



Benthic habitat zonation across oceanographic gradients and seafloor morphology from the mesophotic to the deep zone of the Gulf of Aqaba and the Northern Red Sea

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Abstract. The Gulf of Aqaba and Northern Red Sea are among the least explored basins of the Indo-Pacific region. There, while the shallow Red Sea coastal benthic habitats have been extensively characterised and their zonation in relation to environmental factors described, mesophotic and deep-sea habitats remain comparatively poorly characterised. These habitats develop in a water column that, unlike in most of the global ocean, remains warm (~21 °C) and hypersaline (~40.6) below the pycnocline. In this context, we present the first regional assessment of benthic habitat zonation from the mesophotic to the deep zone (70–700 m) along the Saudi Arabian margin of the Gulf of Aqaba and Northern Red Sea. Using high-resolution multibeam bathymetry, CTD profiles, and over 135 hours of high-definition footage from underwater vehicles, we developed a hierarchical habitat classification, integrating physiography, substrate, terrain analysis, and visually identified biota. Fourteen distinct benthic habitats were identified, including crustose coralline algae- and rare photic coral-dominated bioconstructions, octocoral-dominated assemblages and deep scleractinian coral frameworks. Oceanographic parameters (temperature, salinity, oxygen concentration) and seafloor morphology were both associated with habitat spatial distribution across the two basins. Multivariate analyses revealed a consistent vertical zonation, with three ecological breaks at approximately 100, 120, and 160–180 m depth, delineating four successive zones from the lower mesophotic to the deep azooxanthellate assemblages. This work fills a major knowledge gap for the Red Sea's deep-water ecosystems, providing a critical baseline to support future monitoring, conservation, and management strategies in a rapidly developing region.



1 Introduction

Over the past five decades, growing demand for marine space and resources has intensified pressures on ocean systems (Jouffray et al., 2020). In response, international frameworks such as the UN Sustainable Development Goals and the EU Marine Strategy Framework Directive have been called upon to establish effective conservation and sustainable marine resource management strategies (Long, 2011; UNGA, 2015). Achieving these goals requires robust knowledge of habitat structure, species distributions, and the environmental drivers shaping benthic communities along the depth gradient. Benthic zonation, defined as the occurrence of distinct biological assemblages within restricted depth bands (Carney et al., 1983) separated by ecological breakpoints of maximal faunal turnover (Braga-Henriques et al., 2022; Carney, 2005; Howell, 2010), is primarily driven by depth-related gradients in light, temperature, pressure, food supply, and seafloor geomorphology (Kahng and Kelley, 2007; Wong et al., 2025). At the broadest scale, depth is commonly partitioned into the mesophotic zone, defined between ~30 m and ~150 m depth with debated and variable boundaries regionally (Pyle and Copus, 2019), the rariphotic zone between ~130 and ~300 m (regionally variable, Baldwin et al., 2018), and the aphotic deep-sea zone below it, each harbouring high diversity and unique, often endemic communities structured by habitat-forming corals and sponges (Danovaro et al., 2008; Kahng et al., 2010; Soares et al., 2020). These vertical patterns have been documented across ocean basins worldwide, from the Atlantic (Carney et al., 1983; Howell, 2010; Liddell et al., 1988), Indo-Pacific (Colin et al., 1986; Kahng and Kelley, 2007; Wells, 1954), the polar seas (Rowden et al., 2015; Vedenin et al., 2021), the Mediterranean (Dominguez-Carrió et al., 2022; Gili et al., 2014; Laborel, 1987; Pérès and Picard, 1964), and the Gulf of Aqaba (Chimienti et al., 2025; Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Fricke and Schuhmacher, 1983). However, while this broad-scale framework is well established, how benthic habitats are structured and distributed in mesophotic and deep-water environments remains poorly known compared to shallow-water systems (Hinderstein et al., 2010; Menza et al., 2008; Turner et al., 2019). Characterising these patterns at scale requires integrating complementary datasets within standardised classification frameworks to bridge spatial gaps and generate broad-scale habitat maps (Andersen et al., 2018; Monteiro et al., 2015; Vasquez et al., 2015). Hierarchical schemes such as the European Nature Information System (EUNIS) (Davies and Moss, 2000), the broad-scale approaches developed for the South Atlantic (McQuaid et al., 2023), or the conceptual classification proposed by Buhl-Mortensen et al (2015) and the recent CoDeMap scheme (Grande et al., 2025) combine biological descriptors with physical habitat attributes to produce scalable categories useful for monitoring and management. Such integrative approaches are especially critical in mesophotic and deep environments where habitats still remain poorly characterised (Lesser and Slaterry, 2021; Mestdagh et al., 2020; Micallef et al., 2012; Song et al., 2022). The Red Sea is one such region.

The Red Sea is a semi-enclosed, narrow sea located on the northwestern border of the Indian Ocean, extending over 2000 km in length with an average depth of 490 m (Yao et al., 2014a), and a maximum depth of approximately 2860 m (Augustin et al., 2014). The Gulf of Aqaba (GoA), its northeastern arm, is a narrower basin, ~180 km long, reaching 1765 m at the Aragonese Deep (Friedman, 1985; Purkis et al., 2022a; Ribot et al., 2021). As the Red Sea connects to the Indian Ocean only through the shallow (137 m) Hanish Sill at the Strait of Bab-al-Mandab (Murray and Johns, 1997; Sofianos et al., 2002), the GoA connects



65 to the Northern Red Sea (NRS) only through the shallow sill at the Strait of Tiran (~200 m), which restricts exchange between the water masses of the two basins (Plähn et al., 2002). This restriction of water exchange with the Indian Ocean, combined with a hyperarid climate and the absence of freshwater input, drives a high evaporation rate of ~2 m yr⁻¹ (Purkis et al., 2025; Siddall et al., 2004; Sofianos et al., 2002). This, in turn, produces steep north-south gradients in temperature and salinity that weaken with distance from Bab-al-Mandab, where the influence of Indian Ocean water is greatest (Sofianos, 2002; Xie et al., 70 2019). Along the depth gradient, water temperature declines until ~300 m and then stabilises at ~21 °C even below 2000 m, while salinity below the pycnocline remains close to ~40.6 (Quadfasel, 2001; Yao et al., 2014b). This thermohaline stability at depth, unlike in most other ocean basins, is one of the Red Sea's defining anomalies. The GoA maintains its own deep-water mass, with higher salinity and lower temperature than the deep water of the Red Sea (Manasrah, 2002), so that despite their proximity the two basins present contrasting oceanographic regimes at depth.

75 The Red Sea is globally recognised for its high biodiversity and endemism across marine taxa in shallow tropical ecosystems (Briggs and Bowen, 2012; DiBattista et al., 2016). Its shallow coastal benthic habitats, including mangroves, seagrass beds and coral reefs, have been characterised and their zonation addressed (El Shaffai, 2011; Mergner, 1967; Price et al., 1987; Sheppard et al., 1992; Sheppard and Sheppard, 1991). Yet, consistent with trends observed worldwide, benthic habitat composition and zonation across the Red Sea's mesophotic and deep-water zones remain comparatively understudied 80 (Berumen et al., 2019, 2013; Eyal et al., 2019; Eyal and Pinheiro, 2020; Loya et al., 2016) despite historical and recent exploration efforts.

Research on Red Sea mesophotic ecosystems has long focused on reef-building corals of the upper mesophotic zone near Eilat (Alamaru et al., 2009; Einbinder et al., 2009; Fricke and Schuhmacher, 1983; Mass et al., 2007; Nir et al., 2011; Stambler et al., 2008), with fewer studies targeting the lower mesophotic (Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Fricke 85 and Schuhmacher, 1983; Schlichter et al., 1986) or exploring mesophotic coral distributions along the coasts of Israel, Egypt, and Sudan (Fricke, 1996; Kühlmann, 1970). However, as noted by Ziegler et al. (2015), this body of work has been geographically limited to the northernmost sector of the GoA. Further research on other Red Sea mesophotic ecosystems has addressed the diversity, community structure, and growth forms of other non-scleractinian taxa. These include octocoral species richness and depth zonation (Eyal et al., 2019; Shoham and Benayahu, 2017), bryozoan growth forms and 90 bioconstructions (Hillmer et al., 1996; Scholz and Hillmer, 1995), and the taxonomy and reef-framework contribution of crustose coralline algae in the GoA (Hottinger, 1983) and along the Sudanese coast (Dullo et al., 1990). Similarly, deep-sea benthic ecosystems in the Red Sea have been explored since the early 20th century, beginning with the *Pola* expedition (Marenzeller, 1907). Despite subsequent efforts, knowledge of the deep Red Sea benthos remains fragmented and taxonomically limited (Janssen and Taviani, 2015). Most studies have focused on specific taxa such as deep-water corals 95 (Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Fricke and Schuhmacher, 1983; Gardiner and Waugh, 1939; Marenzeller, 1907; Scheer and Pillai, 1983; Taviani et al., 2007) and molluscs (Janssen, 1989; Rützen-Kositzkau, 1999; Sturany, 1904, 1900), whereas more comprehensive syntheses have attempted to characterise the overall composition of the deep-sea macro- and megabenthic invertebrate fauna (Türkay, 1996).



More recently, exploration of the Saudi Arabian Red Sea has intensified, targeting the discovery and characterisation of benthic habitats and various taxa, mostly representing undescribed species, in the mesophotic and deep zones (Anker et al., 2023; Bracchi et al., 2023; Chimienti et al., 2025, 2022; Macrina et al., 2025a, 2025b, 2024; Maggioni et al., 2022; Nolan et al., 2025, 2024; Nunes Peinemann et al., 2023; Purkis et al., 2022a, 2022b; Qurban et al., 2020, 2014; Roder et al., 2013; Stuhr et al., 2025; Terraneo et al., 2023, 2022; Vicario et al., 2026, 2024b, 2024a; Vimercati et al., 2024, 2023; Westphal et al., 2025; Ziegler et al., 2015). Weinstein et al. (2021) provided the first combined assessment of mesophotic benthic communities and geomorphological features in the northern GoA down to approximately 150 m depth, defining benthic habitat classes integrated with seafloor geomorphology. Nolan et al. (2024, 2025) provided the first models of distribution of mesophotic and deep coral-dominated habitats in the northern Saudi Arabian Red Sea. Beyond these pioneering studies, a broader understanding of benthic mesophotic and deep zonation from continuous spatial datasets in the Red Sea remains limited, a gap directly relevant to Saudi Arabia's coastal development plans, which require comprehensive, standardised habitat assessments to support conservation and management (Howell, 2010).

In 2020, the first modern exploration effort of the Saudi Arabian GoA and NRS mesophotic and deep zones was undertaken during the OceanX-NEOM Deep Blue Expedition, enabling the collection of unprecedented datasets including high-resolution seafloor mapping, imagery from deep-diving underwater vehicles, environmental data, and benthic biological observations. Here, we investigate whether, and how, zonation patterns at depth differ between the GoA and the NRS, given their contrasting oceanographic and geological settings. We present an integrated assessment of mesophotic and deep-sea benthic habitats along the northern Saudi Arabian Red Sea coast and the GoA, laying the foundation for future ecological assessments and management strategies. Specifically, this work (i) characterises benthic habitats, (ii) analyses their patterns of vertical zonation in response to physicochemical and depth-related environmental gradients, (iii) investigates the relationship between habitat distribution and seafloor geomorphology, (iv) compares habitat patterns between two adjacent but oceanographically distinct basins, and (v) proposes the first benthic habitat classification framework for mesophotic and deep environments of the region.

2 Materials and Methods

2.1 Data Acquisition and Processing

High-resolution bathymetric, oceanographic, and imagery data were acquired during the OceanX-NEOM Deep Blue Expedition (October–November 2020) aboard the RV *OceanXplorer*, using a hull-mounted multibeam echosounder, CTD probes, and an ROV (*Chimaera*, CHR) and submersible (*Neptune*, NTN) equipped for synchronised logging of video, navigation, and water-column parameters. Full survey design, vehicle specifications, and acquisition protocols are described in companion studies using the same dataset (Nolan et al., 2025, 2024; Purkis et al., 2022b, 2022a) and in supplementary material (Tables S1 and S2).

Bathymetric data were processed into a 30 m resolution digital elevation model (Fig. 1), from which slope was derived and seafloor landforms were classified into 10 geomorphological phenotype using the Geomorphon tool (Di Stefano and Mayer,

2018; Jasiewicz and Stepinski, 2013), providing the geomorphological framework used throughout this study (Fig. S1). Dive tracks were georeferenced and, after removing stationary points, attributed with geomorphometric variables based on their geographic coordinates and depth, and with oceanographic variables based on temporal synchronisation between the RBR CTD and USBL datasets. Benthic habitat classes identified from video footage were then assigned to the corresponding georeferenced points to build the annotated dataset used in all subsequent statistical analyses.

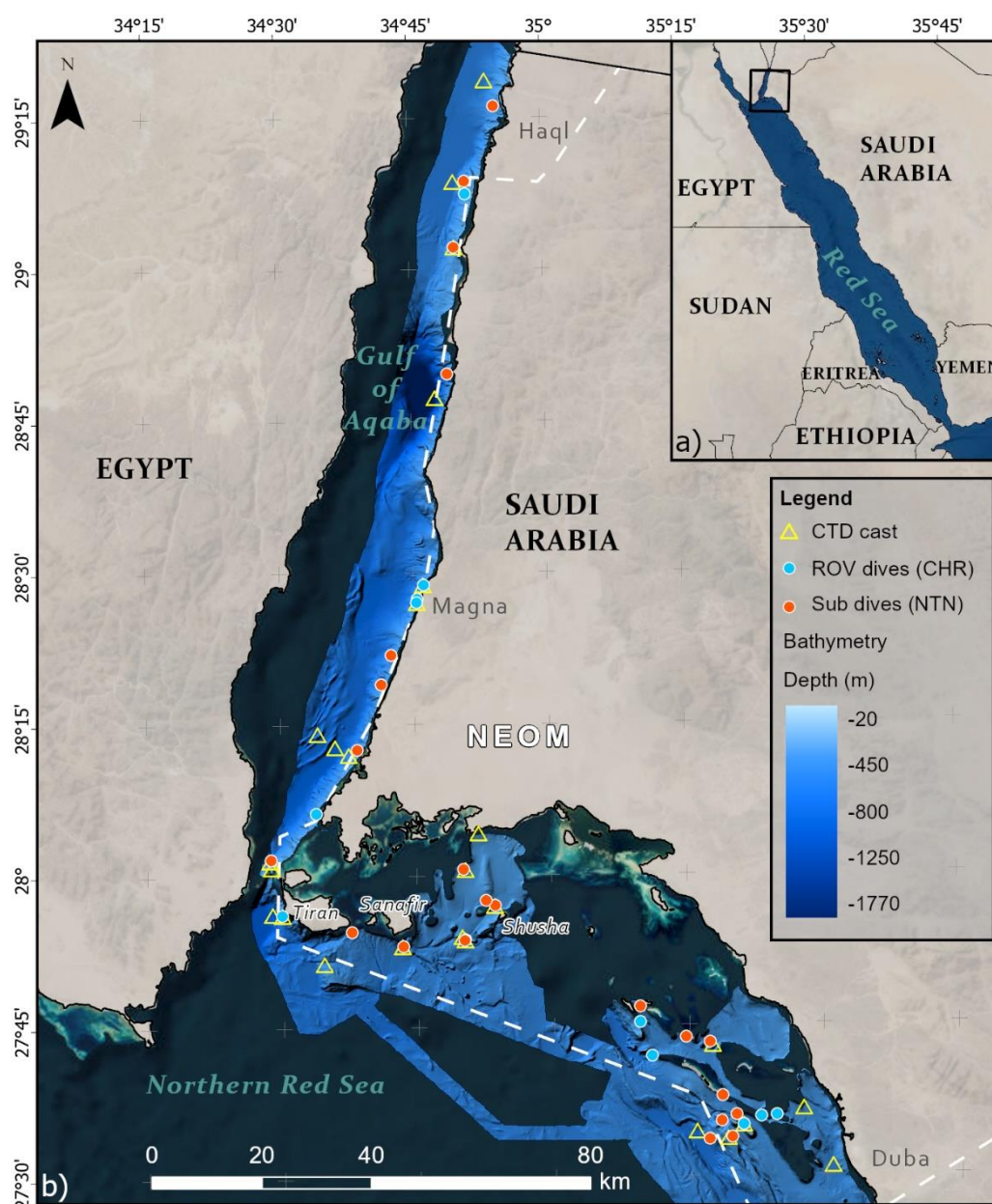




Figure 1: a) Regional geographic context showing the position of the study area within the Northern Red Sea (NRS) and the Gulf of Aqaba (GoA), with the inset box highlighting the extent of panel b). b) Bathymetric map of the study area along the Saudi Arabian margin of the NRS and GoA, derived from a 30 m-resolution digital elevation model. Sampling locations are superimposed on the seafloor topography and include ROV dives (blue points), submersible dives (orange points), and CTD casts (yellow triangles) (Tables S1 and S2). NEOM coastal boundary is indicated by a white dashed line. Coastlines from the GSHHG database (Wessel and Smith, 1996)

2.2 Development of the Benthic Habitat Classification Framework

Our classification adopts the habitat definition by Kostylev et al. (2001), in which a habitat is a spatially defined area where the physical, chemical, and biological environment is distinctly different from its surroundings. This approach assumes that benthic organisms distribute themselves along environmental gradients, with assemblages reflecting consistent sets of environmental conditions. Accordingly, benthic habitats were initially discriminated by video analysis, and their environmental distinctiveness was subsequently tested using permutational multivariate analysis of variance with the environmental variables extracted from the bathymetry and the CTD.

The habitat classification scheme was specifically developed for associations of visually observable benthic taxa and broad substrate type along the continental slope and shelf of the study area. We followed a hierarchical structure incorporating physiographic domain, substrate type, observed slope, and dominant benthic taxa adapted from previous studies (Buhl-Mortensen et al., 2015; Greene et al., 1999) and international frameworks such as EUNIS (Davies and Moss, 2000) and Coastal and Marine Ecological Classification Standard (CMECS; Federal Geographic Data Committee and Marine and Coastal Spatial Data Subcommittee, 2012). In this context, a dominant taxon or structural group is qualitatively defined as the biological component providing the primary ecological and structural signature of a habitat class (Costello, 2009). Given the logistical constraints of deep-sea imagery, where absolute quantification is often restricted, dominance was determined through expert assessment of visual prominence (Kahng and Kelley, 2007; Misiuk and Brown, 2024), a widely accepted methodological standard in benthic habitat classification (Beijbom et al., 2015; Greene et al., 1999; Ierodiaconou et al., 2011; Marin et al., 2025; Tebbett et al., 2023). Specifically, a taxon was considered dominant when it represented the most conspicuous proportion of the live benthic cover or consistently characterised the biogenic framework, thereby distinguishing a specific biotope from its surroundings (Costello, 2009). This qualitative identification of dominant biological groups or diagnostic taxa is used as a reliable surrogate to delineate biological patterns across environmental and geomorphological gradients (Brown et al., 2011; Ierodiaconou et al., 2011; Misiuk and Brown, 2024).

Classification was initially performed through visual interpretation of video footage, relying on the visible dominance of diagnostic taxa and/or on substrate characteristics. To ensure taxonomic accuracy despite the inherent limitations of underwater imagery, video analysis was integrated with the study of specimens collected and described from the same expedition (Bracchi et al., 2023; Chimienti et al., 2025, 2022; Macrina et al., 2025a; Maggioni et al., 2022; Nolan et al., 2025, 2024; Terraneo et al., 2022; Vicario et al., 2024b, 2026; Vimercati et al., 2024). A decision tree tailored to the resolution and quality of the imagery was developed to guide classification in both mesophotic and deep-sea settings. The system distinguishes biotically defined habitats, where diagnostic taxa are clearly identifiable and classification is based on assemblage structure, from



physically defined habitats, where biotic visibility is low or absent and classification relies primarily on substrate type and physiographic context. This dichotomous structure reflects a pragmatic adaptation to the decreasing detectability of fauna with depth and organism size in video surveys.

175 Although qualitative in origin, the classification can be considered semi-quantitative through frequency analyses across depth and geomorphological strata. This procedure allowed for consistent ecological interpretation across environmental gradients.

2.3 Structure of the Classification Scheme

The habitat classification scheme was implemented through a decision-tree structure that reflects observable features extracted from video analyses (Fig. S2). The scheme is organised across four hierarchical levels: physiographic domain, substrate type, 180 observed slope, and dominant benthic biota, each of which progressively narrows the classification path toward the final habitat assignment.

Physiographic domain. The first division separates habitats of the continental shelf from those of the continental slope, based on large-scale seabed morphology (Brown et al., 2011; Greene et al., 1999). This categorisation is derived primarily from regional bathymetric and geomorphological context, although in some cases the shelf break was directly observable in video 185 frames, typically at depths of 90–120 m in our dataset.

Substrate type. Substrate was broadly classified according to its physical consistency as either mobile (e.g., sand or mud) or non-mobile (e.g., consolidated rock, crust, reef framework). Substrate interpretation was based on visual assessment of texture and consolidation, with further subdivision into categories such as sand/mud, nodules, rocky outcrops, crust, and biogenic structures. In parallel, extensive collection of biotic and abiotic samples took place during the same expedition and allowed us 190 to determine the biogenic origin of the structures (Bracchi et al., 2023; Chakraborty et al., 2025; Nolan et al., 2025, 2024).

Observed slope. Slope was estimated visually from the video frame using the relative inclination of the seabed and grouped into three categories: flat or gentle slopes ($\lesssim 10^\circ$), medium or moderate slopes ($\sim 10\text{--}40^\circ$), and steep slopes or vertical walls ($\gtrsim 40^\circ$).

Dominant benthic biota. Where benthic organisms were sufficiently large to be visible in the examined videos (ca. > 2 cm), 195 habitat definition was refined by the presence of a dominant taxon or structural group (e.g., scleractinians, octocorals, bryozoans, foraminiferans). In the absence of a clearly dominant taxon, classification relied primarily on substrate and slope, thus distinguishing between biotically defined and physically defined habitats under otherwise similar environmental settings. Each branch of the decision tree leads to a defined habitat class, with corresponding labels and colour codes shown in Fig. S2. Observational ambiguities (e.g., uncertain slope category, cryptic fauna) were resolved using a majority-rule approach along 200 each transect segment, based on the most consistently visible features.



2.4 Statistical Approach

Statistical analyses of benthic habitat and environmental variables were conducted to characterise multivariate environmental gradients and assess differences among habitat groups, support the benthic habitat classification and help understand the vertical zonation patterns across the two basins. Depth-related environmental thresholds were identified through broken-stick (segmented regression) models (Toms and Lesperance, 2003). A machine learning approach using a multiway regression tree was used to detect ecological breakpoints (Collin et al., 2011) and classify deep benthic habitats under heterogeneous environmental conditions. These analyses were performed using Orange Data Mining v3.34 (Demšar et al., 2013), OriginPro v2022b (OriginLab Corporation, 2022), and R Statistical Software (R Core Team, 2025).

Environmental variability was first summarised through a principal component analysis (PCA), and the first principal component (PC1), which accounted for the largest proportion of the total variance, was used as a synthetic environmental axis. To test whether habitats classified through video analysis correspond to distinct environmental conditions, we performed a permutational multivariate analysis of variance (PERMANOVA) using 999 permutations and Euclidean distances. Piecewise linear regression models were fitted using the *segmented* package in R (Muggeo, 2003), testing models with one to six breakpoints ($n = 1-6$) (Table 3). The n -range reflects the need to balance improvements in model fit with the risk of overfitting and loss of ecological interpretability: models with a high number of breakpoints may capture local noise rather than genuine ecological transitions. Breakpoints were estimated independently for each model, and a consensus threshold was defined as the two most recurring breakpoints in the models within a ± 10 m window. This procedure was adopted because, given the large dataset, objective model selection between sharp and smooth transitions was not straightforward (Toms and Lesperance, 2003), and recurrence across models provided a robust criterion for threshold identification. Breakpoint values are reported throughout as the bin-centres of the ± 10 m window. Where a given breakpoint differed numerically between the basins, the continuous point estimates (ψ) from the segmented models were compared and independently verified using two approaches: a delta-method z-test on the difference in breakpoint location, and a non-parametric bootstrap (1000 resamples per basin), from which 95% confidence intervals (CI) were derived using the percentile method.

A machine learning approach using a multiway regression tree was used to evaluate whether shifts in habitat composition align with these environmental breakpoints and to classify benthic habitats under heterogeneous environmental conditions (Collin et al., 2011). The algorithm we used recursively partitions the predictor space by selecting at each node the environmental variable that maximises the reduction in target heterogeneity. Since the target variable consisted of habitat classes, the model operated as a classification tree, with terminal leaves representing the class composition of the samples falling within each partition. This approach provides an interpretable hierarchical structure that identifies key environmental thresholds associated with habitat transitions.

The analysis was performed in Orange Data Mining (TreeLearner; *binarize* = False). Two separate models were built, one for the NRS and one for the GoA. Both models were configured with a minimum of 10 instances per leaf and a maximum tree



depth of 5 levels. The choice of 10 instances was derived from a preliminary “Test & Score” module using Area Under the
 235 Curve (AUC), Classification Accuracy (CA), and F1-score as validation metrics.

3 Results

3.1 Bathymetry and Terrain Analysis

The resulting DEM spans from 34°23.48' E to 35°50.65' E and from 27°10.87' N to 29°25.17' N, covering 4,505.1 km² of
 Saudi Arabian territorial waters along the NEOM coastline (Fig. 1). The bathymetry in the GoA ranges from 20 m at the Strait
 240 of Tiran to 1,765 m in the Aragonese Deep. Within the GoA, slope steepness varies distinctly along the north-south axis, from
 moderately inclined surfaces in the northern sector to steep gradients (>40°) in the central sector, and a combination of steep
 upper slopes and gentler lower slopes in the southern sector. The NRS DEM extends from 20 m at the Strait of Tiran to 1,420
 m in the Hume Deep. Slopes are generally gentle (<10°) along the Saudi coastal margin but become significantly steeper
 (>40°) around islands and barrier reefs.

245 The geomorphon classification (Fig. S1) reveals a seafloor dominated by slope morphologies and extensive flat areas. Slope
 classes represent the largest portion of the terrain (~1,847 km²), reflecting the steep and continuous margins that characterise
 both the GoA and NRS, as well as the flanks of fringing reefs and the salt-tectonically controlled drowned reef morphologies
 of the NRS. Flat surfaces are also abundant, accounting for ~1,067 km², and correspond largely to the deepest basins within
 the study area. Intermediate morphologies are well represented too. Foothills (~362 km²), spurs and hollows (~299 km²), and
 250 shoulders (~279 km²) capture the transition between the shelf-break zone, the steep continental slope, and the deeper basins.
 Ridges (~156 km²) and valleys (~147 km²) also occur frequently and illustrate the complexity of the margin. These features
 highlight erosional morphologies of the continental slope, including gullies, canyons, and mass-wasting scars, which are
 particularly marked along the southern margin of Tiran and Sanafir Islands in the NRS and throughout the GoA coast. Summits
 and depressions are the least represented and most spatially scattered classes, restricted to isolated topographic highs and small,
 255 enclosed depressions.

3.2 Oceanographic Parameters

A total of 25 CTD casts (Table S1) were used to characterise the hydrographic structure of the two basins, with 13 profiles
 collected in GoA and 12 in NRS (Fig. 2). Although the casts did not all reach the same maximum depth, all extended to at
 least 200 m, allowing consistent characterisation of the surface and intermediate layers. They were collected in the fall when
 260 the stratification weakened (see MLD, Fig. 2; Biton and Gildor, 2011; Carlson et al., 2014; Ismail Badran, 2001).

At the time of our surveys in the fall of 2020, the GoA was consistently saltier (40.72 ± 0.05 vs 40.42 ± 0.14 , mean $\pm$ SD),
 slightly cooler (22.02 ± 1.72 °C vs 24.05 ± 2.84 °C) and more oxygenated (175 ± 16 $\mu\text{mol L}^{-1}$ vs 148 ± 60 $\mu\text{mol L}^{-1}$) than the
 NRS. In the upper 250 m, GoA waters ($T > 21.53$ °C) remained markedly saltier, while NRS waters were warmer ($T > 22.05$
 °C) and fresher, reflecting stronger stratification and surface heating. Between ~100 and 200 m, weak salinity minima



265 occasionally appeared in the GoA, likely remnants of summer stratification (Fig. 2). Several GoA profiles also revealed a reduction in dissolved oxygen between ~150 and 250 m, coinciding with the sill depth of the Strait of Tiran (Fig. 2). Below ~250 m, the GoA intermediate layer ($T \sim 21.20\text{--}21.53\text{ }^{\circ}\text{C}$) exhibited a distinct oxygen maximum of $\sim 200\text{ }\mu\text{mol L}^{-1}$ between 330 and 550 m, while concentrations were more stable between 200 and 330 m. In the NRS, the intermediate layer ($T \sim 21.53\text{--}22.05\text{ }^{\circ}\text{C}$) contained two contrasting oxygen features: a shallow reduction at 150–250 m, and a deeper oxygen

270 minimum zone (OMZ) between 400 and 600 m.

Below 600 m depth, the water mass characteristics in both basins converged toward cooler, denser conditions, though with subtle differences. In the GoA, waters below 600 m were slightly colder ($T \lesssim 21.20\text{ }^{\circ}\text{C}$) and more oxygenated. In the NRS, deep waters ($T < 21.53\text{ }^{\circ}\text{C}$) were less oxygenated.

The mixed layer depth (MLD) was systematically deeper in the GoA ($69 \pm 38\text{ m}$) than in the NRS ($50 \pm 23\text{ m}$), consistent with

275 stronger stratification in the latter. In both basins, a persistent deep chlorophyll maximum (DCM) was observed between ~80 and 120 m, coinciding with the base of the euphotic zone.

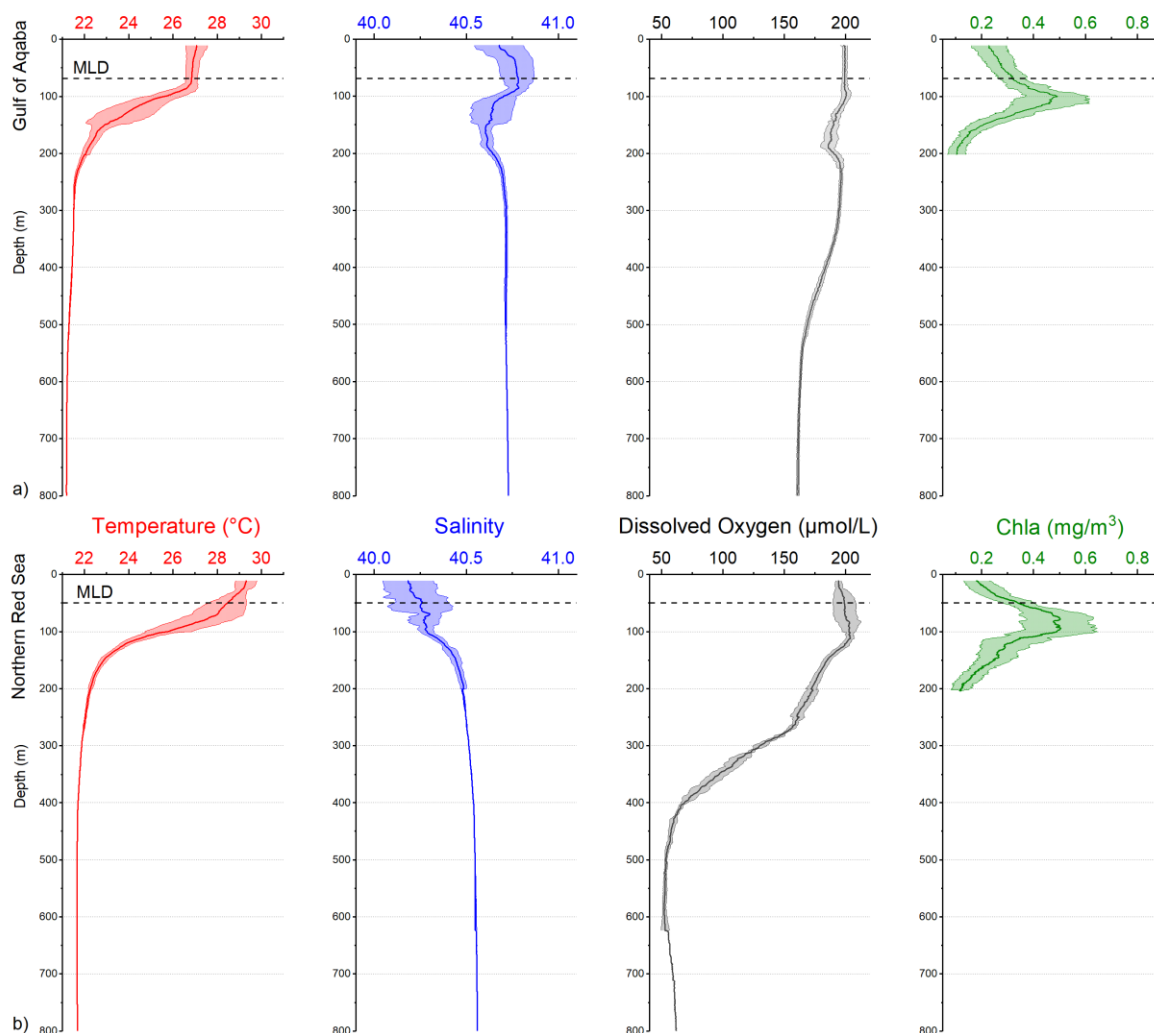


Figure 2: Mean vertical profiles of temperature (°C), salinity, dissolved oxygen ($\mu\text{mol L}^{-1}$), and chlorophyll-a concentration (mg m^{-3}) in the Gulf of Aqaba (top panels, $n = 13$) and the Northern Red Sea (bottom panels, $n = 12$) collected during the Deep Blue Expedition in fall 2020 (October–November). Shaded envelopes represent one standard deviation (SD) around the mean (solid line). The dashed horizontal line marks the mixed layer depth (MLD).

The potential temperature (θ) and salinity (S) diagram (Fig. S3) shows the hydrographic differences between the two basins. GoA waters are characterised by distinctly higher salinities (>40.6) across the entire water column, while the NRS shows comparatively lower salinities (<40.5) and warmer surface signatures. In the depth range of 150–250 m, the transitional θ – S properties of the water close to the Strait of Tiran show that the data from both basins partially overlap, reflecting the exchange between the two basins. The isopycnal contours highlight the vertical layering already evident in the CTD profiles, with saltier and denser GoA waters underlying the lighter stratified layers of the NRS. In the potential temperature–salinity plot, the depth colour scale confirms that these θ – S signatures extend across the full water column, supporting the distinction between GoA



and NRS hydrographic domains. These basin-scale contrasts are consistent with prior hydrographic and tracer studies of the region (Asfahani et al., 2020; Kheireddine et al., 2017; Torfstein and Kienast, 2018).

3.3 Benthic Habitat Characterisation

A total of 35 underwater vehicle dives ($n = 5$ CHR and $n = 8$ NTN in the GoA, $n = 8$ CHR and $n = 14$ NTN in the NRS) were conducted along depth-stratified transects derived from the acoustic dataset, collecting over 135 hours of high-resolution video footage (Fig. 1, Table S2). From these observations, and by applying the hierarchical decision-tree framework, we identified and classified 14 distinct benthic habitats (Fig. 3-6; Table S3), which are described in detail below.

Foralgal reefs (FAR) (Fig. 3a) are highly three-dimensional biogenic structures whose morphology spans from small patchy buildups to extensive biogenic ridges. Corallinaceae, Peyssonneliaceae and foraminifera constitute the primary framework (Dullo et al., 1990), while scleractinian corals from the families Agariciidae, Dendrophylliidae, Caryophylliidae, Pocilloporidae, Merulinidae and Fungiidae act as secondary components. Octocorals from the families Melithaeidae, Siphonogorgiidae, Acanthogorgiidae, Euplexauridae and Ellisellidae are present. Antipatharians from the families Antipathidae, Aphanipathidae and Stichopathidae may locally dominate. Additional contributors include bryozoans, sponges and annelids. FAR were observed between 69 and 135 m in the NRS (97 ± 14 m) and 70–154 m in the GoA (106 ± 16 m), occurring on substrates ranging from flat terraces to gentle and steep slopes and vertical walls.

Foralgal nodules (FANs) *sensu* Bracchi et al. (2023) (Fig. 3b) consist of low-relief, free-living spheroidal nodules forming extensive fields or isolated patches draping the seafloor, often representing an ecotone with FAR. Crustose coralline algae (CCA) and encrusting foraminifera constitute the primary framework, while scleractinian corals from the families Agariciidae (*Leptoseris* cf. *striatus*), Dendrophylliidae, Caryophylliidae and Merulinidae, octocorals from the families Melithaeidae, Siphonogorgiidae, Acanthogorgiidae and Ellisellidae, and antipatharians from the families Antipathidae, Aphanipathidae, Myriopathidae and Stichopathidae occur sporadically, remaining functionally subordinate to the algal–foraminiferal matrix. Additional contributors include sponges and other encrusting invertebrates. FANs were observed between 69 and 150 m in the NRS (92 ± 15 m) and 79–122 m in the GoA (102 ± 8 m), developing primarily on flat or gently sloping hard or mixed substrates.

Scattered biogenic patches interspersed with sandy bottom (SBPS) (Fig. 3c) consist of isolated colonies or decimetre-scale small bioconstructions, with dominant structural components often unclear and highly localised. The biogenic elements typically require close observation to be distinguished. The assemblage is mainly composed of CCA, foraminifera and small scleractinians from the family Dendrophylliidae, with octocorals from the superfamily Pennatulioidea and indistinguishable small wire morphologies of octocorals and antipatharians. Both octocorals and antipatharians appear only sporadically and are rarely dominant, resulting in fine-grained patch mosaics without continuous framework development. This habitat is ecotonal with bryozoan bioconstructions (BB) and rariphotic mixed coral assemblages (RCA), possibly representing a transitional system from deeper zones toward FAR or FANs, with scattered patches reflecting both the influence of adjacent frameworks and limitations imposed by light penetration, sediment mobility and substrate inclination. SBPS were recorded between 112



and 192 m in the NRS (156 ± 26 m) and 113–248 m in the GoA (170 ± 33 m), typically occurring on gentle slopes over mobile sandy substrates.

Bryozoan bioconstructions (BB) (Fig. 3d) consist of centimetric to decimetric erect and encrusting bryozoan skeletal meshes forming highly structured frameworks, similar to those already described in the GoA (Hillmer et al., 1996; Scholz and Hillmer, 1995). Azooxanthellate scleractinian corals, including *Madracis interjecta* and *Dendrophyllia minuscula*, are present together with other taxa from the families Agariciidae (e.g., *D. cervicornis*) and Caryophylliidae, but do not form the dominant structure as in RCA. Octocorals from the families Melithaeidae, Siphonogorgiidae, Acanthogorgiidae, Ellisellidae, and the superfamily Pennatuloidae, together with antipatharians from the families Antipathidae, Aphanipathidae, Myriopathidae, and Stichopathidae are frequent associates. Foraminifera, annelids and sponges are also present. CCA may persist near the upper range (~100 m), accompanied by zooxanthellate scleractinians from the genus *Leptoseris*, marking the transition to shallower FAR or FANs. BB represent a consistently dominated habitat, with bryozoans acting as the principal consolidating agents and providing structural stability and complex microhabitats for associated invertebrates and fish. They are ecotonal with RCA but differ in having bryozoans rather than corals as the main biogenic framework, which reduce the scale of the three-dimensional complexity. BB were observed between 105 and 200 m in the NRS (147 ± 26 m) and between 151 and 186 m in the GoA (162 ± 9 m), mainly occurring on vertical walls where they enhance three-dimensional complexity.

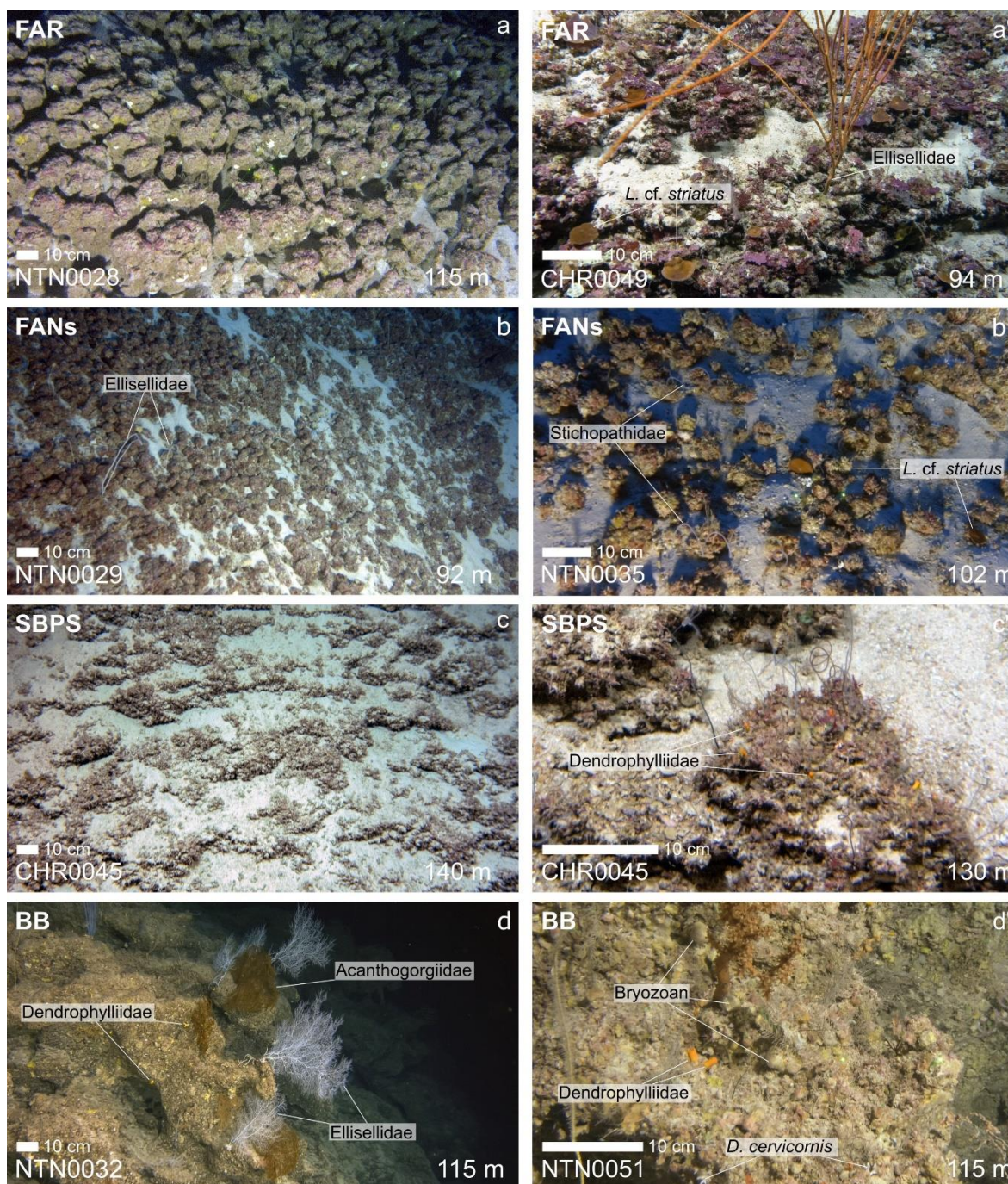


Figure 3: *In situ* images of the benthic habitats observed along the Northern Red Sea and Gulf of Aqaba transects. For each habitat the wider-field overview is shown on the left and a representative higher-magnification detail on the right. a, a') Foralgal Reef (FAR, 115 m and 94 m); b, b') Foralgal Nodules (FANs, 92 m and 102 m); c, c') Scattered biogenic patches interspersed with sandy bottom (SBPS, 140 m and 130 m); d, d') Bryozoan Bioconstruction (BB, 115 m and 115 m). The dive code is indicated in the bottom-left corner of each frame, and taxon labels identify diagnostic organisms visible within each panel. All scale bars represent 10 cm, derived from the spacing of the parallel laser pointers.



Rariphotic mixed coral assemblages (RCA) (Fig. 4a) are characterised by highly three-dimensional biogenic frameworks forming shelf-like overhangs and complex reliefs. The structural matrix is primarily built by encrusting and branching azooxanthellate scleractinian corals, notably *D. minuscula*, *M. interjecta* and *Rhizopsammia compacta*, reinforced by other scleractinian corals, bryozoans, foraminifera, molluscs and annelids, which enhance rigidity and surface complexity (Chimienti et al., 2025; Fricke and Hottinger, 1983). Additional scleractinians from the families Agariciidae, Dendrophylliidae, Caryophylliidae and Flabelliidae are present, together with octocorals from the families Melithaeidae, Siphonogorgiidae, Acanthogorgiidae and Ellisellidae, and antipatharians from the families Antipathidae, Aphanipathidae, Myriopathidae, Pteridopathidae and Stichopathidae. Octocorals and antipatharians contribute to the highest three-dimensional complexity, creating a mixed animal forest that hosts sponges and abundant associated fish fauna. RCA represent one of the most biologically diverse and structurally complex assemblages of the mesophotic zone. A finer-scale, site-specific characterisation of RCA community composition and biogenic structure is provided by Chimienti et al. (2025). RCA were observed between 129 and 173 m in the NRS (154 ± 13 m) and 112–211 m in the GoA (148 ± 20 m), developing on hard substrates ranging from steep slopes to vertical walls and overhanging structures.

Deep octocoral aggregations (DOCA) (Fig. 4b) are characterised by dense arborescent stands of octocorals belonging primarily to the families Ellisellidae and Acanthogorgiidae, which form the main association. Scleractinian corals from the families Dendrophylliidae (*Dendrophyllia* cf. *horsti*, *sensu* Re et al., 2026) and Pocilloporidae (*M. interjecta*) are present, occasional occurrences of octocorals belong to the family Siphonogorgiidae, while antipatharians appear as few, indistinguishable small wire morphologies. Annelids and sponges may occur secondarily but never exceed gorgonians in structural relevance. DOCA were restricted to the NRS, occurring between 164 and 216 m (174 ± 12 m), on rocky substrates either on planar areas or steep slopes.

Dendrophylliids and serpulid associations (DS) (Fig. 4c) consist of encrusting layers formed by small corals from the family Dendrophylliidae (*D. cf. horsti*), forming a matrix with dense serpulids tubes, with the framework predominantly sustained by the dendrophylliid–serpulid association. Associated octocorals belong to the families Siphonogorgiidae and Euplexauridae. Occasional occurrences of sponges and subordinate hard corals (e.g., *Rhizotrochus typus*) were recorded. DS were restricted to the GoA, occurring between 290 and 362 m (328 ± 33 m), developing on vertical to overhanging rocky substrates.

Caryophylliids and solitary flabellids on rocky substrate (CF) (Fig. 4d) develop on exposed rock or consolidated deposits and are dominated by azooxanthellate scleractinian corals from the families Caryophylliidae and Flabelliidae, with *R. typus* occurring at notably high densities. Occasional dendrophylliids and sponges were also observed. The distribution remains small-scale and patchy, similar to the DS habitat. CF were recorded between 410 and 426 m in the NRS (416 ± 6 m) and between 258 and 284 m in the GoA (274 ± 10 m).

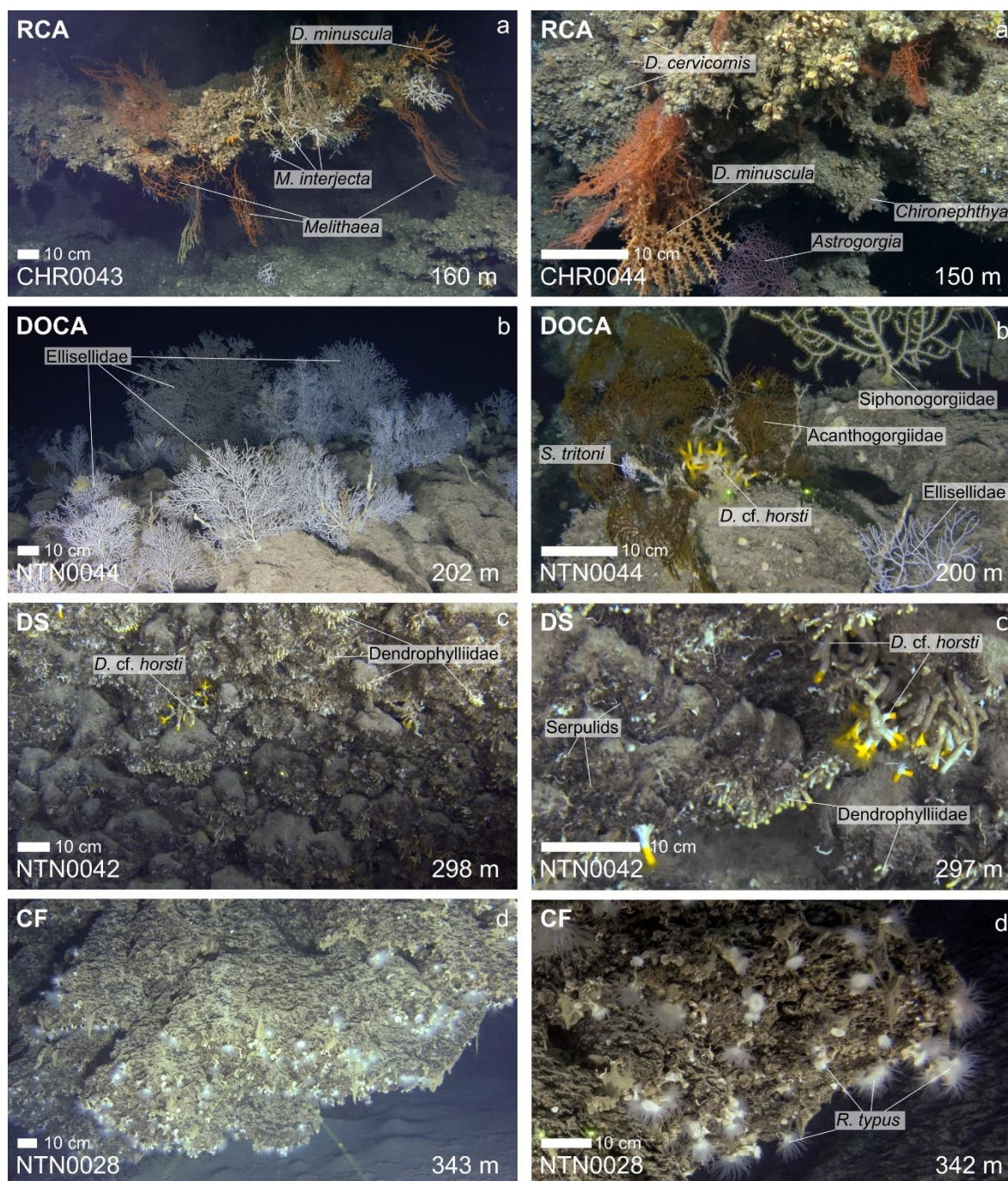


Figure 4: *In situ* images of the benthic habitats observed along the Northern Red Sea and Gulf of Aqaba transects. For each habitat the wider-field overview is shown on the left and a representative higher-magnification detail on the right. a, a') Rariphotic Mixed Coral Assemblages (RCA, 160 m and 150 m); b, b') Deep Octocoral Aggregations (DOCA, 202 m and 200 m); c, c') Dendrophylliid and Serpulid associations (DS, 298 m and 297 m); d, d') Caryophylliids and solitary Flabellids on rocky substrate (CF, 343 m and 342 m). The dive code is indicated in the bottom-left corner of each frame, and taxon labels identify diagnostic organisms visible within each panel. All scale bars represent 10 cm, derived from the spacing of the parallel laser pointers.



380 **Dendrophylliid coral frameworks dominated by *Eguchipsammia fistula* (DCF-EF)** (Fig. 5a) form highly three-dimensional, extensive structures, often displaying hood-like morphologies where *Eguchipsammia fistula* dominates. The primary framework is built by colonial azooxanthellate dendrophylliid *E. fistula*, supporting secondary accreting organisms including other azooxanthellate scleractinians such as *D. cf. horsti*, *R. typus*, and taxa from families Caryophylliidae and Agariciidae (e.g., *D. cervicornis*). Associated octocorals belong to the families Acanthogorgiidae, Ellisellidae and superfamily Pennatuloidae, while antipatharians are represented by the families Myriopathidae, Antipathidae and Schizopathidae (*Bathypathes thermophila*). Other associated taxa include stylasterids (the endemic *Stylaster tritoni*), crinoids, sponges and annelids. Occasional sediment pockets host sea pens and echinoids. Structural complexity is strongly influenced by colony density and slope exposure, producing locally dense and architecturally intricate habitats. DCF-EF were observed between 266 and 440 m in the NRS (365 ± 41 m), developing on substrates ranging from gentle slopes to steep escarpments, primarily in areas dominated by rocky substrate but also occasionally on relict structures within sediment-dominated settings.

390 **Dendrophylliid coral frameworks dominated by *Dendrophyllia cf. horsti* (DCF-DH)** (Fig. 5b) are built primarily by *D. cf. horsti*, typically forming smaller and more discrete structures compared to DCF-EF. Associated fauna are the same as those observed on DCF-EF. Morphologies are generally more compact than *E. fistula*-dominated frameworks, and sediment pockets occasionally host sea pens and echinoids. Structural dominance alternates between dendrophylliids and associated taxa depending on local hydrodynamics and substrate inclination. DCF-DH were observed between 277 and 345 m in the GoA (302 ± 25 m), within a depth range similar to DCF-EF, developing mainly on gentle slopes and hard substrates derived from relict structures within sediment-dominated areas.

Caryophylliid bioconstructions (CBR) (Fig. 5c) are composed of colonial caryophylliids, primarily *Rhizosmilia valida* or a second, yet undescribed species (*Caryophyllia* sp.) (Nolan et al., 2024), which form complex frameworks. On flat seafloor, CBR occur as positive morphologies possibly related to pre-existing hard substrate, generating mixed fields of skeletal rubble and sparse live colonies. Secondary associates include solitary caryophylliids, solitary flabellids (*R. typus*), octocorals from the families Acanthogorgiidae, Siphonogorgiidae and Keroeidae, and other taxa such as sea urchins, annelids and sponges. CBR were recorded between 363 and 701 m in the NRS (478 ± 91 m) and 604 to 650 m in the GoA (623 ± 20 m), occurring on flat substrates where they form positive seafloor structures and in small patches along vertical walls.

405 **Deep hardground with sediment patches (HS)** (Fig. 5d) is characterised by a thin sedimentary crust formed through the lithification of fine sediment, sometimes bioturbated and draped by a mobile sediment layer. These crusts are intermittently covered by sediment and can be buried on the seafloor, creating a layered structure. Like the other substrate-dominated habitats, described in the next paragraphs (see MS and RE), no dominant biota can be defined for this habitat, although HS supports a benthic community primarily characterised by the azooxanthellate scleractinian corals *R. typus*, octocorals (Acanthogorgiidae, Ellisellidae and Siphonogorgiidae) and the antipatharian *B. thermophila*. Secondary groups are scattered throughout. Colonization is restricted to exposed patches, producing a discontinuous and heterogeneous distribution of sessile fauna. Together with other substrate-dominated habitats, HS represents one of the most abundant habitats, prevalent across all

transects, ranging from 128 to 683 m in the NRS and 143 to 1247 m in the GoA, primarily found on deep flat areas or gentle slopes and occasionally observed in the deepest portion of the mesophotic zone.

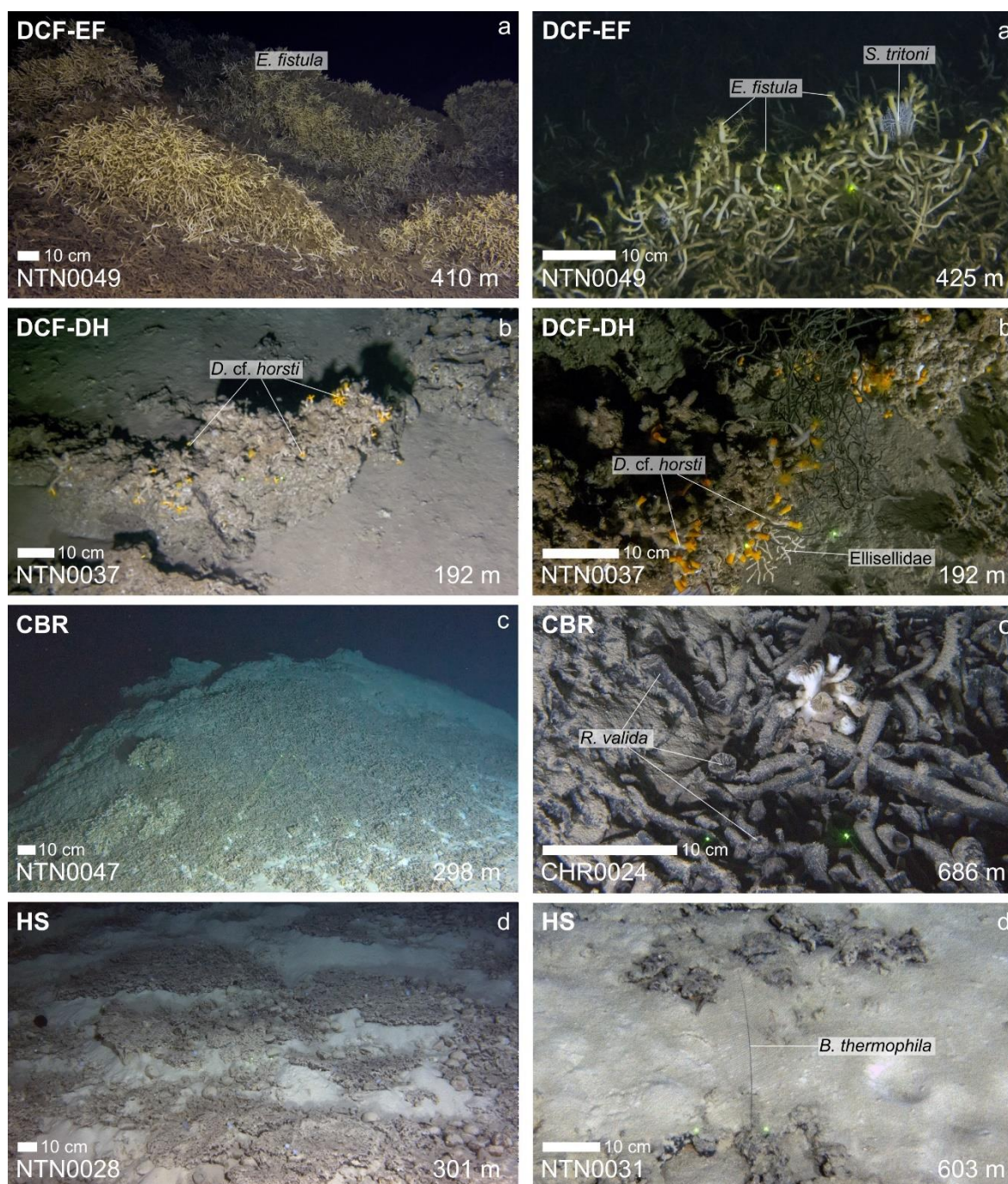


Figure 5: *In situ* images of the benthic habitats observed along the Northern Red Sea and Gulf of Aqaba transects. For each habitat the wider-field overview is shown on the left and a representative higher-magnification detail on the right. a, a') Dendrophylliid coral framework dominated by *Eguchipsammia fistula* (DCF-EF, 410 m and 425 m); b, b') Dendrophylliid coral framework



420 dominated by *Dendrophyllia* cf. *horsti* (DCF-DH, 192 m and 192 m); c, c') Caryophylliid Bioconstructions (CBR, 298 m and 686 m);
 d, d') Deep Hardground with sediment patches (HS, 301 m and 603 m). The dive code is indicated in the bottom-left corner of each
 frame, and taxon labels identify diagnostic organisms visible within each panel. All scale bars represent 10 cm, derived from the
 spacing of the parallel laser pointers

Mobile sediment (MS) (Fig. 6a) consists of unconsolidated fine to coarse sandy bottom or muddy sediment, inhabited
 primarily by vagile infauna and sparse epifauna in a bioturbated mobile sediment matrix. Among the most frequently observed
 425 taxa are the antipatharian *B. thermophila*, as well as octocorals of the superfamily Pennatulioidea, which can utilize the shells
 of dead sea urchins as substrates for growth. In areas near high slopes and vertical walls, boulders resulting from gravity
 processes provide hard substrates for small colonies of azooxanthellate scleractinian corals (mainly from the families
 Flabellidae and Dendrophylliidae), antipatharians (Stichopathidae and Myriopathidae), octocorals (family Acanthogorgiidae
 and superfamily Pennatulioidea) and sponges. The presence and grain size of MS are closely related to seafloor depth and
 430 geomorphological context. On the continental platform, MS is surrounded by FANs, FAR and SBPS, with natural bioerosion
 contributing to grain sizes ranging from fine to coarse sand. Along steep slopes near shallow water areas, MS is characterised
 by fine to coarse sand influenced by gravity processes and the on-land wadi system. In deeper areas, where the gradient is
 generally flat or gently sloping, MS results from pelagic sedimentation processes, leading to finer grain sizes from fine sand
 to mud. MS spanned from approximately 88 to 1054 m in the NRS and 121 to 1761 m in the GoA, typically found on flat
 435 areas, gentle slopes and steep slopes.

Rocky bottom with epifauna (RE) (Fig. 6b) consists of rock draped by thin sediment layers and hosts sparse colonization by
 solitary scleractinian corals, octocorals, antipatharians, stylasterids, crinoids, sponges and annelids. Despite variability in
 inclination and sediment cover, the assemblage remains compositionally consistent, representing a generalist hardground
 community. Azooxanthellate scleractinian corals (mainly from the families Caryophylliidae, Dendrophylliidae and
 440 Flabellidae), antipatharians (Aphanipathidae, Antipathidae, Myriopathidae and Pteridopathidae) and octocorals
 (Acanthogorgiidae, Ellisellidae and Siphonogorgiidae) might be patchily present, although no dominant biota can be defined.
 RE represents one of the most abundant habitats, prevalent across all transects at all depths, occurring between 97 and 699 m
 in the NRS and 140 to 1250 m in the GoA, primarily on steep slopes characterising the continental slope and walls throughout
 the Red Sea, but also on flat areas or gentle slopes as patchy rocky outcrops in the deep.

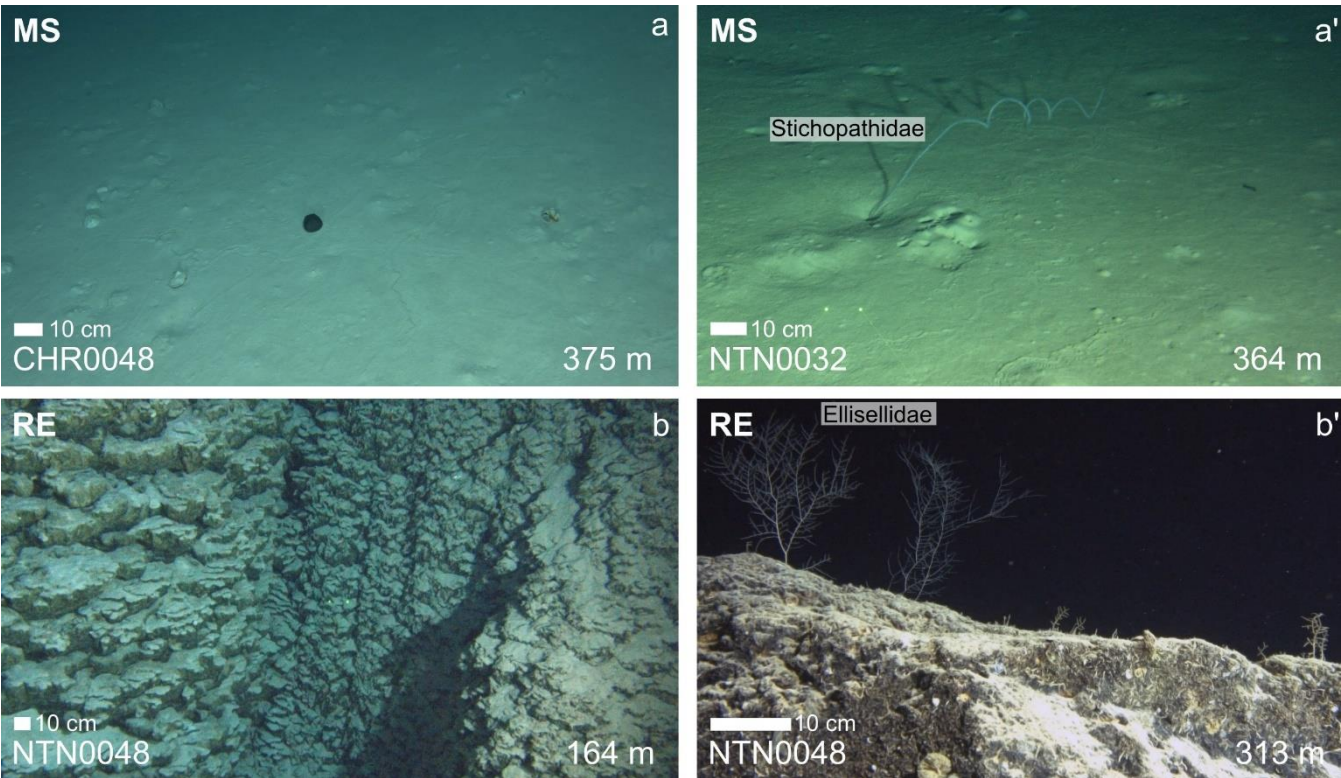


Figure 6: *In situ* images of the benthic habitats observed along the Northern Red Sea and Gulf of Aqaba transects. For each habitat the wider-field overview is shown on the left and a representative higher-magnification detail on the right. a, a') Mobile Sediment (MS, 375 m and 364 m); b, b') Rocky bottom with Epifauna (RE, 164 m and 313 m). The dive code is indicated in the bottom-left corner of each frame, and taxon labels identify diagnostic organisms visible within each panel. All scale bars represent 10 cm, derived from the spacing of the parallel laser pointers.

3.4 Habitat Environmental Setting

A partial set of variables is summarised in Table 1 and reported separately for the NRS and the GoA, reflecting the oceanographic regimes of the two basins. Profile curvature, plan curvature, and Vector Ruggedness Measure (VRM) were not included in this table because they are dimensionless indices and therefore not directly comparable to the other environmental parameters summarised here, however, they were still included in the statistical analysis.

Table 1: Summary of benthic habitat types surveyed during the Deep Blue Expedition 2020 in the Northern Red Sea (NRS) and Gulf of Aqaba (GoA). Each habitat includes depth ranges (mean $\pm$ SD), water temperature ($^{\circ}\text{C}$, $\pm$ SD), dissolved oxygen (μM , $\pm$ SD), salinity range ($\pm$ SD), slope ($^{\circ}$, $\pm$ SD), and aspect ($^{\circ}$, $\pm$ SD). Water column parameters were extracted from RBR CTDs collected along each CHR or NTN dive, slope and aspect were derived from the 30 m resolution DEM

Habitat	Depth NRS (m)	Depth GoA (m)	Temp. NRS ($^{\circ}\text{C}$)	Temp. GoA ($^{\circ}\text{C}$)	O ₂ NRS ($\mu\text{mol/l}$)	O ₂ GoA ($\mu\text{mol/l}$)	Salinity NRS ($\text{}$)	Salinity GoA ($\text{}$)	Slope NRS ($^{\circ}$)	Slope GoA ($^{\circ}$)	Aspect NRS ($^{\circ}$)	Aspect GoA ($^{\circ}$)
FANS	69–150 (92 $\pm$ 15)	79–122 (102 $\pm$ 8)	26.77 $\pm$ 1.30	25.38 $\pm$ 0.37	223.7 $\pm$ 4.9	223.1 $\pm$ 4.7	40.32– 40.67	40.32– 40.67	22.2 $\pm$ 17.0	15.6 $\pm$ 13.1	188 $\pm$ 55	273 $\pm$ 92
FAR	69–135 (97 $\pm$ 14)	70–154 (106 $\pm$ 16)	25.83 $\pm$ 1.40	25.26 $\pm$ 0.84	226.4 $\pm$ 5.5	223.1 $\pm$ 4.5	40.32– 40.71	40.32– 40.71	44.4 $\pm$ 22.0	23.2 $\pm$ 13.2	209 $\pm$ 86	19 $\pm$ 113



BB	105–200 (147 ± 26)	151–186 (162 ± 9)	23.25 ± 0.73	22.97 ± 0.21	217.1 ± 12.1	215.1 ± 4.2	40.44– 40.58	40.44– 40.58	65.6 ± 10.5	28.9 ± 5.9	176 ± 48	300 ± 30
SBPS	112–192 (156 ± 26)	113–248 (170 ± 33)	22.89 ± 0.64	23.02 ± 0.83	206.3 ± 14.1	218.6 ± 6.4	40.46– 40.63	40.46– 40.63	27.7 ± 15.0	35.1 ± 7.4	156 ± 115	269 ± 131
DOCA	164–216 (174 ± 12)	–	22.39 ± 0.05	–	198.2 ± 0.99	–	40.50 ± 0.01	–	14.1 ± 10.8	–	175 ± 94	–
RCA	129–173 (154 ± 13)	112–211 (148 ± 20)	22.90 ± 0.51	23.67 ± 0.72	201 ± 15	220 ± 6	40.48 ± 0.04	40.63 ± 0.04	62.4 ± 8.9	41.4 ± 12.3	114 ± 91	271 ± 112
DS	–	290–362 (328 ± 33)	–	21.48 ± 0.02	–	213.7 ± 5.3	–	40.72 ± 0.004	–	31.2 ± 3.5	287 ± 15	–
CF	410–426 (416 ± 6)	258–284 (274 ± 10)	21.71 ± 0.02	21.55 ± 0.05	78.9 ± 14.4	217.4 ± 2.0	40.55 ± 0.003	40.73 ± 0.01	46.3 ± 17.7	12.3 ± 3.5	195 ± 28	12 ± 2
DCF-EF	266–440 (365 ± 41)	–	21.79 ± 0.10	–	110 ± 27	–	40.53 ± 0.03	–	16.7 ± 10.4	–	145 ± 106	–
DCF-DH	–	277–345 (302 ± 25)	–	21.54 ± 0.04	–	216 ± 2.5	–	40.73 ± 0.01	–	15.5 ± 1.8	–	15–16
CBR	363–701 (478 ± 91)	604–650 (623 ± 20)	21.68 ± 0.02	21.23 ± 0.01	76.2 ± 12.5	195.4 ± 0.7	40.55 ± 0.01	40.73 ± 0.01	16.8 ± 13.9	40.1 ± 4.4	215 ± 104	314 ± 2

460 3.5 Cross-Basin Habitat Distribution

The integration of video observations with navigational data resulted in a comprehensive dataset of 35,965 georeferenced points, representing annotated seafloor characteristics recorded along the USBL dive tracks of the CHR and NTN vehicles. This dataset provides a high-resolution record of the spatial distribution of the 14 identified benthic habitats across depth gradients, water column characteristics, and seafloor morphologies. Due to the opportunistic nature of sampling during the survey, effort was not evenly distributed between the two basins in the full dataset, with 68% of annotated points located in the NRS (n = 24,453) and 32% in the GoA (n = 11,512). This difference includes the omnipresent substrate-dominated habitats (rocky bottom, hardgrounds with sediments, and mobile sediments: RE, HS, MS), which occur across all depths and locations and provide limited information on their vertical zonation at our scale of analysis. When these habitat categories are excluded and only habitats dominated by visually detectable organisms from the video data are considered, the distribution of observations is more balanced, with 55.2% occurring in the NRS (n = 6,543) and 44.8% in the GoA (n = 5,303) (Fig. S4). The dataset across depth gradients reveals how the annotated points are distributed within each basin (Fig. 7 and Fig. S5). The bar plots in Fig. S5 illustrate these proportions and the relative abundance of annotated habitats within each basin, providing a quantitative overview of survey representativeness prior to multivariate comparisons. The GoA showed a bimodal pattern, with most observations occurring between 100 and 200 m, representing lower mesophotic-rariphotic habitats, and a smaller cluster below 200 m where deeper azooxanthellate communities were observed (Fig. 7a). In contrast, in the NRS, annotated points are more evenly distributed across the 70–500 m range, with local peaks between 90 and 200 m, in the lower mesophotic-rariphotic zone, corresponding to higher occurrences of FAR, RCA, and BB. A second group is observed between 300 and 500 m, matching the distribution of DCF (Fig. 7b). Depths beyond 500 m were explored almost exclusively in the NRS, due



to the consistent presence of the deep CBR. This pattern stems from a more continuous exploration of depth zones in the NRS compared to the more clustered sampling in the GoA.

Across the surveyed depth range, we observed distinct patterns of benthic habitat occurrence between the NRS and the GoA (Fig. 7). Shallower mesophotic habitats such as FANs and FAR were well represented in both basins, consistently occurring between 70 and 150 m under warm, oxygen-rich conditions. These benthic habitats occurred on steeper, south- to southwest-facing slopes in the NRS, whereas in the GoA they were associated with gentler, north- or west-oriented surfaces. BB occupied slightly deeper settings, mostly between 100 and 200 m, and were abundant in the NRS but rare in the GoA. They thrived under cooler and less oxygenated conditions than foralgal frameworks and typically colonised steep southern slopes. SBPS and RCA were present in both basins, but more frequent in the GoA. These habitats occurred at intermediate depths (110–250 m) and reflected transitional environments, characterised by moderate slopes and variable orientations. Water column temperature conditions were slightly warmer in the GoA and more oxygen-depleted in the NRS, in line with the general oceanographic contrast between basins.

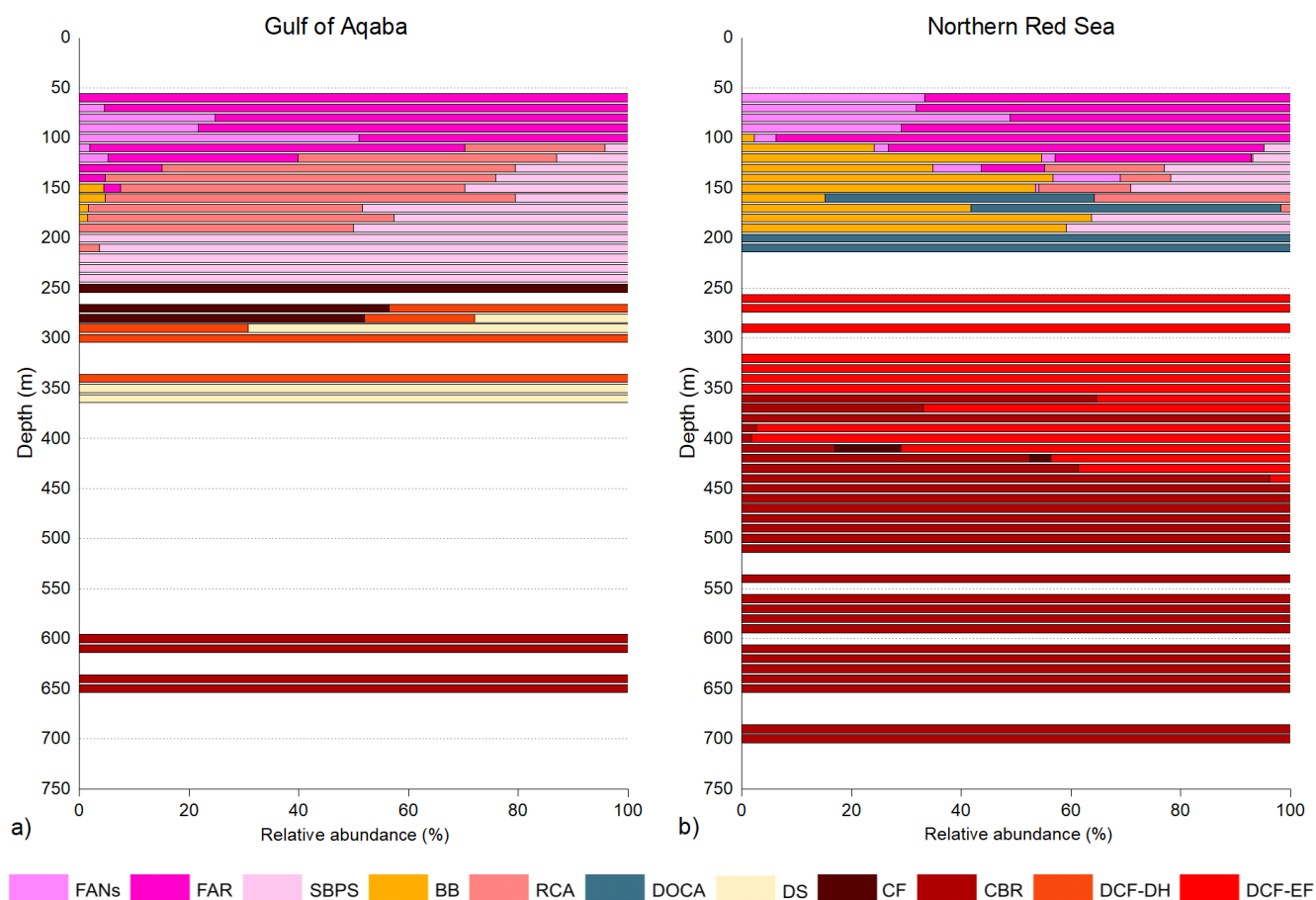


Figure 7: Relative abundance and distribution of the benthic habitats identified in the video transects in a) the Gulf of Aqaba (GoA) and b) Northern Red Sea (NRS). The x-axis represents the percentage of georeferenced points within each basin (GoA: n = 11,512;



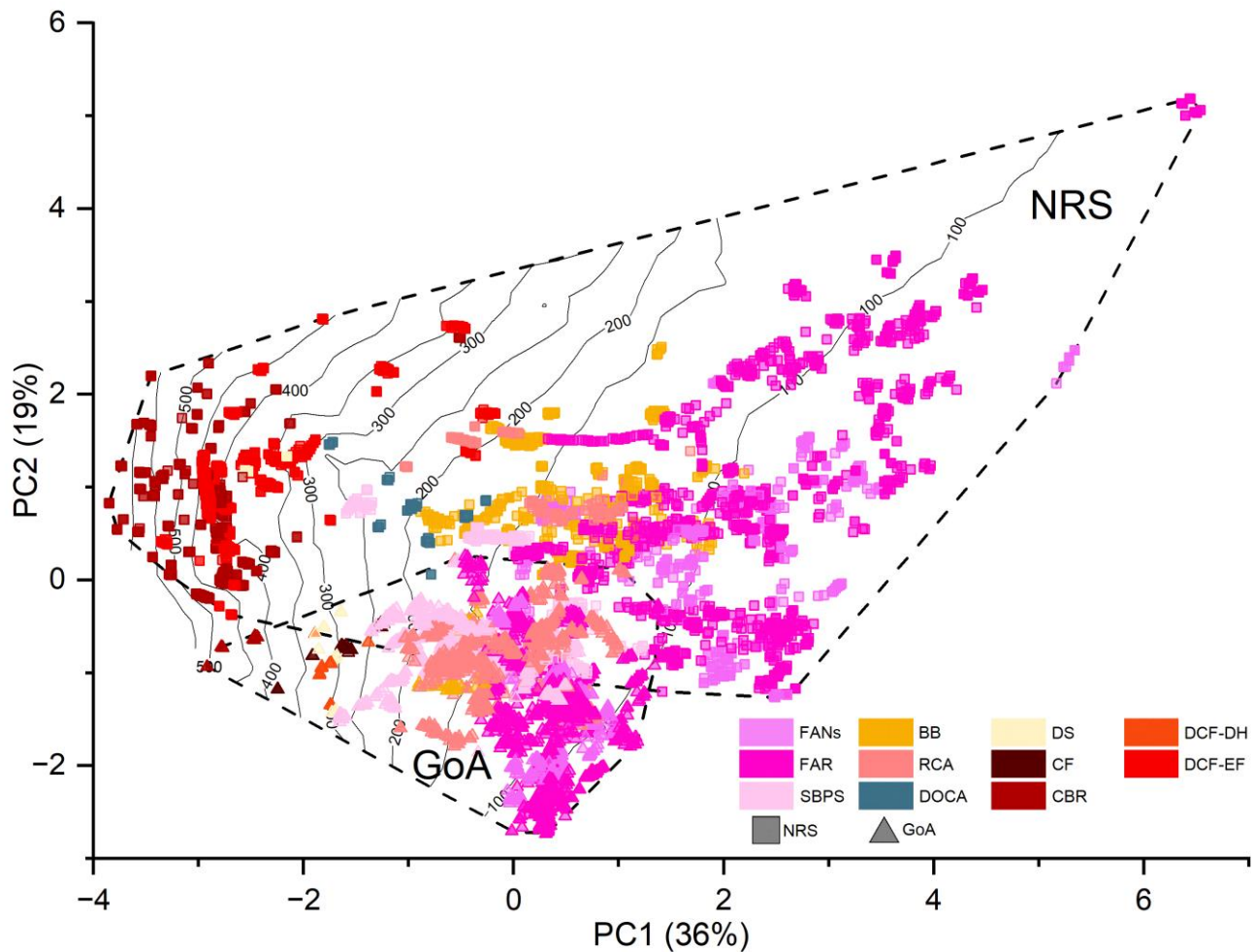
495 **NRS: n = 24,453, recorded at 5-second intervals along USBL tracks) assigned to each habitat class within 10-m depth intervals. The legend is consistent across panels and includes only the biotically defined habitat types.**

Deeper assemblages showed clearer differences in distribution. DOCA were found exclusively in the NRS between 160 and 220 m, on planar to steep, south-facing slopes under cool and oxygen-poor conditions. DS and CF occurred mainly in the GoA between 260 and 360 m, where oxygen levels remained relatively high compared to equivalent depths in the NRS (Fig. 2). DCF were present in both basins but far more abundant in the NRS, extending from approximately 260 to 440 m and
 500 developing under cool, low-oxygen conditions on southeast-facing slopes. The deepest habitat, CBR, was largely confined to the NRS and occurred beyond 600 m, forming under cold, oxygen-depleted conditions on moderately sloping, south-oriented substrates. Overall, the distribution of these habitats along the depth gradient observed in Fig. 7 suggests consistent vertical patterns across basins, with shallow foralgal frameworks transitioning to intermediate coral-bryozoan assemblages and finally to deep azooxanthellate communities. These observational trends denote a depth-dependent distribution of habitats, which is
 505 further analysed in the following sections. Despite differences in sampling intensity and depth coverage, the comparable representation of non-substrate-dominated habitats in both basins supports the robustness and representativeness of the dataset for cross-basin analysis across the 70–700 m depth range.

3.6 Statistical Analysis

3.6.1 Multivariate Analysis

510 The principal component analysis (PCA) of the classified benthic habitats (Fig. 8, Table 2) revealed a clear separation of benthic habitats along the first two components, which together explained 55% of the total variance (PC1: 36%, PC2: 19%). PC1, primarily driven by water temperature (-0.48), dissolved oxygen (-0.45), and density anomaly (0.52), represents vertical zonation along depth and associated environmental gradients. Habitats in both the NRS and GoA showed a similar PC1 trend, reflecting comparable depth-related patterns and confirming that vertical zonation is maintained across both basins. In contrast,
 515 PC2, dominated by aspect (0.49), salinity (0.48), and VRM (-0.46), differentiated the two basins along a combined geomorphological and oceanographic gradient. NRS habitats were distributed around intermediate to positive PC2 values, indicating moderate topography and variable seafloor orientation, whereas GoA habitats were exclusively associated with negative PC2 values, reflecting more irregular terrain and distinct aspect orientations. Salinity also contributed to this separation, differing consistently between the two basins along PC2. RCA and SBPS occupied intermediate positions along
 520 both axes, partially overlapping between the two basins. BB were located primarily in the NRS at moderate PC1 and positive PC2 values, consistent with intermediate depth and topographic conditions. Overall, the PCA highlights that while vertical zonation patterns are similar across both basins, environmental differentiation between NRS and GoA along PC2 is driven by differences in seafloor orientation, topographic complexity (VRM), and salinity.



525 **Figure 8: Principal Component Analysis (PCA) of the classified benthic habitats. PC1 (36% variance) is primarily influenced by**
temperature, dissolved oxygen, and density anomaly, representing vertical zonation along depth. PC2 (19% variance), is dominated
by aspect, salinity, and VRM, differentiates the two basins along a combined geomorphological and physico-chemical gradient.
Contour lines represent interpolated depth value between basins points Dashed polygons refer to the basin: the Gulf of Aqaba (GoA) and
the Northern Red Sea (NRS).

530

Table 2: PC variance and variables contribution to PC1 and PC2 of the classified benthic habitat

Components	Variance	Slope	VRM	Temperature	Dissolved O ₂ Concentration	Salinity	Density Anomaly	Aspect	ProCurv	PlanCurv
PC1	0.36	-0.21	-0.29	-0.48	-0.45	0.25	0.52	-0.08	-0.32	0.08
PC2	0.19	-0.17	-0.46	0.22	0.30	0.48	-0.20	0.49	-0.31	-0.11

A complementary nMDS analysis (Fig. S6) confirmed the consistency of the multivariate structure. Both PCA and nMDS revealed a consistent multivariate structure, indicating that the environmental gradients separating habitats are robust and



independent of the ordination method used. PCA was therefore adopted as the primary ordination approach, as it provides a more interpretable representation of the dominant gradients.

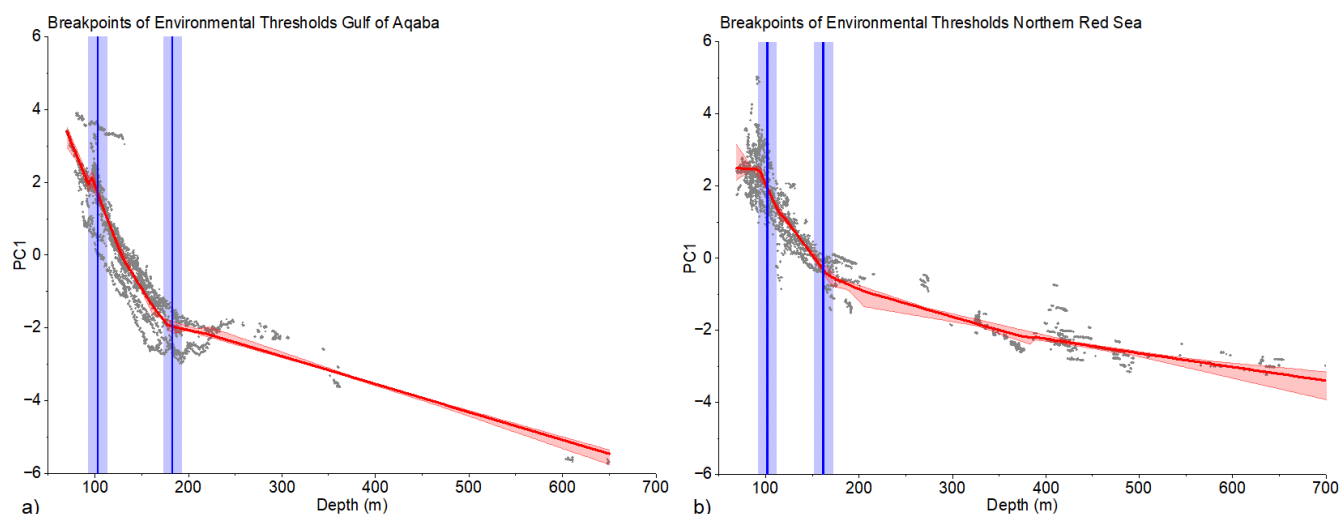
The PERMANOVA analysis confirmed significant differences among habitat groups (pseudo-F = 827.23, $R^2 = 0.411$, $p = 0.001$), indicating that 41.1% of the variance in the environmental variables was explained by habitat groupings (Table S4).

3.6.2 Environmental Thresholds

The segmented regression analysis consistently identified three ecological transitions along the depth gradient in the GoA and NRS (Fig. 9, Table 3). Two primary consensus breakpoints, defined by their higher recurrence across models (Table 3) and represented in Fig. 9, were detected at 103 ± 10 m (GoA) and 102 ± 10 m (NRS), and at 161 ± 10 m (NRS) and 183 ± 10 m (GoA). The first primary threshold marks the transition out of the lower mesophotic zone into the mesophotic-rariphotic transition zone. A secondary breakpoint at 123 ± 10 m (GoA) and 122 ± 10 m (NRS), while recurring less frequently across models, is ecologically significant: its near-identical position across both basins marks the point where foralgal-dominated habitats (FAR and FANs) begin to decline while transition-zone habitats (RCA, BB, SBPS) become more dominant. The second primary breakpoint, showing slight basin-specific variation, corresponds to the transition from intermediate habitats (RCA, BB, SBPS) to the deep azooxanthellate zone (DCF, CBR). The depth difference between basins suggests that the onset of truly deep-sea conditions occurs shallower in the NRS compared to the GoA, likely driven by the distinct water mass signatures (temperature and oxygen) identified in the oceanographic profiles.

Table 3: Depth breakpoints detected across six broken-stick segmented regression models for the Gulf of Aqaba (GoA) and the Northern Red Sea (NRS). Breakpoints represent statistically inferred transitions along the depth–PC1 relationship. The frequency column (f) indicates how many of the six models identified each breakpoint.

Gulf of Aqaba		Northern Red Sea	
Breakpoints	f	Breakpoints	f
93,113	9	92,112	6
113,133	4	112,132	3
133,153	1	151,171	5
153,173	1	192,212	1
173,193	5	352,372	3



555 **Figure 9: Segmented (broken-stick) regression applied to the environmental gradient (PC1) as a function of depth in both basins, a-**
Gulf of Aqaba and b-Northern Red Sea. Grey points represent individual point from the video analysis shapefile. The red curve
shows the mean fitted relationship across six segmented models (with 1–6 breakpoints), and the shaded red ribbon indicates model
variability. Vertical blue lines mark the two consensus environmental thresholds, defined as the two most recurrent breakpoints in
the models within a ± 10 m buffer. The light-blue shading represents the breakpoint uncertainty range. These depth intervals
 560 **correspond to statistically supported changes in the slope of the environmental gradient.**

The ~20 m difference between the NRS and GoA deep breakpoints was tested independently with a delta-method z-test on the segmented regression model and a non-parametric bootstrap (1000 resamples per basin), using the continuous point estimates (ψ) from the underlying model (NRS $\psi = 155$ m, CI 151–158 m; GoA $\psi = 177$ m, CI 176–179 m). Both approaches confirmed the offset as statistically robust: the z-test gave $z = 13.75$ ($p < 0.001$), and the bootstrap confidence intervals for the two basins
 565 did not overlap, indicating that the asymmetry reflects a genuine basin-level difference rather than sampling noise.

3.6.3 Regression Tree Analysis

The regression tree models showed consistently high performance in both basins: a) GoA, AUC = 0.979, CA = 0.890, F1 = 0.886 and b) NRS, AUC = 0.991, CA = 0.930, F1 = 0.930. These values indicate a high ability to discriminate among habitat classes, high overall accuracy, and an excellent balance between model precision and recall.
 570 In the GoA, the regression tree (Fig. S7) shows its primary split at 124 m on Node 1, separating the dataset into two major habitat domains: a left branch dominated by FAR (63.7%) and a right branch dominated by RCA (55.4%). From this point onward, the two branches evolve under different environmental controls. In the FAR branch, Node 2 introduces a second split based exclusively on depth, generating Nodes 4 and 5, both of which retain FAR as the dominant habitat, indicating a coherent shallow–mid-depth assemblage. In contrast, the RCA branch is structured by temperature, with Node 3 producing two distinct
 575 pathways that already separate SBPS (Node 6) from RCA (Node 7).

At deeper levels, the internal zonation of the basin becomes apparent (Fig. S7). From Node 4, a key split on salinity forms Node 8, which leads to the FANs-dominated terminal leaves, while Node 9 remain FAR-dominated together with their



descendant branches. From Node 5, slope drives the subdivision into Node 10 and Node 11, identifying in the latter an RCA-dominated leaf associated with steep terrain. The deeper RCA-related pathway, defined by Node 6, captures SBPS at depths shallower than 248 m, while deeper branches converge toward Node 12, the four azooxanthellate coral habitats typical of the lower mesophotic and rariphotic zones in the GoA (DCF-DH, CF, DS, CBR). Finally, Node 13 delineate RCA-dominated environments structured by successive splits on morphological variables, confirming the increasing influence of geomorphology at intermediate depths.

In the NRS, the regression tree (Fig. S8) identifies its main division on Node 1, splitting at a temperature of 21.9 °C, which corresponds to approximately 200 m depth. This separates a deep-water branch dominated by DCF-EF (57.4%) from a shallower branch dominated by FAR (44.2%). In the deep-water domain, Nodes 2 and 4 introduce depth-driven splits that distinguish two major deep assemblages: a CBR-dominated environment emerging from Node 7, and a DCF-EF-dominated pathway descending from Node 8. A first CBR leaf is already produced directly from Node 2, indicating the early separation of this habitat type in the deep branch.

On the shallower side of the tree, the split at Node 3 generates two contrasting habitat domains. The first, defined by Node 5, corresponds to a purely shallow assemblage dominated by FAR and FANs. The second, descending from Node 6, differentiates into two structurally distinct deeper assemblages: Node 11, dominated by SBPS and DOCA with minor contributions from FAR and FANs, and Node 12, which identifies an environment primarily characterised by BB, with increasing representation of FAR and RCA toward the terminal leaves.

Together, the splits in the NRS and GoA reveal a zonation pattern in which depth, temperature and slope drive the major structural boundary, while geomorphological variables, salinity and oxygen refine the partitioning. Moreover, the primary temperature-based split in the NRS regression tree (~200 m, corresponding to 21.9°C) is slightly deeper than the broken-stick breakpoint identified for the same basin (161 ± 10 m). This discrepancy likely reflects the influence of GoA water masses south of Tiran Island on the generalised environmental model used for the NRS, as also suggested by the potential temperature-salinity diagram (Fig. S3).

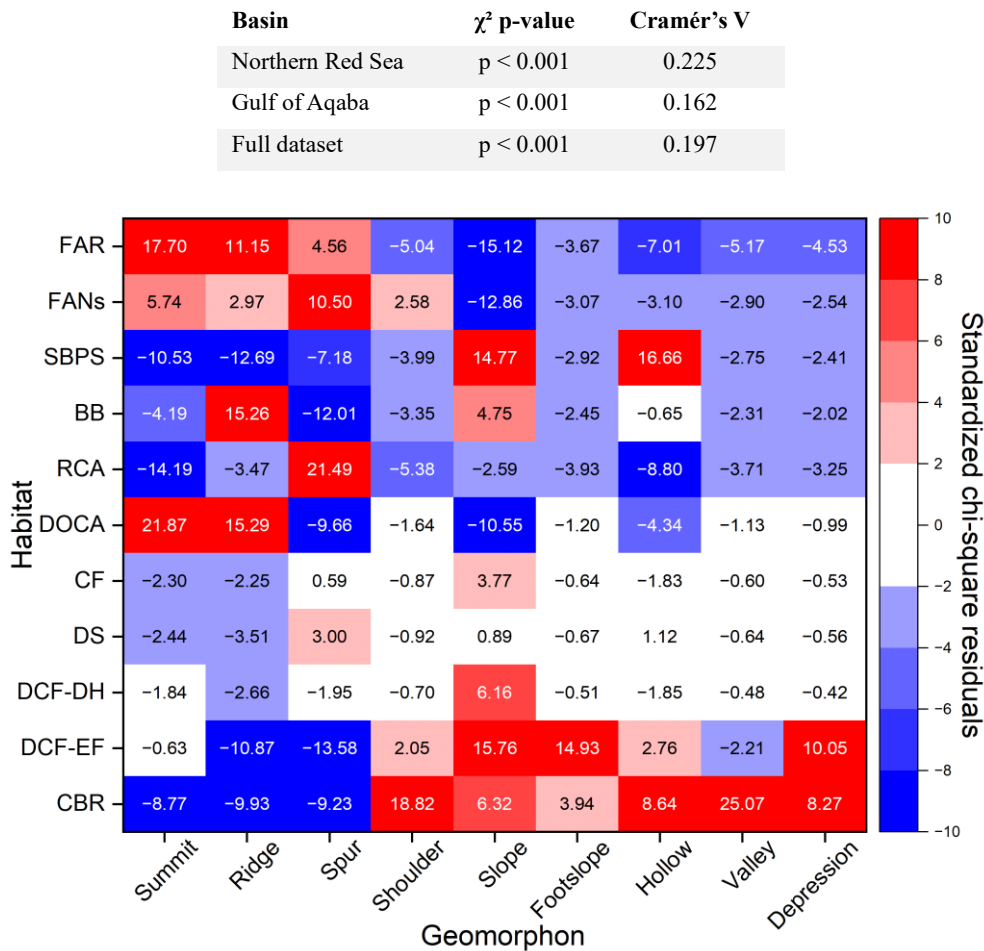
3.6.4 Geomorphon - Habitat Associations

The results of the contingency analysis between benthic habitats and geomorphon classes showed a highly significant across the full dataset ($\chi^2 = 12504.5$, $df = 117$, $p < 0.001$), with a moderate effect size (Cramér's $V = 0.197$) indicating a non-random but not exclusive association between habitat type and terrain morphology. When analysed separately, the association remained significant in both basins (NRS: $\chi^2 = 11193.9$, $df = 99$, $p < 0.001$; $V = 0.225$; GoA: $\chi^2 = 2120.2$, $df = 77$, $p < 0.001$; $V = 0.162$), indicating that habitat-morphology relationships are consistent but slightly stronger in the NRS.

Table 4: Results of the Chi-square (χ^2) contingency analysis assessing the association between classified benthic habitats and geomorphon landforms in the Northern Red Sea (NRS), the Gulf of Aqaba (GoA), and for the full dataset. The results allowed us to formally reject the null hypothesis of no relationship between habitat distribution and seafloor landforms, across the full dataset



610 and within each basin. Although the Cramér’s V values (ranging from 0.162 in the GoA to 0.225 in the NRS) indicate a moderate rather than exclusive effect size, they confirm a highly significant, non-random association between terrain morphology and habitats.



615 **Figure 10: Standardised chi-square residual heatmap showing deviations from expected frequencies in the contingency analysis of habitats versus geomorphon classes. Positive residuals (red hues) indicate habitat–morphology combinations occurring more often than expected under independence, while negative residuals (blue hues) denote under-representation.**

Heatmaps of standardised residuals (Fig. 10, Table 4) showed distinct over- and under-representation patterns for specific benthic habitat-geomorphon combinations. Positive residuals ($> +2$) for FAR, FANs, BB, RCA and DOCA occurred predominantly on summit, ridge and spur classes, indicating a higher frequency on convex landforms. Conversely, DCF (both DH and EF variants) and CBR were consistently over-represented on foothslope, hollow, valley and depression classes, corresponding to concave or downslope morphologies. Intermediate positions were observed for SBPS and CF, which displayed positive associations on slope-like forms. Shoulder and foothslope classes were shared by both mesophotic and deeper habitats, but with higher residuals in the latter. No habitat showed strong positive residuals on planar morphologies. These findings confirm that habitat occurrence is non-randomly distributed across morphological classes, with consistent differentiation between convex and concave settings across both basins. These results indicate that while geomorphology is



not the sole driver of habitat occurrence, it acts as a robust secondary control that modulates the broad-scale vertical zonation established by depth and water mass characteristics.

3.7 Vertical Zonation Framework

To synthesize the patterns emerging from habitat observations and quantitative analyses, we propose an integrated vertical zonation framework. Video observations and statistical analyses converged on a four-tiered vertical zonation (Fig. 7–9). Lower mesophotic assemblages (~70–100 m) were dominated by foralgal frameworks (FAR, FANs). A relatively narrow transition zone (~100–120 m) marked the decline of foralgal habitats and the establishment of rariphotic communities. The rariphotic zone (~120–161 m in the NRS and ~120–183 m in the GoA) was characterised by RCA, BB, and SBPS. Below ~161 m (NRS), and ~183 m (GoA), benthic communities transitioned into the aphotic deep azooxanthellate zone, dominated by deep coral frameworks (DCF-EF, DCF-DH), CBR, and associated CF and DS habitats. Three statistically supported environmental breakpoints (~102 m, ~122 m, and 161–183 m) corresponded to these transitions (Fig. 9, Table 3). Overall, the combined evidence from visual observations and statistical analyses defines a coherent vertical zonation of benthic habitats structured along the depth gradient and consistently observed across both basins.

4 Discussion

The NRS and the GoA represent a unique case study for mesophotic, rariphotic and deep-sea ecology due to their distinctive physicochemical structure. Unlike most global ocean basins, where deep-water temperatures decrease to ~4 °C, the Red Sea maintains a remarkably stable thermal regime of approximately 21 °C and higher salinity (~40.6) down to abyssal depths (Fig. 2). The deep scleractinian-dominated habitats we describe develop under conditions with no equivalent in classical cold-water coral provinces, and we refer to them as warm-water deep coral frameworks (*sensu* Nolan et al., 2024).

The habitat classification proposed here provides a structured framework to describe benthic habitats based on video analysis of macroscopic features along depth and environmental gradients, supported by both visual observations and quantitative analyses. Individual habitat types had already been reported in localised areas of the GoA and the Red Sea (Bracchi et al., 2023; Chimienti et al., 2025; Dullo et al., 1990; Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Fricke and Schuhmacher, 1983; Hottinger, 1983; Nolan et al., 2025, 2024; Qurban et al., 2020, 2014; Roder et al., 2013). This study extends their characterisation across a broader spatial and environmental range, integrating them into a depth-structured framework comparable to schemes proposed for other regions (Diaz et al., 2023; Stefanoudis et al., 2019).

The results highlight a hierarchical structuring of the observed benthic habitats, in which large-scale oceanographic gradients act as a primary regulator on their vertical distribution, while seafloor geomorphology acts as a secondary modulating factor (Fig. 8, Table 2). The shallowest ecological transition, associated with the upper portion of the thermocline, is consistent with patterns described in other continental margins (e.g., Braga-Henriques et al., 2022). However, deeper habitat transitions in the Red Sea occur under different conditions. In most oceanic basins, progressive cooling with depth limits benthic habitats



thermally (Graiff et al., 2025), while in the deep Red Sea the isothermal conditions remove this constraint and habitat-forming organisms persist across extended bathymetric ranges (Table 1, DCF and CBR). As a result, the controls on vertical distribution of aphotic habitats in the Red Sea shift from temperature to dissolved oxygen availability and seafloor geomorphology, consistent with the comparable PC1 loadings of temperature and dissolved oxygen (Fig. 8, Table 2) and the secondary influence of geomorphology reported above (Fig. 10).

4.1 Development of the Benthic Habitat Classification Scheme

While international frameworks such as EUNIS (Davies and Moss, 2000), CMECS (Federal Geographic Data Committee and Marine and Coastal Spatial Data Subcommittee, 2012), and the scheme of Buhl-Mortensen et al. (2015) provide valuable structural templates for benthic habitat classification, they were developed for temperate Atlantic and Nordic systems, and cannot be transposed to the Red Sea without adaptation. The basin's anomalous physicochemical conditions, the limited knowledge of the mesophotic and deep zones, and its endemic fauna define an ecological context that differs from the systems on which these frameworks were calibrated. Applying them unchanged would risk misclassifying habitat-forming taxa that, while functionally analogous to Atlantic or Mediterranean counterparts, develop under fundamentally different physicochemical conditions, such as the *E. fistula*-dominated frameworks (Qurban et al., 2020) or the foraminiferal-algal nodule beds documented here and in Bracchi et al. (2023).

Prior to this study, habitat characterisation in the Red Sea mesophotic and deep zones was fragmented across localised and/or taxonomically focused investigations (Fricke and Hottinger, 1983; Fricke and Knauer, 1986; Qurban et al., 2020, 2014; Roder et al., 2013; Weinstein et al., 2021). Nevertheless, these works provided the taxonomic and ecological foundation on which the present classification is built, even though no prior study spanned both basins continuously or combined biological observations with geomorphological and oceanographic data at regional scale. The classification proposed here fills this gap by producing 14 habitat classes that are directly linked to quantifiable environmental gradients, enabling cross-basin and cross-depth comparisons.

4.2 Habitat Diversity and Global Ecological Significance

The habitats identified in this study show strong evidence of functional convergence with benthic systems described in other ocean basins, despite differences in taxonomic composition. The Red Sea habitats are rarely direct taxonomic equivalents of Atlantic or Mediterranean systems, but their habitat-forming taxa fulfil comparable ecological, functional and structural roles. For example, FAR and FANs are ecological analogues to coralligenous build-ups and rhodolith beds documented in the Mediterranean (Ballesteros, 2006; Basso et al., 2017; Dominguez-Carrió et al., 2022), serving as primary carbonate producers and biodiversity hotspots in dim-light environments. Similar rhodolith-foraminiferal assemblages have been documented worldwide (Bracchi et al., 2023; Matsuda and Iryu, 2011; Prager and Ginsburg, 1989; Reid and MacIntyre, 1988), where they act as ecosystem engineers and provide recruitment and nursery habitats.



The rariphotic coral ecosystems of the GoA (Chimienti et al., 2025) represent a globally distinctive case with no equivalents worldwide, and only a partial analogue in *Dendrophyllia cornigera* beds on Mediterranean muddy bottoms (Enrichetti et al., 2023).

690 The scleractinian frameworks identified at aphotic depths, including the caryophylliid bioconstructions (CBR) and the dendrophylliid frameworks (DCF-EF and DCF-DH), find functional parallels with the deep azooxanthellate cold water coral (CWC) frameworks in the Atlantic Ocean and the Mediterranean Sea (Chimienti et al., 2019; Freiwald, 2002; Roberts et al., 2009; Vinha et al., 2025), and in the Indo-Pacific, where dendrophylliids such as the genera *Eguchipsammia*, *Dendrophyllia*, and *Cladopsammia* are recognised as key habitat-forming taxa in the South China Sea, Indian Ocean and the Philippine Sea
 695 (Davies and Guinotte, 2011; Lu et al., 2024; Zhao et al., 2023). Globally, these azooxanthellate bioconstructions are among the most three-dimensionally complex habitats of the deep ocean and host hundreds of associated species.

4.3 A Globally Consistent Vertical Zonation

The four-tiered vertical zonation documented in this work includes the lower mesophotic (FAR/FANs, <100 m), mesophotic-rariphotic transition (decline of FAR/FANs, emergence of RCA/BB/SBPS ~100–120 m), the rariphotic zone (RCA, BB, SBPS; NRS: ~120–161 m, GoA: ~120–183 m) and the deep azooxanthellate zone (DOCA, DCF, CF, DS, CBR; NRS: >~161 m, GoA: >~183 m). This zonation scheme closely matches the framework formalised by Stefanoudis et al. (2019) for Bermuda, where benthic communities turn over sharply at ~150 m and again near 200 m, and is consistent with patterns described from the Indo-Pacific (Diaz et al., 2024; Kahng and Kelley, 2007; Stefanoudis et al., 2023), the Azores mesophotic-deep transition (Braga-Henriques et al., 2022), and Pacific temperate mesophotic-rariphotic systems (Wong et al., 2025). The convergence is
 705 highly notable given the very different oceanographic settings of these systems and indicates that depth-driven gradients in light, food supply, and water-mass properties impose comparable structural constraints on benthic habitat architecture across ocean basins (Carney, 2005; Howell, 2010).

The absolute depths of the breakpoints differ between regions, reflecting regional calibration of the main drivers. In Bermuda and the Bahamas, the mesophotic-rariphotic transition occurs at ~130–150 m (Reed, 1985; Stefanoudis et al., 2019), in Indo-Pacific oligotrophic systems near 120–150 m (Kahng and Kelley, 2007), and in Tasmanian temperate margins between 70 and 90 m (Wong et al., 2025). Our consensus breakpoints at 102 ± 10 m and 122 ± 10 m place the Red Sea transitions at the shallower end of this global range, consistent with the high water clarity and oligotrophic regime, which extend euphotic conditions deeper than in turbid temperate areas but compress them slightly compared to tropical Pacific systems. The deeper breakpoint at 161–183 m falls within the global rariphotic-to-deep transition window (Baldwin et al., 2018; Stefanoudis et al.,
 715 2019), reinforcing the universality of this second turnover.

4.4 Regional Vertical Zonation: Asymmetries Between NRS and GoA

The four-tiered zonation framework documented in this study is preserved across both basins, with the lower mesophotic boundary (~102 m) identical between the GoA and the NRS (Fig. 9, Table 3). The two basins diverge at the deeper end of the



gradient: the transition from rariphotic to deep azooxanthellate communities occurs at ~161 m in the NRS and at ~183 m in the GoA, a systematic ~20 m offset that places the upper boundary of the deep zone shallower in the NRS. Our delta-method z-test and bootstrap analyses showed that this offset is statistically robust, indicating that the asymmetry reflects a basin-level difference rather than sampling noise. This asymmetry is consistent with the oceanographic contrast documented in our CTD profiles (Fig. 2). The NRS shows a shallow oxygen reduction at 150–250 m linked to heterotrophic activity, and a deeper oxygen minimum zone (OMZ) between 400 and 600 m, whereas the GoA maintains comparatively higher oxygen and stable conditions throughout the upper bathyal due to active winter convection (Carlson et al., 2014; Manasrah, 2002; Plähn et al., 2002). Several GoA profiles also showed a localised oxygen reduction between ~150 and 250 m, coinciding with the sill depth of the Strait of Tiran, consistent with intermittent intrusion of relatively warm, less saline, oxygen-depleted NRS water into the GoA (Plähn et al., 2002), a direct water-column signature of the same cross-basin exchange that structures the ~20 m offset in the deep zonation boundary. Because the breakpoint analysis was performed on the environmental gradient rather than on biological data directly, the agreement between the modelled depth offset and the habitat transitions documented in the video transects is independent evidence that the local water-column structure shapes the bathymetric organisation of benthic communities, consistent with the regression tree analysis, which was specifically designed to identify the environmental variables driving habitat transitions. This view is also supported by recent work showing that vertical water-mass structure controls the bathymetric distribution of deep-sea octocorals (Radice et al., 2016) and more broadly the deep coral communities (Auscavitch et al., 2020).

Beyond the systematic shift in the deep breakpoint, some habitat classes were observed in only one basin: Deep octocoral aggregations (DOCA, 164–216 m) only in the NRS, and dendrophylliid-serpulid associations (DS, 290–362 m) only in the GoA. These exclusivities may reflect either uneven sampling effort linked to opportunistic dive-site selection, or genuine environmental constraints. With the current dataset we cannot distinguish between these two possibilities, and balanced surveys of both basins will be required to resolve this point. The clearest case is the absence of *E. fistula* frameworks (DCF-EF) from the GoA, despite the availability of comparable depth ranges and hard substrates. In the Saudi Arabian NRS, *E. fistula* is a major framework-builder, forming extensive structures across a wide depth range from ~266 m down to over 680 m (Nolan et al., 2024; Qurban et al., 2014, 2020; this study). The species thrives under low-oxygen, isothermal conditions (Roder et al., 2013; Roik et al., 2015) that match the upper bathyal regime of the NRS but differ from the better-oxygenated water column of the GoA.

4.5 Warm-Water Deep Coral Frameworks: A Red Sea Peculiarity with Global Implications

The deep coral frameworks documented in this work (DCF-EF, DCF-DH, CBR) overlap the architectural niche that is globally occupied by CWC habitats dominated by *Desmophyllum pertusum*, *Madrepora oculata*, *Enallopsammia rostrata* and *Desmophyllum dianthus* (Freiwald, 2002; Roberts et al., 2009). The CWC habitats share with the Red Sea deep frameworks their three-dimensional skeletal architecture, suspension-feeding ecology and associated fauna, but they operate under a fundamentally different physico-chemical context. CWCs in the North Atlantic and Mediterranean develop in waters of 4–13



°C, salinity ~35–38.5, and aragonite saturation states (Ω_{Ar}) currently above 1 but increasingly threatened by the shoaling of the aragonite saturation horizon under ocean acidification (Guinotte et al., 2006; Tittensor et al., 2010). In contrast, Red Sea deep-water corals occur at ~21 °C and ~40.6, within a water column that remains supersaturated with respect to aragonite ($\Omega_{Ar} > 1$) down to abyssal depths, effectively removing one of the principal chemical constraints on deep-sea scleractinian calcification. Without carbonate limitation, the distribution of Red Sea deep coral frameworks reflects other controls such as oxygen availability, food supply, substrate, and potentially upper thermal tolerance. In this context, the Red Sea represents a natural end-member system where the decoupling of temperature and carbonate chemistry allows direct testing of the limits of deep coral persistence under projected ocean warming and ongoing changes in carbonate saturation.

4.6 Geomorphology as a Secondary Structuring Axis

The seafloor of the NRS and GoA reveals a physiography dominated by steep continental slopes transitioning into broad flat basins, with a diverse set of intermediate landforms (Fig. S1). This terraced physiography, with marginal areas stepping down from the shelf toward deeper basins, is consistent with previous descriptions of the NRS rift margins (Cochran, 2005; Martinez and Cochran, 1988). Slopes are generally gentle along the Saudi Arabian margin but become significantly steeper around islands and barrier reefs, a pattern that reflects the interplay of gravity-driven processes, salt-tectonic structuring (Mitchell et al., 2017), sediment dynamics, and carbonate build-up (Rowlands and Purkis, 2015) characteristic of the NRS and GoA margins. Against this physiographic background, heatmaps of standardised chi-square residuals (Fig. 10) revealed a robust association between habitat type and seafloor morphology. Mesophotic and rariphotic habitats (FAR, FANs, BB, RCA) were over-represented on convex landforms (summits, ridges, spurs). This pattern matches the known role of topographic highs in accelerating bottom flows, enhancing food supply, and minimising sediment burial, and the preference of arborescent octocorals and erect filter-feeding taxa for elevated, current-exposed landforms in high-energy mesophotic-rariphotic systems (Wong et al., 2025).

In the deep azooxanthellate coral zone, the octocoral-dominated DOCA shows the strongest positive residuals on summit and ridge classes. The dendrophylliid-dominated frameworks (DCF-EF, DCF-DH), in contrast, were over-represented on slope and footslope classes, such as the inclined flanks and bases of larger convex structures. This distribution matches the known preference of cold-water coral framework-builders for current-exposed flanks of bathyal mounds, where bottom-flow acceleration enhances food supply and prevents sediment burial (Bargain et al., 2017; Savini et al., 2014). At the 30 m DEM resolution of our analysis, the geomorphometric signal of the DCF framework captures the broader slope architecture rather than the small-scale positive relief of individual coral frameworks.

CBR showed the strongest positive residuals on valley, hollow, depression and shoulder classes. CBR occur as sparse, small-scale positive biogenic structures developing within or at the margins of larger concave morphologies. At the 30 m resolution of the geomorphon analysis, the positive relief generated by these isolated bioconstructions is not resolved, and their classification reflects instead the surrounding negative morphological context. The association with the shoulder class is

consistent with their occurrence at the lateral margins of concave features, where the transition to steeper terrain may locally
785 reduce sediment cover and expose hard substrate.

These findings refine the simple convex–concave dichotomy and suggest that geomorphology acts as a secondary structuring
axis that modulates habitat partitioning within the broader vertical zonation defined by depth and water-mass identity.

4.7 A Rapoport-Depth Perspective

Rapoport's rule postulates that species at higher latitudes tend to have larger latitudinal ranges (Stevens, 1989). Stevens (1996)
790 extended Rapoport's latitudinal rule to depth, predicting that the bathymetric ranges of marine species and the depth zones
should scale inversely with the steepness of the underlying environmental gradient. As a consequence, where temperature,
salinity, and oxygen change rapidly with depth, zonal bands are narrow, but where they are nearly invariant, zonal bands
expand.

The deep Red Sea, with temperatures stable at ~21 °C and salinity at ~40.6 from below the pycnocline to abyssal depths (Roder
795 et al., 2013; Yao et al., 2014a, b; this work), is an endmember of a compressed thermohaline gradient unmatched by other
open-ocean basins. Our dataset cannot test species-level depth ranges, which is a known limit of video-based surveys (see the
next section), but the habitat-level evidence is qualitatively consistent with the Rapoport-depth prediction. In the upper 200 m,
where light, temperature and oxygen vary steeply, our analyses resolve five habitat classes (FAR, FANs, BB, RCA, plus the
transitional SBPS) packed within ~130 m of vertical extent. By contrast, the deep azooxanthellate zone (operating under near-
800 isothermal, isohaline, and aragonite-supersaturated conditions) hosts six habitat classes (DOCA, CF, DS, DCF-EF, DCF-DH,
CBR) distributed across more than 500 m of depth. This contrast between a finely stratified upper zone and an extensively
developed deep zone is the asymmetry Rapoport-depth would predict for a system in which the temperature gradient becomes
homogeneous below the pycnocline (Fernández and Marchant, 2025).

Comparison of habitat depth-range distributions across regions with contrasting deep-water stratification, such as the Red Sea
805 (compressed gradient, Yao et al., 2014a, b), the Mediterranean Sea (homothermal at ~13 °C and well-ventilated below the
thermocline, Tanhua et al., 2013) and the North Atlantic (steeply stratified, Roberts et al., 2009), would provide a community-
level extension of Rapoport-depth that complements existing species-level work (Fernández and Marchant, 2025; Hernández
et al., 2005; Smith and Gaines, 2003; Stevens, 1996). Such comparisons require standardised habitat classification frameworks
across regions, an argument for the type of regional schemes proposed in the present study.

810 4.8 Study Limitations

Underwater video surveys allow extensive coverage of mesophotic and deep habitats with minimal environmental disturbance,
but they impose known constraints on taxonomic resolution and detection of small-sized and/or sediment dwelling organisms
(Davies et al., 2014; Lesser and Slattery, 2021; Pawlik et al., 2022). High-definition imagery often lacks sufficient detail to
identify fine morphological characters, limiting reliable identification to genus or family for many taxa, including habitat
815 formers (Bo et al., 2012; Marin et al., 2025). Light conditions, camera angle, background complexity, field of view, and vehicle



stability further influence the accuracy of visual assessments (Song et al., 2022). Survey designs that optimise species-level identification, through shorter transects or more close-up footage, would reduce spatial coverage, a trade-off between taxonomic resolution and habitat extent. We mitigated this trade-off by integrating physical specimen collections from the same expedition (Bracchi et al., 2023; Chimienti et al., 2022; Macrina et al., 2025a; Maggioni et al., 2022; Nolan et al., 2025, 820 2024; Terraneo et al., 2022; Vicario et al., 2024b, 2026), which anchored the visual classification to species-level identifications for key habitat-forming taxa.

The spatial representativeness of the dataset was also affected by the opportunistic nature of the surveys. Transects were conducted in areas considered promising based on seafloor morphology or preliminary investigation, rather than through a fully randomised design. Consequently, some habitats (particularly those occurring at depths >500 m in the GoA, or in the 825 deepest parts of the NRS) may be over- or under-represented, and basin-level habitat proportions should be interpreted accordingly. Nevertheless, when substrate-dominated habitats are excluded, relative proportions of biologically structured habitats become comparable between NRS and GoA, indicating that the dataset remains robust for assessing broad-scale patterns.

The absence in our dataset of key environmental variables, such as in situ light attenuation profiles and bottom current 830 velocities, may limit the ability to further resolve the drivers of vertical and spatial zonation in this study. Light availability is a primary driver of mesophotic-rariphotic habitat transitions, particularly for the boundary between phototrophic and heterotrophic communities (Diaz et al., 2023; Lesser et al., 2018; Tamir et al., 2019), yet no direct irradiance measurements were available across the depth gradient. Bottom currents strongly influence sediment mobility, food supply, and the distribution of suspension-feeding taxa (Davies et al., 2009; Mienis et al., 2007). Including these variables in future surveys 835 would substantially improve model accuracy, refine breakpoint estimates, and better constrain the mechanisms responsible for basin-specific differences in deep habitat transitions.

Finally, the resolution of digital elevation models used to extract geomorphological variables imposes additional constraints. Fine-scale bedform features may be underrepresented, affecting the scale of habitat-morphology associations (Lecours et al., 2016; Misiuk and Brown, 2024). Despite these limitations, this work represents the first attempt to a spatially explicit 840 classification of mesophotic and deep benthic habitats across our study area and provides an exploratory baseline. Future efforts should integrate higher-resolution mapping, specimen-based taxonomy, and molecular tools to improve both the spatial and ecological resolution of deep-sea habitat assessments for conservation and management.

4.9 Implications for Monitoring, Management, and Conservation

The hierarchical classification of benthic habitats presented here, combined with their spatial characterisation from ROV and 845 submersible surveys, provides a documented baseline for monitoring and management in the NRS and GoA. Several outcomes of this study translate directly into operational tools.

First, the association between habitat types and geomorphon classes allows predictive habitat mapping from multibeam bathymetry alone (Misiuk and Brown, 2024). Convex landforms such as summits, ridges and spurs consistently host



mesophotic and rariphotic assemblages, while slope and footslope classes are indicative of deep dendrophylliid frameworks.

850 This relationship potentially enables managers to identify priority areas for protection or impact assessment before committing to costly ROV surveys, using bathymetric data that is increasingly available at regional scale.

Second, the three statistically supported depth breakpoints (~100, ~122, and ~161–183 m) provide ecologically grounded boundaries for depth-based zoning in the GoA and the NRS, replacing the arbitrary depth limits commonly adopted from studies outside the Red Sea in marine spatial planning with transitions that reflect shifts in community composition and

855 environmental conditions.

Third, the mesophotic and rariphotic habitats of the GoA, including structurally complex foralgal reefs, bryozoan bioconstructions and mixed coral assemblages, develop on steep slopes within a few hundred metres of the coastline. Their proximity to the shore exposes them to high sedimentation, anchoring disturbance and physical impacts from coastal construction, and highlights the need for buffer zones that extend well below the shallow reef into the mesophotic range.

860 Furthermore, the deep coral frameworks (DCF-EF, DCF-DH, CBR) are functional analogues of cold-water coral habitats that benefit from formal protection in multiple jurisdictions such as the Marine Strategy Framework Directive (MSFD; The European Parliament and the Council of the European Union, 2008) and OSPAR (OSPAR Commission, 1992). Granting equivalent recognition for these warm-water deep frameworks in the Red Sea regulatory context would represent a concrete management outcome directly supported by our characterisation.

865 Finally, the dataset of 35,965 georeferenced habitat observations provides a quantitative baseline against which future change can be measured. Without a standardised classification, temporal comparisons of habitat state are not possible. In the context of Saudi Arabia's Vision 2030 and large-scale coastal development along the NEOM coastline, this baseline is timely for designing monitoring programmes that can detect and respond to habitat change before it becomes irreversible.

5 Conclusions

870 This study provides a regional-scale, multidisciplinary characterisation of mesophotic and deep benthic habitats along the Saudi Arabian North Red Sea and Gulf of Aqaba. By integrating ~135 hours of high-definition underwater imagery collected during the OceanX-NEOM Deep Blue Expedition 2020 with high-resolution multibeam bathymetry and CTD casts, we provided a quantitative, basin-comparative description of benthic habitat distribution and zonation across this region between 70 and ~700 m depth. Fourteen distinct benthic habitats were identified across the analysed depth range, among them foralgal-

875 foraminiferal dominated habitats (FAR, FANs), mixed mesophotic and rariphotic habitats (BB, RCA, SBPS), three deep coral framework habitats (DCF-EF, DCF-DH, CBR), and substrate-dominated habitats. They are structured in a four-tiered vertical zonation framework, with three statistically supported environmental breakpoints at ~100, ~120, and ~161–183 m depth that separate the lower mesophotic, the lower mesophotic-rariphotic transition, the rariphotic, and the deep azooxanthellate zone. This framework is preserved between the two basins but with regional asymmetries: the deep breakpoint sits ~20 m shallower

880 in the NRS than in the GoA, the rariphotic band extends deeper in the GoA, with some habitats (DOCA, DS, DCF-EF) confined



to one basin, consistent with basin-specific oceanography. Seafloor geomorphology emerged as a robust secondary structuring axis, with mesophotic and rariphotic habitats associated with convex landforms and deep frameworks with inclined slopes and footslopes. The deep coral frameworks documented here represent warm-water deep coral systems operating under a different physico-chemical regime from classical cold-water coral provinces: their distribution is decoupled from temperature and aragonite saturation, and appears instead controlled by dissolved oxygen availability and geomorphological variables. Together, these findings establish a regionally adapted habitat classification framework and provide a baseline for monitoring, conservation, and management strategies in a rapidly developing region. The absence of comprehensive habitat inventories from adjacent regions (Egyptian, Sudanese, Eritrean, Yemeni coasts) currently limits our ability to assess whether these 14 habitat types represent the full diversity of Red Sea deep benthos. Future basin-wide surveys integrating higher-resolution mapping, in situ irradiance and current measurements, and specimen-based and molecular taxonomy will be essential to refine these results and extend their relevance across the broader Red Sea.

6 Data availability

The dataset used in the statistical analyses (35,965 georeferenced observations of benthic habitat class and environmental variables) is publicly available in Zenodo at <https://doi.org/10.5281/zenodo.23293694> (Marchese and Benzoni, 2026). No custom code was developed for this study. The analyses used the software and settings described in Sect. 2.4.

7 Author contributions

FM: Writing – original draft, Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Validation, Writing – review & editing. **GC:** Investigation, Methodology, Writing – review & editing. **MO:** Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **TIT:** Investigation, Validation, Writing – review & editing. **MAEW:** Methodology, Validation, Writing – review & editing. **SV:** Validation, Writing – review & editing. **LM:** Validation, Writing – review & editing. **SJP:** Investigation, Project administration, Supervision, Writing – review & editing. **VP:** Project administration, Resources, Writing – review & editing. **MR:** Investigation, Project administration, Resources, Writing – review & editing. **AC:** Investigation, Resources, Writing – review & editing. **AAE:** Project administration, Funding acquisition, Writing – review & editing. **FB:** Supervision, Conceptualization, Funding acquisition, Project administration, Investigation, Validation, Writing – review & editing..

8 Competing interests

The authors declare that they have no conflict of interest.



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