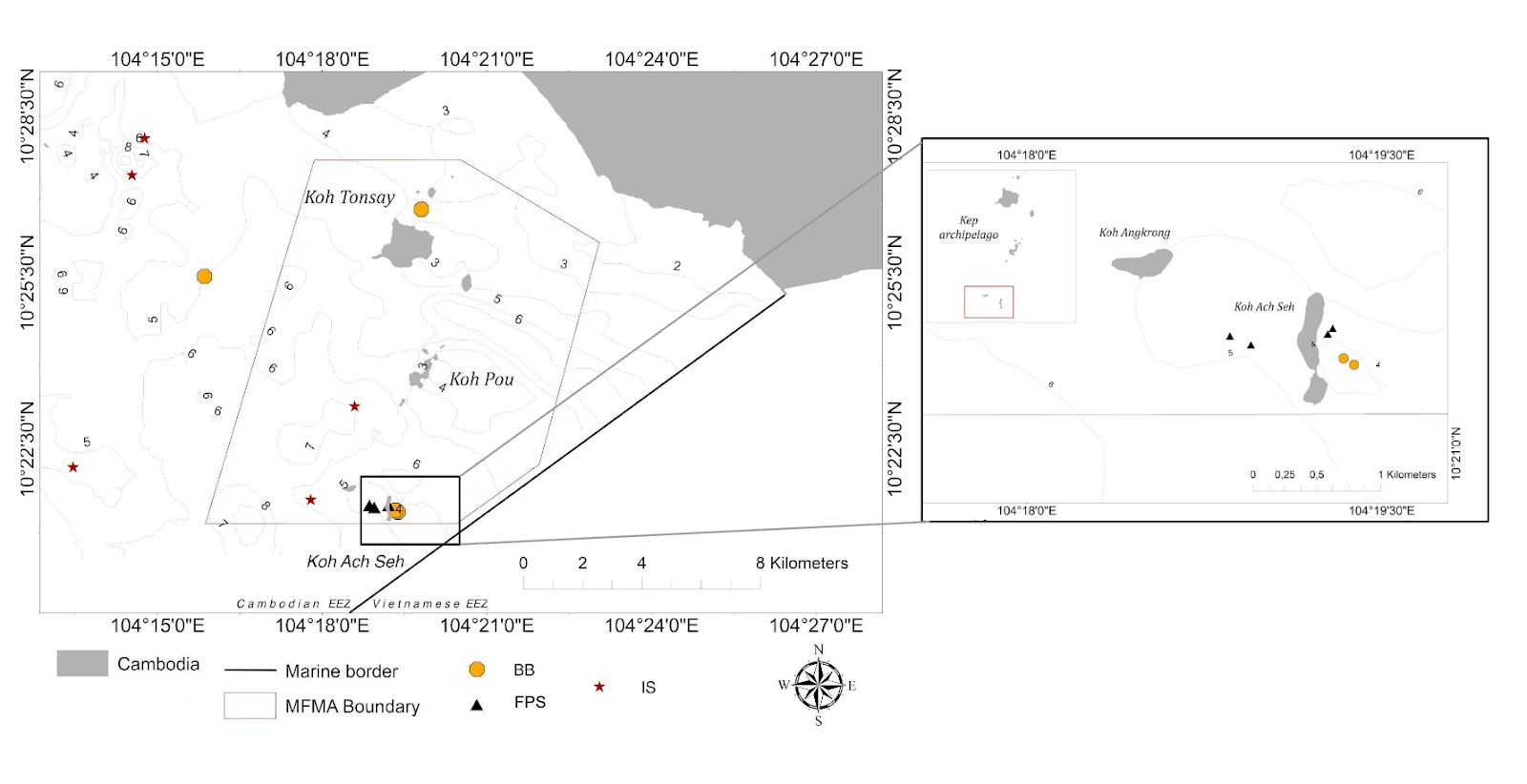
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Figures and Tables:

**Fig. 1 (below). Overview of Study Area.** The study area of sample stations: Bivalve Beds (BB, orange circles), Fisheries Production Structures (FPS, black triangles), and Impacted Stations (IS, red stars), surveyed within Kep Archipelago. The Kingdom of Cambodia is a Southeast Asian country in the Gulf of Thailand, sharing marine borders with Thailand and Vietnam. The majority of sample stations occurred near the Cambodian-Vietnamese border and fall within the Marine Fisheries Management Area (MFMA boundary; grey solid line); however, they remain subject to illegal fishing (pers. obvs., Amick Haissoune, pers. comm.). Map courtesy of Simon Valerio, MCC.

**Table 1 (below). Description of sampling stations.** Key environmental variables, including light availability, temperature, anoxic sediment layer depth, mean grain size, are presented. Meiofauna higher taxonomic diversity measured at representative stations (denoted with an asterisk). Stations are identified by their respective categories: BB = bivalve bed, FPS = habitat restoration site, IS = impacted station. This work was conducted at Marine Conservation Cambodia (MCC).

|  |  |  |  |
| --- | --- | --- | --- |
| Station ID | Location (degree °) | Description | FPS Deployment year (estimated age in years during study) |
| BB\_01\* | 10.44707 N, 104.33016 E | Mixed bivalve bed with light fishing activity observed |  |
| BB\_02\* | 10.35621 N, 104.32305 E | Mix of seagrass and bivalve beds near Koh Ach Seh (protected by MCC) |  |
| BB\_03 | 10.35665 N, 104.32232 E | Offshore of BB\_02 (similar habitat) |  |
| BB\_04 | 10.42693 N, 104.26429 E | Dense bivalve bed ner Koh Pou |  |
| FPS\_01 | 10.3576 N, 104.31579 E | FPS located west of Koh Ach Seh | 2018 (5) |
| FPS\_02 | 10.35822 N, 104.31431 E | FPS located west Koh Ach Seh | 2019 (4) |
| FPS\_03 | 10.35821 N, 104.32012 E | FPS near MCC (east of Koh Ach Seh) | 2017 (6) |
| FPS\_04 | 10.357772 N, 104.321137 E | FPS near coral reef (east of Koh Ach Seh, protected by MCC) | 2018 (5) |
| FPS\_05 | 10.357715 N, 104.321202 E | Prototype near MCC and coral reef (east of Koh Ach Seh) | 2017 (6) |
| IS\_01\* | 10.36976 N, 104.2244 E | Active trawling grounds with remnant patches of seagrass |  |
| IS\_02 | 10.35996 N, 104.29659 E | Known fishing grounds |  |
| IS\_03 | 10.38805 N, 104.3099 E | Fishing grounds nearby |  |
| IS\_04 | 10.46854 N, 104.24616 E | Fishing ground near Koh Kron and channel, [~10-15 vessels within 2 km radius] |  |
| IS\_05\* | 10.45751 N, 104.24229 E | 10-m deep channel, near Kampot |  |

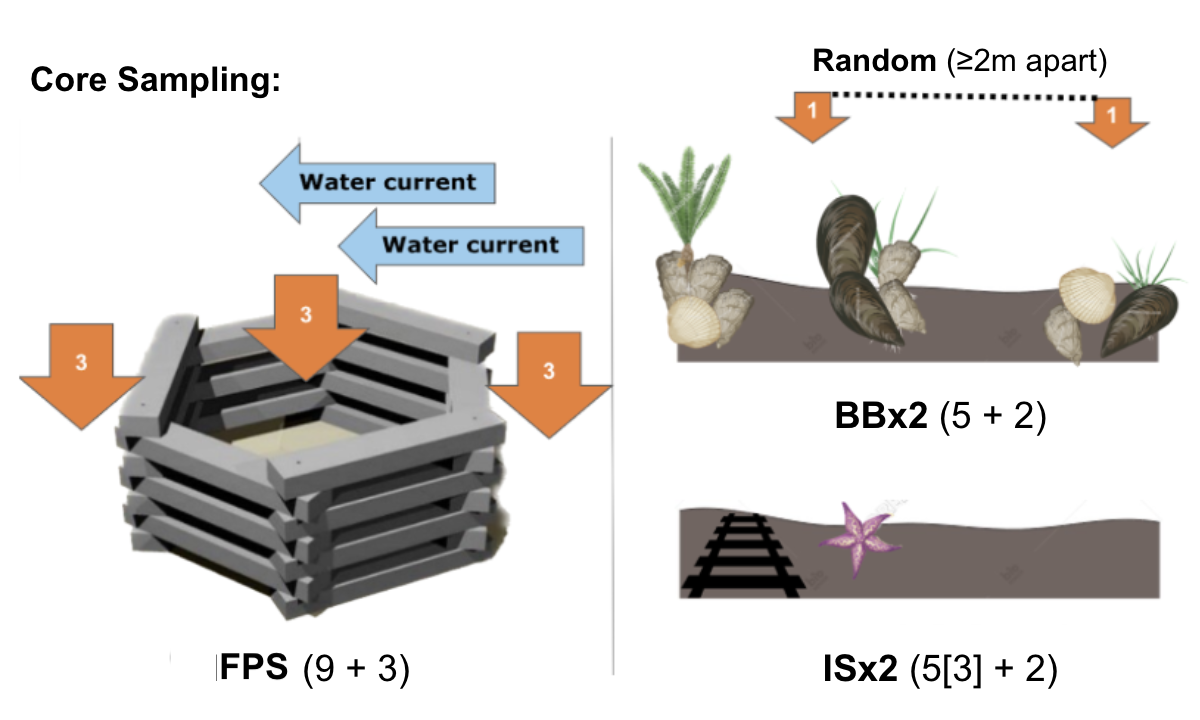
**Table 2 (below). Environmental variables.** Measurements were estimated across stations (BB=Bivale Beds, FPS= Fisheries Production Structures, IS= Impacted Stations). Temperature (°C) was recorded with dive computers, while average temperature (avg. °C) and light intensity (avg. lux, lm/m²) were recorded at depths of 0 and 1 metre at reference stations (\*) using HOBO data loggers. The control sensor captured ambient conditions. Temperature sensor resolution: 0.14°C at 25°C with response times of 2 m/s response in air, and 5 minutes in water. Substrate types: ST = Silt, SS = Sand/Shell, SST = Sand/Silt, SSTPB = Sand/Silt/Pebble, SSSTPB = Sand/Shell/Silt/Pebble, NS = No Survey.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Station | Depth (m) | Visibility (m) | Temperature (℃) | Salinity (ppt) | Light (avg. lux) | | Temperature (avg. ℃) | | Dominant  Substrate |
|  |  |  |  |  | 0m [SD] | 1m [SD] | 0m [SD] | 1m [SD] |  |
| BB\_01\* | 3.5 | 3.5 | 27 | 30 | 526.6 [889.12] | 353.3 [527.47] | 28 [0.38] | 28 [0.39] | ST |
| BB\_02\* | 3 | 4.3 | 29 | 32 | 2166.3 [156.73] | 6747.6 [11312.89] | 28.9 [0.25] | 29.1 [0.43] | NS |
| BB\_03 | 2.2 | 2.5 | 30 | - | - | - | - | - | SS |
| BB\_04 | 6 | 6 | 30 | - | - | - | - | - | SSSTPB |
| FPS\_01 | 5.3 | 1.5 | 31 | 32 | 545. 4 [896.35] | 1911.4 [2969.69] | 28 [0.42] | 28 [0.43] | ST |
| FPS\_02 | 5.5 | 2 | 29 |  | - | - | - | - | ST |
| FPS\_03 | 1.9 | 2.5 | 30 |  | - | - | - | - | SS |
| FPS\_04 | 1.9 | 3 | 30 |  | - | - | - | - | SS |
| FPS\_05 | 1.7 | 2.5 | 29 |  | - | - | - | - | SS |
| IS\_01\* | 5.1 | 4 | 32 | 32 | 2483.7 [4088.90] | 1854.9 [3265.21] | 27.8 [0.28] | 27.81 [0.28] |  |
| IS\_02 | 5.8 | - | 33 |  | - | - | - | - | SSTPB |
| IS\_03 | 7.3 | 2.6 | 31 |  | - | - | - | - | SSTPB |
| IS\_04 | 5.6 | 4 | 31 |  | - | - | - | - | SST |
| IS\_05\* | 10.9 | 2 | 29 | 34 | 12.6 [27.28] | 44.4 [77.14] | 28.9 [0.11] | 28.9 [0.13] | NS |
| Control | - | - | - | - | 43262.5 [64221.92] | | 29.5 [4.76] | |  |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Average anoxic layer  depth (cm) [SD] | ncores | Median grain size (DX90 μm) [SD] | Wentworth (1922) grain size classification |
| Station |  |  |  |  |
| BB\_01 | 3.11 [0.50] | 7 | 136.22 [45.02] | Fine to medium sand |
| BB\_02 | 3.71 [0.95] | 7 | 619.67 [60.26] | Coarse sand |
| BB | 3.41 [0.79] | 14 | 377.94 [257.52] | Medium sand |
| FPS\_in | 1.78 [1.32] | 4 | 644.33 [243.82] | Coarse sand |
| FPS\_up | 1.33 [1.04] | 3 | - | - |
| FPS\_down | 1.30 [1.17] | 4 | - | - |
| FPS\_adjacent | 3 [na] | 1 | 347.30 [8.14] | Medium sand |
| FPS\_01\* | 1.51 [1.13] | 12 | 495.83 [224.20] | Medium sand |
| IS\_01 | 0 [na] | 7 | 1035.67 [280.54] | Very coarse sand |
| IS\_05 | 0 [na] | 5 | 143.67 [42.19] | Fine sand |
| IS | 0 | 12 | 589.67 [503.57] | Coarse sand |

\*includes sample taken on the side of the structure

**Table 3. (above). Sediment characteristics across reference stations.** The anoxic layer depth and median grain size (where over 90% of the sample is smaller than the given value in micrometres ) and their associated standard deviations were calculated and averaged for each station and habitat type (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations). The average anoxic depth measurement does not include the adjacent sample collected at FPS\_01.

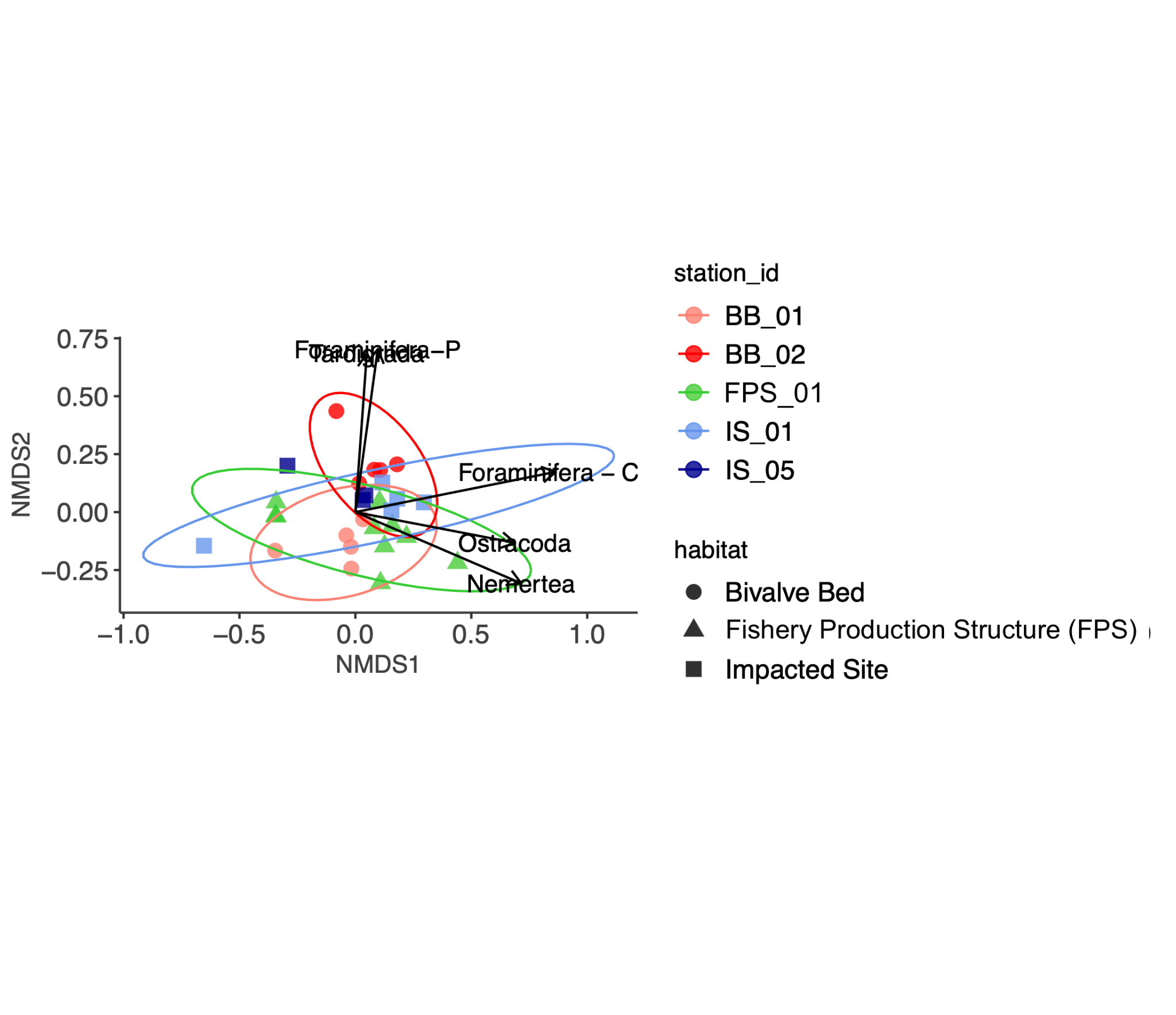


**Fig. 2 Sediment core sampling strategy.** The sampling strategy for core collection was designed to reflect key attributes of the different habitats (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations). Five cores were collected randomly (spaced at least two m apart) for BB and IS habitats (right), except for three at IS\_05 (out of interest). In a patchy BB, such as BB\_01, cores were collected near clusters of bivalves. For IS habitats, like IS\_01, cores were taken inside and outside visible trawling paths to assess potential impacts. A modified core sampling procedure at FPS (left) considered the possible influence of altered current dynamics due to vertical relief. Thus, three cores were collected up-current, down-current, and inside the structure to capture potential variations in sediment characteristics. Additionally, another core was obtained inside the FPS at a deeper profile (i.e., 10 cm vs. 5 cm) to assess meiofauna community assemblage, as the presence of pinkish-red clay at this depth could indicate specific ecological conditions.

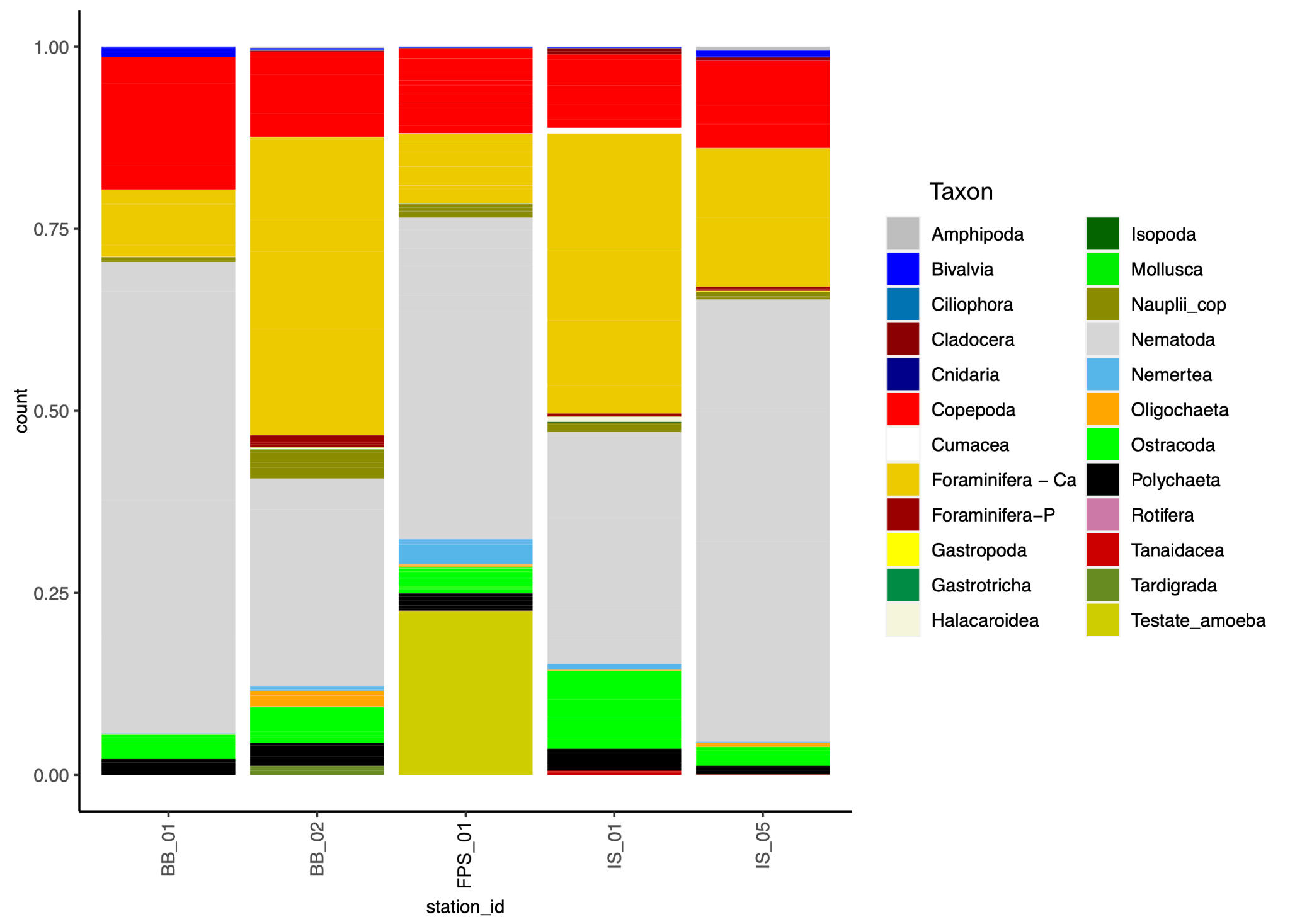
Table 4. Meiofauna average density across stations (below).

The average densities (ind. 10 cm-2) and associated standard deviations (shown in brackets) of permanent meiofauna across representative stations (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | BB | | FPS | IS | |
|  | 01 | 02 | 01 | 01 | 05 |
| Taxa |  |  |  |  |  |
| Amphipoda | 0 [na] | 2.6 [1.67] | 0.5 [1.07] | 0.5 [1.0] | 8.5 [6.36] |
| Bivalvia | 22.4 [21.96] | 1.6 [1.52] | 2.78 [4.29] | 2.25 [1.26] | 6.0 [0] |
| Cladocera | 0 [na] | 2 [2.35] | 2.5 [5.24] | 8.5 [5.80] | 7.5 [0.71] |
| Copepoda | 286.36 [189.30] | 116.35 [92.98] | 218.58 [109.64] | 104.5 [44.59] | 105.5 [16.26] |
| Cumacea | 0.8 [0.84] | 1.2 [1.30] | 2 [2.39] | 8.75 [5.38] | 0.5 [0.71] |
| Foraminifera (P) | 0.5 [1.0] | 16.8 [12.54] | 0.5 [1.27] | 3.8 [8.50] | 7 [2.65] |
| Foraminifera (C) | 143.4 [172.82] | 409.6 [289.05] | 192.89 [137.45] | 344 [271.04] | 339 [1.41] |
| Gastrotricha | 0 [na] | 0.4 [0.55] | 0.125 [0.35] | 0.25 [0.5] | 0 [na] |
| Halacaridae | 0.2 [0.45] | 1.8 [1.79] | 0.56 [0.88] | 7.25 [11.30] | 0 [na] |
| Nauplii | 10.8 [11.97] | 39.8 [29.15] | 34.3 [30.98] | 11.0 [14.27] | 12.33 [8.39] |
| Nematoda | 1017.8 [465.02] | 285.6 [150.13] | 765.9 [811.94] | 313 [191.86] | 722.3 [227.78] |
| Ostracoda | 52.6 [74.79] | 49.4 [65.87] | 80 [48.81] | 117.0 [44.31] | 37.0 [24.04] |
| Polychaeta | 34.6 [17.02] | 31.4 [10.14] | 49.75 [22.86] | 27.0 [23.34] | 15.5 [4.95] |
| Rotifera | 0 [na] | 0.2 [0.45] | 0.25 [0.71] | 0 [na] | 0 [na] |
| Tanaidacea | 0 [na] | 0 [na] | 0.25 [0.71] | 6.75 [5.56] | 0.5 [0.71] |
| Tardigrada | 0 [na] | 12.4 [10.53] | 0 [na] | 0 [na] | 0 [na] |
| Testate Amoeba | 0 [na] | 0 [na] | 1371 [2374.06] | 0 [na] | 0 [na] |



**Fig. 3 (above).** Non-metric Multidimensional Scaling (NMDS) plot showing four distinct groups based on habitat (BB = Bivalve Beds, FPS = Fisheries Production Structures, IS = Impacted stations) and station\_id. Taxa contributing most to within-site differences include calcareous foraminifera, Nemertea, and Ostracoda on NMDS1, and proteinaceous foraminifera and Tardigrada on NMDS2. The analysis was based on taxa filtered with a p-value = 0.001 (R² = 0.97, linear fit R² = 0.878, Stress = 0.17).



**Fig. 4** Stacked bar plot showing the multivariate relative abundances of the higher taxon meiofauna across stations (n=24) where BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations.

###### 

###### **Fig. 5.** The taxon richness of meiofauna taxa varies significantly across sample stations (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations; F = 5.499, p < 0.01). The median richness is 15 taxa per site, the thick horizontal black bands represent the median for each station, while the boxplot margins indicate the first and third quartiles. Among the stations, the lowest taxon richness was observed at BB\_01 (11.6 ∓ 1.62), and the highest was at BB\_02 (17.8 ∓ 0.75).

**Table 5. (below)**. SIMPER results: between station contrasts (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations). Top three taxa contributing to station contrasts. The asterisk indicates the level of significance corresponding to taxa, such that ‘\*\*\*’ = p < 0.001, ‘\*\*’ = p < 0.01, ‘\*’ = p < 0.05.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Contrast: BB\_01, BB\_02  Dissimilarity: 34.8% | | Contrast: BB\_01, FPS\_01  Dissimilarity: 30.9% | | Contrast: BB\_01, IS\_01  Dissimilarity: 33.8% | | Contrast: BB\_01, IS\_05  Dissimilarity: 28.9 % | | Contrast: BB\_02, FPS\_01  Dissimilarity: 34.1 % | |
| Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib |
| Tardigrada\*\*\* | 19.6 | Bivalvia\*\*\* | 21.8 | Nematoda\*\*\* | 23.8 | Amphipoda\*\*\* | 23.7 | Tardigrada\*\*\* | 18.8 |
| Foraminifera(P)\*\*\* | 28.4 | Oligochaeta\* | 43.0 | Copepoda\*\* | 38.0 | Foraminifera (P)\* | 33.0 | Foraminifera (P)\*\*\* | 27.0 |
| Oligochaeta\*\* | 44.0 | Naupauli\* | 54.3 | Tanaidacea\*\* | 62.5 | Oligochaeta\* | 40.7 | Amphipoda\* | 42.6 |
| Contrast: IS\_01, BB\_02  Dissimilarity: 32.3% | | Contrast: IS\_05, BB\_02  Dissimilarity: 27.3% | | Contrast: IS\_01, FPS\_01  Dissimilarity: 33.6% | | Contrast: IS\_05, FPS\_01  Dissimilarity: 32.3% | | Contrast: IS\_05, IS\_01  Dissimilarity: 32.6% | |
| Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib | Taxa | Cum. Contrib |
| Tardigrada\*\*\* | 19.0 | Tardigrada\* | 21.0 | Tanaidacea\*\* | 37.0 | Amphipoda\*\* | 18.6 | Amphipoda\*\* | 34.7 |
| Foraminifera (P)\*\* | 27.5 | - | - | Halacaridae\* | 42.0 | Foraminifera (P)\* | 26.0 | Halacaridae\* | 40.8 |
| Tanaidacea\* | 43.4 | - | - | - | - | Cnidaria\* | 94.7 | Cumacea\* | 46.8 |

**Table 6.** **Shannon diversity and taxon richness of cores across stations.** Shannon diversity and taxon richness is described below for respective stations (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations).

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Core\_ID | | Shannon  Diversity | Taxon richness | ind./core |  | Core\_ID | Shannon  Diversity | Taxon  richness | ind./core |
| Station | | | |  | Station |  |  |  |  |
| BB\_01 | #001 | 1.95 | 10 | 1302 | BB\_02 | #027 | 2.65 | 18 | 1332 |
|  | #002.2 | 2.30 | 14 | 2446 |  | #028 | 2.59 | 17 | 901 |
|  | #003 | 2.04 | 11 | 1904 |  | #029 | 2.63 | 18 | 1274 |
|  | #004 | 2.22 | 13 | 1588 |  | #030 | 2.57 | 17 | 1140 |
|  | #005 | 1.91 | 10 | 625 |  | #031 | 2.74 | 19 | 366 |
|  |  |  | 11.6 [+/-1.62] | 7683 |  |  |  | 17.8 [+/-0.75] | 5012 |
| FPS\_01 |  |  |  |  |  |  |  |  |  |
|  | #008 | 2.10 | 11 | 1358 |  | #013 | 2.24 | 13 | 581 |
|  | #009 | 2.15 | 12 | 4173 |  | #014 | 2.61 | 18 | 1667 |
|  | #010 | 2.26 | 13 | 734 |  | #015 | 2.63 | 18 | 1241 |
|  | #011 | 2.34 | 14 | 1383 |  | #016 | 2.51 | 16 | 581 |
|  | #012 | 2.36 | 14 | 5960 |  | #019 | 2.21 | 12 | 677 |
|  |  |  |  |  |  |  |  | 15 [+/-2.34] | 18474 |
| IS\_01 |  |  |  |  | IS\_05 |  |  |  |  |
|  | #020 | 2.55 | 16 | 519 |  | #034 | 2.56 | 17 | 1563 |
|  | #021 | 2.46 | 15 | 881 |  | #035 | 2.44 | 15 | 1143 |
|  | #022 | 2.57 | 17 | 1341 |  | #036 | 2.45 | 15 | 872 |
|  | #023 | 2.55 | 17 | 1633 |  |  |  |  |  |
|  | #024 | 2.04 | 10 | 105 |  |  |  |  |  |
|  |  |  | 15 [+/-2.61] | 4479 |  |  |  | 15.7 [+/-0.94] | 3578 |

**Table 7. Mean Pielou’s Evenness J and Hill’s Index. (below).** The number of replicate cores (R), Mean and associated standard deviation (SD),Mean Pielou's Evenness J and values for Hill’s Index (N0, N1, N2) were calculated for each station based on raw counts estimated within each replicate core. Significant differences for both Mean Pielou's Evenness J (factor “Core ID”, F = 1.144, p = 0.113) and Hill’s Index, including: taxon richness, N0 (F = 5.088, Pr(>F) = 0.00437); Shannon Entropy Index, N1 (F = 7.301, Pr(>F) = 0.00059); and Simpson’s Concentration Index, N2 (F = 4.534, Pr(>F) = 0.00757) using the factor “Core ID”. The Hill’s Index values are averaged for stations (BB=Bivalve Beds, FPS=Fisheries Production Structures, IS=Impacted stations).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Station | replicate number (R) | Mean (species richness) | Mean Pielou’s  Evenness J | Taxon Richness (N0) | Shannon Entropy Index (N1) | Simpson’s Concentration Index (N2) |
| BB\_01 | 5 | 11.6 [+/- 1.62] | 0.416 | 9.6 | 2.70 | 2.05 |
| BB\_02 | 5 | 17.8 [+/-0.75] | 0.543 | 15.4 | 4.59 | 3.02 |
| FPS\_01 | 10 | 14.1 [+/-2.34] | 0.498 | 11.5 | 3.65 | 2.72 |
| IS\_01 | 5 | 15 [+/-2.61] | 0.617 | 12.6 | 4.84 | 3.73 |
| IS\_05 | 3 | 15.7 [+/-0.94] | 0.435 | 13.3 | 3.18 | 2.27 |

**Table 8. Statistical summary**. Description of the tests employed to analyse the variables and effects of interest for the overall study.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Variables | Test | Effect | Test stat | Significance | Key take-aways, notes |
| Abiotic |  |  |  |  | Abiotic metrics differ between habitats and stations |
| Median grain size | One-way ANOVA | Between stations | F=30.77 | p=2.51e-09\*\*\* |  |
| Anoxic layer depth | One-way ANOVA | Between habitats | F=14.03 | p=0.0089\*\*\* |  |
| Biotic |  |  |  |  |  |
| Meiofauna |  |  |  |  | Meiofauna metrics differ significantly between habitats |
| Diversity | One-way ANOVA  (richness, Shannon diversity);  PERMANOVA (on relative abundances, nperm=999);  DbRDA (squared-Bray distance) | Between habitats  (inc. env. vars.[[1]](#footnote-1)) | F=5.499 (richness),  F=7.323 (div.);  pseudo-F:2.5,  R2=2.4482;  Total inertia: 0.43 | p<0.01\*\*  (richness, div.);  p=0.002\*\*  (Permdisp: n.s.);  n.s. | Significant differences in meiofauna richness and diversity, as well as relative abundances between assemblages. A pair-wise PERMDISP was shown insignificant; similarly, community variability was not sufficiently explained by environmental variables, as more replicates are likely necessary |
| Between-group differences | SIMPER  (based on Bray-Curtis dissimilarity) | Between stations  Driving taxa |  | p=0.05\*  p=0.001\*\*\* | - Most dissimilarity between BB\_01 and BB\_02  - Tardigrada, Oligochaete, Bivalvia (larvae), and Amphipoda drive among-site dissimilarity |

###### 

1. The environmental variables tested include: Anoxic layer depth, median grain size (DX-90), salinity, average water temperature (recorded by HOBO data logger), and average light availability (lux) at the sediment surface and 1 metre above (recorded by the HOBO data logger). [↑](#footnote-ref-1)