Replicating natural topography on marine artificial structures – A novel approach to eco-engineering

Evans, Ally; Lawrence, Peter; Natanzi, Atteyeh; Moore, Pippa; Davies, Andy; Crowe, Tasman; McNally, Ciaran; Thompson, Bryan; Dozier, Amy; Brooks, Paul

Ecological Engineering

DOI:
10.1016/j.ecoleng.2020.106144

Published: 01/02/2021

Replicating natural topography on marine artificial structures – a novel approach to eco-engineering

Ally J. Evans*[a], Peter J. Lawrence*[b], Atteyeh S. Natanzi*[c], Pippa J. Moore[a,d], Andrew J. Davies[b,e], Tasman P. Crowe[f], Ciaran McNally[c], Bryan Thompson[f], Amy E. Dozier[g], Paul R. Brooks[f]

[a]Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, SY233DA, UK

[b]School of Ocean Sciences, Bangor University, Menai Bridge, LL595AB, UK

[c]School of Civil Engineering, University College Dublin, Dublin, Ireland

[d]School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, NE17RU, UK [Present address]

[e]Biological Sciences, University of Rhode Island, Kingston, RI02881, USA [Present address]

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

[g]MaREI, the SFI Research Centre for Energy, Climate and Marine, Environmental Research Institute, University College Cork, Ringaskiddy, Ireland

Corresponding author: Ally.Evans@aber.ac.uk

*Joint first authorship

Abstract

Ocean sprawl is a growing threat to marine and coastal ecosystems globally, with wide-ranging consequences for natural habitats and species. Artificial structures built in the marine environment often support less diverse communities than natural rocky marine habitats because of low topographic complexity. Some structures can be eco-engineered to increase their complexity and promote biodiversity. Tried-and-tested eco-engineering approaches include building-in habitat designs to mimic features of natural reef topography that are important for biodiversity. Most designs mimic discrete microhabitat features like crevices or holes and are geometrically-simplified. Here we propose that directly replicating the full fingerprint of natural reef topography in habitat designs makes a novel addition to the growing toolkit of eco-engineering options. We developed a five-step process for designing natural topography-based eco-engineering interventions for marine artificial structures. Given that topography is highly spatially variable in rocky reef habitats, our targeted approach seeks to identify and replicate the 'best' types of reef topography to satisfy specific eco-engineering objectives. We demonstrate and evaluate the process by designing three natural topography-based habitat units for intertidal structures, each targeting one of three hypothetical eco-engineering objectives. The process described can be adapted and applied according to user-specific priorities. Expanding the toolkit for eco-engineering marine structures is crucial to enable ecologically-informed designs that maximise biodiversity benefits from burgeoning ocean sprawl.

Keywords: artificial structures, eco-engineering, marine management, ocean sprawl, topography, urban ecology

1. Introduction

Ocean sprawl is a growing threat to marine and coastal ecosystems globally, with wide-ranging consequences for habitats and species (Firth et al., 2016a). Aside from the environmental impacts of building artificial structures in the sea (Bishop et al., 2017; Heery et al., 2017), structures generally provide poor quality habitats for biodiversity compared with natural rocky marine habitats (Moschella et al., 2005; Wilhelmsson & Malm, 2008). In nature, topographic heterogeneity generates variation in the physical environment and plays an important role in sustaining biodiversity and functioning (Levin, 1974). Species exist within the bounds of their differing evolutionary adaptations to physical stresses and a complex interplay of biotic interactions (Huston, 1999). On rocky reefs, many habitat features that offer refugia from physical stressors and predation (Aguilera et al., 2019; Hereu et al., 2005; Menge & Lubchenco, 1981), such as crevices, bumps and holes, are generated as a function of substrate topography. On artificial structures, topographic complexity is generally much lower (Moschella et al., 2005; Wilhelmsson & Malm, 2008); for example, plain concrete seawalls, uniform rock armour, and smooth jetty pilings. This is a key reason for their reduced biodiversity compared with natural rocky habitats (Firth et al., 2013; Moschella et al., 2005; Wilhelmsson & Malm, 2008). In some circumstances, absence of surface complexity and colonisation of marine life is desirable on structures. For example, on wave and tidal energy infrastructure, where local hydrodynamics are key (Langhamer et al., 2009). But where marine developments contribute to the loss or fragmentation of natural reefs (Hall et al., 2018), or where reef habitats and species are in decline for other reasons (Jackson & McIlvenny, 2011; Perkol-Finkel et al., 2012), it would be ecologically-beneficial if structures provide effective surrogate habitats for these communities, or indeed for other vulnerable/valued target species.

There is a growing toolkit of options for eco-engineering marine structures to enhance their biodiversity value by increasing their topographic complexity (O'Shaughnessy et al., 2020; Strain et al., 2018b). For example, researchers have trialled creating textured surfaces (Perkol-Finkel & Sella, 2016; Sella & Perkol-Finkel, 2015), microhabitats like holes and crevices (Chapman & Underwood, 2011; Hall et al., 2018; Langhamer & Wilhelmsson, 2009), rock pools (Evans et al., 2016; Morris et al., 2017; Waltham & Sheaves, 2020), and scaled-up habitat units (Firth et al., 2014; Sella & Perkol-Finkel, 2015). Others have transplanted target species onto structures (Ng et al., 2015; Perkol-Finkel et al., 2012). The evidence base for if and how biodiversity can be promoted through such 'greening-the-grey' (Firth et al., 2020; Naylor et al., 2017) eco-engineering interventions is growing rapidly (Strain et al., 2018b). The popularity of the concept is also growing amongst developers tasked with demonstrating how their proposals align with increasingly-proactive conservation and planning legislation (Dafforn et al., 2015; Evans et al., 2019).

The ecological benefits that can be delivered by greening-the-grey options from the eco-engineering toolkit are variable and context-dependent (Strain et al., 2018b). In most cases, novel habitat designs have been successfully colonised by reef organisms, but have not always functioned in the same way as comparable natural habitats (e.g. Chapman & Blockley, 2009; Evans et al., 2016; Langhamer & Wilhelmsson, 2009). This may be partly because of stressful environmental conditions around artificial structures, such as poor water quality in urban areas (Pinedo et al., 2007), unfavourable thermal conditions (Waltham & Sheaves, 2020) or high disturbance regimes (Airoldi & Bulleri, 2011). It may also be because many designs are geometrically-simplified representations of natural habitat features. For example, eco-engineered pit, crevice and rock pool habitat designs are commonly drilled or cast in regular forms for convenience or cost reasons (Firth et al., 2014; Hall et al., 2018; Langhamer & Wilhelmsson, 2009). Some habitats have been designed theoretically using computer-aided design to maximise biodiversity benefits (Loke et al., 2014). Others have been designed with an emphasis on aesthetics and public engagement (Hall et al., 2019). Whilst the majority of interventions are inspired by natural rocky habitat features, none have been designed to directly replicate them (but see MacArthur et al., 2019). With increasing affordability and accessibility of 3D habitat modelling and printing technologies (Canessa et al., 2013; D'Urban Jackson et al., 2020), different ecologically-targeted outcomes may be achieved by directly replicating the full fingerprint of natural reef topography in eco-engineering designs.

Here we describe a novel approach for designing eco-engineering interventions (i.e. habitat units) for marine artificial structures that directly replicate natural reef topography on structure surfaces. Given that topography, and hence the distribution of habitat features, physical conditions and biodiversity, is highly spatially variable on rocky reefs (Aguilera et al., 2019; Meager et al., 2011), our targeted approach seeks to identify and replicate the 'best' types of reef topography to satisfy specific eco-engineering objectives. This involves first identifying relationships between features of substrate topography and biodiversity metrics of interest, then selecting areas of topography to replicate accordingly. Acknowledging that eco-engineering options and objectives are likely to be different for different structures in different places, we present a five-step process that can be adapted and applied according to site-specific or species-specific priorities. We then describe and evaluate our own application of the process to promote three hypothetical eco-engineering objectives for intertidal artificial structures.

2. Designing Natural Topography-Based Eco-engineering Habitat Units: A Five-Step Process

We propose a five-step process for designing ecologically-targeted natural topography-based eco-engineering habitat units for marine artificial structures (Fig. 1). Prior to applying this process, the options and objectives of the eco-engineering intervention must be known. In particular, the species or communities that are the desired targets of the intervention must be identified, and these must be realistic targets of topography-based intervention. Following this, Step 1 is to conduct a baseline survey to sample the biology and topography of local reef habitats that support those target species/communities to varying degrees. The location, scale, timing and method of baseline survey must be appropriate to their biology and ecology. Biological sampling must be appropriate for subsequently identifying and selecting the 'best' and 'worst' samples for target species/communities, according to the user's objectives. If a single species is the target (e.g. for conservation/fisheries interest), simple measures of presence, abundance and/or population demographics may be sufficient. If groups of species or full communities are the target (e.g. to promote natural reef communities), then community-level biodiversity metrics or indices may be necessary and data should be collected accordingly. Topographic sampling must allow for the construction of three-dimensional digital habitat models (e.g. digital elevation models (DEMs) or point clouds) of appropriate scale and resolution (e.g. using structure-from-motion (SfM) photogrammetry or laser-scanning; D'Urban Jackson et al., 2020).

Step 2 is a biological selection step to identify subsets of the 'best' and 'worst' samples from the baseline survey for target species/communities. Using appropriate biodiversity metrics, samples can be scored, ranked and filtered pragmatically to select subsets of the 'best' and 'worst' samples that contain enough samples for subsequently detecting associations with topographic features. Step 3 is a topographic selection step to identify topographic features characteristic of the 'best' but not the 'worst' samples, then to shortlist the 'best candidates' based on these. This step should include a rigorous method (e.g. statistical modelling) for identifying relationships between the target species/communities and features of the underlying topography. Step 4 is an engineering selection step to identify potential practical issues for manufacturing eco-engineering habitat units based on the 'best candidates'. Step 5 is to manufacture habitat units replicating the ultimately selected 'best' samples of reef substrate.

3. Application of the Five-Step Process

We applied the five-step process (Fig. 1) to design natural topography-based eco-engineering habitat units for artificial structures in our region (Fig. 2). We aimed to design experimental-scale (25 x 25 cm) habitat units for mid-shore seaward-facing surfaces on intertidal structures. We applied the approach with three hypothetical eco-engineering objectives in mind: (A) to maximise the richness of colonising communities; (B) to promote local rocky reef species that are normally deficient on artificial structures; and (C) to promote rocky reef species that are rare in our region.

3.1 Step 1 – Baseline Survey

3.1.1 Survey Sites

Natural and artificial intertidal rocky habitats were surveyed at 54 sites around the Irish Sea coasts of Ireland and Wales during summer 2018 (Fig. 2; Table S1). For every natural habitat sampled (n = 27), a nearby artificial habitat was sampled (n = 27) with comparable aspect and wave exposure. Natural habitats were bedrock reefs formed of mixed sand/mudstones, limestone or granite. Artificial habitats were walls and rock armour constructed from limestone, granite or concrete. Artificial habitats were sampled because biodiversity metrics calculated for two of our hypothetical eco-engineering objectives required data on the biodiversity colonising artificial structures (see Section 3.2 below).

3.1.2 Biological Sampling

The biological communities in natural and artificial habitats were sampled using ten 25 x 25 cm quadrats. Five quadrats were placed haphazardly on mid-shore seaward-facing surfaces in each of two patches (approx. 20 m long, ≥20 m apart) in each site. We sampled steep/vertical surfaces (60–90°) on walls and sloping/horizontal surfaces (0–40°) on rock armour. Surface inclination was matched at the natural site loosely paired with each artificial structure. Surfaces with rugosity features >10 cm were avoided. This was on account of the small size (25 x 25 cm) of the experimental habitat units we wished to produce: (i) to avoid the surface being dominated by a single microhabitat feature; and (ii) to avoid size/integrity issues when producing and deploying the units.

The percent cover of canopy algae within quadrats was recorded then the canopy was removed by cutting just above the holdfast. Mobile fauna were shaken from the canopy and counted. The percent cover of sub-canopy algae and encrusting fauna, and counts of mobile fauna remaining within the quadrat, were then recorded. Barnacles and cryptic gastropods were counted from photoquadrats.

3.1.3 Topographic Sampling

The topography of each 25 x 25 cm quadrat was recorded using structure-from-motion (SfM) photogrammetry. All organisms were removed from within quadrats and the substrate was cleaned using a wire brush. A 50 x 50 cm checkerboard frame, with six control points covering three dimensions, was placed centrally around each cleared area. Photographs were taken from each corner angled at 45° towards the centre. Then 16 overlapping perpendicular photographs were taken in a four-by-four grid. From the total of 20 photographs per quadrat, we generated accurately-scaled (0.1 mm) DEMs with Cartesian co-ordinates using Agisoft Photoscan Professional v1.4 (Agisoft LLC, 2018). The central 25 x 25 cm area was clipped from each model so that the final topography sample was the substrate directly beneath the biological community sampled.

3.2 Step 2 – Biological Selection

To identify the 'best' and 'worst' natural substrate samples for our three hypothetical eco-engineering objectives, three corresponding biodiversity indices were calculated: (A) Richness; (B) Diversity Deficit; and (C) Rare Taxa. Each index was used to rank the 270 natural quadrats sampled (Fig. S1). The top and bottom 5–10% of quadrats in each ranked list were selected as the 'best' and 'worst' sample subsets. This equated to 13–27 samples in each 'best' or 'worst' subset. We considered this a reasonable balance between selecting only the highest/lowest scores, whilst retaining large enough sample sizes to maintain power to detect associations in the subsequent topographic selection step. The exact number in each subset varied according to sensible cut-offs for each index – this was necessarily subjective, given that there were many joint ranks.

*3.2.1 (A) Richness Index (***R***)*

The Richness Index (*R*) was calculated as the number of taxa per quadrat. Richness in natural quadrats ranged from 1 to 20 (mean 8.3 ± 4.1SD) (Fig. S1a). Natural quadrats were ranked from high to low *R*. The top 14 quadrats contained >16 taxa (*R* = 17–20). These were selected as the 'best' samples. They were all sampled from sloping/horizontal surfaces. The bottom 24 quadrats from matching substrate inclination contained <5 taxa (*R* = 1–4). To reduce this bottom selection, only quadrats from sites in which some had scored above average for *R* (*R* ≥ 8.3) were included. This ensured that low richness was not due to paucity in the local species pool, thus there was higher likelihood that topography had contributed to the low *R* scores. The bottom 15 quadrats that met this criterion were selected as the 'worst'.

*3.2.2 (B) Diversity Deficit Index (***DD***)*

The Diversity Deficit Index (*DD*) was derived by identifying key characteristic members of the mid-shore community that were consistently present in natural quadrats but absent or consistently less abundant in artificial quadrats. Eight diversity-deficit taxa groups were identified using SIMPER analysis (Table S2). Each natural quadrat was scored and ranked according to the number of these taxa groups that were present in higher than average abundances (i.e. > mean across all natural quadrats; Table S2). The top 29 quadrats contained higher than average abundances of more than four of the eight groups (*DD* = 5–6) and were selected as the 'best' samples (Fig. S1b). These were all sampled from sloping/horizontal surfaces. The bottom 28 quadrats from matching substrate inclination did not contain any diversity-deficit groups in higher than average abundance (*DD* = 0) and were selected as the 'worst'.

*3.2.3 (C) Rare Taxa Index (***RT***)*

The Rare Taxa Index (*RT*) was derived by identifying taxa that occurred most infrequently in our survey (i.e. recorded in ≤5% quadrats sampled). Nine rare taxa groups were identified (Table S3). Each natural quadrat was scored and ranked according to the number of these taxa groups that were present. The top 16 quadrats contained more than two of the nine groups (*RT* = 3–4) and were selected as the 'best' samples (Fig. S1c). These were all sampled from sloping/horizontal surfaces. The bottom 99 quadrats from matching substrate inclination did not contain any rare groups (*RT* = 0). To reduce this bottom selection, only quadrats from sites in which some had scored highly for *RT* (*RT* > 2) were included. This ensured that the absence of rare taxa was not because they were absent at the site level, thus there was higher likelihood that topography had contributed to the zero *RT* scores. The bottom 23 quadrats that met this criterion were selected as the 'worst'.

3.3 Step 3 – Topographic Selection

This step aimed to identify and select features of substrate topography that were characteristic of the 'best' but not the 'worst' quadrat samples for each biodiversity index. We first identified the most important topographic variables for discriminating between the 'best' and 'worst' subsets for each index (see details below). These variables were then used to re-rank the 'best' subsets and to select five 'best candidate' quadrats for each biodiversity index. 'Best candidates' were thus the 'best' in terms of biodiversity scores and importantly, had meaningful topographies that were able to distinguish them from the 'worst'. Therefore, features of the underlying topography are likely to have contributed, at least in part, to their high biodiversity scores.

For each quadrat, 13 topographic variables were calculated from the DEMs of the 25 x 25 cm substrate areas (Table 1). To identify the most important variables for discriminating between the 'best' and 'worst' subsets, we used two statistical methods based on a random forest framework. This allowed us to review variable importance and provide estimates of class prediction skill (i.e. 'best'/'worst' subset), whilst being robust to correlation within predictors (Breiman, 2001). We first used 10-fold (5-repeat) cross-validated recursive feature selection (CV-RFS) within the 'caret' package in R (Kuhn, 2008; R Development Core Team 2011) to identify the best reduced models for predicting class membership of quadrats (Table S5) and to calculate variable importance ranks (Fig. 3). We then used the 'randomForest' package in R (Liaw & Wiener, 2002) with 500 trees to validate variable importance scores and ranks within those best reduced models (Fig. 3), and provide overall model performance (i.e. prediction error rates; Table S6).

The best performing model for predicting the ‘best’ and ‘worst’ quadrat subsets for the Richness Index (*R*) included four topographic variables (Fig. 3a; Table S5a) and had a 3% prediction error rate (Table S6a). The best model for predicting the Diversity Deficit Index (*DD*) included seven variables (Fig. 3b; Table S5b) and had a 16% error rate (Table S6b). The best model for predicting the Rare Taxa Index (*RT*) included all 13 variables (Fig. 3c; Table S5c) and had a 31% error rate (Table S6c). Variable importance ranks from the CV-RFS analysis, and corroborated by the additional random forest analysis, revealed the top three most important variables for model performance for each biodiversity index (Fig. 3; Table 1). The ‘best’ quadrats for each of the three biodiversity indices were scored according to the number of these key topographic variables that had above average values (i.e. > mean of all ‘best’ quadrats for each index). The ‘best’ quadrats were then re-ranked according to these scores and the top five quadrats for each biodiversity index were selected as the ‘best candidates’.

3.4 Step 4 – Engineering Selection

The DEMs of the five ‘best candidate’ quadrats selected for each biodiversity index were inspected for their suitability for moulding and casting into eco-engineering habitat units. The overall height (and therefore weight) of units was considered for practicality and feasibility of deployment. For us, deployment would require manual handling to install experimental units on artificial structures. For scaled-up eco-engineering intervention, different engineering considerations may apply. The fragility and completeness of substrate features when the 25 x 25 cm quadrat area was clipped from the DEM was also considered. For example, if this resulted in partial loss of continuous features of topography that may have influenced the distribution of species on the natural shore (e.g. a ridge adjacent to an indentation that would have retained water), the quadrat was considered unsuitable. Subjectivity employed at this stage maximised the chances that eco-engineered habitat units could replicate the topographic (and thus physico-environmental) conditions available to species on the natural shores from which they were modelled. Ultimately, one 'best' quadrat was selected for each biodiversity index and the DEMs of these were converted to stereolithography (STL) files for mould creation.

3.5 Step 5 – Manufacture

The STL files of the three selected 'best' natural topography samples were 3D printed on a Prusa MK3 printer using polylactic acid, with 215°C extruder temperature and 60°C bed temperature. Cura software was used for slicing the STL files into machine-readable g-code. Mould-making silicone rubber was poured in layers over the printed samples until 10 mm thick and cured for 16 h. A rigid support shell was built around each mould using two layers of Plasti-Paste© urethane resin and cured for two hours. Concrete was poured into the moulds to cast habitat units replicating the original topography samples. These were cured in water for 30 days.

4. Results

By following our five-step process (Fig. 1), we selected three of the 'best' natural topography samples from our baseline survey to promote three hypothetical eco-engineering objectives. We then replicated them into three experimental-scale eco-engineering habitat units (Fig. 4).

When plotted amongst all 270 natural quadrats sampled, the 'best' biological subsets (i.e. the top 5–10% of biodiversity scores) were clearly dissimilar to the 'worst' (i.e. the bottom 5–10%) in terms of their multivariate species compositions (Fig. 5 left). This was largely pre-determined, given that the biological selection used elements of these full assemblages to identify and select the 'best' and 'worst' subsets. The 'best' selected quadrats for the *R* and *DD* Indices (Figs 5a,b left) were more similar to one another than the 'best' subsets for the

RT Index (Fig. 5c left). Numerous quadrat samples *not* selected by our process apparently had very similar community structure to those that were (Fig. 5 left). This likely reflects the use of univariate biodiversity indices for selection, which inevitably obscure much detail in community structure.

The three biodiversity indices (Fig. 5 middle) and the top three topographic variables (Fig. 5 right) used in the selection process were correlated with the direction of separation between the 'best' and 'worst' subsets for each index (Fig. 5 left). However, the 'best candidate' samples and the ultimately-selected 'best' quadrats were not always plotted in the quadrant of maximum values for these (i.e. in the top right corner of the data cloud; Fig. 5 left). For example, for *DD* (Fig. 5b left), several 'best candidates', including the ultimately-selected 'best' sample, plotted relatively central. These quadrats did not have the highest *DD* scores compared to others in the 'best' subset. Neither did they have the highest values for VRM (cm), Slope (mm) and Rugosity (mm). Nevertheless, the combination of being in the top 5–10% of *DD* scores and having above average topography scores led to them being shortlisted.

The manufactured habitat units were deployed experimentally on artificial structures around Irish Sea coasts during 2019. While monitoring is ongoing, preliminary observations were encouraging. Limpet recruits appeared in pools and shaded channels provided by the replicated natural topography within one week (Figs 6a,c). Juvenile and adult limpets were again observed in these refuge areas several months later (Figs 6b,d), in some cases creating grazing halos amongst pioneer algal growth (Fig. 6d).

5. Discussion

We propose a novel five-step approach for designing natural topography-based eco-engineering habitat units for marine artificial structures. We applied the approach to design three experimental-scale units for intertidal artificial structures in our region. Each design targeted one of three hypothetical eco-engineering objectives: (A) to maximise the richness of colonising communities; (B) to promote local rocky reef species that are normally deficient on artificial structures; and (C) to promote rocky reef species that are rare in our region. The habitat units replicated the topography from within three of the 'best' natural rocky reef quadrat samples from our baseline survey, and observations of early colonisation are promising.

The habitat design to maximise richness had high mm-scale Vector Ruggedness Measure (VRM), Arc-Chord Ratio and Surface Area: Planar Area Ratio. The designs to reduce the diversity deficit and promote rare species also had high VRM, as well as high mm-scale Rugosity and Slope. These parameters each indicate high surface ruggedness and complexity: qualities known to be instrumental in supporting diversity on intertidal reefs by modulating temperature, light, humidity and water flow (Aguilera et al., 2019; Guichard & Bourget, 1998; Meager et al., 2011), and providing refuge from predation (Menge & Lubchenco, 1981). Millimetre-scale ruggedness influences barnacle settlement (MacArthur et al., 2019), creating habitat structure and promoting succession of colonising communities (Harley, 2006). These were not the only topographic variables that characterised the surfaces replicated in our habitat units. Several others were similarly associated with the 'best' samples for biodiversity metrics and were unintended features of our topographic designs (Fig. S4). In contrast, Topographic Position Index, the position of a point in relation to its neighbours, was inversely associated (Fig. S4). Thus, surfaces with more concave than convex features – more dips than bumps – were better for biodiversity. This reflects the value of water-retaining features, even at the mm–cm scale, for intertidal biodiversity (Firth et al., 2013).

A number of topographic variables combined were necessary for accurate discrimination between the ‘best’ and ‘worst’ quadrat subsets for each biodiversity index. The Richness Index required the fewest (i.e. 4) topographic variables to predict the ‘best’ samples and had the highest accuracy. This suggests that species richness on the rocky shores we sampled was closely associated with those features of the underlying topography. Promoting richness, therefore, would be a realistic target of topography-based eco-engineering for intertidal structures in our region. In contrast, for the Rare Taxa Index, all 13 topographic variables were required in the best predictive model and this still had relatively low accuracy. This was likely due to the observed greater dissimilarity amongst the ‘best’ samples for this index. It may reflect a more complex relationship between rare taxa and substrate topography, e.g. if different rare species have different specialist niche requirements (Verberk, 2011). A single-species approach may, therefore, have been more effective for identifying topographies (at the 25 x 25 cm scale) to promote rare species in our region. Alternatively, it may indicate a relatively weak relationship, i.e. that topography was a poor predictor of rare species, and their distributions were driven by other factors (as seen in different systems: Gunatilleke et al., 2006, Wang et al., 2009). In this case, a topography-based eco-engineering approach may not be suitable for the rare species we were targeting. Further work is necessary to improve our understanding of which species and communities are feasible targets for natural topography-based eco-engineering.

The fact that four or more topographic variables were required to differentiate the ‘best’ from the ‘worst’ samples for all three biodiversity indices lends support to our suggestion that habitat designs based on a single element of topography (e.g. regularly-shaped pits/grooves) are unlikely to be effective in achieving community-level objectives, compared with an approach that replicates natural topography directly. Each element of topography influences and is influenced by its surroundings, within the context of the wider topographic mosaic. It also suggests that shortlisting our ‘best candidates’ based on only the top three topographic variables was perhaps over-simplistic. The quadrat samples on which our designs were modelled are unlikely to have been the absolute best for biodiversity *or* the most aligned with the key topographic drivers out of all the samples from which we could have selected. It was inevitable that selecting samples based on biodiversity, topography and engineering practicality would lead to compromise. However, our selection process ensured that each of the ultimately-selected topography designs satisfy three criteria: 1) the samples were amongst the top 5–10% of biodiversity scores, thus the units have the capacity to support the ‘best’ biodiversity for our eco-engineering objectives; 2) the samples scored above average for the top three most important topographic variables for biodiversity, thus meaningful features of the topography were likely to have contributed to their high biodiversity scores; and 3) there were no practical barriers to replicating the sample topography in concrete habitat units, thus the units have the capacity to replicate the topography-driven physico-environmental conditions available to species on the natural shore from which they were modelled.

Given that eco-engineering options and objectives vary for different structures in different locations, our approach can be adapted and applied to user-specific scenarios. In our application, we chose three community-level objectives that could be reasonable goals of eco-engineering. Objectives may alternatively focus on individual target species of conservation (Perkol-Finkel et al., 2012) or commercial concern (Langhamer & Wilhelmsson, 2009). Or they may focus on the functional value of organisms/assemblages (Strain et al., 2018a). If objectives are multi-functional, or include a mixture of community-level and species-specific targets, more than one ‘best’ topography could be replicated and arranged in a mosaic. They could also be combined with other single-microhabitat interventions from the eco-engineering toolkit, like rock pools or crevices. Multiple ‘best’ topographies, each targeting a different species/assemblage, would likely fulfil their roles better than one single topography that is ‘OK’ for everything all at once. However, further experimental work is necessary to understand what objectives can feasibly be targeted using topography-based eco-engineering and how different patches would interact. Principally, it is critical that the objectives of eco-engineering are clear before applying our five-step process. This is a golden rule in restoration ecology (Ehrenfeld, 2000). The baseline survey would need to be planned and executed accordingly. Biodiversity metrics and topographic parameters used to identify optimal areas of topography to replicate would need to be relevant. Prior to this, though, the essential first step would be to determine whether replicating natural topography is likely to be effective for the eco-engineering objectives and site-specific characteristics in the first place. If target species are not likely to be influenced by substrate topography, or if the context of the site is such that the influence of topography is likely to be overwhelmed by other factors (e.g. water chemistry, larvae/propagule/food supply, disturbance/hydrodynamic regime), then this approach is probably unsuitable.

If the user determines that our approach *is* suitable, the next question would be one of scale, both spatial and temporal. The spatial scale of sampling units in our baseline survey matched the small size of the experimental units we wished to produce (25 x 25 cm). We measured topographic variables at the mm- and cm-scale since we anticipated encountering taxa that are influenced by habitat complexity at these scales; e.g. larval settlement and refugia for mobile invertebrates (MacArthur et al., 2019). These scales are likely to be relevant for early lifeforms of many rocky reef species but may be largely irrelevant for larger-bodied adult fish and crustaceans that require much larger habitat niches (Caddy & Stamatopoulos, 1990). Although higher trophic level organisms rely on small-bodied organisms and primary producers for food and habitat, eco-engineering designs targeting them would also need to target larger-scale topography. We undertook our baseline survey at the end of summer when intertidal communities are likely to be well-developed in our region, i.e. with little sand-scour from storms. Baseline surveys should, in practice, match the timing when target species/communities/life stages are expected to be encountered. Repeat surveys (seasonal, annual) would improve confidence in species distributions but may not be feasible in the timeframe of planning eco-engineering enhancements for development proposals. Other key considerations are the orientation, tidal level/depth and aspect of the structures subject to eco-engineering intervention. Habitat units featuring topography from a horizontal orientation would be unlikely to provide the same niche conditions for organisms if installed vertically, and vice-versa (Connell, 1999), although this is yet to be formally tested in an eco-engineering context. Similarly, features important for niche provision are likely to be different for different intertidal levels, subtidal depths, and aspects to wave/current and sunlight exposure (Firth et al., 2016b; Guichard & Bourget, 1998; Letourneur et al., 2003; Menge & Lubchenco, 1981). We recommend matching each of these factors in baseline surveys to the context of the structures to be eco-engineered.

Finally, we do not suggest that this novel approach to eco-engineering marine structures should replace existing approaches that mimic discrete microhabitats on structure surfaces. Indeed, different approaches may be complementary. Decision-makers should weigh-up the options available to them according to their biodiversity objectives, engineering limitations and budget, consulting the evidence base for what they can expect the cost-benefits to be. We do not specify how to physically apply scaled-up areas of natural reef topography to different types of artificial structures, since the mechanics of this are subject to innovation by designers and civil engineers. Formliners, textured encasements and specialised moulds have been used in eco-engineering previously (Firth et al., 2014; Perkol-Finkel & Sella, 2016; Perkol-Finkel et al., 2018; Sella & Perkol-Finkel, 2015; see also the Living Seawalls project https://www.sims.org.au/page/130/living-seawalls-landing) and could feasibly replicate natural topography on structure surfaces during construction or retrospectively. Although likely to be more expensive than manually drilling holes and crevices into structure surfaces, the development and use of specialised formliners to impart textured surfaces on concrete is well-established in the construction sector to add aesthetic value to products. Formliners can now be re-used repeatedly, leading to by-area cost reductions and making their use economically viable (Naylor et al. 2017). Using formliners or moulds for the application described in this paper, however, would involve a bespoke ecologically-driven design process, which may add to the cost of production. Some of the design-associated costs, however, may already exist in project budgets for new developments. For example, environmental assessments may already include surveys of target species/communities in local natural habitats. Further work is needed to rigorously weigh up the cost-benefits of all the different approaches to eco-engineering artificial structures (but see Naylor et al., 2017). In particular, for our proposed natural topography-based addition to the eco-engineering toolkit, understanding the effects of patch size and configuration on the potential for topographies to target certain biodiversity outcomes will be key to assessing the potential costs and benefits of scaled-up implementation. Nevertheless, digital habitat modelling and 3D printing technologies have become increasingly affordable and accessible in recent years (Canessa et al., 2013; D'Urban Jackson et al., 2020), opening the door to great unrealised potential for natural topography-based eco-engineering.

Acknowledgements

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 2014–2022. Data collection was also part-funded by Aberystwyth University through the AberForward scheme. Thanks to Derek Holmes, John Ryan, Jennifer

Coughlan and Veronica Farrugia-Drakard of UCD, Harry Thatcher and Hannah Earp of Aberystwyth University, and Siobhan Vye and Tim D'Urban Jackson of Bangor University, plus all other research assistants for considerable help in the workshop/field. Thanks also to authorities/landowners for granting site access. Finally, we are grateful to two anonymous reviewers for their insightful and constructive comments that improved the manuscript.

References

Aguilera, M. A., Arias, R. M., & Manzur, T. (2019). Mapping microhabitat thermal patterns in artificial breakwaters: Alteration of intertidal biodiversity by higher rock temperature. *Ecology and Evolution*, *9*(22), 12915–12927. doi: 10.1002/ece3.5776

Airoldi, L., & Bulleri, F. (2011). Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *PloS ONE*, *6*(8), e22985. doi: 10.1371/journal.pone.0022985

Bishop, M. J., Mayer-Pinto, M., Airoldi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., … Dafforn, K. A. (2017). Effects of ocean sprawl on ecological connectivity: impacts and solutions. *Journal of Experimental Marine Biology and Ecology*, *492*, 7–30. doi: 10.1016/j.jembe.2017.01.021

Breiman, L. (2001). Random Forests. *Machine Learning*, *45*, 5–32.

Caddy, J. F., & Stamatopoulos, C. (1990). Mapping growth and mortality rates of crevice-dwelling organisms onto a perforated surface: the relevance of "cover" to the carrying capacity of natural and artificial habitats. *Estuarine, Coastal and Shelf Science*, *31*, 87–106. doi: 10.1016/0272-7714(90)90030-U

Canessa, E., Fonda, C., & Zennaro, M. (2013). *Low-cost 3D printing for science, education* *and sustainable development* (E. Canessa, C. Fonda, & M. Zennaro, eds.). ICTP Science Dissemination Unit.

Chapman, M. G., & Blockley, D. J. (2009). Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. *Oecologia*, *161*(3), 625–635. doi: 10.1007/s00442-009-1393-y

Chapman, M. G., & Underwood, A. J. (2011). Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. *Journal of Experimental Marine Biology and Ecology*, *400*, 302–313. doi: 10.1016/j.jembe.2011.02.025

Connell, S. D. (1999). Effects of surface orientation on the cover of epibiota. *Biofouling*, *14*(3), 219–226. doi: 10.1080/08927019909378413

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. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1920), 20192383. doi: 10.1098/rspb.2019.2383

Dafforn, K. A., Glasby, T. M., Airoldi, L., Rivero, N. K., Mayer-pinto, M., & Johnston, E. L. (2015). Marine urbanization: an ecological framework for designing multifunctional artificial structures. *Frontiers in Ecology and the Environment*, *13*(2), 82–90. doi: 10.1890/140050

Ehrenfeld, J. G. (2000). Defining the limits of restoration: The need for realistic goals. *Restoration Ecology*, *8*(1), 2–9. doi: 10.1046/j.1526-100X.2000.80002.x

Evans, A. J., Firth, L. B., Hawkins, S. J., Hall, A. E., Ironside, J. E., Thompson, R. C., & Moore, P. J. (2019). From ocean sprawl to blue-green infrastructure – A UK perspective on an issue of global significance. *Environmental Science and Policy*, *91*(August 2018), 60–69. doi: 10.1016/j.envsci.2018.09.008

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. *Marine and Freshwater Research*, *67*, 123–130. doi: 10.1071/MF14244

Firth, L. B., Airoldi, L., Bulleri, F., Challinor, S., Chee, S. -Y., Evans, A. J., … Hawkins, S. J. (2020). Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development. *Journal of Applied Ecology, 57*(9), 1762–1768. doi: 10.1111/1365-2664.13683

Firth, L. B., Knights, A. M., Bridger, D., Evans, A. J., Mieszkowska, N., Moore, P. J., … Hawkins, S. J. (2016a). Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanography and Marine Biology: An Annual Review, 54,* 193–269.

Firth, L. B., Thompson, R. C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T. J., … Hawkins, S. J. (2014). Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, *87*(SI), 122–135. doi: 10.1016/j.coastaleng.2013.10.015

Firth, L. B., Thompson, R. C., White, F. J., Schofield, M., Skov, M. W., Hoggart, S. P. G., … Hawkins, S. J. (2013). The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. *Diversity and Distributions*, *19*(10), 1275–1283. doi: 10.1111/ddi.12079

Firth, L. B., White, F. J., Schofield, M., Hanley, M. E., Burrows, M. T., Thompson, R. C., … Hawkins, S. J. (2016b). Facing the future: The importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. *Marine and Freshwater Research*, *67*(1), 131–143. doi: 10.1071/MF14163

Guichard, F., & Bourget, E. (1998). Topographic heterogeneity, hydrodynamics, and benthic community structure:a scale-dependent cascade. *Marine Ecology Progress Series*, *171,* 59–70. doi: 10.3354/meps171059

Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Esufali, S., Harms, K. E., Ashton, P. M. S., Burslem, D. F. R. P., & Ashton, P. S. (2006). Species-habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology*, *22*(4), 371–384. doi: 10.1017/S0266467406003282

Hall, A. E., Herbert, R. J., Britton, R. J., Boyd, I., & George, N. (2019). Shelving the coast with vertipools: Retrofitting artificial rock pools on coastal structures as mitigation for coastal squeeze. *Frontiers in Marine Science*, *6*(JUL), 1–11. doi: 10.3389/fmars.2019.00456

Hall, A. E., Herbert, R. J. H., Britton, J. R., & Hull, S. L. (2018). Ecological enhancement techniques to improve habitat heterogeneity on coastal defence structures. *Estuarine, Coastal and Shelf Science*, *210*(June), 68–78. doi: 10.1016/j.ecss.2018.05.025

Harley, C. (2006). Effects of physical ecosystem engineering and herbivory on intertidal community structure. *Marine Ecology Progress Series*, *317*, 29–39. doi: 10.3354/meps317029

Heery, E. C., Bishop, M. J., Critchley, L. P., Bugnot, A. B., Airoldi, L., Mayer-Pinto, M., … Dafforn, K. A. (2017). Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology*, *492*, 31–48. doi: 10.1016/j.jembe.2017.01.020

Hereu, B., Zabala, M., Linares, C., & Sala, E. (2005). The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Marine Biology*, *146*(2), 293–299. doi: 10.1007/s00227-004-1439-y

Huston, M. A. (1999). Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos, 86*(3), 393–401. doi: 10.2307/3546645

Jackson, A. C., & McIlvenny, J. (2011). Coastal squeeze on rocky shores in northern Scotland and some possible ecological impacts. *Journal of Experimental Marine Biology and Ecology*, *400*(1–2), 314–321. doi: 10.1016/j.jembe.2011.02.012

Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of Statistical Software*, *28*, 1–26. Retrieved from http://www.jstatsoft.org/

Langhamer, O., & Wilhelmsson, D. (2009). Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes - A field experiment. *Marine Environmental Research*, *68*(4), 151–157. doi: 10.1016/j.marenvres.2009.06.003

Langhamer, O., Wilhelmsson, D., & Engstrom, J. (2009). Artificial reef effect and fouling impacts on offshore wave power foundations and buoys - a pilot study. *Estuarine, Coastal and Shelf Science*, *82*(3), 426–432. doi: 10.1016/j.ecss.2009.02.009

Letourneur, Y., Ruitton, S., & Sartoretto, S. (2003). Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, *83*, 193–204. doi: 10.1017/S0025315403006970h

Levin, S. A. (1974). Dispersion and population interactions. *American Society of Naturalists*, *108*, 207–228.

Liaw, A., & Wiener, M. (2002). Classification and regression by RandomForest. *R News*, *2*(3), 18–22. Retrieved from https://www.researchgate.net/publication/228451484

Loke, L. H. L., Jachowski, N. R., Bouma, T. J., Ladle, R. J., & Todd, P. a. (2014).

Complexity for artificial substrates (CASU): software for creating and visualising habitat complexity. *PloS ONE*, *9*(2), e87990. doi: 10.1371/journal.pone.0087990

MacArthur, M., Naylor, L. A., Hansom, J. D., Burrows, M. T., Loke, L. H. L., & Boyd, I. (2019). Maximising the ecological value of hard coastal structures using textured formliners. *Ecological Engineering: X*, *1*, 100002. doi: 10.1016/j.ecoena.2019.100002

Meager, J. J., Schlacher, T. A., & Green, M. (2011). Topgraphic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Marine Ecological Progress Series*, *428*, 1–12. doi: 10.3354/meps09124

Menge, B. A., & Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs*, *51*(4), 429–450.

Morris, R. L., Chapman, M. G., Firth, L. B., & Coleman, R. A. (2017). Increasing habitat complexity on seawalls: Investigating large- and small-scale effects on fish assemblages. *Ecology and Evolution*, *7*(22), 9567–9579. doi: 10.1002/ece3.3475

Moschella, P. S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J. M., Bacchiocchi, F., … Hawkins, S. J. (2005). Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coastal Engineering*, *52*(10–11), 1053–1071. doi: 10.1016/j.coastaleng.2005.09.014

Naylor, L. A., Kippen, H., Coombes, M. A., Horton, B., MacArthur, M., & Jackson, N. (2017). *Greening the Grey: A Framework for Integrated Green Grey Infrastructure (IGGI)*. University of Glasgow.

Ng, C. S. L., Lim, S. C., Ong, J. Y., Teo, L. M. S., Chou, L. M., Chua, K. E., & Tan, K. S. (2015). Enhancing the biodiversity of coastal defence structures: transplantation of nursery-reared reef biota onto intertidal seawalls. *Ecological Engineering*, *82*, 480–486. doi: 10.1016/j.ecoleng.2015.05.016

O'Shaughnessy, K. A., Hawkins, S. J., Evans, A. J., Hanley, M. E., Lunt, P., Thompson, R. C., … Firth, L. B. (2020). Design catalogue for eco-engineering of coastal artificial structures: a multifunctional approach for stakeholders and end-users. *Urban Ecosystems*, *23*(2), 431–443. doi: 10.1007/s11252-019-00924-z

Perkol-Finkel, S, & Sella, I. (2016). Blue is the new green - harnessing urban coastal infrastructure for ecological enhancement. In *Coastal Management: Changing Coast, Changing Climate, Changing Minds* (pp. 139–149). ICE Publishing.

Perkol-Finkel, S., Ferrario, F., Nicotera, V., & Airoldi, L. (2012). Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. *Journal of Applied Ecology*, *49*(6), 1457–1466. doi: 10.1111/j.1365-2664.2012.02204.x

Perkol-Finkel, S., Hadary, T., Rella, A., Shirazi, R., & Sella, I. (2018). Seascape architecture - incorporating ecological considerations in design of coastal and marine infrastructure. *Ecological Engineering*, *120*, 645–654. doi: 10.1016/j.ecoleng.2017.06.051

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. *Marine Pollution Bulletin*, *55*(1–6), 126–135. doi: 10.1016/j.marpolbul.2006.08.044

Sella, I., & Perkol-Finkel, S. (2015). Blue is the new green - ecological enhancement of concrete based coastal and marine infrastructure. *Ecological Engineering*, *84*, 260–272. doi: 10.1016/j.ecoleng.2015.09.016

Strain, E. M. A., Morris, R. L., Coleman, R. A., Figueira, W. F., Steinberg, P. D., Johnston,

E. L., & Bishop, M. J. (2018a). Increasing microhabitat complexity on seawalls can reduce fish predation on native oysters. *Ecological Engineering*, *120,* 637–644. doi: 10.1016/j.ecoleng.2017.05.030

Strain, E. M. A., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R. L., Bugnot, A. B., … Bishop, M. J. (2018b). Eco-engineering urban infrastructure for marine and coastal biodiversity: Which interventions have the greatest ecological benefit? *Journal of Applied Ecology, 55,* 426–441. doi: 10.1111/1365-2664.12961

Verberk, W. (2011). Explaining general patterns in species abundance and distributions. *Nature Education Knowledge, 3,* 38. Retrieved from https://www.nature.com/scitable/knowledge/library/explaining-general-patterns-in-species-abundance-and-23162842/

Waltham, N. J., & Sheaves, M. (2020). Thermal exposure risks to mobile tropical marine snails: Are eco-engineered rock pools on seawalls scale-specific enough for comprehensive biodiversity outcomes? *Marine Pollution Bulletin*, *156*, 111237. doi: 10.1016/j.marpolbul.2020.111237

Wang, Z., Ye, W., Cao, H., Huang, Z., Lian, J., Li, L., … Sun, I. F. (2009). Species-topography association in a species-rich subtropical forest of China. *Basic and Applied Ecology*, *10*(7), 648–655. doi: 10.1016/j.baae.2009.03.002

Wilhelmsson, D., & Malm, T. (2008). Fouling assemblages on offshore wind power plants and adjacent substrata. *Estuarine, Coastal and Shelf Science*, *79*(3), 459–466. doi: 10.1016/j.ecss.2008.04.020

Table 1 Topographic variables calculated from quadrat DEMs. Where indicated, variables were calculated at two scales (mm, cm) appropriate to the organisms present. Scale-independent variables were calculated once per quadrat. Rank Importance indicates the three most important variables for discriminating the 'best' from 'worst' quadrats for three biodiversity indices (Fig. 3). See Table S4 for references.

Variable	Scale	Definition	Rank Importance
Topographic Position Index (TPI)	mm	The relative elevation of a point to its neighbours.	
	cm		
Slope	mm	The angle of a surface.	*DD*2, *RT*2
	cm		
Rugosity (Rug.)	mm	The standard deviation of surface elevation.	*DD*3, *RT*1
	cm		
Curvature (Curv.)	mm	The rate and direction of surface change.	
	cm		
Vector Ruggedness Measure (VRM)	mm	The dispersal of surface aspects (surface unpredictability).	*R*1, *RT*3
	cm		*DD*1
Surface Area: Planar Area Ratio (SA:PA)	n/a	The area of surface contained within a 2D space.	*R*3
Typical Elevation	n/a	The net protrusion/depression of a surface.	
Arc-Chord Ratio (ACR)	n/a	Rugosity index quantifying 3D structural complexity.	*R*2

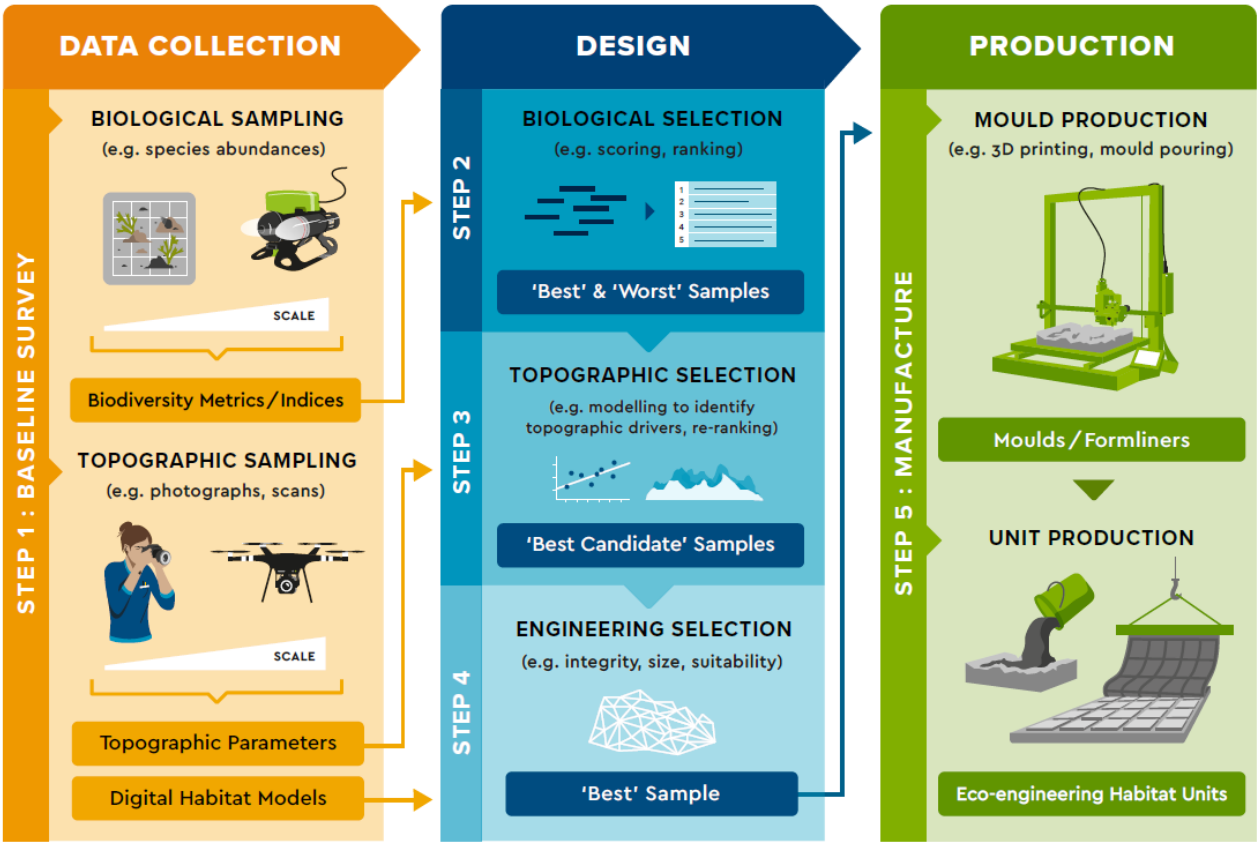

Figure 1 Five-step process for designing natural topography-based eco-engineering habitat units for marine artificial structures. Figure by Amy Dozier.

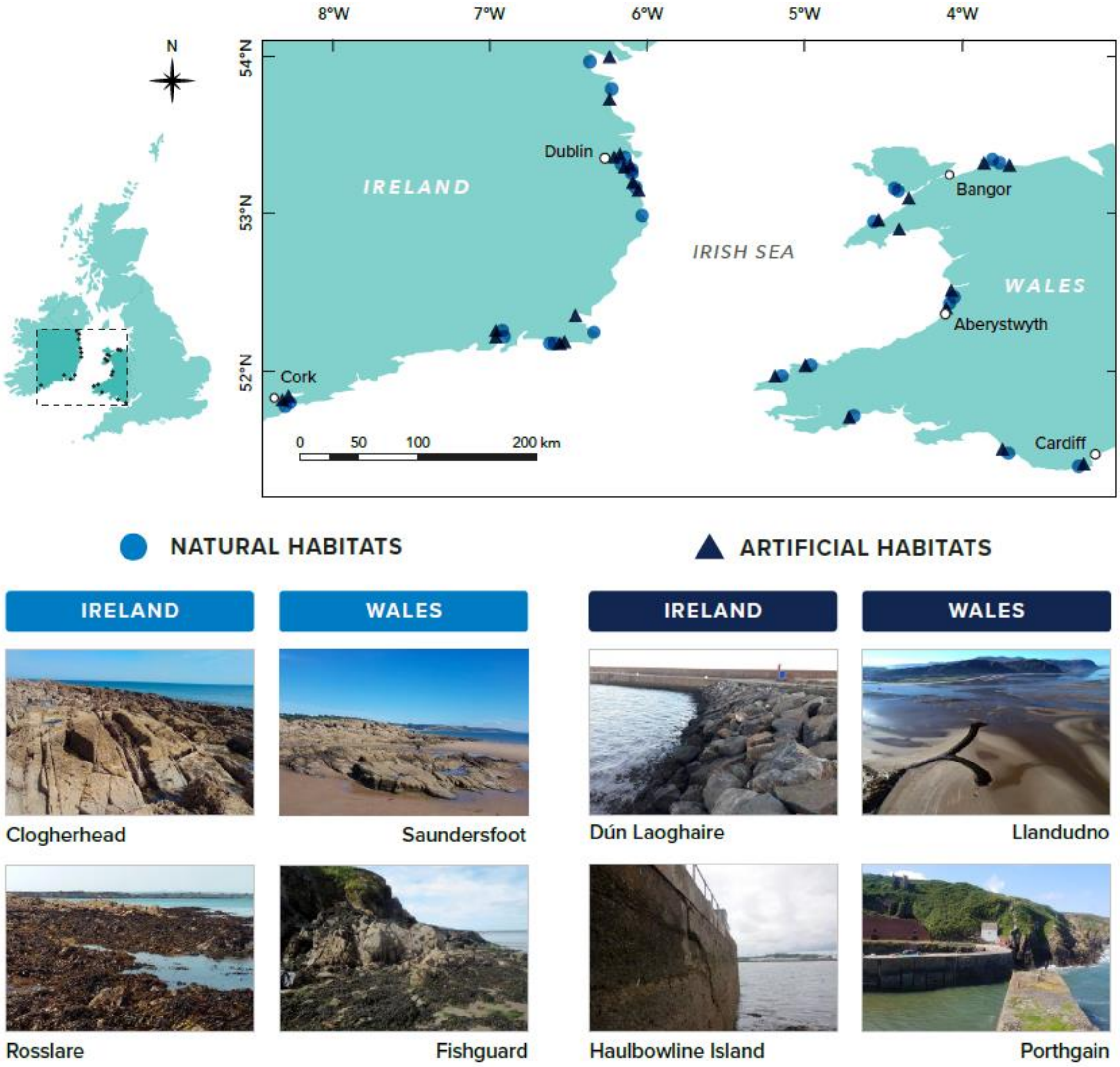

Figure 2 Fifty-four natural and artificial survey sites around Irish Sea coasts, with examples of intertidal rocky habitats surveyed (see Table S1 for site details). Figure by Amy Dozier.

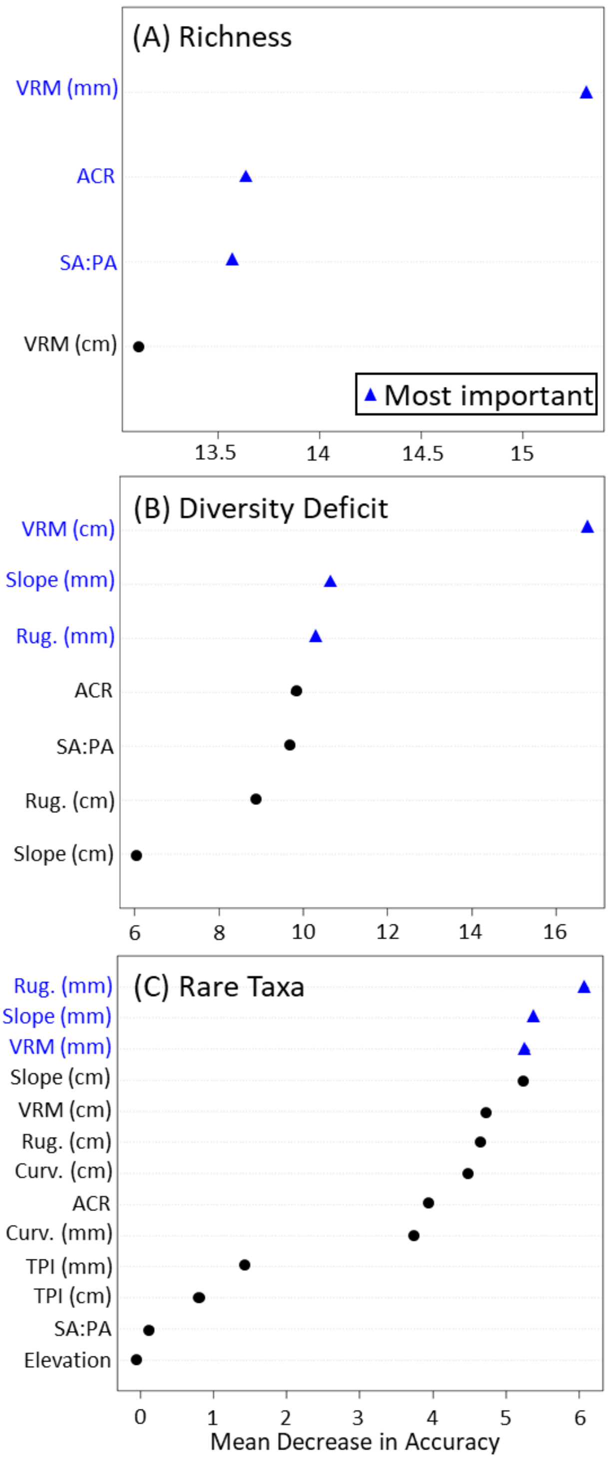

Figure 3 Variable importance plots indicating the three most important topographic variables (Table 1) for predicting quadrat membership to the 'best' and 'worst' subsets for three biodiversity indices (A–C). Analyses based on the best predictive models for each index (Table S5).

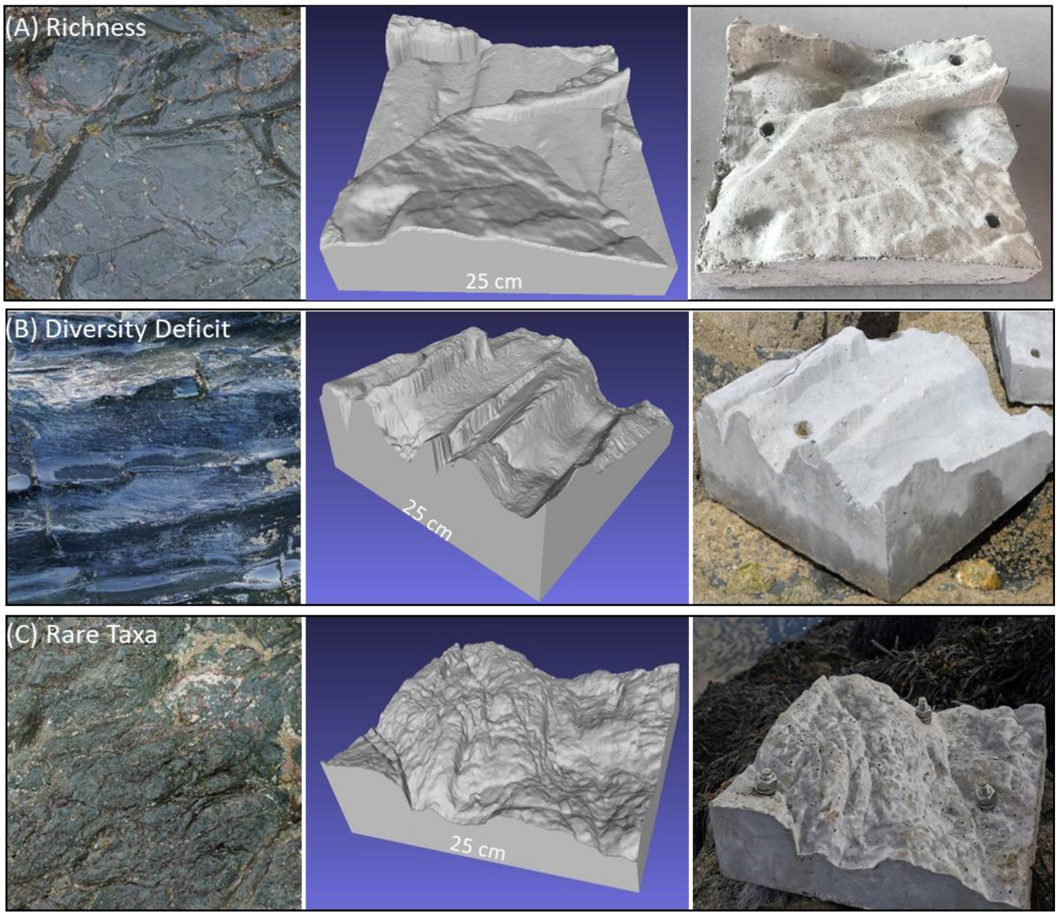

Figure 4 Left-to-right: *in situ* photographs, STLs and concrete habitat units of the 'best' selected topography samples for three biodiversity indices (A–C). Examples of the 'worst' samples are shown in Fig. S3.

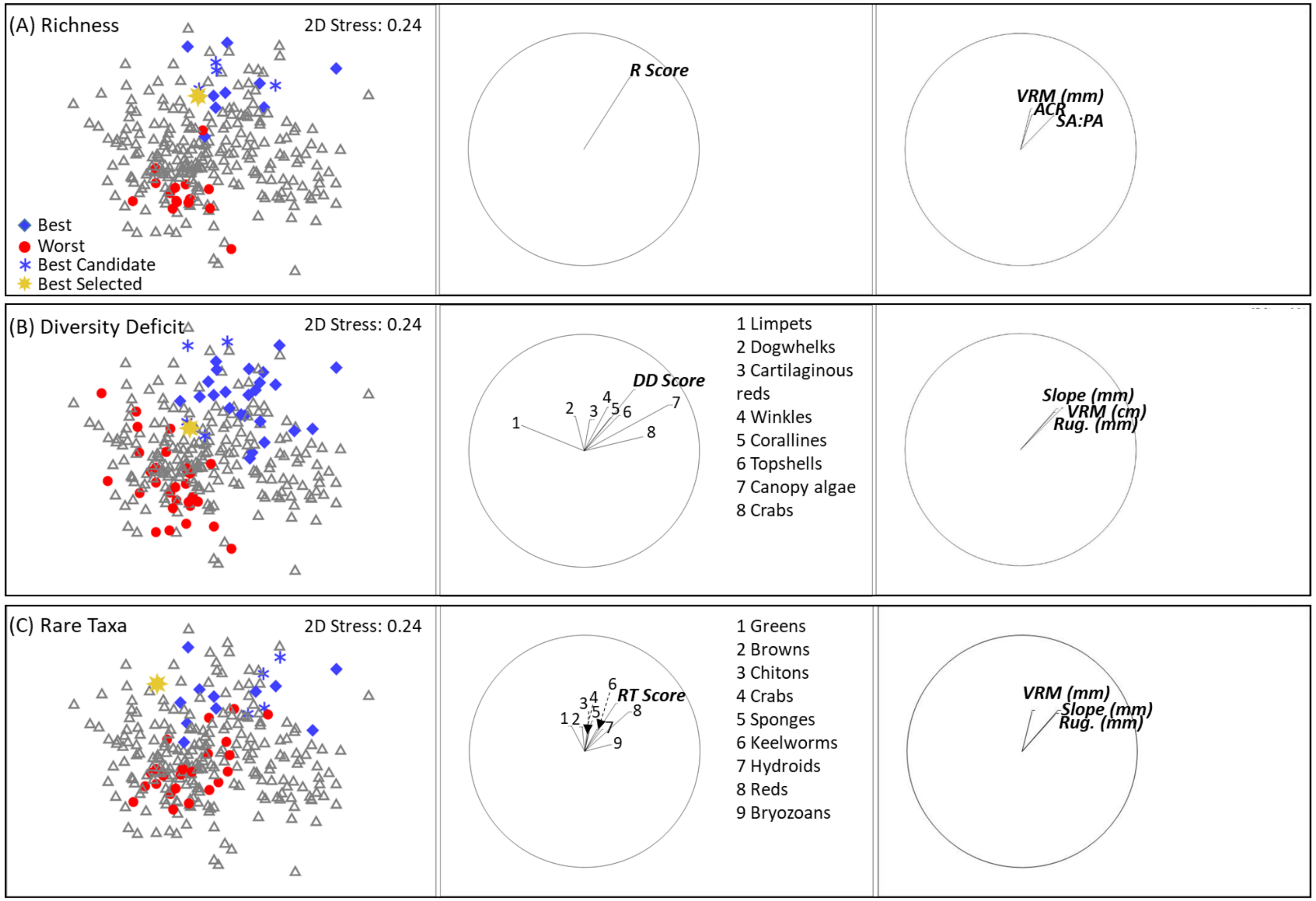

Figure 5 Left: nMDS ordination of multivariate species composition in 270 natural rocky reef quadrats. The ‘best’ and ‘worst’ quadrat subsets, five ‘best candidates’ and the ultimately-selected ‘best’ quadrats for three biodiversity indices (A–C) are highlighted. Middle/right: vectors represent the direction and strength of multiple Pearson correlations between biodiversity indices (middle) and topographic variables (right; Table 1) used in the selection process within the multi-dimensional space. Outer circles represent correlation of 1. Ordination based on Gower-Excluding 0–0 similarities of 4th-root transformed abundances. Analyses carried out in PRIMER v7 (PRIMER-E Ltd., 2015). Vector overlays of all 13 topographic variables are shown in Fig. S4.

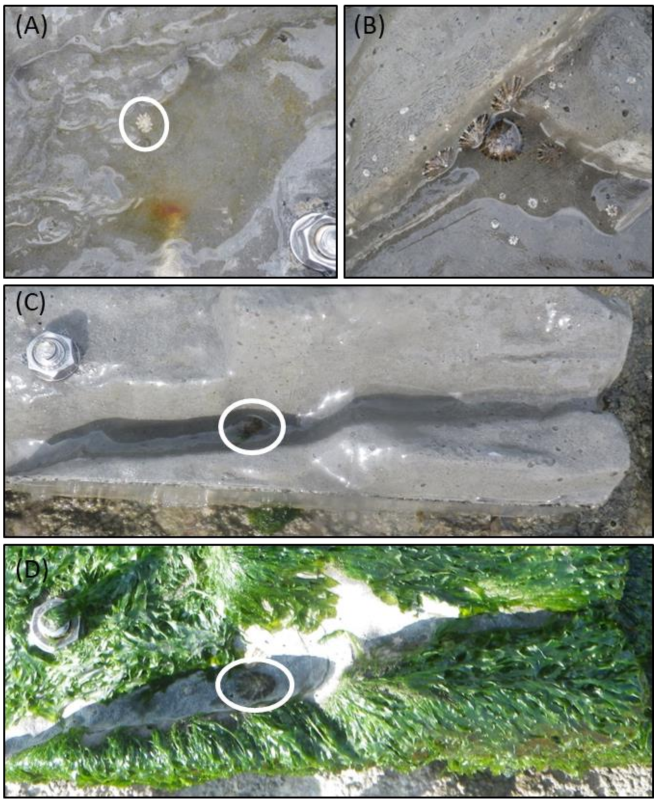

Figure 6 (A–B): Water pooling in depressions, with (A) limpet recruit on Rare Taxa habitat unit after one week and (B) adult and juvenile limpets on Richness habitat unit after four months. (C–D): Shaded channels on Diversity Deficit unit, with (C) juvenile limpet after one week and (D) limpet creating a grazing halo amongst pioneer *Ulva* after two months.