Habitat structure shapes temperate reef assemblages across regional environmental gradients

Jackson-Bue, Tim; Evans, Ally J; Lawrence, Peter; Brooks, Paul; Ward, Sophie; Jenkins, Stuart; Moore, Pippa J.; Crowe, Tasman; Neill, Simon; Davies, Andrew

Science of the Total Environment

Published: 01/01/2024

Peer reviewed version

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Jackson-Bue, T., Evans, A. J., Lawrence, P., Brooks, P., Ward, S., Jenkins, S., Moore, P. J., Crowe, T., Neill, S., & Davies, A. (2024). Habitat structure shapes temperate reef assemblages across regional environmental gradients. *Science of the Total Environment*, Article 167494. https://www.sciencedirect.com/science/article/pii/S0048969723061211

Habitat structure shapes temperate reef assemblages across regional environmental gradients

Tim Jackson-Bué*[1], Ally J. Evans[2], Peter J. Lawrence[3], Paul R. Brooks[4], Sophie L. Ward[1], Stuart R. Jenkins[1], Pippa J. Moore[2,5], Tasman P. Crowe[4], Simon P. Neill[1], Andrew J. Davies[6,7]

* Corresponding author. Email: t.d.jackson@bangor.ac.uk

[1] School of Ocean Sciences, Bangor University, Askew St, Menai Bridge, LL59 5AB, UK

[2] Department of Life Sciences, Aberystwyth University, Aberystwyth SY23 3DA, UK

[3] Institute of Science and Environment, University of Cumbria, Ambleside LA22 9BB, UK

[4] Earth Institute and School of Biology and Environmental Science, University College Dublin, Dublin, Ireland

[5] Dove Marine Laboratory, School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, NE1 7RU, UK

[6] University of Rhode Island, Department of Biological Sciences, 120 Flagg Road, Kingston, RI 02881, USA

[7] University of Rhode Island, Graduate School of Oceanography, Narragansett, RI, 02882, USA

ORCID IDs:

TJB: 0000-0001-7077-2186

AJE: 0000-0003-4039-1467

PJL: 0000-0002-9809-0221

PRB: 0000-0002-8105-0813

SLW: 0000-0001-5146-9325

SRJ: 0000-0002-2299-6318

PJM: 0000-0002-9889-2216

TPC: 0000-0001-9583-542X

SPN: 0000-0002-1674-3445

AJD: 0000-0002-2087-0885

Abstract

Intertidal artificial habitats are proliferating, but are generally simpler in structure and host lower biodiversity than natural rocky reefs. Eco-engineering aims to enhance the biodiversity of coastal infrastructure, often through physical structural modifications that mimic topographic properties of natural shores. Relationships between biotic assemblages and structural properties of natural and artificial reefs have been extensively studied at sampling scales of up to 1 m^2. But evidence that quantified local structural variation has an appreciable influence on biotic assemblages, at a shore-wide scale across regional environmental gradients, is lacking. Here we addressed this knowledge gap with an observational study at 32 natural and artificial intertidal reef sites in Wales, UK. We used multivariate community analysis and permutation tests to examine associations between local physical structure, regional environmental variables and sessile biotic assemblages. A potential influence of local habitat structure on assemblage composition was evident across regional-scale environmental gradients. Compared to natural sites, artificial reefs had lower taxonomic richness, distinct and more variable assemblage composition, and different physical structure. After removing the effect of habitat (natural or artificial), canonical correspondence analysis showed that environmental variables (wave exposure, sea surface temperature and salinity variation), along with two metrics of physical structure (standard deviation in log-transformed detrended roughness and skewness of surface verticality, both at 0.5 m scale), explained 40% of the variation in assemblage composition among sites. The two structural metrics independently explained 14.5% of the variation. Associations identified between individual taxa and environmental variables indicated that sites with a higher proportion of horizontal surfaces hosted more canopy macroalgae, which in turn support other algae and invertebrates. Our findings provide evidence to inform scaling-up of structural eco-engineering interventions from experimental contexts to enhance the biodiversity of coastal infrastructure across regional extents.

Keywords:

Littoral, rocky shore, eco-engineering, habitat complexity, topography, terrestrial laser scanning.

1. Introduction

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

Many studies have shown an effect of physical habitat structure on assemblages in intertidal reefs, defined as any intertidal hard-substrate habitat (Firth et al., 2013; Harley, 2008; Knott et al., 2004). For example, on natural rocky shores, several studies have shown that surface complexity measured in various ways is positively correlated with species richness (Kohn and Leviten, 1976; Kostylev et al., 2005; Menge et al., 1985). Other studies have shown mixed results. For example, Beck (2000) found that the effect of complexity on gastropod species richness varied with measurement method, time and site, and Meager and Schlacher (2013) found a relationship only when a novel metric of complexity was used. In artificial reef habitats similar variability has been found. Using small concrete panels, Loke and Todd (2016) found a positive effect of habitat complexity on species richness, while Strain et al. (2021) reported 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 using quadrats or panels of up to 1 m^2, and controlling for external environmental variation. But structure influences ecological interactions across a range of scales that may be specific to species, functional groups or life stages. Across broader spatial scales of 100 m to 100 km in eastern Canada, Archambault and Bourget (1996) found no statistical relationship between categorised surface heterogeneity and sessile species richness. Across 20° of latitude in Australia, Bracewell et al. (2018) found positive effects of increased settlement panel complexity on biodiversity only at higher latitudes. Such variable results pose difficulties for leveraging habitat structure in environmental management applications (Evans et al., 2021).

As human demands on coastal regions intensify, hard artificial coastal infrastructure is proliferating, with environmental impacts like habitat loss, pollution and increased risk of invasive species (Bugnot et al., 2020; Heery et al., 2017; Komyakova et al., 2022). There is increasing demand for mitigation of the negative impacts of intertidal infrastructure with biodiversity-enhancing modifications, which has been widely termed eco-engineering (Evans et al., 2017). Eco-engineering interventions to structure design, construction methods or retrofitting features such as pits, grooves, pools and complex tiles have shown positive effects on biodiversity at local scales in certain contexts (Chapman and Underwood, 2011; Evans et al., 2021; Strain et al., 2018). But to be implementable and effective, eco-engineering interventions need to be cost-effective, scalable, and have ecological impacts measurable against defined management goals. Currently these goals are challenging to define because there is limited evidence to predict the effects of scaled-up eco-engineering interventions on intertidal 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 work has been conducted, but over regional spatial scales at which environmental managers operate, environmental gradients may mask the effects of structure. No previous studies have investigated the relationship between quantified physical structure and assemblage composition at scales relevant to both direct ecological interactions (centimetre resolution) and management units (hundreds of m^2 extent separated by kilometres) across regional environmental gradients.

Here, we address gaps in our understanding of how physical habitat structure may influence sessile intertidal assemblages in natural and artificial temperate intertidal reef habitats. Specifically, we investigate: 1) whether artificial and natural reefs host different biotic assemblages at a regional scale; 2) whether physical habitat structure quantified at centimetre resolution and hundreds of m^2 sampling extent has an observable association with reef assemblages across a region spanning more than 1000 km of coastline; and 3) how the strength of associations between assemblages and local or regional environmental variables differ. By addressing these knowledge gaps, we generate valuable information to inform scaling-up of coastal eco-engineering.

2. Methods

2.1 Data collection

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

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

$$V = 1 - N_z \qquad \text{Equation 1}$$

Where N_z is the z-axis normal vector of the local plane, such that for a horizontal plane $N_z = 1$ and for a vertical plane $N_z = 0$. We calculated verticality using the *Geometric Features* tool. We calculated both metrics using circular focal windows of 0.1, 0.2, 0.3, 0.4 and 0.5 m diameter centred on each point in the dataset to capture scale-dependent variation. We randomly subsampled 10,000 points from each site dataset, each with a roughness and verticality 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 log-transformed detrended roughness at 0.1 and 0.5 m scales, and skewness in verticality at 0.5 m scale (Supporting information, Table S1).

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

2.2 Data analysis

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

We used a permutation test to examine the effect of habitat (artificial or natural) on median taxonomic richness, with 99999 permutations of habitat labels among sites and an alpha level of 0.05. Permutation tests are non-parametric and have few assumptions, generating the null distribution by permuting observations over different arrangements (Berry et al., 2011). We then calculated a Bray-Curtis dissimilarity matrix of sites and visualised the multivariate assemblage data using a non-metric multidimensional scaling plot. This enabled us to explore overall dissimilarity in assemblage composition among sites and whether artificial and natural sites clustered together. We tested for an effect of habitat (artificial or natural) on group centroid and dispersion using the *adonis2* and *betadisper* functions from the *vegan* package implemented in R (Oksanen et al., 2020; R Core Team, 2023), with 9999 permutations under a reduced model. We used the *simper* function to identify taxa that were the highest contributors to between-habitat variation using similarity percentage analysis (SIMPER, Clarke, 1993). To explore the ways in which assemblages on artificial and natural sites differed we categorised taxa into functional groups based on authors' knowledge, literature and the Biological Traits Information Database (BIOTIC, https://www.marlin.ac.uk/biotic/) (Supporting information Table S3), and plotted sites' median density scores for each group and habitat. Each functional group data point represented the median of one to several numeric density scores, so it was inappropriate to analyse these data statistically. Instead, we visually interpreted patterns in 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 0.05.

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

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).

A non-metric multidimensional scaling plot of assemblage data from all sites showed that natural and artificial sites clustered separately (Figure 4). Artificial sites were more variable than natural sites and showed some clustering of structure types (Figure 4). Statistical tests showed that group centroids and dispersion of artificial and natural sites both differed significantly (Table 1). SIMPER tests indicated that the 12 taxa with the highest contribution to between-habitat differences were found in higher density on natural sites (Table 2). Only five taxa had higher density in artificial habitats, including the non-native species *Austrominius modestus*. The only other non-native species we recorded was *Sargassum muticum*, which was not included in multivariate analysis due to its rarity in our dataset, only being found at two 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 metrics of standard deviation in log-transformed detrended roughness and skewness in verticality, both at 0.5 m scale, together explained 40% of the variation in assemblage composition (overall $P = 0.001$, for each term $P < 0.05$). Habitat independently explained 6.4% of assemblage variation and 53.6% remained unexplained. Partial canonical correspondence analysis with habitat and environmental variables as conditional variables showed that the two structural metrics independently explained 14.5% of assemblage variation ($P = 0.001$).

We interpreted the potential influence of local and regional environmental variables on assemblages from a canonical correspondence biplot (Figure 6). The biplot indicated that wave exposure and mean sea surface temperature were associated with assemblage variation along an axis approximately perpendicular to that of the influence of salinity variation and the opposing influences of the two structural metrics: standard deviation in log-transformed detrended roughness, and skewness in verticality (Figure 6). Higher variation in salinity correlated with higher skewness in verticality, and the medium and high mean sea surface temperature categories were more closely associated to each other than to the low category (Figure 6). The algae *Ascophyllum nodosum* and its common epiphyte *Vertebrata lanosa* were strongly associated with high skewness in verticality, indicating association with a high proportion of horizontal surfaces, low standard deviation in roughness and high standard deviation in salinity. The macroalgae *Fucus serratus* and *Fucus vesiculosus*, and the gastropod *Littorina obtusata* were less strongly associated with these variables. The sponge *Halichondria panicea* and the red alga *Palmaria palmata* were associated with high standard deviation in roughness and low skewness in verticality. The gastropods *Patella depressa*, *Patella 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.

4. Discussion

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

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 habitats has been observed across a range of structure types including sea walls, groynes and breakwaters (Chapman, 2003; Firth et al., 2013; Gacia et al., 2007; Moschella et al., 2005). The mechanisms proposed to drive this pattern have included a lack of physical structural complexity on artificial structures providing a smaller range of niches compared to natural rocky reefs (Aguilera et al., 2014; Moschella et al., 2005), and artificial infrastructure experiencing different stressors and disturbance regimes (Bulleri and Chapman, 2010; Moschella et al., 2005). In pairing artificial and natural sites in their environmental settings we attempted to control for differences in environmental variables, so that artificial and natural sites differed only in certain physical structural characteristics. The more variable physical structure of our artificial sites, comprising rock armour, dolos and sea walls, contributed to more variable biotic assemblages found on these sites compared to the natural rocky shores.

Our results support previous work showing higher abundances in natural compared to artificial hard substrate habitats (for reviews see: Bulleri and Chapman, 2010; Moschella et al., 2005). Both canopy and understory algae were notably lower in density on artificial shores in our study. On Mediterranean coasts, lower abundance and growth of the canopy algae *Cystoseira* spp. on artificial structures compared to natural rocky shores was attributed to differences in biotic pressures of herbivory and non-consumptive disturbance by fish and crabs (Ferrario et al., 2016). Canopy algae are important mediators of local environmental conditions experienced by intertidal organisms such as thermal fluctuations, light and hydrodynamic forces. They also provide physical refuge for small prey organisms, substrate for epibiota, and forage for grazers. 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

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

4.2 Environmental variables explained most variation in assemblages

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

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 that the metrics of skewness in surface verticality and standard deviation in log-transformed detrended roughness had the strongest association with assemblage variation. Skewness in verticality described the relative proportions of vertical and horizontal surfaces in the habitat and was lower at artificial sites than at natural sites, indicating a higher proportion of vertical surfaces at artificial sites. Surface orientation is known to influence assemblage variation (Benedetti-Cecchi et al., 2001; Vaselli et al., 2008). Organisms on vertical surfaces facing the sea could be expected to experience higher stresses from wave action, although local topography mediates these forces in unpredictable ways (Helmuth and Denny, 2003). On intertidal reefs during low tides, moisture is retained for longer in depressions on horizontal surfaces, supporting diverse assemblages (Firth et al., 2013). While we did not directly measure water retention, it is likely that more water retaining features were present at sites with a high proportion of locally horizontal surfaces, promoting their biodiversity compared to more vertical sites.

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

4.4 Taxon associations with structural metrics and management implications

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

Metrics of physical structure emerged as key potential drivers of assemblage variation that could be targeted for eco-engineering intervention and design. Indeed, evidence that structural modifications can promote biodiversity at a local scale have led to a range of imaginative design interventions (Evans et al., 2021; O’Shaughnessy et al., 2020). But quantifying structural characteristics is challenging, requiring multiple metrics across a range of scales. Even then, this information provides little insight into consistent mechanistic effects. Modifications to artificial coastal structures can be expensive, so having confidence that they will have a desired effect at a particular scale is important. At the start of this study, we considered whether structural differences were likely to influence assemblages across regional gradients in environmental variables. Our findings indicate that physical structure quantified at centimetre resolution across hundreds of m^2 of a shore is a likely driver of assemblage variation across regional extents. Although it was not directly tested in this study, these results give support to the idea that structural eco-engineering modifications implemented across entire coastal habitats may be effective in shaping intertidal biodiversity. In particular, we showed that a high proportion of 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 biodiversity across a whole shore are likely to be those that generate high microhabitat diversity. By including large extents of horizontal and rugged areas in the mid- to low-shore to promote macroalgal growth, water retaining features, overhangs, and multi-scale complexity, microhabitat diversity can be enhanced (Aguilera et al., 2014; Evans et al., 2021; Sebens, 1991). However, cost-effective intervention planning must consider the fact that the primary function, site, and environmental conditions of coastal infrastructure can constrain the intended outcomes of interventions.

4.5 Artificial coastal structures are poor surrogates for natural rocky shores

Many eco-engineering interventions are based on the premise that enhanced biodiversity on artificial structures can be achieved by simulating structural properties of natural rocky shores (Firth et al., 2013; O'Shaughnessy et al., 2020). However, due to their fundamental structural differences across scales (Lawrence et al., 2021), it may not be possible for assemblages on artificial habitats to resemble those on natural shores (Bulleri and Chapman, 2010). This raises the question of how to measure the ecological value of these novel habitats and determine the success of eco-engineering interventions. Efficient ecosystem management needs SMART (Specific, Measurable, Achievable, Realistic, and Timebound) targets (Wood, 2011). But in many cases, it is not clear what the measurable targets should be for eco-engineering of coastal structures. If an artificial habitat is unlikely to support an assemblage equivalent to that of a natural habitat in many contexts (Perkol-Finkel et al., 2006), what can we expect its ideal assemblage to look like? What level of species richness, diversity or abundance of functional groups should be targeted? Perhaps, as they are novel systems, targets based on ecosystem services or ecosystem functioning would be more appropriate than attempting to replicate a 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 novel habitat provided ecosystem services of water filtration and food (Chee et al., 2021). In another example, positive effects of an artificial habitat's physical and biogenic complexity on biodiversity contrasted with negative effects on ecosystem functioning measured as primary productivity and nutrient cycling (Mayer-Pinto et al., 2022). However, seeding experiments have had limited long-term success (Perkol-Finkel et al., 2012; Strain et al., 2020), and there is a risk that promoting non-natural communities will disproportionately favour colonisation by non-native species, exacerbating negative impacts of marine infrastructure (Komyakova et al., 2022).

4.6 Limitations

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

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

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

Acknowledgements

The authors wish to thank Harry Thatcher, Hannah Earp, Siobhan Vye, Melanie Prentice, Macauley Chapman, Tomos Jones and Irene Barriga for their contributions to fieldwork. We also wish to acknowledge the work of the wider Ecostructure team in building and supporting a productive collaborative research environment, in particular project lead Joe Ironside and project manager Liz Humphreys. We wish to thank two anonymous reviewers and Associate Editor Martin Drews whose comments helped us to improve the manuscript.

Funding

This work formed part of the Ecostructure project (www.ecostructureproject.eu), part-funded by the European Regional Development Fund (ERDF) through the Ireland-Wales Cooperation Programme 2014– 2020. A.J.D. was supported by the USDA National Institute of Food and Agriculture, Hatch Formula project accession no. 1017848.

Competing interests

The authors declare that we have no competing interests.

Data availability

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

5. References

Aguilera, M.A., Broitman, B.R., Thiel, M., 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: Lack of microhabitats suppresses intertidal biodiversity. Mar. Pollut. Bull. 87, 257–268. https://doi.org/10.1016/j.marpolbul.2014.07.046

Archambault, P., Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Mar. Ecol. Prog. Ser. 136, 111–121. https://doi.org/10.3354/meps136111

Beck, M.W., 2000. Separating the elements of habitat structure: Independent effects of habitat complexity and structural components on rocky intertidal gastropods. J. Exp. Mar. Bio. Ecol. 249, 29–49. https://doi.org/10.1016/S0022-0981(00)00171-4

Beck, M.W., 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169, 165–178. https://doi.org/10.3354/meps169165

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar. Ecol. Prog. Ser. 215, 79–92. https://doi.org/10.3354/meps215079

Benedetti-Cecchi, L., Bulleri, F., Acunto, S., Cinelli, F., 2001. Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean. Mar. Ecol. Prog. Ser. 209, 131–141. https://doi.org/10.3354/MEPS209131

Berry, K.J., Johnston, J.E., Mielke, P.W., 2011. Permutation methods. Wiley Interdiscip. Rev. Comput. Stat. 3, 527–542. https://doi.org/10.1002/WICS.177

Bracewell, S.A., Clark, G.F., Johnston, E.L., 2018. Habitat complexity effects on diversity and abundance differ with latitude: an experimental study over 20 degrees. Ecology 99, 1964–

1974. https://doi.org/10.1002/ecy.2408

Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P., Strain, E.M.A., Morris, R.L., Loke, L.H.L., Bishop, M.J., Sheehan, E. V., Coleman, R.A., Dafforn, K.A., 2020. Current and projected global extent of marine built structures. Nat. Sustain. 2020 41 4, 33–41. https://doi.org/10.1038/s41893-020-00595-1

Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x

Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Mar. Ecol. Prog. Ser. 264, 21–29. https://doi.org/10.3354/MEPS264021

Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of “armoured” shorelines to improve their value as habitat. J. Exp. Mar. Bio. Ecol. 400, 302–313. https://doi.org/10.1016/J.JEMBE.2011.02.025

Chappuis, E., Terradas, M., Cefalì, M.E., Mariani, S., Ballesteros, E., 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. Estuar. Coast. Shelf Sci. 147, 113–122. https://doi.org/10.1016/j.ecss.2014.05.031

Chee, S.Y., Yee, J.C., Cheah, C.B., Evans, A.J., Firth, L.B., Hawkins, S.J., Strain, E.M.A., 2021. Habitat complexity affects the structure but not the diversity of sessile communities on tropical coastal infrastructure. Front. Ecol. Evol. 9, 685. https://doi.org/10.3389/fevo.2021.673227

Chiba, S., Noda, T., 2000. Factors maintaining topography-related mosaic of barnacle and mussel on a rocky shore. J. Mar. Biol. Assoc. United Kingdom 80, 617–622. https://doi.org/10.1017/S0025315400002435

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

D'Urban Jackson, T., Williams, G.J., Walker-Springett, G., Davies, A.J., 2020. Three-dimensional digital mapping of ecosystems: A new era in spatial ecology. Proc. R. Soc. B Biol. Sci. 287, 1–10. https://doi.org/10.1098/rspb.2019.2383

Denny, M.W., Helmuth, B., Leonard, G.H., Harley, C.D.G., Hunt, L.J.H., Nelson, E.K., 2004. Quantifying scale in ecology: Lessons from a wave-swept shore. Ecol. Monogr. 74, 513–532. https://doi.org/10.1890/03-4043

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Evans, A.J., Firth, L.B., Hawkins, S.J., Morris, E.S., Goudge, H., Moore, P.J., 2016. Drill-cored rock pools: An effective method of ecological enhancement on artificial structures. Mar. Freshw. Res. 67, 123–130. https://doi.org/10.1071/MF14244

Evans, A.J., Garrod, B., Firth, L.B., Hawkins, S.J., Morris-Webb, E.S., Goudge, H., Moore, P.J., 2017. Stakeholder priorities for multi-functional coastal defence developments and steps to effective implementation. Mar. Policy 75, 143–155. https://doi.org/10.1016/J.MARPOL.2016.10.006

Evans, A.J., Moore, P.J., Firth, L.B., Smith, R.K., Sutherland, W.J., 2021. Enhancing the biodiversity of marine artificial structures - Global evidence for the effects of interventions. Cambridge, UK.

Ferrario, F., Iveša, L., Jaklin, A., Perkol-Finkel, S., Airoldi, L., 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. J. Appl. Ecol. 53, 16–24. https://doi.org/10.1111/1365-2664.12533

Firth, L.B., Harris, D., Blaze, J.A., Marzloff, M.P., Boyé, A., Miller, P.I., Curd, A., Vasquez, M., Nunn, J.D., O'Connor, N.E., Power, A.M., Mieszkowska, N., O'Riordan, R.M., Burrows, M.T., Bricheno, L.M., Knights, A.M., Nunes, F.L.D., Bordeyne, F., Bush, L.E., Byers, J.E., David, C., Davies, A.J., Dubois, S.F., Edwards, H., Foggo, A., Grant, L., Green, J.A.M., Gribben, P.E., Lima, F.P., McGrath, D., Noël, L.M.L.J., Seabra, R., Simkanin, C., Hawkins, S.J., 2021. Specific niche requirements underpin multidecadal range edge stability, but may introduce barriers for climate change adaptation. Divers. Distrib. 27, 668–683. https://doi.org/10.1111/ddi.13224

Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M., Hawkins, S.J., 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Divers. Distrib. 19, 1275–1283. https://doi.org/10.1111/ddi.12079

Forbes, E., 1858. The distribution of marine life, illustrated chiefly by fishes and molluscs and radiata, in: AK Johnston's Physical Atlas. Edinburgh, pp. 99–101.

Frost, N.J., Burrows, M.T., Johnson, M.P., Hanley, M.E., Hawkins, S.J., 2005. Measuring surface complexity in ecological studies. Limnol. Oceanogr. Methods 3, 203–210. https://doi.org/10.4319/lom.2005.3.203

Gacia, E., Satta, M.P., Martin, D., 2007. Low crested coastal defence structures on the Catalan coast of the Mediterranean Sea: how they compare with natural rocky shores. Sci. Mar. 71, 259–267. https://doi.org/10.3989/SCIMAR.2007.71N2259

Garza, C., 2019. Landscape Ecology in the Rocky Intertidal: Opportunities for Advancing Discovery and Innovation in Intertidal Research. Curr. Landsc. Ecol. Reports 4, 83–90. https://doi.org/10.1007/s40823-019-00042-8

Guichard, F., Bourget, E., 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: A scale-dependent cascade. Mar. Ecol. Prog. Ser. 171, 59–70. https://doi.org/10.3354/meps171059

Halley, J.M., Hartley, S., Kallimanis, A.S., Kunin, W.E., Lennon, J.J., Sgardelis, S.P., 2004. Uses and abuses of fractal methodology in ecology. Ecol. Lett. 7, 254–271. https://doi.org/10.1111/J.1461-0248.2004.00568.X

Harley, C.D.G., 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Mar. Ecol. Prog. Ser. 371, 37–46. https://doi.org/10.3354/meps07711

Hawkins, S., Hartnoll, R., 1985. Factors determining the upper limits of intertidal canopy-forming algae. Mar. Ecol. Prog. Ser. 20, 265–271. https://doi.org/10.3354/meps020265

Hawkins, S.J., Pack, K.E., Firth, L.B., Mieszkowska, N., Evans, A.J., Martins, G.M., Åberg, P., Adams, L.C., Arenas, F., Boaventura, D.M., Bohn, K., Debora Borges, C.G., Castro, J.J., Coleman, R.A., Crowe, T.P., Cruz, T., Davies, M.S., Epstein, G., Faria, J., Ferreira, J.G., Frost, N.J., Griffin, J.N., Hanley, M.E., Herbert, R.J.H., Hyder, K., Johnson, M.P., Lima, F.P., Masterson-Algar, P., Moore, P.J., Moschella, P.S., Notman, G.M., Pannacciulli, F.G., Ribeiro, P.A., Santos, A.M., Silva, A.C.F., Skov, M.W., Sugden, H., Vale, M., Wangkulangkul, K., Wort, E.J.G., Thompson, R.C., Hartnoll, R.G., Burrows, M.T., Jenkins, S.R., 2019. The Intertidal Zone of the North-East Atlantic Region: Pattern and Process, in: Interactions in the Marine Benthos: Global Patterns and Processes. Cambridge University Press, pp. 7–46. https://doi.org/10.1017/9781108235792.003

Heery, E.C., Bishop, M.J., Critchley, L.P., Bugnot, A.B., Airoldi, L., Mayer-Pinto, M., Sheehan, E. V., Coleman, R.A., Loke, L.H.L., Johnston, E.L., Komyakova, V., Morris, R.L., Strain, E.M.A., Naylor, L.A., Dafforn, K.A., 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. J. Exp. Mar. Bio. Ecol. 492, 31–48. https://doi.org/10.1016/j.jembe.2017.01.020

Helmuth, B., Denny, M.W., 2003. Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? Limnol. Oceanogr. 48, 1338–1345. https://doi.org/10.4319/lo.2003.48.3.1338

Hiscock, K. (Ed.), 1996. Marine Nature Conservation Review: Rationale and methods. Coasts and seas of the United Kingdom. Joint Nature Conservation Committee, Peterborough.

Jenkins, S.R., Hawkins, S.J., Norton, T.A., 1999. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. Mar. Ecol. Prog. Ser. 188, 81–92. https://doi.org/10.3354/MEPS188081

Jenkins, S.R., Moore, P., Burrows, M.T., Garbary, D.J., Hawkins, S.J., Ing??lfsson, A., Sebens, K.P., Snelgrove, P.V.R., Wethey, D.S., Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: Do differences in players matter for process? Ecology 89. https://doi.org/10.1890/07-1155.1

Johnson, M.P., Frost, N.J., Mosley, M.W.J., Roberts, M.F., Hawkins, S.J., 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecol. Lett. 6, 126–132. https://doi.org/10.1046/J.1461-0248.2003.00404.X

Johnson, M.P., Hughes, R.N., Burrows, M.T., Hawkins, S.J., 1998. Beyond the predation halo: Small scale gradients in barnacle populations affected by the relative refuge value of crevices. J. Exp. Mar. Bio. Ecol. 231, 163–170. https://doi.org/10.1016/S0022-0981(98)00055-0

Knott, N.A., Underwood, A.J., Chapman, M.G., Glasby, T.M., 2004. Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. J. Mar. Biol. Assoc. United Kingdom 84, 1117–1130. https://doi.org/10.1017/S0025315404010550h

Kohn, A.J., Leviten, P.J., 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia 25, 199–210. https://doi.org/10.1007/BF00345098

Komyakova, V., Jaffrés, J.B.D., Strain, E.M.A., Cullen-Knox, C., Fudge, M., Langhamer, O., Bender, A., Yaakub, S.M., Wilson, E., Allan, B.J.M., Sella, I., Haward, M., 2022. Conceptualisation of multiple impacts interacting in the marine environment using marine infrastructure as an example. Sci. Total Environ. 830, 154748.

https://doi.org/10.1016/J.SCITOTENV.2022.154748

Kostylev, V.E., Erlandsson, J., Mak, Y.M., Williams, G.A., Ming, M.Y., Williams, G.A., Mak, Y.M., Williams, G.A., Ming, M.Y., Williams, G.A., 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. Ecol. Complex. 2, 272–286. https://doi.org/10.1016/j.ecocom.2005.04.002

Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: Approaches and future directions. Hydrobiologia 685, 1–17. https://doi.org/10.1007/s10750-011-0974-z

Lague, D., Brodu, N., Leroux, J., 2013. Accurate 3D comparison of complex topography with terrestrial laser scanner: Application to the Rangitikei canyon (N-Z). ISPRS J. Photogramm. Remote Sens. 82, 10–26. https://doi.org/10.1016/j.isprsjprs.2013.04.009

Lawrence, P.J., Evans, A.J., Jackson-Bué, T., Brooks, P.R., Crowe, T.P., Dozier, A.E., Jenkins, S.R., Moore, P.J., Williams, G.J., Davies, A.J., 2021. Artificial shorelines lack natural structural complexity across scales. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2021.0329

Legendre, P., Legendre, L., 2012. Numerical Ecology, 3rd Englis. ed. Elsevier.

Lewis, J.R., 1968. Water movements and their role in rocky shore ecology. Sarsia 34, 13–36. https://doi.org/10.1080/00364827.1968.10413369

Lewis, J.R., 1961. The Littoral Zone on Rocky Shores: A Biological or Physical Entity? Oikos 12, 280. https://doi.org/10.2307/3564701

Lindegarth, M., Gamfeldt, L., 2005. Comparing categorical and continuous ecological analyses: Effects of “wave exposure” on rocky shores. Ecology 86, 1346–1357. https://doi.org/10.1890/04-1168

Liversage, K., Chapman, M.G., 2018. Coastal ecological engineering and habitat restoration: incorporating biologically diverse boulder habitat. Mar. Ecol. Prog. Ser. 593, 173–185.

https://doi.org/10.3354/MEPS12541

Loke, L.H.L., Chisholm, R.A., 2022. Measuring habitat complexity and spatial heterogeneity in ecology. Ecol. Lett. 25, 2269–2288. https://doi.org/10.1111/ele.14084

Loke, L.H.L., Todd, P.A., 2016. Structural complexity and component type increase intertidal biodiversity independently of area. Ecology 97, 383–393. https://doi.org/10.1890/15-0257.1

MacArthur, R.H., MacArthur, J.W., 1961. On Bird Species Diversity. Ecol. Soc. Am. 42, 594–598.

Mayer-Pinto, M., Bugnot, A.B., Johnston, E.L., Potts, J., Airoldi, L., Glasby, T.M., Strain, E.M.A., Scanes, P., Ushiama, S., Dafforn, K.A., 2022. Physical and biogenic complexity mediates ecosystem functions in urban sessile marine communities. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14347

McCoy, E.D., Bell, S.S., 1991. Habitat Structure, Habitat Structure. Springer Netherlands. https://doi.org/10.1007/978-94-011-3076-9

Meager, J.J., Schlacher, T.A., 2013. New metric of microhabitat complexity predicts species richness on a rocky shore. Mar. Ecol. 34, 484–491. https://doi.org/10.1111/maec.12049

Meager, J.J., Schlacher, T.A., Green, M., 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. Mar. Ecol. Prog. Ser. 428, 1–12. https://doi.org/10.3354/meps09124

Menge, B.A., Lubchenco, J., Ashkenas, L.R., 1985. Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. Oecologia 1985 653 65, 394–405. https://doi.org/10.1007/BF00378915

Menge, B.A., Olson, A.M., 1990. Role of scale and environmental factors in regulation of community structure. Trends Ecol. Evol. 5, 52–57. https://doi.org/10.1016/0169-5347(90)90048-I

Moschella, P.S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J.M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M., Gacia, E., Granhag, L., Jonsson, P.R., Satta, M.P., Sundelöf, A., Thompson, R.C., Hawkins, S.J., 2005. Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coast. Eng. 52, 1053–1071. https://doi.org/10.1016/J.COASTALENG.2005.09.014

Nash, K.L., Graham, N.A.J., Wilson, S.K., Bellwood, D.R., 2013. Cross-scale Habitat Structure Drives Fish Body Size Distributions on Coral Reefs. Ecosystems 16, 478–490. https://doi.org/10.1007/s10021-012-9625-0

O'Shaughnessy, K.A., Hawkins, S.J., Evans, A.J., Hanley, M.E., Lunt, P., Thompson, R.C., Francis, R.A., Hoggart, S.P.G., Moore, P.J., Iglesias, G., Simmonds, D., Ducker, J., Firth, L.B., 2020. Design catalogue for eco-engineering of coastal artificial structures: a multifunctional approach for stakeholders and end-users. Urban Ecosyst. 23, 431–443. https://doi.org/10.1007/s11252-019-00924-z

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.5-7.

Pearson, K., 1894. Contributions to the Mathematical Theory of Evolution. Philos. Trans. R. Soc. London. A 185, 71–110. https://doi.org/10.1007/BF02464423

Perkol-Finkel, S., Ferrario, F., Nicotera, V., Airoldi, L., 2012. Conservation challenges in urban seascapes: Promoting the growth of threatened species on coastal infrastructures. J. Appl. Ecol. 49, 1457–1466. https://doi.org/10.1111/j.1365-2664.2012.02204.x

Perkol-Finkel, S., Shashar, N., Benayahu, Y., 2006. Can artificial reefs mimic natural reef communities? The roles of structural features and age. Mar. Environ. Res. 61, 121–135. https://doi.org/10.1016/J.MARENVRES.2005.08.001

Pinedo, S., García, M., Satta, M.P., Torres, M. de, Ballesteros, E., 2007. Rocky-shore communities as indicators of water quality: A case study in the Northwestern Mediterranean. Mar. Pollut. Bull. 55, 126–135. https://doi.org/10.1016/J.MARPOLBUL.2006.08.044

Prentice, M., Ward, S., Robins, P., Shaw, P., Earp, H., Sauze, C., Skujina, I., Jenkins, S., Ironside, J., 2022. Oceanographic currents, geographic patterns and local environment contribute to neutral and adaptive genetic structure in two intertidal marine gastropods with contrasting life-histories. Authorea Prepr. https://doi.org/10.22541/AU.164873607.76071489/V1

R Core Team, 2023. R: A Language and Environment for Statistical Computing.

Robins, P.E., Neill, S.P., Giménez, L., Stuart, R., Jenkins, S.R., Malham, S.K., 2013. Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. Limnol. Oceanogr. 58, 505–524. https://doi.org/10.4319/lo.2013.58.2.0505

Sebens, K.P., 1991. Habitat structure and community dynamics in marine benthic systems. Habitat Struct. 211–234. https://doi.org/10.1007/978-94-011-3076-9_11

Simberloff, D., 2004. Community ecology: Is it time to move on? (An american society of naturalists presidential address). Am. Nat. 163, 787–799. https://doi.org/10.1086/420777/ASSET/IMAGES/LARGE/FG1.JPEG

Strain, E.M.A., Cumbo, V.R., Morris, R.L., Steinberg, P.D., Bishop, M.J., 2020. Interacting effects of habitat structure and seeding with oysters on the intertidal biodiversity of seawalls. PLoS One 15, e0230807. https://doi.org/10.1371/journal.pone.0230807

Strain, E.M.A., Steinberg, P.D., Vozzo, M., Johnston, E.L., Abbiati, M., Aguilera, M.A., Airoldi, L., Aguirre, J.D., Ashton, G., Bernardi, M., Brooks, P., Chan, B.K.K., Cheah, C.B., Chee, S.Y., Coutinho, R., Crowe, T., Davey, A., Firth, L.B., Fraser, C., Hanley, M.E., Hawkins, S.J., Knick, K.E., Lau, E.T.C., Leung, K.M.Y., McKenzie, C., Macleod, C., Mafanya, S., Mancuso, F.P., Messano, L.V.R., Naval-Xavier, L.P.D., Ng, T.P.T., O'Shaughnessy, K.A., Pattrick, P., Perkins, M.J., Perkol-Finkel, S., Porri, F., Ross, D.J., Ruiz, G., Sella, I., Seitz, R., Shirazi, R., Thiel, M., Thompson, R.C., Yee, J.C., Zabin, C., Bishop, M.J., 2021. A global analysis of complexity–biodiversity relationships on marine artificial structures. Glob. Ecol. Biogeogr. 30, 140–153. https://doi.org/10.1111/GEB.13202

Strain, E.M.A.A., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B., Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P.R., Bishop, M.J., 2018. Eco-engineering urban infrastructure for marine and coastal biodiversity: Which interventions have the greatest ecological benefit? J. Appl. Ecol. 55, 426–441. https://doi.org/10.1111/1365-2664.12961

Strong, J.A., Johnson, M., 2020. Converting SACFOR data for statistical analysis: Validation, demonstration and further possibilities. Mar. Biodivers. Rec. 13, 1–18. https://doi.org/10.1186/s41200-020-0184-3

ter Braak, C.J.F., 1986. Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. Ecology 67, 1167–1179. https://doi.org/10.2307/1938672

ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 57, 255–289. https://doi.org/10.1007/BF00877430

Tomanek, L., Helmuth, B., 2002. Physiological Ecology of Rocky Intertidal Organisms: A Synergy of Concepts. Integr. Comp. Biol. 42, 771–775. https://doi.org/10.1093/icb/42.4.771

Torres-Pulliza, D., Dornelas, M.A., Pizarro, O., Bewley, M., Blowes, S.A., Boutros, N., Brambilla, V., Chase, T.J., Frank, G., Friedman, A., Hoogenboom, M.O., Williams, S., Zawada, K.J.A., Madin, J.S., 2020. A geometric basis for surface habitat complexity and biodiversity. Nat. Ecol. Evol. 4, 1495–1501. https://doi.org/10.1038/s41559-020-1281-8

Valdivia, N., Scrosati, R.A., Molis, M., Knox, A.S., 2011. Variation in Community Structure across Vertical Intertidal Stress Gradients: How Does It Compare with Horizontal Variation at Different Scales? PLoS One 6, e24062. https://doi.org/10.1371/JOURNAL.PONE.0024062

Van Diggelen, A.D., Montagna, P.A., 2016. Is Salinity Variability a Benthic Disturbance in Estuaries? Estuaries and Coasts 39, 967–980. https://doi.org/10.1007/s12237-015-0058-9

Vaselli, S., Bertocci, I., Maggi, E., Benedetti-Cecchi, L., 2008. Assessing the consequences of sea level rise: Effects of changes in the slope of the substratum on sessile assemblages of rocky seashores. Mar. Ecol. Prog. Ser. 368, 9–22. https://doi.org/10.3354/meps07625

Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141, 171–178. https://doi.org/10.1007/S00442-004-1644-X/FIGURES/1

Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol. Evol. 3, 89–101. https://doi.org/10.1111/J.2041-210X.2011.00127.X

Wood, L., 2011. Global marine protection targets: How S.M.A.R.T are they? Environ. Manage. 47, 525–535. https://doi.org/10.1007/S00267-011-9668-6/FIGURES/1

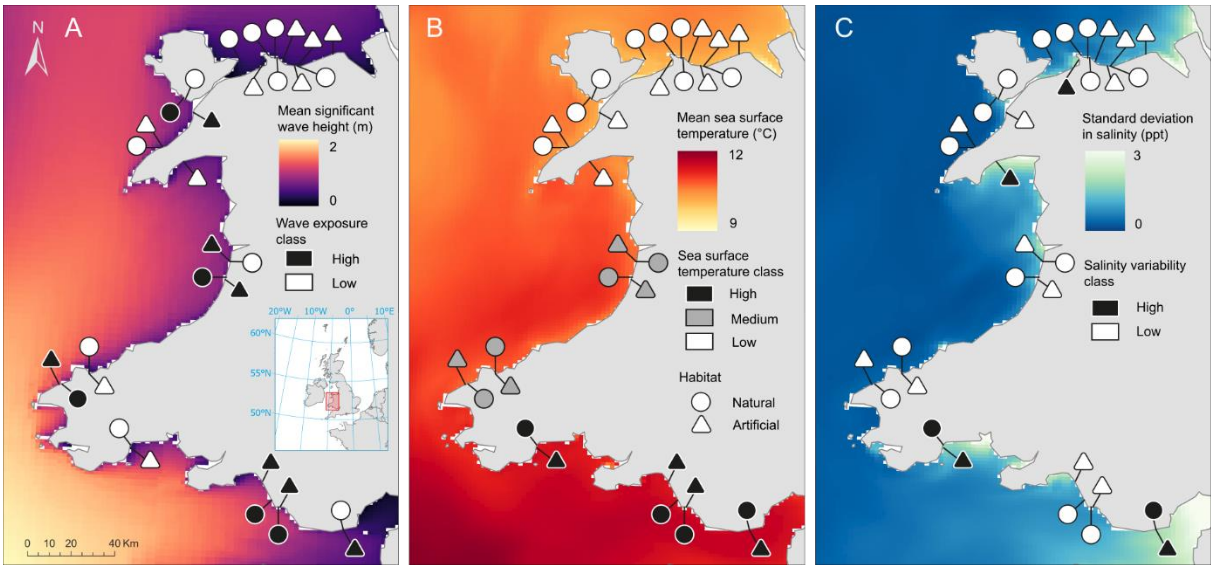


Figure 1. Intertidal study sites along the coastline of Wales, UK at 16 natural and 16 artificial reefs, with three environmental variables. Black lines from symbols indicate precise site locations and are identical in all three panels. A) Mean significant wave height (40 year) was combined with local 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.

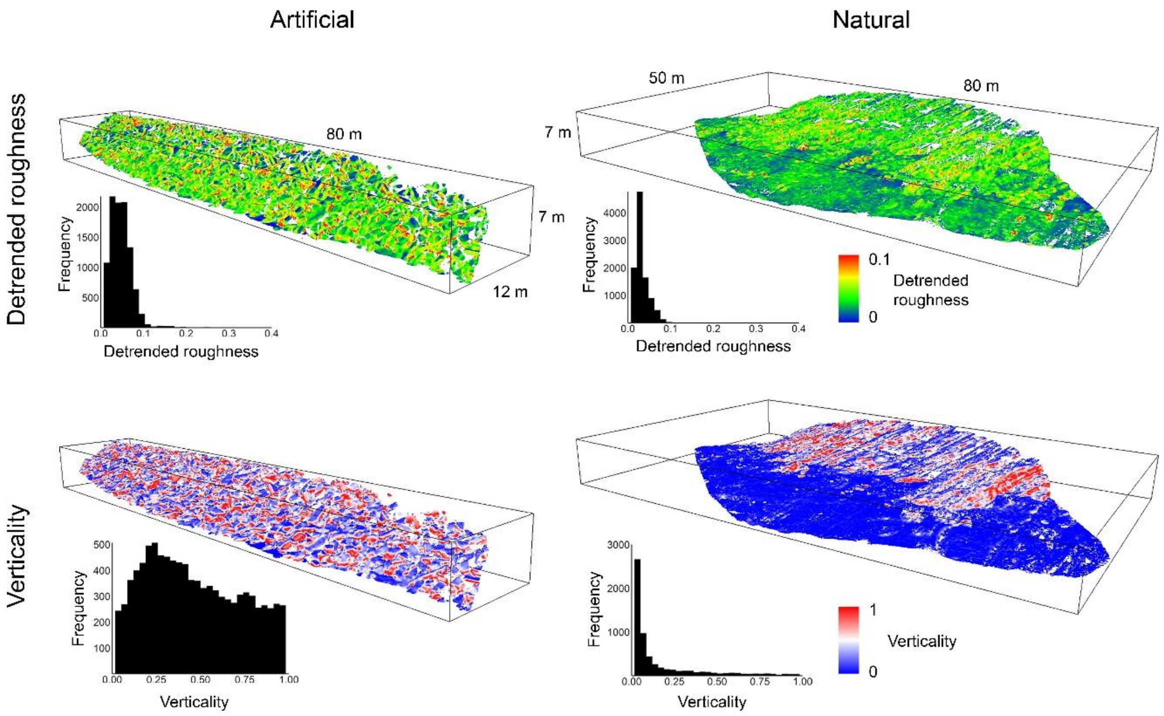


Figure 2. Metrics characterising the physical structure of artificial and natural intertidal reefs were calculated for each 3D data point at multiple scales. In this example, 3D point clouds of an artificial (rock armour) and a natural reef at Barry are displayed with points coloured by detrended roughness 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.

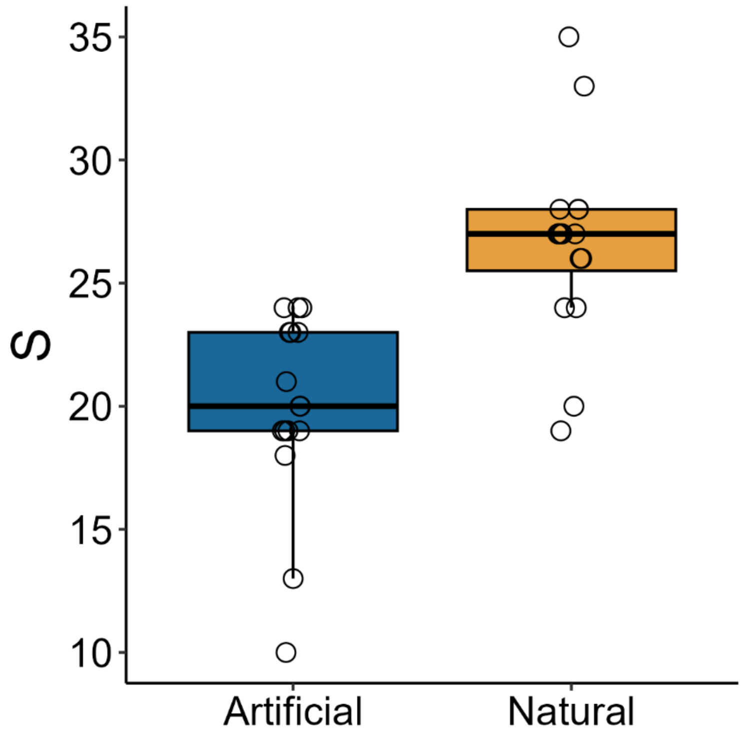
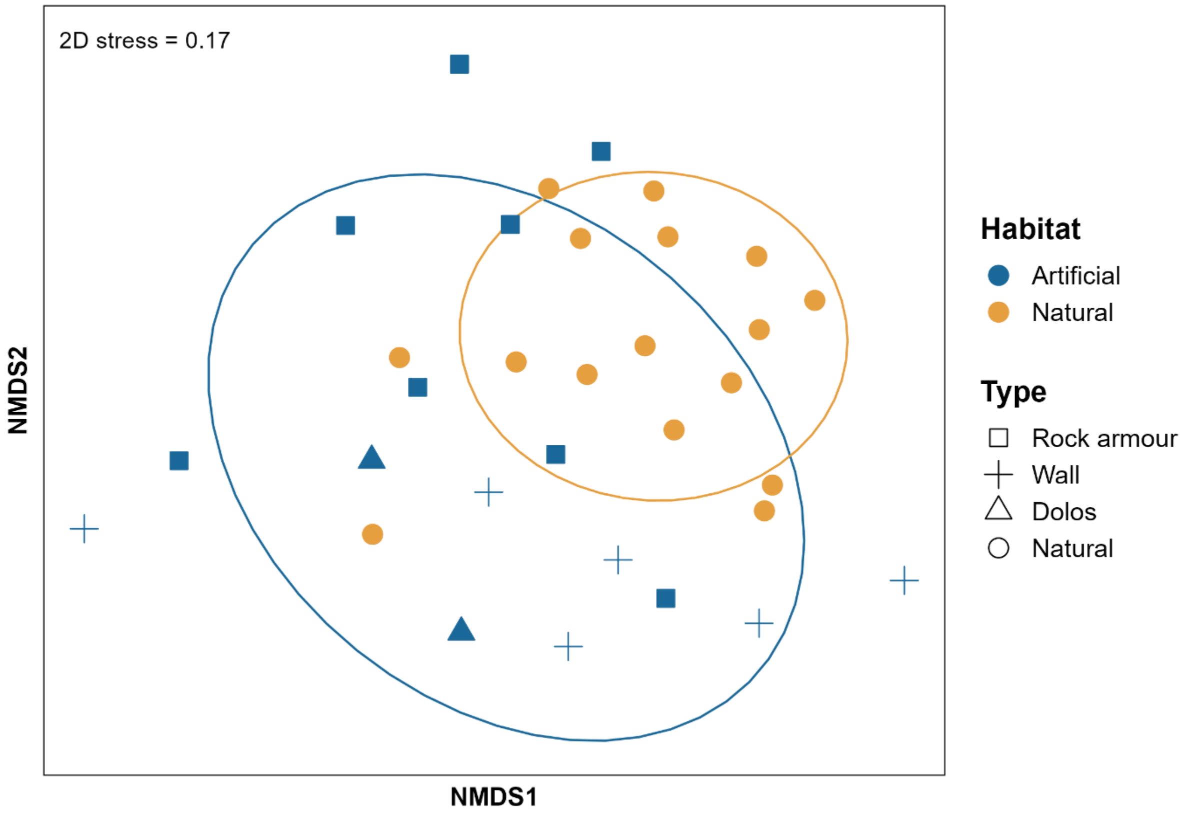


Figure 3. Boxplot and point data showing taxonomic richness (S) at artificial and natural reefs (n = 16 per habitat). Median taxonomic richness (bold black bar) was higher in natural habitats (*P* = 0.001).



847

848 Figure 4. Non-metric multidimensional scaling plot from a Bray-Curtis dissimilarity matrix of

849 sites, using ordinal density scores with no further transformation (n = 32). Natural and artificial

850 reef habitats had different assemblages and artificial habitats had higher within-group

851 variation, with some clustering of structure types. Elipses indicate 75% confidence level for a

852 multivariate t-distribution to guide visual interpretation.

853

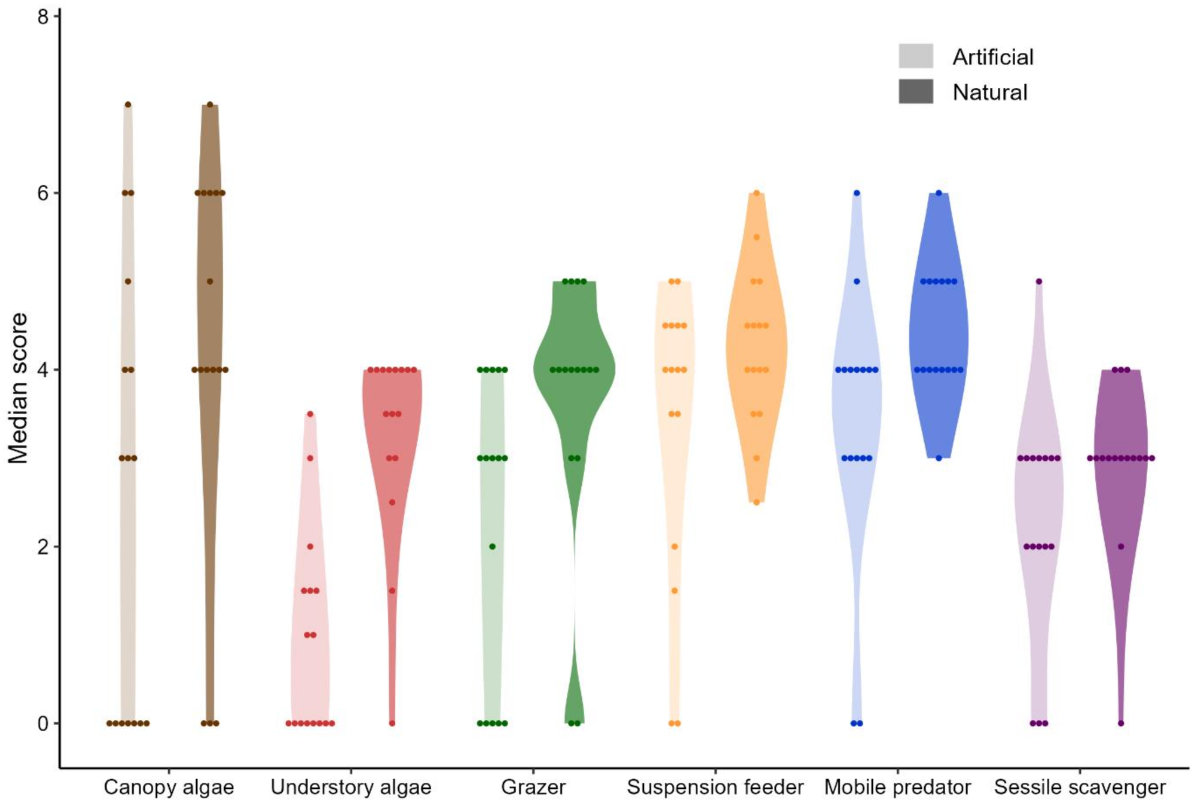


Figure 5. Violin and dot plot of median ordinal density scores of functional groups recorded in artificial (light shade) and natural (dark shade) habitats. Each dot represents the median ordinal score for a site, such that n = 16 for each functional group in each habitat. The mobile predator and sessile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

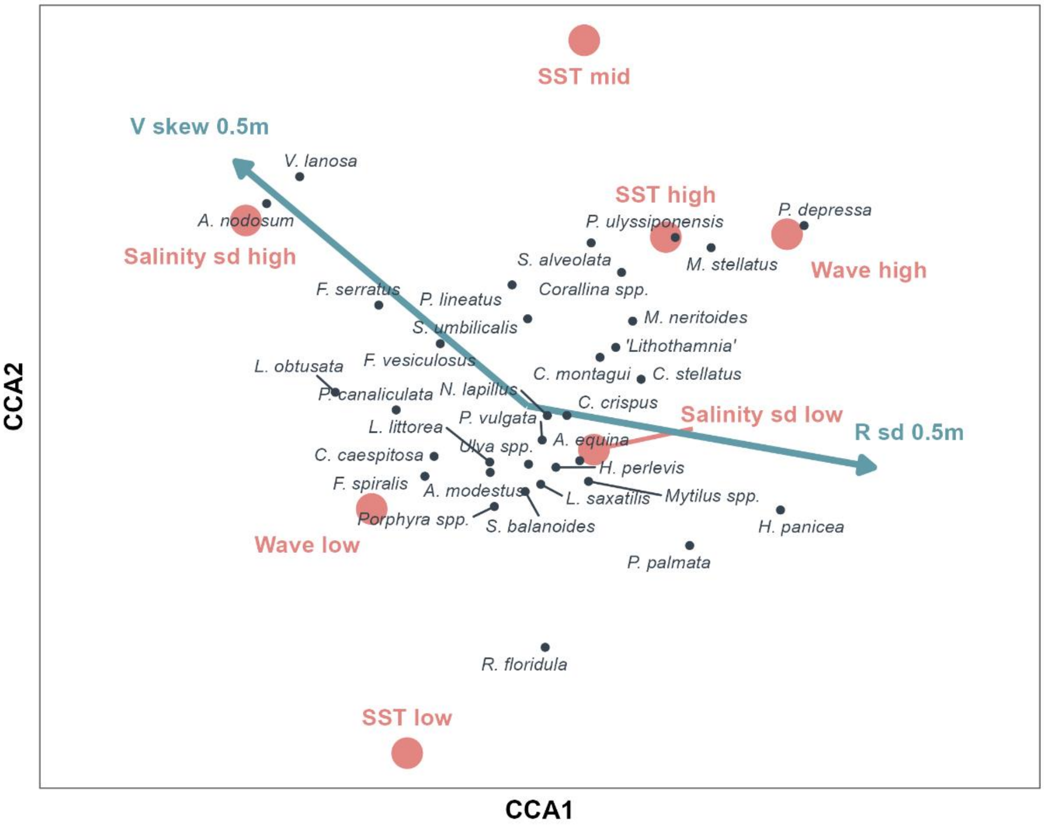


Figure 6. Canonical correspondence analysis biplot of a model with environmental variables and forward selection of structural metrics, removing the effect of habitat (artificial or natural) by including it as a conditional variable. Taxa are dark grey points; discrete variable centroids are red points,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

	df	SS	F	*P*
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.

Taxon	Median abundance score			Contribution	
	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
Mytilus 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

Supporting information

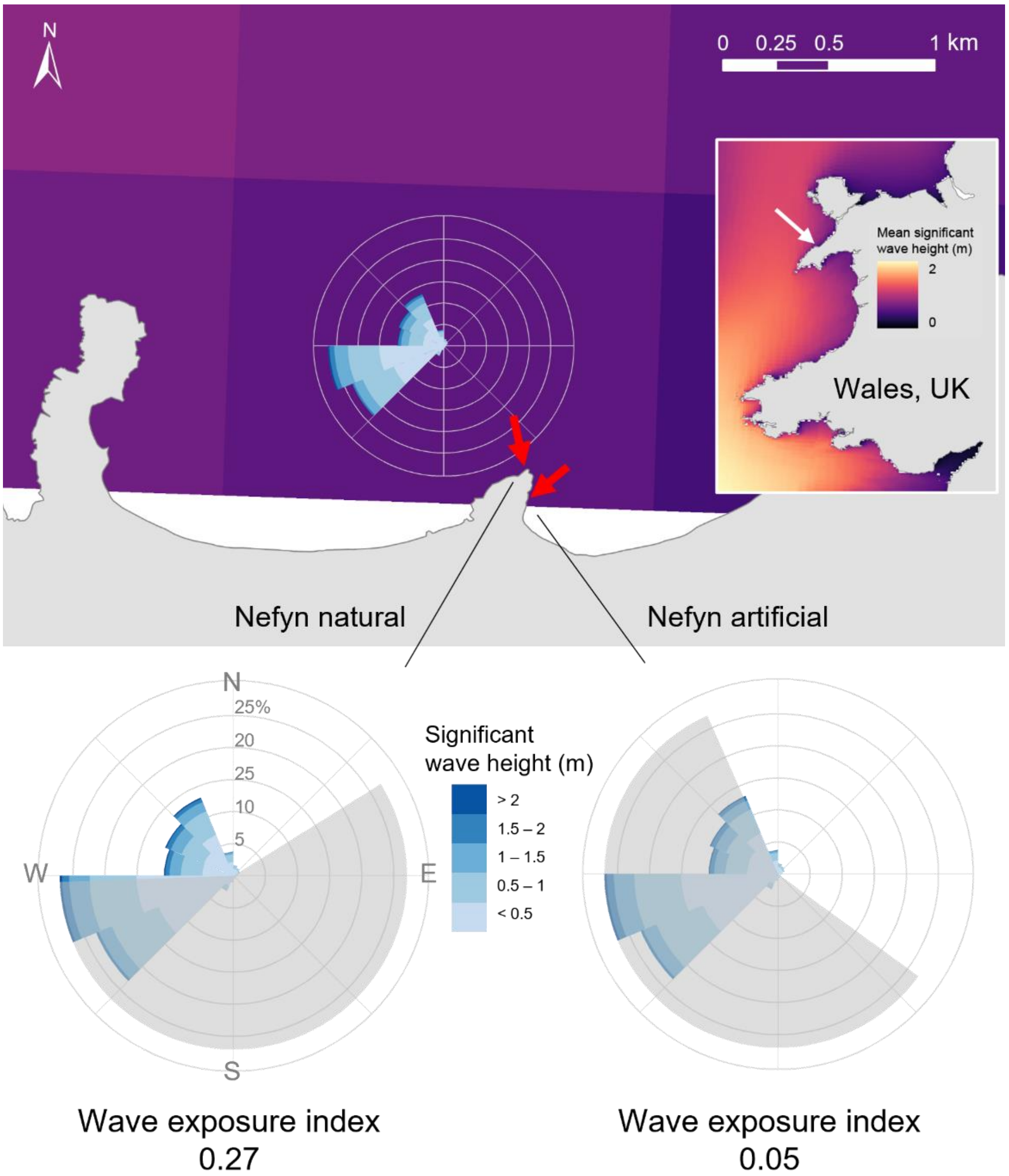


Figure S1. Wave exposure index incorporating significant wave height and onshore wave occurrence using 40 year hindcast data (https://doi.org/10.48670/moi-00060) and local site aspect. In this example, two sites at Nefyn use data from the same grid cell of the hindcast dataset, summarised here by a wave 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 occurrence is shown by the length of directional sectors as percentage. In this example, the distribution of significant wave heights is similar from all directions, but waves mostly arrive from the southwest. Because local site aspect differs (red arrow bearings), different windows of onshore angles are calculated (unshaded sectors on wave rose diagrams) to adjust the model data. All wave heights with directions outside of the 150° onshore windows are set to zero (grey sectors on wave rose diagrams), before calculating mean significant wave height. The resulting wave exposure index is lower at the artificial site because the local aspect faces away from the prevailing waves.

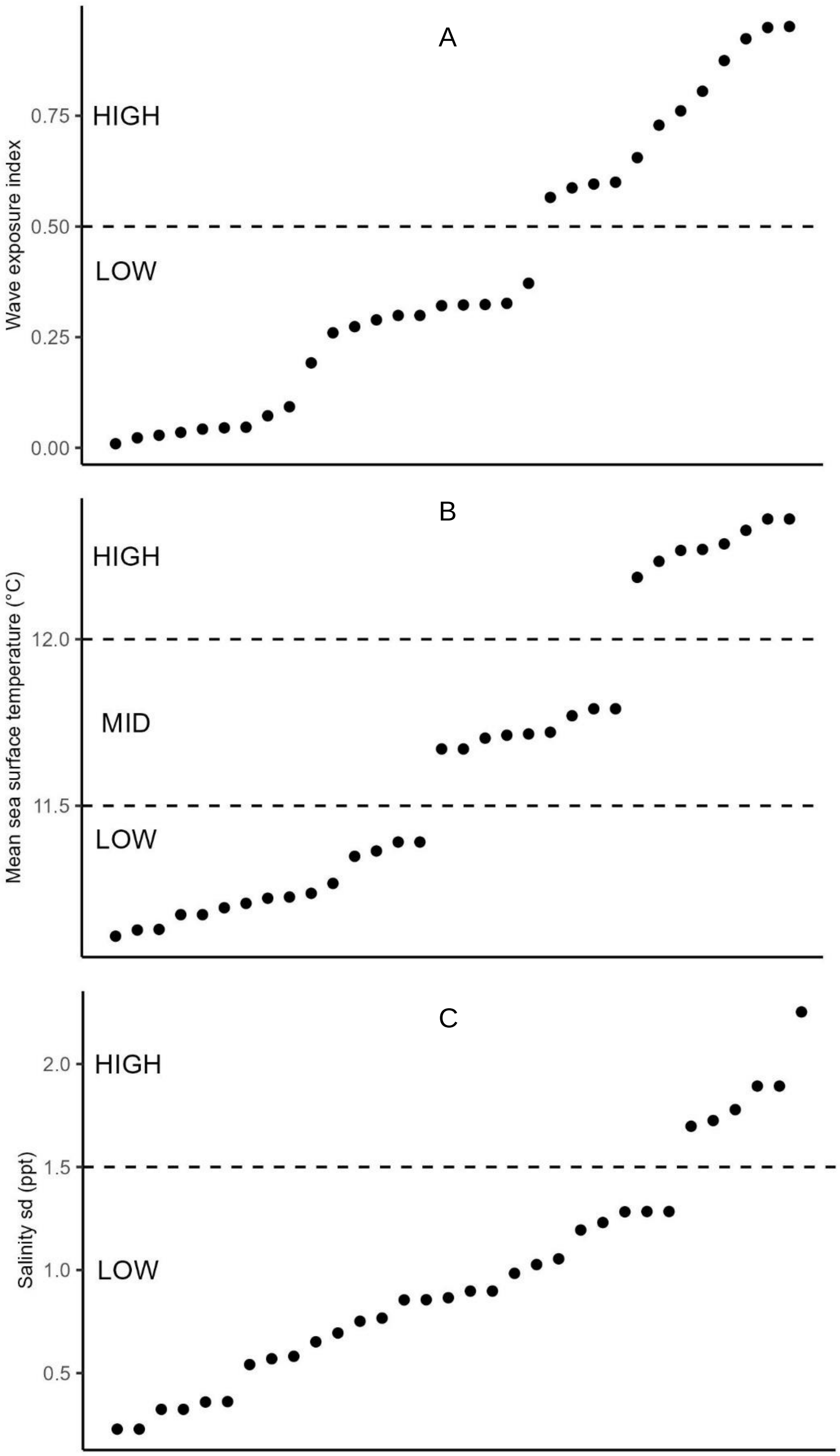


Figure S2. Environmental variables of A) wave exposure index, B) mean sea surface temperature and C) standard deviation in salinity discretised by ordering sites by each variable and finding natural breaks.

Table S1. See attached file Supporting_information_table_S1.xlsx

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

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)
Mytilus 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.

References

BIOTIC. Biological Traits Information Catalogue. https://www.marlin.ac.uk/biotic/

Chintiroglou, C., Koukouras, A., 1992. The feeding habits of three Mediterranean sea anemone species, Anemonia viridis (Forskål), Actinia equina (Linnaeus) and Cereus pedunculatus (Pennant). Helgoländer Meeresuntersuchungen 46, 53–68. https://doi.org/10.1007/BF02366212

Davenport, J., Moloney, T. V., Kelly, J., 2011. Common sea anemones Actinia equina are predominantly sessile intertidal scavengers. Mar. Ecol. Prog. Ser. 430, 147–155. https://doi.org/10.3354/meps08861

Hawkins, S.J., Watson, D.C., Hill, A.S., Harding, S.P., Kyriakides, M.A., Hutchinson, S., Norton, T.A., 1989. A COMPARISON OF FEEDING MECHANISMS IN MICROPHAGOUS, HERBIVOROUS, INTERTIDAL, PROSOBRANCHS IN RELATION TO RESOURCE PARTITIONING. J. Molluscan Stud. 55, 151–165. https://doi.org/10.1093/MOLLUS/55.2.151

Hayward, P.J., Ryland, J.S. (Eds.), 2017. Handbook of the Marine Fauna of North-West Europe, 2nd ed. Oxford University Press.

Laurand, S., Riera, P., 2006. Trophic ecology of the supralittoral rocky shore (Roscoff, France): A dual stable isotope (δ13C, δ15N) and experimental approach. J. Sea Res. 56, 27–36. https://doi.org/10.1016/J.SEARES.2006.03.002

MarLIN. The Marine Life Information Network. Species list. https://www.marlin.ac.uk/species

Otero-Schmitt, J., Cruz, R., García, C., Rolán-Alvarez, E., 2012. Feeding strategy and habitat choice in Littorina saxatilis (Gastropoda: Prosobranchia) and their role in the origin and maintenance of a sympatric polymorphism. http://dx.doi.org/10.1080/00785326.1997.10432879 46, 205–216. https://doi.org/10.1080/00785326.1997.10432879

Rainbow, P.S., 1984. An introduction to the biology of British littoral barnacles. F. Stud. 6, 1–51.

Watson, D.C., Norton, T.A., 1987. The habitat and feeding preferences of Littorina obtusata (L.) and L. mariae sacchi et rastelli. J. Exp. Mar. Bio. Ecol. 112, 61–72. https://doi.org/10.1016/S0022-0981(87)80015-1