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Habitat structure shapes temperate reef assemblages across regional environmental gradients

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29 Abstract

30 Intertidal artificial habitats are proliferating, but are generally simpler in structure and host 31 lower biodiversity than natural rocky reefs. Eco-engineering aims to enhance the biodiversity of 32 coastal infrastructure, often through physical structural modifications that mimic topographic 33 properties of natural shores. Relationships between biotic assemblages and structural 34 properties of natural and artificial reefs have been extensively studied at sampling scales of up 35 to 1 m². But evidence that quantified local structural variation has an appreciable influence on 36 biotic assemblages, at a shore-wide scale across regional environmental gradients, is lacking. 37 Here we addressed this knowledge gap with an observational study at 32 natural and artificial 38 intertidal reef sites in Wales, UK. We used multivariate community analysis and permutation 39 tests to examine associations between local physical structure, regional environmental 40 variables and sessile biotic assemblages. A potential influence of local habitat structure on 41 assemblage composition was evident across regional-scale environmental gradients. Compared 42 to natural sites, artificial reefs had lower taxonomic richness, distinct and more variable 43 assemblage composition, and different physical structure. After removing the effect of habitat 44 (natural or artificial), canonical correspondence analysis showed that environmental variables 45 (wave exposure, sea surface temperature and salinity variation), along with two metrics of 46 physical structure (standard deviation in log-transformed detrended roughness and skewness 47 of surface verticality, both at 0.5 m scale), explained 40% of the variation in assemblage 48 composition among sites. The two structural metrics independently explained 14.5% of the 49 variation. Associations identified between individual taxa and environmental variables 50 indicated that sites with a higher proportion of horizontal surfaces hosted more canopy 51 macroalgae, which in turn support other algae and invertebrates. Our findings provide evidence 52 to inform scaling-up of structural eco-engineering interventions from experimental contexts to 53 enhance the biodiversity of coastal infrastructure across regional extents.

54

- 55 Keywords:
- 56 Littoral, rocky shore, eco-engineering, habitat complexity, topography, terrestrial laser
- 57 scanning.

58 1. Introduction

59 The physical structure of habitats has an important influence on the composition of biological 60 assemblages across systems and scales (McCoy and Bell, 1991). Examples include bird diversity 61 varying with vertical vegetation profile (MacArthur and MacArthur, 1961), freshwater 62 macrophyte structure shaping predator-prey relationships (Warfe and Barmuta, 2004), and 63 coral reef fish assemblages varying with cross-scale substrate complexity (Nash et al., 2013). In 64 general, habitats with more complex physical structure host greater biodiversity (Kovalenko et 65 al., 2012). However, the relationship is not ubiquitous, and difficulties in quantifying physical 66 structure in a system-independent manner at a range of ecologically relevant scales have 67 precluded a firm understanding of its contribution to assemblage variation among other driving 68 variables (Beck, 1998; Frost et al., 2005; Halley et al., 2004; Loke and Chisholm, 2022; Torres-69 Pulliza et al., 2020).

70 Many studies have shown an effect of physical habitat structure on assemblages in intertidal 71 reefs, defined as any intertidal hard-substrate habitat (Firth et al., 2013; Harley, 2008; Knott et 72 al., 2004). For example, on natural rocky shores, several studies have shown that surface 73 complexity measured in various ways is positively correlated with species richness (Kohn and 74 Leviten, 1976; Kostylev et al., 2005; Menge et al., 1985). Other studies have shown mixed 75 results. For example, Beck (2000) found that the effect of complexity on gastropod species 76 richness varied with measurement method, time and site, and Meager and Schlacher (2013) 77 found a relationship only when a novel metric of complexity was used. In artificial reef habitats 78 similar variability has been found. Using small concrete panels, Loke and Todd (2016) found a 79 positive effect of habitat complexity on species richness, while Strain et al. (2021) reported 80 context dependent effects varying from neutral to positive.

Ecological interactions and the relative influence of community structuring variables are
typically scale-dependent (Menge and Olson, 1990). Investigations of the effects of intertidal
habitat structure on assemblages tend to focus on interactions at local spatial scales, sampling

84 using quadrats or panels of up to 1 m², and controlling for external environmental variation. But 85 structure influences ecological interactions across a range of scales that may be specific to 86 species, functional groups or life stages. Across broader spatial scales of 100 m to 100 km in 87 eastern Canada, Archambault and Bourget (1996) found no statistical relationship between 88 categorised surface heterogeneity and sessile species richness. Across 20° of latitude in 89 Australia, Bracewell et al. (2018) found positive effects of increased settlement panel 90 complexity on biodiversity only at higher latitudes. Such variable results pose difficulties for 91 leveraging habitat structure in environmental management applications (Evans et al., 2021). 92 As human demands on coastal regions intensify, hard artificial coastal infrastructure is 93 proliferating, with environmental impacts like habitat loss, pollution and increased risk of 94 invasive species (Bugnot et al., 2020; Heery et al., 2017; Komyakova et al., 2022). There is 95 increasing demand for mitigation of the negative impacts of intertidal infrastructure with 96 biodiversity-enhancing modifications, which has been widely termed eco-engineering (Evans et 97 al., 2017). Eco-engineering interventions to structure design, construction methods or 98 retrofitting features such as pits, grooves, pools and complex tiles have shown positive effects 99 on biodiversity at local scales in certain contexts (Chapman and Underwood, 2011; Evans et al., 100 2021; Strain et al., 2018). But to be implementable and effective, eco-engineering interventions 101 need to be cost-effective, scalable, and have ecological impacts measurable against defined 102 management goals. Currently these goals are challenging to define because there is limited 103 evidence to predict the effects of scaled-up eco-engineering interventions on intertidal

104 assemblages across entire shores under a range of environmental regimes.

Regional gradients in multiple environmental stressors mediate biological patterns and
processes on intertidal reefs (Tomanek and Helmuth, 2002). Simultaneously, local physical
structure mediates environmental stressors and biological interactions including predation and
competition (Guichard and Bourget, 1998; Menge et al., 1985). It is feasible that structural
variation is critical to assemblage variation at local spatial scales, where most experimental

110 work has been conducted, but over regional spatial scales at which environmental managers 111 operate, environmental gradients may mask the effects of structure. No previous studies have 112 investigated the relationship between quantified physical structure and assemblage 113 composition at scales relevant to both direct ecological interactions (centimetre resolution) and 114 management units (hundreds of m² extent separated by kilometres) across regional 115 environmental gradients. 116 Here, we address gaps in our understanding of how physical habitat structure may influence 117 sessile intertidal assemblages in natural and artificial temperate intertidal reef habitats. 118 Specifically, we investigate: 1) whether artificial and natural reefs host different biotic 119 assemblages at a regional scale; 2) whether physical habitat structure quantified at centimetre 120 resolution and hundreds of m² sampling extent has an observable association with reef 121 assemblages across a region spanning more than 1000 km of coastline; and 3) how the strength 122 of associations between assemblages and local or regional environmental variables differ. By 123 addressing these knowledge gaps, we generate valuable information to inform scaling-up of 124 coastal eco-engineering.

125 **2. Methods**

126 2.1 Data collection

127 We collected biological, environmental, and physical structural data at 32 intertidal sites around 128 the coast of Wales, UK, in two habitats: 16 natural reefs (rocky shores) and 16 artificial reefs 129 (rock armour, dolos and seawalls) (Figure 1, supporting information Table S1). Our sites were 130 distributed around the coast to capture a broad range in environmental conditions. We loosely 131 paired artificial and natural sites with similar environmental conditions to achieve balance in 132 conditions between the two habitats. The minimum separation between paired sites was 260 m, 133 with 14 out of 16 pairs within 10 km of each other and the remaining two separated by 28 km 134 and 42 km. Sites were not strictly paired for statistical analysis. 135 For consistency, a single experienced surveyor recorded the sessile biotic assemblage at all

136 sites, targeting the mid-shore by the presence of indicative mid-shore species like *Fucus* 137 vesiculosus. A single plot per site was surveyed, with a distance parallel to the sea of 138 approximately 60 m, and a distance perpendicular to the sea varying according to the shore 139 gradient, being close to zero for vertical seawalls and tens of metres for gently sloping shores. 140 The surveyor recorded density or percent cover for all taxa found to the lowest possible 141 taxonomic level using the semi-quantitative SACFOR scale (Hiscock, 1996) for approximately 30 142 minutes, recording their position at 1 second intervals with a GPS logger. By sampling a single 143 large plot representative of each site, our biological sampling matched the scale of our physical 144 structure sampling.

We quantified the physical structure of sites using high-resolution, three-dimensional (3D)
remote sensing. We used a terrestrial laser scanner (Leica Geosystems HDS ScanStation C10) to
collect 3D point cloud data merged from 3-8 stations per site at a resolution of 10 cm point
spacing at 100 m range. We georeferenced scanner positions using a differential GPS system
(Leica Geosystems System 1200) with post processed kinematic corrections using the closest
three OS Net RINEX stations. We processed and quality checked laser scanner data following

manufacturer recommended procedures within Cyclone software (Leica Geosystems), to an
accuracy of 6 mm. We cropped the 3D data horizontally to a planar convex hull of GPS logger
positions buffered outwards by 1 m, and vertically to the local mean high-water neap to lowwater neap elevation range, or a maximum of 3 m from the base of extremely vertical sites like
seawalls, to represent the observed survey area. We manually cleaned point cloud data to leave
only data representing hard substrate.

To quantify the physical structure of sites we calculated the metrics of detrended roughness and verticality at multiple scales in the open-source software CloudCompare v2.12 (Figure 2). Both algorithms use a local best fit plane calculated in a user defined focal window. Detrended roughness is defined as the standard deviation of point distances from the local plane in the normal (orientation) direction, calculated using the *Multiscale Model to Model Cloud Comparison* tool (Lague et al., 2013). Verticality (V) is defined as:

- 163
- 164 $V = 1 N_z$ Equation 1
- 165

166 Where N_z is the z-axis normal vector of the local plane, such that for a horizontal plane $N_z = 1$ 167 and for a vertical plane $N_z = 0$. We calculated verticality using the *Geometric Features* tool. We 168 calculated both metrics using circular focal windows of 0.1, 0.2, 0.3, 0.4 and 0.5 m diameter 169 centred on each point in the dataset to capture scale-dependent variation. We randomly 170 subsampled 10,000 points from each site dataset, each with a roughness and verticality 171 attribute at each scale.

We calculated mean and standard deviation of log-transformed detrended roughness for each
site at each scale to describe the average and variability in site surface structure. We calculated
Pearson's second coefficient of skewness (Pearson, 1894) to characterise distribution in
verticality values. Sites with high positive skewness in verticality had a higher proportion of

horizontal surfaces at a given scale (Figure 2). We calculated mean overall slope for each site
from mean elevation of point clouds gridded at 1 m, or 10 cm for sites with steep walls. We
tested the collinearity of structural metrics calculated across scales and removed collinear
variables using stepwise removal and a threshold variance inflation factor of 10 (Dormann et al.,
2013). The structural metrics we retained for analysis were mean and standard deviation of logtransformed detrended roughness at 0.1 and 0.5 m scales, and skewness in verticality at 0.5 m
scale (Supporting information, Table S1).

183 We estimated environmental variables of wave exposure, water temperature and salinity using 184 data from the Copernicus Marine Service. We calculated an index of wave exposure for each site 185 using the Atlantic-European North West Shelf-Wave Physics Reanalysis dataset 186 (https://doi.org/10.48670/moi-00060), to describe mean significant wave height adjusted to 187 account for local shore aspect (Supporting information, Figure S1). This wave dataset is based 188 on the WAVEWATCH III model, with a model resolution of 0.017 x 0.017 degrees, and forced by 189 ECMWF ERA-5 wind fields. We calculated a 150° onshore window of incidence angles centred 190 on the local site aspect bearing estimated using aerial imagery. We then extracted the 3-hourly 191 mean significant wave height and direction between 1980 and 2020 (Figure 1A). We set all 192 wave height values with directions outside of the 150° onshore window to zero, then calculated 193 mean significant wave height for each site. Our wave exposure index therefore represented the 194 mean significant height and occurrence of onshore waves at a site. We used the European North 195 West Shelf-Ocean Physics Analysis and Forecast dataset (https://doi.org/10.48670/moi-00054) 196 with data available from 2019 onwards to calculate mean sea surface temperature (Figure 1B) 197 and standard deviation in salinity (Figure 1C) from daily mean values, for the nearest grid cell to 198 each site over the full year of 2020. Mean sea surface temperature was expected to vary in a 199 biologically meaningful way across the study region because it includes a biogeographic 200 boundary with several intertidal reef species at, or close to, their range edge (Firth et al., 2021; 201 Forbes, 1858; Hawkins et al., 2019). Standard deviation in salinity was used rather than mean 202 salinity because low salinity pulses are a more significant stressor than constant mildly reduced

salinity (Van Diggelen and Montagna, 2016). Our environmental data had low spatial resolution
(approximately 1.5 east-west by 2 km north-south) relative to the scale of biological and
structural observations (< 100 m of shoreline), so to avoid incorporating false precision we
discretised environmental variables based on natural breaks in their ordered sequences (Figure
1, Supporting information Figure S2). Artificial and natural sites had approximately balanced
environmental conditions due to our loosely paired site design (Supporting information Table
S2).

210 2.2 Data analysis

211 We converted SACFOR data to ordinal scores for statistical analysis following Strong and 212 Johnson (2020), enabling us to combine density and cover estimates from taxa with different 213 body sizes and lifeforms. Our data showed a mean-variance relationship in the density scores of 214 rarer taxa. As this can be problematic for distance-based multivariate analysis, we removed 215 seven rare taxa to reduce the effect (Warton et al., 2012). The removed taxa occurred in five or 216 fewer sites and had mean ordinal score of less than 0.6 across all sites. They included four taxa 217 that were only present at natural sites (Supporting information table S3) and the non-native 218 species Sargassum muticum. The remaining taxa included in analysis were all present at both 219 natural and artificial sites.

220 We used a permutation test to examine the effect of habitat (artificial or natural) on median 221 taxonomic richness, with 99999 permutations of habitat labels among sites and an alpha level of 222 0.05. Permutation tests are non-parametric and have few assumptions, generating the null 223 distribution by permuting observations over different arrangements (Berry et al., 2011). We 224 then calculated a Bray-Curtis dissimilarity matrix of sites and visualised the multivariate 225 assemblage data using a non-metric multidimensional scaling plot. This enabled us to explore 226 overall dissimilarity in assemblage composition among sites and whether artificial and natural 227 sites clustered together. We tested for an effect of habitat (artificial or natural) on group 228 centroid and dispersion using the *adonis2* and *betadisper* functions from the *vegan* package

229 implemented in R (Oksanen et al., 2020; R Core Team, 2023), with 9999 permutations under a 230 reduced model. We used the *simper* function to identify taxa that were the highest contributors 231 to between-habitat variation using similarity percentage analysis (SIMPER, Clarke, 1993). To 232 explore the ways in which assemblages on artificial and natural sites differed we categorised 233 taxa into functional groups based on authors' knowledge, literature and the Biological Traits 234 Information Database (BIOTIC, https://www.marlin.ac.uk/biotic/) (Supporting information 235 Table S3), and plotted sites' median density scores for each group and habitat. Each functional 236 group data point represented the median of one to several numeric density scores, so it was 237 inappropriate to analyse these data statistically. Instead, we visually interpreted patterns in 238 functional group densities. We evaluated whether artificial and natural habitats differed in median structural variables using a permutation test with 99999 permutations and an alpha of 239 240 0.05.

241 To explore the relative influence of environmental and structural variables in explaining 242 variation in biotic assemblages we used canonical correspondence analysis (ter Braak, 1986). 243 The results of canonical correspondence analysis can be presented in ordination plots 244 displaying sites, taxa, and variables. The relative positions of points, representing sites, species 245 and discrete variables, and vectors, representing direction and importance of continuous 246 variables, can be interpreted to understand closeness of associations (ter Braak and 247 Verdonschot, 1995). To examine the potential influence of environmental and structural 248 variables on assemblage composition independently of the established strong influence of 249 habitat (artificial or natural), we used partial canonical correspondence analysis. We included 250 environmental variables and forward-selected uncorrelated structural metrics as predictor 251 variables, and habitat (artificial or natural) as a conditional variable, using the package vegan. 252 To examine the amount of variation in biotic assemblages that was explained independently by 253 structural metrics we then performed partial canonical correspondence analysis with habitat 254 and environmental variables as conditional variables. We evaluated the statistical significance

- of each model using permutation tests, with 9999 permutations under a reduced model to reach
- a stable solution.

257 **3. Results**

We recorded 41 taxa across our 32 artificial and natural sites, reduced to 34 taxa after removing rare taxa (Supporting information Table S3). Permutation tests showed that taxonomic richness was higher in natural habitats (median 27, interquartile range 25.5 – 28) compared to artificial habitats (median 20, interquartile range 19 – 23) (*P* = 0.001, Figure 3).

262 A non-metric multidimensional scaling plot of assemblage data from all sites showed that 263 natural and artificial sites clustered separately (Figure 4). Artificial sites were more variable 264 than natural sites and showed some clustering of structure types (Figure 4). Statistical tests 265 showed that group centroids and dispersion of artificial and natural sites both differed 266 significantly (Table 1). SIMPER tests indicated that the 12 taxa with the highest contribution to 267 between-habitat differences were found in higher density on natural sites (Table 2). Only five 268 taxa had higher density in artificial habitats, including the non-native species Austrominius 269 modestus. The only other non-native species we recorded was Sargassum muticum, which was 270 not included in multivariate analysis due to its rarity in our dataset, only being found at two 271 natural sites with "rare" density on the SACFOR scale.

Qualitatively, assemblages found on artificial and natural sites differed in the density of
functional groups (Figure 5). Density of all functional groups was higher on natural shores, but
particularly so for understory algae and grazers. More artificial sites had median scores of zero
compared to natural sites for all categories.

Tests to explore whether habitats differed systematically in their physical structure showed that
artificial sites had lower mean log-transformed detrended roughness at 0.1 m scale and lower
skewness in verticality at 0.5 m scale (P < 0.05). There was no significant difference in mean
roughness at 0.5 m scale or standard deviation in roughness at 0.1 m or 0.5 m scale.

Partial canonical correspondence analysis showed that the environmental variables of wave
exposure, mean sea surface temperature and standard deviation in salinity, and the structural

282 metrics of standard deviation in log-transformed detrended roughness and skewness in 283 verticality, both at 0.5 m scale, together explained 40% of the variation in assemblage 284 composition (overall P = 0.001, for each term P < 0.05). Habitat independently explained 6.4% 285 of assemblage variation and 53.6% remained unexplained. Partial canonical correspondence 286 analysis with habitat and environmental variables as conditional variables showed that the two 287 structural metrics independently explained 14.5% of assemblage variation (P = 0.001). 288 We interpreted the potential influence of local and regional environmental variables on

289 assemblages from a canonical correspondence biplot (Figure 6). The biplot indicated that wave 290 exposure and mean sea surface temperature were associated with assemblage variation along 291 an axis approximately perpendicular to that of the influence of salinity variation and the 292 opposing influences of the two structural metrics: standard deviation in log-transformed 293 detrended roughness, and skewness in verticality (Figure 6). Higher variation in salinity 294 correlated with higher skewness in verticality, and the medium and high mean sea surface 295 temperature categories were more closely associated to each other than to the low category 296 (Figure 6). The algae Ascophyllum nodosum and its common epiphyte Vertebrata lanosa were 297 strongly associated with high skewness in verticality, indicating association with a high 298 proportion of horizontal surfaces, low standard deviation in roughness and high standard 299 deviation in salinity. The macroalgae Fucus serratus and Fucus vesiculosus, and the gastropod 300 Littorina obtusata were less strongly associated with these variables. The sponge Halichondria 301 panicea and the red alga Palmaria palmata were associated with high standard deviation in 302 roughness and low skewness in verticality. The gastropods Patella depressa, Patella 303 ulyssiponensis and the red alga Mastocarpus stellatus were associated with high wave exposure, while *P. ulyssiponensis, M. stellatus, Sabellaria alveolata* and *Corallina* spp. were the taxa most
strongly associated with high mean sea surface temperature.

306 **4.** Discussion

307 We investigated the potential influence of quantified local habitat structure and regional 308 environmental gradients on natural and artificial intertidal reef assemblage at a novel scale 309 relevant to both ecological processes and ecosystem management. Our results show that 310 assemblages found on artificial hard substrates are depauperate and more variable compared to 311 those found on natural rocky shores, contributing information at a novel scale to a body of 312 existing work mostly conducted at more local scales. We found that artificial sites hosted 313 assemblages with lower taxonomic richness that were different at both taxon and functional 314 group level compared to natural sites, with more within-habitat variation. The physical 315 structure of artificial and natural habitats also differed, with artificial sites having lower 316 roughness and a higher proportion of vertical as opposed to horizontal surfaces. After removing 317 the overall effect of a site being artificial or natural, the structural metrics of skewness in 318 verticality and standard deviation in detrended roughness emerged as important potential 319 drivers of assemblage composition, along with the environmental variables of wave exposure, 320 water temperature and variation in salinity. The fact that an association between physical 321 habitat structure and intertidal reef assemblages was observable even within the context of 322 regional-scale variation in environmental conditions highlights potential importance of habitat 323 structure in shaping assemblages. Our findings provide further insight into the ecology of 324 temperate intertidal reef systems and will inform decision making for coastal ecosystem 325 management and eco-engineering.

326 4.1 Habitat was strongly associated with assemblage variation

The assemblage variation we identified between artificial and natural sites is likely due to
differences in the physical structure of these habitats rather than systematic differences in their
environmental settings. Lower taxonomic richness on artificial structures compared to natural

330 habitats has been observed across a range of structure types including sea walls, groynes and 331 breakwaters (Chapman, 2003; Firth et al., 2013; Gacia et al., 2007; Moschella et al., 2005). The 332 mechanisms proposed to drive this pattern have included a lack of physical structural 333 complexity on artificial structures providing a smaller range of niches compared to natural 334 rocky reefs (Aguilera et al., 2014; Moschella et al., 2005), and artificial infrastructure 335 experiencing different stressors and disturbance regimes (Bulleri and Chapman, 2010; 336 Moschella et al., 2005). In pairing artificial and natural sites in their environmental settings we 337 attempted to control for differences in environmental variables, so that artificial and natural 338 sites differed only in certain physical structural characteristics. The more variable physical 339 structure of our artificial sites, comprising rock armour, dolos and sea walls, contributed to 340 more variable biotic assemblages found on these sites compared to the natural rocky shores. 341 Our results support previous work showing higher abundances in natural compared to artificial 342 hard substrate habitats (for reviews see: Bulleri and Chapman, 2010; Moschella et al., 2005). 343 Both canopy and understory algae were notably lower in density on artificial shores in our 344 study. On Mediterranean coasts, lower abundance and growth of the canopy algae Cystoseira 345 spp. on artificial structures compared to natural rocky shores was attributed to differences in 346 biotic pressures of herbivory and non-consumptive disturbance by fish and crabs (Ferrario et 347 al., 2016). Canopy algae are important mediators of local environmental conditions experienced 348 by intertidal organisms such as thermal fluctuations, light and hydrodynamic forces. They also 349 provide physical refuge for small prey organisms, substrate for epibiota, and forage for grazers. 350 As such, the presence of canopy algae facilitates the development of diverse assemblages on

hard substrates (Jenkins et al., 1999).

Differences in densities of specific taxa that we observed support previous findings from the
same region. We found low density of "Lithothamnia", a collective term for unidentified
encrusting red algae (Hawkins and Hartnoll, 1985) and *Corallina* spp. in artificial habitats, and a
high density of the green algae *Ulva* spp. Similarly, Evans et al. (2016) found no Lithothamnia or

356 Corallina spp. and high abundance of Ulva spp. in artificial rock pools built into a breakwater, 357 compared to natural rockpools in Wales. *Ulva* spp. are fast growing, opportunistic species that 358 readily colonise bare substrate, while Lithothamnia and Corallina spp. are slow growing, 359 suggesting that artificial habitats may be regularly disturbed (Moschella et al., 2005). *Ulva* spp. 360 can also be an indicator of poor water quality (Pinedo et al., 2007), suggesting that artificial 361 sites, typically located near urban areas or centres of anthropogenic activity, may be subject to 362 higher levels of pollution than natural rocky shores (Bugnot et al., 2020; Komyakova et al., 363 2022). Several of the taxa we found with higher density in natural sites are associated with rock 364 pools, including *Corallina* spp. and *Chondrus crispus*. This indicates that water retaining features 365 were lacking in the artificial habitats that we sampled, an important category of features for 366 enhancing intertidal hard substrate biodiversity (Evans et al., 2016; Firth et al., 2013; Strain et 367 al., 2018).

368 4.2 Environmental variables explained most variation in assemblages

369 Wave exposure has been the subject of decades of observation and experimentation and is 370 widely accepted as a major driver of rocky reef assemblage composition (Denny et al., 2004; 371 Jenkins et al., 2008; Lewis, 1968). Although water temperature and salinity are also known to 372 influence intertidal assemblages, wave exposure emerged as a more important variable, 373 perhaps because it had a greater range in magnitude among sites. The ranges in temperature 374 and salinity may have been relatively less biologically significant than wave exposure, showing a 375 weaker signal in assemblage structure across the scale investigated among other drivers of 376 variation.

377 4.3 Roughness and verticality were potentially influential structural metrics

The use of contemporary 3D ecosystem mapping technology enabled us to quantify metrics of physical structure at ecologically relevant resolution and extent. Given that there is no generally accepted, single metric to characterise the physical structure or complexity of a habitat, multiple metrics founded in ecological theory should be used (Loke and Chisholm, 2022). Here we found 382 that the metrics of skewness in surface verticality and standard deviation in log-transformed 383 detrended roughness had the strongest association with assemblage variation. Skewness in 384 verticality described the relative proportions of vertical and horizontal surfaces in the habitat 385 and was lower at artificial sites than at natural sites, indicating a higher proportion of vertical 386 surfaces at artificial sites. Surface orientation is known to influence assemblage variation 387 (Benedetti-Cecchi et al., 2001; Vaselli et al., 2008). Organisms on vertical surfaces facing the sea 388 could be expected to experience higher stresses from wave action, although local topography 389 mediates these forces in unpredictable ways (Helmuth and Denny, 2003). On intertidal reefs 390 during low tides, moisture is retained for longer in depressions on horizontal surfaces, 391 supporting diverse assemblages (Firth et al., 2013). While we did not directly measure water 392 retention, it is likely that more water retaining features were present at sites with a high 393 proportion of locally horizontal surfaces, promoting their biodiversity compared to more 394 vertical sites.

395 In intertidal reef habitats surface complexity has been proposed to influence assemblages by 396 modifying substrate and refuge space, environmental conditions like thermal landscape and 397 hydrodynamic forces, and biological processes like recruitment, predation and competition 398 (Chiba and Noda, 2000; Johnson et al., 2003, 1998; Meager et al., 2011; Menge et al., 1985). 399 Several studies have reported positive effects of increased structural complexity on intertidal 400 reef biodiversity, but technological limitations have constrained methods, most notably limiting 401 the scales investigated or necessitating the use of human-centric qualitative site categorisation 402 (Garza, 2019). Such limitations call into question the relevance of scaling findings from highly 403 controlled studies with limited environmental variation to real-world observational contexts 404 that feature regional-scale variation in multiple variables. Until recently, robust quantification of 405 physical structure at organism-centric resolution and across whole shores was not 406 technologically feasible. In the last decade, however, close range remote sensing technologies 407 with the capacity for quantifying detailed habitat structure have become practical for use in 408 intertidal mapping (D'Urban Jackson et al., 2020; Lawrence et al., 2021). This capability is

important in ecology because conclusions about the ecological effects of a variable can be
different, improved or explored in novel ways when the variable is robustly quantified
compared to using qualitative categories (Lindegarth and Gamfeldt, 2005).

412 4.4 Taxon associations with structural metrics and management implications

413 Ascophyllum nodosum and two Fucus species were associated with shores with a higher 414 proportion of horizontal surfaces. Indeed, these species were less common in artificial habitats 415 than in natural habitats, reflecting the lower proportion of horizontal surfaces in artificial 416 shores compared to natural shores. Two other species with similar environmental associations 417 identified in our results, the epiphytic alga Vertebrata lanosa and the gastropod Littorina 418 obtusata are known to be strongly associated with fucoid macroalgae. This indicates that 419 physical shore structure, specifically a high proportion of intertidal horizontal surfaces, can 420 encourage colonisation by habitat forming species that then facilitate the development of 421 diverse associated assemblages. Other taxa that we found were associated with more vertical 422 surfaces included species that prefer shady, damp areas like Halichondria panicea. This 423 highlights that a higher proportion of vertical surfaces does not necessarily mean featureless 424 walls, but includes sites with large boulders featuring overhangs that can provide important 425 microhabitats not found on more horizontal shores (Liversage and Chapman, 2018).

426 Metrics of physical structure emerged as key potential drivers of assemblage variation that 427 could be targeted for eco-engineering intervention and design. Indeed, evidence that structural 428 modifications can promote biodiversity at a local scale have led to a range of imaginative design 429 interventions (Evans et al., 2021; O'Shaughnessy et al., 2020). But quantifying structural 430 characteristics is challenging, requiring multiple metrics across a range of scales. Even then, this 431 information provides little insight into consistent mechanistic effects. Modifications to artificial 432 coastal structures can be expensive, so having confidence that they will have a desired effect at a 433 particular scale is important. At the start of this study, we considered whether structural 434 differences were likely to influence assemblages across regional gradients in environmental

435 variables. Our findings indicate that physical structure quantified at centimetre resolution 436 across hundreds of m² of a shore is a likely driver of assemblage variation across regional 437 extents. Although it was not directly tested in this study, these results give support to the idea 438 that structural eco-engineering modifications implemented across entire coastal habitats may 439 be effective in shaping intertidal biodiversity. In particular, we showed that a high proportion of 440 horizontal surfaces in the mid intertidal zone may encourage the development of diverse algal and invertebrate assemblages. In practice, the most effective interventions for increasing 441 442 biodiversity across a whole shore are likely to be those that generate high microhabitat 443 diversity. By including large extents of horizontal and rugged areas in the mid- to low-shore to 444 promote macroalgal growth, water retaining features, overhangs, and multi-scale complexity, 445 microhabitat diversity can be enhanced (Aguilera et al., 2014; Evans et al., 2021; Sebens, 1991). 446 However, cost-effective intervention planning must consider the fact that the primary function, 447 site, and environmental conditions of coastal infrastructure can constrain the intended 448 outcomes of interventions.

449 4.5 Artificial coastal structures are poor surrogates for natural rocky shores

450 Many eco-engineering interventions are based on the premise that enhanced biodiversity on 451 artificial structures can be achieved by simulating structural properties of natural rocky shores 452 (Firth et al., 2013; O'Shaughnessy et al., 2020). However, due to their fundamental structural 453 differences across scales (Lawrence et al., 2021), it may not be possible for assemblages on 454 artificial habitats to resemble those on natural shores (Bulleri and Chapman, 2010). This raises 455 the question of how to measure the ecological value of these novel habitats and determine the 456 success of eco-engineering interventions. Efficient ecosystem management needs SMART 457 (Specific, Measurable, Achievable, Realistic, and Timebound) targets (Wood, 2011). But in many 458 cases, it is not clear what the measurable targets should be for eco-engineering of coastal 459 structures. If an artificial habitat is unlikely to support an assemblage equivalent to that of a 460 natural habitat in many contexts (Perkol-Finkel et al., 2006), what can we expect its ideal 461 assemblage to look like? What level of species richness, diversity or abundance of functional

462 groups should be targeted? Perhaps, as they are novel systems, targets based on ecosystem 463 services or ecosystem functioning would be more appropriate than attempting to replicate a 464 reference natural system. For instance, on an artificial habitat seeded with bivalves, investigators found low diversity and a lack of resemblance to nearby rocky shores, but the 465 466 novel habitat provided ecosystem services of water filtration and food (Chee et al., 2021). In 467 another example, positive effects of an artificial habitat's physical and biogenic complexity on 468 biodiversity contrasted with negative effects on ecosystem functioning measured as primary 469 productivity and nutrient cycling (Mayer-Pinto et al., 2022). However, seeding experiments 470 have had limited long-term success (Perkol-Finkel et al., 2012; Strain et al., 2020), and there is a 471 risk that promoting non-natural communities will disproportionately favour colonisation by 472 non-native species, exacerbating negative impacts of marine infrastructure (Komyakova et al., 473 2022).

474 4.6 Limitations

475 The factors shaping composition of biological assemblages are notoriously complex (Simberloff, 476 2004) and there were a number of potentially influential factors that we did not investigate for 477 logistical reasons or because they were confounded with other variables. For instance, spatial 478 variation in hydrodynamic and larval connectivity may have influenced the similarity in 479 assemblages among groups of sites separated by biogeographic obstacles like peninsulas and 480 oceanic fronts (Prentice et al., 2022; Robins et al., 2013). Other potentially influential variables 481 include time since construction, maintenance or cleaning of artificial structures, and 482 anthropogenic factors like pollution and physical disturbance.

We targeted the mid-shore based on the distribution of shore zone indicator taxa like *Fucus vesiculosus*. While this approach is logical and practical in rocky shore ecology (Lewis, 1961),
the taxa recorded indicated that the surveyed zone included some areas that could be
considered high or low shore at some sites. Further, at some sites the upper or lower limits of
the surveyed area were constrained by the vertical limit of hard substrate, for example, where

an artificial structure or rocky habitat abutted sediment at its lower extent. For these reasons
the tidal range of the surveyed area at each site likely differed, adding variation to the results as
assemblages change with both vertical and horizontal position in the intertidal zone (BenedettiCecchi, 2001; Chappuis et al., 2014; Valdivia et al., 2011). In addition, variation in the overall
slope of sites produces variation in the planar area of the mid-shore zone, potentially leading to
unquantified taxa-area effects, whereby available space constrains taxonomic richness.

494 Because our digital surface data represented the whole shore without any clearing of organisms, 495 biotic cover may have influenced structural metrics in places, in particular roughness at finer 496 scales. For instance, in digital representations, barnacles can add roughness to smooth rock at 497 millimetre scales, dense patches of Ascophyllum nodosum have high roughness at centimetre 498 scales, and reef building Sabellaria alveolata colonies can have similar physical structure to 499 boulders at decimetre scales. This could lead to false associations between habitat roughness 500 and organism density but could not be avoided at the scale of our study. While quadrat-sized 501 patches of shores can be cleared to quantify underlying substrate topography (Lawrence et al., 502 2021), clearing epibiota from hundreds of m^2 at several sites would be needed to investigate 503 structural metrics across scales, which is not practical or responsible for an observational 504 ecological study. Finally, while the use of semi-quantitative density scales like the SACFOR scale 505 has advantages for efficiency of data collection, it also means that the scope of numerical 506 analysis is constrained (Legendre and Legendre, 2012; Strong and Johnson, 2020), such that we 507 intentionally limited our statistical analysis to avoid overleveraging our data.

508 4.7 Conclusions

We demonstrate that physical structure quantified at organism-centric resolution likely shapes
biotic assemblage composition in natural and artificial temperate reef habitats across regional
scales relevant to ecosystem management. Despite broad variability in environmental
conditions and inherent differences between artificial and natural habitats, we detected a
potential influence of physical habitat structure on assemblage composition in an observational

- 514 context. Our findings provide evidence to support scaling-up of structural eco-engineering
- 515 interventions from spatially limited experiments to meet ecological targets over broad
- 516 geographical extents.

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530

- 531 Competing interests
- 532 The authors declare that we have no competing interests.
- 533

534 Data availability

- All data and code to support this manuscript are available at the following figshare repository:
- 536 <u>https://doi.org/10.6084/m9.figshare.23959089.v1</u>

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Figure 1. Intertidal study sites along the coastline of Wales, UK at 16 natural and 16 artificial
reefs, with three environmental variables. Black lines from symbols indicate precise site
locations and are identical in all three panels. A) Mean significant wave height (40 year) was
combined with local shore orientation to calculate a wave exposure index, transformed into two
discrete categories. B) Mean sea surface temperature (1 year), transformed into three discrete
categories. C) Standard deviation in salinity (1 year), transformed into two discrete categories.



Figure 2. Metrics characterising the physical structure of artificial and natural intertidal reefs
were calculated for each 3D data point at multiple scales. In this example, 3D point clouds of an
artificial (rock armour) and a natural reef at Barry are displayed with points coloured by
detrended roughness and verticality metrics at 0.5 m scale. Frequency histograms of point
values are shown to highlight differences in the distributions of metric values among habitats.



Figure 3. Boxplot and point data showing taxonomic richness (S) at artificial and natural reefs (n
= 16 per habitat). Median taxonomic richness (bold black bar) was higher in natural habitats (*P*= 0.001).







852 multivariate t-distribution to guide visual interpretation.





Figure 5. Violin and dot plot of median ordinal density scores of functional groups recorded in
artificial (light shade) and natural (dark shade) habitats. Each dot represents the median
ordinal score for a site, such that n = 16 for each functional group in each habitat. The mobile
predator and sessile scavenger categories were each represented by a single species
(Supporting information Table S3).



862 Figure 6. Canonical correspondence analysis biplot of a model with environmental variables and 863 forward selection of structural metrics, removing the effect of habitat (artificial or natural) by 864 including it as a conditional variable. Taxa are dark grey points; discrete variable centroids are 865 red points, and blue arrows indicate the magnitude of association and direction of increase of 866 continuous variables. Continuous variable vectors have been scaled to 50% for readability. 867 Ordinations can be interpreted by the relative positions of points and vectors, with proximity 868 indicating close association. For example, Ascophyllum nodosum was found in higher density at 869 sites with high standard deviation in salinity and high skewness in verticality. Austrominius 870 *modestus* is a non-native species.

Table 1. Permutational multivariate analysis of variance testing for an effect of habitat (artificial or

natural) on assemblage centroid (adonis2) and dispersion (betadisper).
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	df	SS	F	Р
adonis2				
Habitat	1	0.24	4.05	0.002
Residual	30	1.80		
Total	31	2.04		
betadisper				
Habitat	1	0.03	8.88	0.005
Residuals	30	0.10		

Abbreviations: df, degrees of freedom; SS, sum of squares

Table 2. Results from SIMPER analysis showing the individual and cumulative contribution of each taxon to dissimilarity between habitats (artificial or natural). Median abundance scores are shown along with the difference in scores between natural and artificial sites.

Tarran	Median abundance score			Contribution	
Taxon	Artificial	Natural	Difference	Individual	Cumulative
Lithothamnia*	0	5	5	0.047	0.047
Catenella caespitosa	0	4	4	0.043	0.090
Melarhaphe neritoides	1.5	5	3.5	0.042	0.132
Fucus serratus	1.5	4	2.5	0.041	0.173
Fucus vesiculosus	4	5	1	0.040	0.213
Ascophyllum nodosum	0	1.5	1.5	0.040	0.253
Pelvetia canaliculata	1.5	4	2.5	0.040	0.292
Hymeniacidon perlevis	4	5	1	0.036	0.328
Steromphala umbilicalis	2	5	3	0.036	0.364
Corallina spp.	0	4	4	0.035	0.399
Chthamalus montagui	5	5.5	0.5	0.033	0.432
Littorina obtusata	0	4	4	0.032	0.465
Vertebrata lanosa	0	0	0	0.031	0.496
Chthamalus stellatus	4	4	0	0.031	0.526
Fucus spiralis	5	4.5	-0.5	0.030	0.557
Sabellaria alveolata	0	0	0	0.030	0.587
Austrominius modestus †	6	5.5	-0.5	0.030	0.617
Patella ulyssiponensis	0	3	3	0.030	0.647
Phorcus lineatus	0	3.5	3.5	0.029	0.676

Chondrus crispus	3	4	1	0.029	0.705
Rhodothamniella floridula	0	0	0	0.028	0.733
Porphyra spp.	3.5	3	-0.5	0.028	0.761
Patella depressa	0	2	2	0.027	0.788
<i>Mytilus</i> spp.	4	3	-1	0.026	0.814
Littorina littorea	3.5	5	1.5	0.022	0.837
Halichondria panicea	0	0	0	0.022	0.858
Mastocarpus stellatus	0	0	0	0.021	0.880
Littorina saxatilis	4	5	1	0.021	0.900
Semibalanus balanoides	6	6	0	0.020	0.920
Ulva spp.	5	4	-1	0.019	0.940
Nucella lapillus	4	4	0	0.019	0.959
Palmaria palmata	0	0	0	0.018	0.977
Actinia equina	2.5	3	0.5	0.017	0.994
Patella vulgata	5	5	0	0.006	1.000

* Unidentified encrusting red algae. † Non-native species

881 Supporting information



882

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Figure S1. Wave exposure index incorporating significant wave height and onshore wave
occurrence using 40 year hindcast data (https://doi.org/10.48670/moi-00060) and local site
aspect. In this example, two sites at Nefyn use data from the same grid cell of the hindcast
dataset, summarised here by a wave rose diagram. In the wave rose significant wave height is
shown in graduated blue categories, direction is shown in 16 polar bins and frequency of

889 occurrence is shown by the length of directional sectors as percentage. In this example, the 890 distribution of significant wave heights is similar from all directions, but waves mostly arrive 891 from the southwest. Because local site aspect differs (red arrow bearings), different windows of 892 onshore angles are calculated (unshaded sectors on wave rose diagrams) to adjust the model 893 data. All wave heights with directions outside of the 150° onshore windows are set to zero (grey 894 sectors on wave rose diagrams), before calculating mean significant wave height. The resulting 895 wave exposure index is lower at the artificial site because the local aspect faces away from the 896 prevailing waves.



916 **Figure S2.** Environmental variables of A) wave exposure index, B) mean sea surface

917 temperature and C) standard deviation in salinity discretised by ordering sites by each variable

918 and finding natural breaks.

Table S1. See attached file Supporting_information_table_S1.xlsx

Table S2. Number of sites in each habitat - environmental category combination. Artificial and
922 natural sites were approximately balanced in their environmental characteristics due to our
923 loosely paired site design.

	Wave exposure		SST mean			Salinity variation	
	Low	High	Low	Medium	High	Low	High
Artificial	9	7	7	5	4	12	4
Natural	11	5	8	4	4	14	2

927 **Table S3.** Taxa and assigned functional groups, including rare taxa removed before analysis.

Taxon

Functional group Reference(s)

Ascophyllum nodosum	Canopy algae	BIOTIC
Fucus serratus	Canopy algae	BIOTIC
Fucus spiralis	Canopy algae	BIOTIC
Fucus vesiculosus	Canopy algae	BIOTIC
Pelvetia canaliculata	Canopy algae	BIOTIC
Catenella caespitosa	Understory algae	MarLIN
Chondrus crispus	Understory algae	BIOTIC
Corallina spp.	Understory algae	BIOTIC
"Lithothamnia"*‡	Understory algae	
Mastocarpus stellatus	Understory algae	MarLIN
Palmaria palmata	Understory algae	BIOTIC
Porphyra spp.	Understory algae	MarLIN
Rhodothamniella floridula	Understory algae	BIOTIC
Ulva spp.	Understory algae	BIOTIC
Vertebrata lanosa	Understory algae	MarLIN
Littorina littorea	Grazer	BIOTIC
Littorina obtusata	Grazer	(Watson and Norton, 1987)
Littorina saxatilis	Grazer	(Otero-Schmitt et al., 2012)
Melarhaphe neritoides	Grazer	(Laurand and Riera, 2006)
Patella depressa	Grazer	(Hawkins et al., 1989)
Patella ulyssiponensis	Grazer	BIOTIC
Patella vulgata	Grazer	(BIOTIC, Hawkins et al., 1989)
Phorcus lineatus	Grazer	MarLIN
Steromphala umbilicalis	Grazer	(Hawkins et al., 1989)
Austrominius modestus†	Suspension feeder	(Rainbow, 1984)
Chthamalus montagui	Suspension feeder	(Rainbow, 1984)
Chthamalus stellatus	Suspension feeder	(Rainbow, 1984)
Halichondria panicea	Suspension feeder	BIOTIC
Hymeniacidon perlevis	Suspension feeder	(Hayward and Ryland, 2017)
<i>Mytilus</i> spp.	Suspension feeder	BIOTIC
Sabellaria alveolata	Suspension feeder	BIOTIC
Semibalanus balanoides	Suspension feeder	(Rainbow, 1984)
Nucella lapillus	Mobile predator	BIOTIC
Actinia equina	Sessile scavenger	(Davenport et al., 2011)

Rare taxa removed		
Lichina pygmaea*	Lichen	MarLIN
Laminaria digitata	Canopy algae	BIOTIC
Sargassum muticum*†	Canopy algae - INNS	MarLIN
Halidrys siliquosa*	Canopy algae	BIOTIC
Steromphala cineraria	Grazer	Hawkins et al 1989
Anemonia viridis*	Sessile predator	(Chintiroglou and Koukouras, 1992)
Perforatus perforatus	Suspension feeder	(Rainbow, 1984)

* Taxon only present in natural reefs

† Non-native species

‡ Unidentified encrusting red algae.

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