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Biodiversity in intertidal rock pools: Informing engineering criteria for artificial habitat enhancement in the built environment

Louise B. Firth [a,*], Meredith Schofield [a], Freya J. White [a], Martin W. Skov [a], Stephen J. Hawkins [a,b]

[a] *School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, United Kingdom*
[b] *Ocean and Earth Science, National Oceanography Centre Southampton, Waterfront Campus, University of Southampton, European Way, Southampton, Hampshire SO14 3ZH, United Kingdom*

A B S T R A C T

Coastal defence structures are proliferating to counter rising and stormier seas. With increasing concern about the ecological value of built environments, efforts are being made to create novel habitat to increase biodiversity. Rock pools are infrequent on artificial structures. We compared biodiversity patterns between rock pools and emergent rock and assessed the role of pool depth and substratum incline in determining patterns of biodiversity. Rock pools were more taxon rich than emergent substrata. Patterns varied with depth and incline with algal groups being more positively associated with shallow than deeper habitats. Substratum incline had little influence on colonising epibiota, with the exception of canopy algae in deeper habitats where vertical surfaces supported greater taxon richness than horizontal surfaces. The creation of artificial rock pools in built environments will have a positive effect on biodiversity. Building pools of varying depths and inclines and shore heights will provide a range of habitats, increase environmental heterogeneity, therefore creating more possible ecological niches, promoting local biodiversity.

Keywords:
Biodiversity
Conservation
Rock pool
Incline
Depth
Ecological engineering
Habitat enhancement
Artificial habitat
Environmental heterogeneity
Urbanisation

1. Introduction

Environmental heterogeneity promotes the coexistence of competitors, which would not be possible in homogenous environments (Levin, 1992), and therefore is an important mechanism in the maintenance of biological diversity (Levin, 1981; Firth and Crowe, 2008; Griffin et al., 2010). Huston (1979) argued that the environmental heterogeneity hypothesis was the only diversity hypothesis supported by convincing evidence. Traditionally, much of the empirical support for this assertion came from terrestrial (MacArthur and MacArthur, 1961; Tilman, 1994; Dufour et al., 2006; Healy et al., 2008) or freshwater systems (Vinson and Hawkins, 1998), but an increasing body of evidence continues to emerge from marine ecosystems (Gaston et al., 1995; Therriault and Kolasa, 2000; Francis and Hoggart, 2009; Yeager et al., 2011; Hoggart et al., 2012; Firth et al., 2013a). The occurrence of multiple habitat types has a strong influence on the number of species that can coexist. Once a species has become established in a given habitat, its persistence is ultimately determined by the complex interplay between changes in environmental conditions (Garrity, 1984; Williams and Morritt, 1995; Morritt et al., 2007; Firth et al., 2011; Wethey et al., 2011; O'Connor and Donohue, 2013) and species interactions (Jonsson et al., 2006; Moore et al., 2007; O'Connor and Crowe, 2008; Knights and Walters, 2010) both individually and in combination (Firth and Williams, 2009; O'Connor, 2009; Atalah and Crowe, 2010; Knights et al., 2012).

Marine intertidal systems comprise a variety of habitats with varying degrees of heterogeneity. Habitat complexity and spatial heterogeneity are important factors in the structure and functioning of rocky shore communities (Underwood and Denley, 1984; Menge et al., 1995), contributing to community diversity and species coexistence in marine benthic systems (Sebens, 1991; Johnson et al., 2003; Kostylev et al., 2005). In addition to the diversity of habitats available, the type and quality of the habitat is an important determinant of local biodiversity. Rock pools (hereafter pools) are ubiquitous features of rocky shores across the world. In comparison to emergent rock substrata relatively little is known about the processes determining the structure and functioning of biotic communities in pools (but see Underwood and Skilleter, 1996; van

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* Corresponding author. Current address: Ryan Institute, National University of Ireland Galway Ireland, University Road, Galway, Ireland. Tel.: +353 (0)91 493744.
E-mail address: louise.firth@nuigalway.ie (L.B. Firth).

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Tamelen, 1996; O'Connor and Crowe, 2005; Martins et al., 2007). Pools provide important nursery grounds (Orton, 1929; Norris, 1963; Lewis and Bowman, 1975; Thompson, 1980; Bennett, 1987; Delany et al., 1998), feeding habitat (Wai and Williams, 2006a,b; Noël et al., 2009) and refugia (Schonbeck and Norton, 1978; Underwood and Jernakoff, 1984; Moran, 1985; Fairweather, 1988) for a wide range of organisms. Biological communities of pools differ greatly to those on emergent rock. Rock pools can extend the upper vertical limits of many organisms that are susceptible to desiccation and whilst some species tend to aggregate in pools, other species avoid them (Johnson and Skutch, 1928; Goss-Custard et al., 1979; Metaxas and Scheibling, 1993; Araujo et al., 2006; Firth and Crowe, 2008, 2010; Firth et al., 2013a).

Although pools can offer refuge from the harsh conditions encountered on emergent rock (e.g. temperature and desiccation stress), they may also become stressful environments, with large fluctuations in temperature, salinity, pH, carbon dioxide and dissolved oxygen (Goss-Custard et al., 1979; Metaxas and Scheibling, 1994; Chan, 2000; Firth and Williams, 2009). Upper shore pools are exposed to longer periods of emersion and exhibit greater variability in environmental conditions than pools located lower on the shore (Pyefinch, 1943; Huggett and Griffiths, 1986). Furthermore, pools of lower volume are more extreme environments as there is less water to buffer changes in environmental conditions (Ganning, 1971; Metaxas and Scheibling, 1994; Therriault and Kolasa, 2000; Firth and Williams, 2009). Despite exhibiting dramatic fluctuations in physico-chemical conditions, natural rock pools often support greater diversity, abundance and/or biomass of organisms than emergent rock (Goss-Custard et al., 1979; Chapman and Johnson, 1990). Whilst this is a very common assertion in ecology, there is surprisingly little evidence in the literature to support this statement (but see Firth et al., 2013a).

Pools are complex habitats that can vary greatly in their area, depth and substratum incline. Of these physical properties, area is considered to have little influence on the biological structure of pools (Underwood and Skilleter, 1996; Martins et al., 2007), depth is known to strongly influence species performance, diversity and community composition (Goss-Custard et al., 1979; Kooistra et al., 1989; Astles, 1993; van Tamelen, 1996; Moschella et al., 2005; Bussell et al., 2007; Martins et al., 2007; Browne and Chapman, 2014) whereas little is known about the effect of incline. The relationship of diversity and functioning with depth varies depending on the response variable measured. Bussell et al. (2007) found higher diversity and richness of invertebrates (associated with *Corallina officinalis*) at shallower depths nearer the pool edges. Conversely, both Moschella et al. (2005) and Martins et al. (2007) found that species diversity was positively correlated with pool depth on shores in southeast England. Johnson and Skutch (1928) describe the associations of some individual species to substratum incline in pools (e.g. *Corallina* was commonly found on vertical surfaces) but there is a paucity of literature describing the relationship between species richness and community structure with substratum incline.

In response to the growing need to defend infrastructure from sea level rise and coastal erosion, hard-substrate defence structures are becoming ubiquitous features of coastal landscapes in intertidal and shallow subtidal environments (Airoldi et al., 2005; Bulleri and Chapman, 2010; Chapman and Underwood, 2011; Airoldi and Bulleri, 2011; Firth and Hawkins, 2011; Firth et al., 2013b). For example, more than 50% of Italian coastline on the Adriatic sea is protected by hard defence structures (Airoldi and Bulleri, 2011); 50% of Sydney Harbour in Australia is protected by seawalls (Chapman and Underwood, 2011); 45% of England's coastline is protected by either hard structures or artificial beaches (Masselink and Russell, 2010). Ecological-engineering is an emerging field which integrates engineering and ecological expertise to create more ecologically-friendly urban environments (Schulze, 1996; Bergen et al., 2001; Chapman and Underwood, 2011). Recent studies of artificial coastal defence structures in intertidal habitats (e.g. seawalls, breakwaters and groynes) have revealed that the incorporation of water retaining features that mimic natural rock pools can dramatically increase the diversity of colonising epibiota (Chapman and Blockley, 2009; Browne and Chapman, 2011, 2014; Chapman and Underwood, 2011; Firth et al., 2014).

To better inform engineering design of coastal infrastructure, we investigated the importance of pools in determining patterns of biodiversity on natural rocky shores. Furthermore, with the view to the artificial creation of pools in built environments, we investigated the role of depth and incline in determining patterns of biodiversity to inform engineering criteria for the creation of these pools. For example, is there a particular depth or incline for optimal biodiversity? Specifically we tested the following hypotheses:

(1) Pool habitats will support greater taxon richness than emergent rock habitats.
(2) Deeper pool habitats will support greater taxon richness than shallower habitats.
(3) Species richness will vary with incline.
(4) Community structure will vary among habitats (pool and emergent rock, depth and incline).

2. Methods

2.1. Study locations

Thirteen study locations were investigated in Norway, Scotland, England, Wales and Ireland (Fig. 1). All locations were characterised by an abundance of rock pools and emergent rock, and were either moderately exposed or exposed. In Norway locations were located at Sulesund (62°39′ N, 5°16′ E) and Vigra (62°53′ N, 6°02′ E). In Scotland a single location was located at Port Patrick (54°50′ N, 5°07′ W); in England, at Newquay (50°25′ N, 5°05′ W), Brixham (50°24′ N, 3°29′ W), Torquay (50°27′ N, 3°30′ W) and Flamborough Head (54°07′ N, 0°04′ W). In Wales the locations were located at Penmon (53°18′ N, 4°02′ W) and Porth Dinllaen (52°56′ N, 4°34′ W) and locations in Ireland were located at Muighinis Island (53°17′ N, 9°50′ W), Spiddal (53°14′ N, 9°18′ W), Carraroe (53°15′ N, 9°37′ W) and Carnsore Point (52°10′ N, 6°21′ W). Tidal ranges vary between a minimum of ~2–4 m in Norway to a maximum of 6–8 m in Wales. Subsets of these locations were compared to address specific questions and are discussed in the relevant sections below.

2.2. Sampling method

2.2.1. Study 1. Comparison of species richness and community structure among rock pools and emergent substrata

All thirteen locations were sampled during low-water spring tides in the summer/autumn of 2011 and 2012. At each location, 10 quadrats (0.1 × 0.1 m) were haphazardly placed on horizontal surfaces both in shallow (<12 cm) rock pools and on the adjacent emergent rock. Shallow rock pools were investigated as it was expected that deeper pools would support greater species richness than shallow pools. Therefore, if differences were detected using shallow pools, even greater differences would be expected with deeper pools. A small quadrat size was selected for sampling rock pools due to variation in area among rock pools and topography over small spatial scales. The following response variables were recorded in each quadrat: (a) overall percentage cover of canopy algae (based on 25 intersection points), (b) after moving canopy aside,

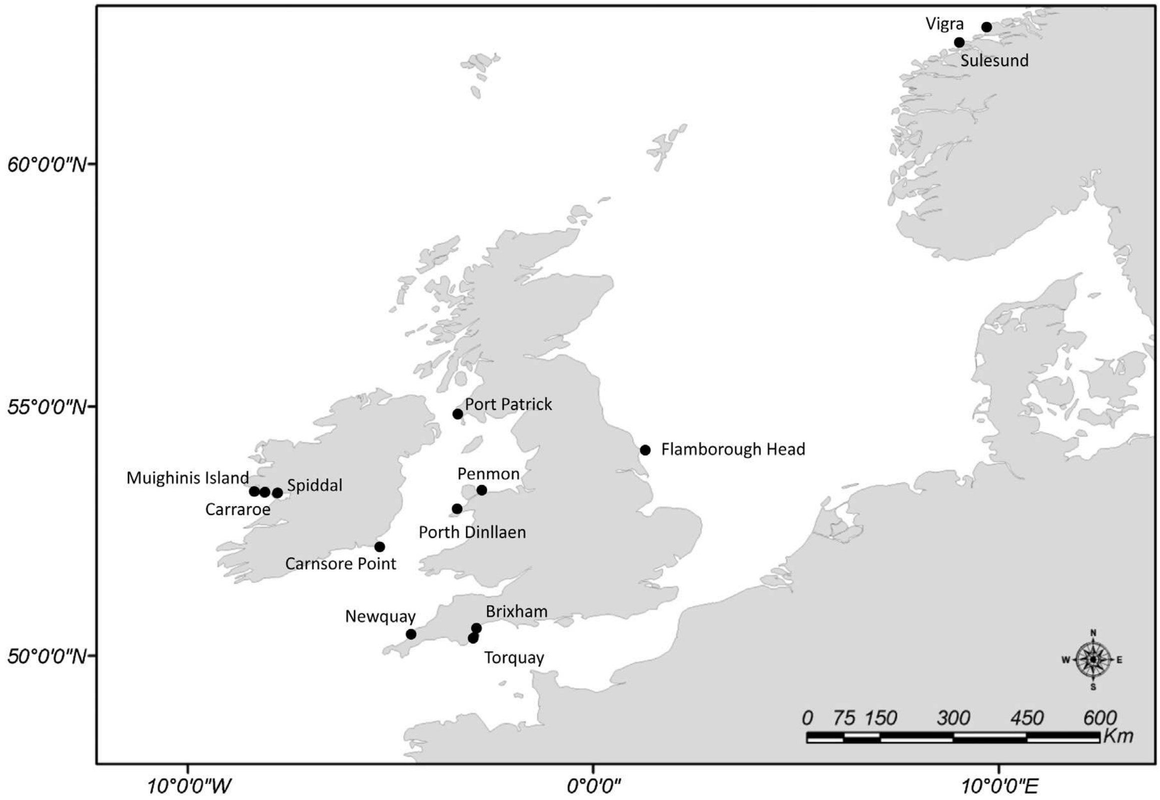

Fig. 1. Map showing study locations in northwest Europe. All locations were used to compare biological communities in rock pools and on emergent rock. Penmon and Porth Dinllaen were used for investigation of the role of depth and incline in community structure.

percentage cover of sessile organisms (particularly mussels, barnacles and sponges) and other algal species (e.g. turfs, encrusting species). Sessile species that were present but did not fall below an intersection were given an arbitrary value of 1% cover in the analyses; (c) abundances of mobile species (mainly gastropods).

2.2.2. Study 2. Comparison of species richness and community structure among depth and incline in rock pools

The influence of depth and incline on community structure and diversity in pools were examined for both low and mid tidal levels at two locations in North Wales, Penmon and Porth Dinllaen (Fig. 1). A 2-factor orthogonal design was employed using distinct categories: depth (3 levels: shallow: $<$10 cm, medium: 10–20 cm, deep: $>$20 cm) and three different inclines (3 levels: horizontal: 0–20°, sloping: 40–60°, vertical: 70–90°). Ten quadrats (0.1×0.1 m) were randomly placed in each combination of depth and incline resulting in 90 quadrats sampled in each low and mid shores of Penmon and Porth Dinllaen ($90 \times 4 = 360$ quadrats in total across the whole survey). Efforts were made to avoid placing multiple quadrats in the same pools and to only sample larger pools that comprised a multitude of the required habitat combinations (i.e. small shallow pools were avoided). Previous studies have found that pool area has little influence on community structure and diversity (Underwood and Skilleter, 1996; Martins et al., 2007), therefore pool area was not taken into consideration in this study. The same response variables and sampling procedures as described in study 1 above were employed here.

2.3. Statistical analyses

Permutational multivariate analyses of variance (PERMANOVA, McArdle and Anderson, 2001; Anderson, 2005) were used to test hypotheses of differences in both taxon richness and community structure. In the case of univariate data (i.e. taxon richness) Euclidean distances were used as the measure of similarity. Non-metric multidimensional scaling (nMDS) was used to test differences in overall community structure. nMDS is an ordination technique based on rank dissimilarity, in this case measured with the Bray–Curtis index on presence-absence transformed data (Clarke, 1993). SIMPER analysis in the PRIMER package was used to assess which species were most influential in causing similarity among plots within treatments and dissimilarity among different treatments (Clarke and Warwick, 1994).

For each of Study 1 and 2, the same design was employed for both univariate and multivariate comparisons. To test hypotheses about the differences in taxon richness and community structure among rock pools and emergent substrata (study 1) factors were Location (13 levels: listed above; random) and Habitat (two levels: pool, rock; fixed & orthogonal). To test hypotheses about the differences in taxon richness and community structure among depth and incline (study 2) factors were Location (2 levels: Penmon, Porth Dinllaen; random), Height (2 levels: low, mid; fixed & orthogonal), Depth (3 levels: shallow, medium, deep; fixed & orthogonal) and Incline (3 levels: horizontal, sloping, vertical; fixed & orthogonal).

Data for both taxon richness and community structure were partitioned into (i) all taxa, (ii) canopy and sub-canopy algae, (iii) turf algae, (iv) encrusting algae, (v) filter feeders, (vi) predators and (vii) grazing gastropods.

3. Results

3.1. Study 1. Comparison of species richness and community structure among rock pools and emergent substrata

A total of 88 taxa were recorded across all 13 locations and habitats (rock pool and emergent rock). Of these taxa, 74 were

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recorded in pools and 40 on emergent rock. 48 taxa were unique to pools and 14 were unique to emergent rock. Canopy and sub-canopy algae contributed most to this diversity (43 taxa), followed by filter feeders (13 taxa), grazing gastropods (11 taxa), turf algae (10 taxa), predators (5 taxa), encrusting algae (3 taxa), lichens (2 taxa), and cyanobacteria (1 taxon).

There was a significant interaction in the analysis comparing taxon richness among locations and habitats. Post-hoc pairwise comparisons revealed that at all but three locations (Porth Dinllaen, Brixham, Torquay) pools supported significantly greater taxon richness than emergent rock (Fig. 2, Table 1). Although the results were not significant at Porth Dinllaen, Brixham and Torquay, there were more taxa in the pools than emergent rock. There was also a significant interaction between habitat and location in the community analysis (Table 1). Dissimilarity between habitats at each location were driven by different species but in general, barnacles and the limpet *Patella vulgata* were more commonly found on emergent rock, whilst the algae *Corallina* spp., Lithothamnia, *Ulva* spp. and the gastropods *Patella ulyssiponensis* and *Gibbula umbilicalis* were more commonly found in pools.

3.2. Study 2. Comparison of species richness and community structure among depth and incline in rock pools

A total of 128 taxa were recorded across the two locations (Porth Dinllaen and Penmon), shore heights, depths and slopes. Canopy and sub-canopy algae contributed most to this diversity (50 taxa), followed by filter feeders (30 taxa), turf algae (22 taxa), grazing gastropods (17 taxa), predators (6 taxa), encrusting algae (3 taxa).

In an effort to associate differential responses of the various groups to the factors depth and incline, changes in total taxon richness were explored first and then partitioned into morpho-functional groups of canopy and sub-canopy algae, turf algae, encrusting algae, filter feeders, predators and grazing gastropods.

3.2.1. All taxa

There was a significant three-way interaction between location, height and depth for taxon richness (Table 2). Taxon richness generally appeared to be greater in shallow compared to deeper habitats but this was only significant in the low shore at Penmon (Fig. 3a) and in the mid shore at Porth Dinllaen (Fig. 3b). There was no significant effect of incline on colonising epibiota. Community analyses revealed significant three-way interactions between location, height and depth, and location, height and incline (Table 3). SIMPER analysis did not reveal any clear associations of any taxa with any particular depth or incline across locations.

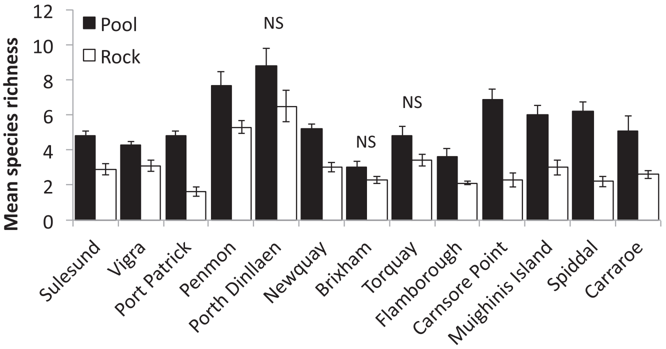

Fig. 2. Mean taxon richness (±SE) in rock pools (black bars) and on emergent rock (white bars) at 13 locations in northwest Europe. Norway: Sulesund & Vigra. Scotland: Port Patrick. Wales: Penmon & Porth Dinllaen. England: Newquay, Brixham, Torquay & Flamborough. Ireland: Carnsore Point, Muighinis Island, Spiddal & Carraroe. ($n = 10$; NS = Not significant).

Table 1
Results for comparison of taxon richness (PERMANOVA) and community composition (PERMANOVA) among rock pool and emergent rock habitats. Analyses were based on Euclidian distance (taxon richness) and Bray–Curtis similarities (community composition) of data. All tests used 9999 permutations under a reduced model. ($^{**} = P < 0.01$,$^{***} = P < 0.001$).

	Taxon richness			Community composition	
Source	df	MS	Pseudo-F	MS	Pseudo-F
Location (Lo)	12	38.47	16.59***	12724.00	9.69***
Habitat (Ha)	1	367.23	59.38***	277520.00	29.84***
Lo × Ha	12	6.18	2.67**	9299.60	7.08***
Residual	234	2.32		1313.70	

3.2.2. Canopy and sub-canopy algae

There was a significant three-way interaction between location, depth and incline for taxon richness (Table 2). On horizontal inclines, taxon richness was significantly greater in shallow compared to deep habitats at both Penmon and Porth Dinllaen (Fig. 4). Results for medium depths varied, being more similar to shallow at Penmon and more similar to deep at Porth Dinllaen (Fig. 4). Taxon richness was significantly greater on vertical than horizontal inclines in deep habitats at Penmon and in both medium and deep habitats at Porth Dinllaen (Fig. 4). In each case the sloping incline category varied, being more similar to vertical (deep depth Penmon) or horizontal (medium depth Porth Dinllaen), or significantly different to both horizontal and vertical (deep depth Porth Dinllaen). Community analyses revealed a significant three-way interaction between location, depth and incline (Table 3). SIMPER analysis did not reveal any clear associations of any taxa with any particular depth or incline across locations.

3.2.3. Turf algae

There was a significant three-way interaction between location, height and depth for taxon richness, reflecting the same trend as for all species (Table 2). Taxon richness generally appeared to be greater in shallow compared to deeper habitats but this was only significant on both the low and the mid shore at Porth Dinllaen (Fig. 5). There was no significant effect of incline on colonising epibiota. Community analyses revealed significant two-way interactions between location and height, and location and depth (Table 3). SIMPER analysis did not reveal any clear associations of any taxa with any particular depth or incline across locations.

3.2.4. Encrusting algae

There were significant two-way interactions between location and incline, and location and depth for taxon richness (Table 2). The results were very variable and post-hoc pairwise comparisons revealed no clear trend with taxon richness and either depth or incline (Fig. 6). Community analyses revealed no significant effect of any factor apart from location (Table 3).

3.2.5. Filter feeders, predators and grazing gastropods

There were no significant differences among factors (except location for grazing gastropods) for taxon richness for any of the faunal groups (Table 2). Community analyses revealed significant interactions among location, height and depth for both filter feeders and grazing gastropods (Table 3) but SIMPER analyses did not reveal any clear associations of any taxa with any particular depth or height across locations.

4. Discussion

Taxon richness was consistently greater in pools than on adjacent emergent rock. The presence of pools increased diversity by a factor

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Table 2

PERMANOVA test results for effects of location (Penmon and Porth Dinllaen), tidal height (low and mid), pool depth (shallow (<10 cm), medium (10–20 cm), deep (>20 cm)) and substratum incline (horizontal, sloping, vertical) on taxon richness. Analyses were based on Euclidian distance similarities of data. All tests used 9999 permutations under a reduced model. ($^{*} = P < 0.05$,$^{**} = P < 0.01$,$^{***} = P < 0.001$).

		All taxa		Canopy & subcanoy algae		Turf algae		Encrusting algae		Filter feeders		Predators		Grazers	
	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Location (Lo)	1	810	78.4***	46.9	11.3***	36.1	34.7***	62.8	512.6***	0.2	0.1	4.40E-02	0.2	48.4	136.1***
Height (He)	1	0.54	0.01	2.5	4.10E-02	1.6	1	0.2	9.1	0.9	0.1	0.3	6.3	1.6	1
Depth (De)	2	73.64	5.1	16.5	4.6	10.5	1.6	0.4	0.9	0.5	0.8	0.3	91	0.3	0.7
Incline (In)	2	149.95	5.9	46.9	3.8	2.4	1.2	1.30E-02	1.8E-2	31.4	7.2	0.2	1.8	0.5	2
Lo × He	1	51.38	4.9*	60.8	14.7***	1.6	1.5	2.40E-02	0.2	6.9	3.6	4.40E-02	0.2	1.6	4.5
Lo × De	2	14.53	1.4	3.5	0.9	6.8	6.5**	0.4	3.2*	0.7	0.4	2.70E-03	1.20E-02	0.4	1.1
Lo × In	2	25.53	2.5	12.1	2.9	2	1.9	0.7	6.1**	4.3	2.3	0.1	0.5	0.2	0.7
He × De	2	26.84	0.5	5.4	0.4	5.80E-02	1.70E-02	5.90E-03	2.6E-2	5	3.6	1.90E-02	0.3	0.9	0.9
He × In	2	4.04	0.7	6.3	2253**	1.6	2.3	2.30E-02	0.1	0.2	0.1	0.1	1	0.4	1
De × In	4	32.89	1.6	22.6	2	0.8	1.7	0.1	3.4	2.5	1.2	0.1	0.2	0.3	0.6
Lo × He × De	2	50.98	4.9**	15	3.6*	3.4	3.2*	0.2	1.8	1.4	0.7	6.90E-02	0.3	0.9	2.7
Lo × He × In	2	5.42	0.5	2.70E-03	6.70E-04	0.7	0.7	0.2	1.3	3.5	1.8	0.1	0.6	0.4	1.2
Lo × De × In	4	20.88	2	11	2.6***	0.5	0.5	4.30E-02	0.4	2.1	1.1	0.5	1.9	0.5	1.3
He × De × In	4	6.41	1.2	2	0.8	1.6	1.9	0.2	4.5	2.5	2.6	0.2	1.7	0.4	0.7
Lo × He × De × In	4	5.34	0.5	2.4	0.6	0.8	0.8	4.90E-02	0.4	0.9	0.5	9.80E-02	0.4	0.5	1.4
Residual	324	10.33		4.1		1		0.1		1.9		0.2		0.4	

of three. In natural habitats, pools are sometimes considered to support greater abundance, biomass and diversity than emergent rock (Goss-Custard et al., 1979; Chapman and Johnson, 1990). Similarly, recent work in artificial habitats has found that water-retaining features on coastal defence structures (mimicking rock pools) support greater species richness than adjacent emergent rock habitats (Moschella et al., 2005; Pinn et al., 2005; Firth et al., 2013a). In the present study community structure varied significantly with both habitat and location. The identity of the species driving the dissimilarities between pools and emergent rock varied with location and tidal height, most likely in response to differences in local physical conditions and available species pool. Previous studies have found that community structure and functioning appears to differ between pools and emergent rock (Metaxas et al., 1994; Araujo et al., 2006; Firth and Crowe, 2008, 2010; Firth et al., 2009).

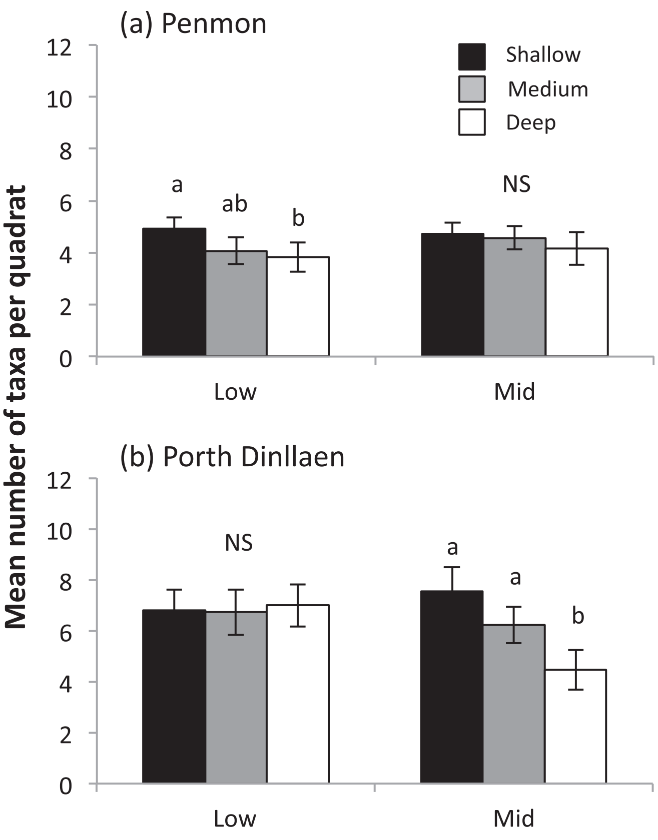

Fig. 3. Mean total taxon richness (±SE) across all inclines in shallow (<10 cm, black bars), medium (10–20 cm, grey bars) and deep (>20 cm, white bars) rock pool habitats on the low and mid shore at Penmon (a) and Porth Dinllaen (b). ($n = 30$; NS = Not significant; lettering denotes instances where results were significant).

Organisms within pools are continually submerged, and hence are not subjected to the same aerial stresses as those on emergent rock, providing a refuge for a variety of marine organisms (Underwood, 1980; Underwood and Jernakoff, 1984; Martins et al., 2007). Species that inhabit pools are, nevertheless subject to stressful environmental conditions during the low-water period (Ganning, 1971; Huggett and Griffiths, 1986). Several studies have suggested that deeper pools may support more algal and invertebrate species (Ranta, 1982; Fairweather and Underwood, 1991; Moschella et al., 2005), whilst the opposite was found in our study. In the present study, there was never a main effect of depth on taxon richness or community structure. There was a general trend towards taxon richness being slightly higher in shallow habitats than deep for some groups (all taxa, canopy and subcanopy algae (horizontal only), turf algae). It appears that these differences are primarily driven by algae with faunal taxa showing no relationship with pool depth. Browne and Chapman (2014) created artificial "rock pools" on Sydney seawalls using modified planters and found that the shallow pools (22 cm) pools supported greater diversity than the deeper pools (38 cm). Despite deeper habitats generally supporting lower algal taxon richness than shallow pools, some species that were found in deep habitats were rarely found elsewhere (e.g. *Dilsea carnosa*). Deeper rock pools tend to experience smaller fluctuations in temperature, salinity, oxygen concentration and pH than shallow rock pools (Ganning, 1971; Metaxas and Scheibling, 1994; Firth and Williams, 2009) making them a more stable environment for some more stress-sensitive species. In larger rock pools, vertical zonation can often be seen where clear patterns can be seen with particular species and depths (Kooistra et al., 1989; van Tamelen, 1996).

Only three relatively shallow depth categories were investigated in the present study. These depth categories were selected as they are within the depths that could reasonably be engineered on artificial structures. Further investigation of deeper pools (>30 cm) is likely to yield even more information in terms of taxon richness and community structure.

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Table 3
PERMANOVA test results for effects of location (Penmon and Porth Dinllaen), tidal height (low and mid), pool depth (shallow (<10 cm), medium (10–20 cm), deep (>20 cm)) and substratum incline (horizontal, sloping, vertical) on community composition. Analyses were based on Bray–Curtis similarity distance similarities of presence/absence (all species and filter feeders) square-root transformed (canopy, turf, encrusting, predators and grazers) data. All tests used 9999 permutations under a reduced model. ($^{*} = P < 0.05$,$^{**} = P < 0.01$,$^{***} = P < 0.001$). P/A = Presence/absence transformation; SQRT = square root transformation.

		All taxa		Canopy & subcanopy algae		Turf algae		Encrusting algae		Filter feeders		Predators		Grazers	
	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Location (Lo)	1	1.30E+05	68.5***	54764	20.3***	1.10E+05	61.7***	4539	663.7***	57593	52.6***	3268	11.3***	16724	33.2***
Height (He)	1	17666	0.8	25433	0.9	8097	1.3	3.2	2.3	8943	0.7	366	1.8	6398	0.9
Depth (De)	2	7817	1.2	11747	1.8	6939	1.1	6	1.5	2217	0.9	213	2.7	1226	0.9
Incline (In)	2	10155	2.8	9373	2.5	4341	1.6	9.6	0.9	9180	5.7	602	1.5	756	1.2
Lo × He	1	22503	11.4***	28346	10.5***	6167	3.3*	1.4	0.2	12523	11.4***	198	0.7	7056	13.9***
Lo × De	2	6403	3.2***	6536	2.4***	6040	3.3**	4.1	0.6	2244	2.1*	78	0.3	1275	2.5**
Lo × In	2	3670	1.9**	3685	1.4	2694	1.5	9.8	1.4	1607	1.5	404	1.4	632	1.3
He × De	2	4991	1.1	6327	0.9	3433	0.9	11.2	1.8	2248	0.9	628	1.1	1128	0.9
He × In	2	2504	0.7	4640	1.2	1255	0.5	7.5	0.7	638	0.6	400	0.8	538	0.9
De × In	4	3705	1.5	5427	1.1	1630	1.1	7.8	1.2	1643	1.8	432	1.5	616	1.1
Lo × He × De	2	4736	2.4***	7255	2.7***	3542	1.9	6.3	0.9	2459	2.2*	559	1.9	1164	2.3***
Lo × He × In	2	3465	1.8*	3918	1.5	2441	1.3	10.2	1.5	990	0.9	509	1.8	61	1.2
Lo × De × In	4	2400	1.2	4771	1.8**	1469	0.8	6.6	0.9	904	0.8	281	0.9	567	1.1
He × De × In	4	2174	1.2	3344	0.9	2884	1.3	8.5	1.7	1198	1.9	139	0.9	401	0.9
Lo × He × De × In	4	1814	0.9	3396	1.2	2113	1.1	5	0.7	626	0.6	150	0.5	462	0.9
Residual	324	1974		2693		1846		6.8		1094		288		504	
Transform		P/A		SQRT		SQRT		SQRT		P/A		SQRT		SQRT	

Substratum incline was found to have little effect on colonising epibiota. The only group which exhibited any response to substratum incline was canopy and subcanopy algae and this was only true at deeper depths, where vertical inclines supported greater taxon richness than horizontal inclines. While much is known about the effect of incline in terrestrial systems (e.g. Bazzaz, 1975; Lieffers and Larkin-Lieffers, 1987), little is known about the effect of substratum incline on community structure and functioning on natural rocky shores despite rocky shores being very variable in their topography. Of the few studies that have been carried out, the majority have investigated incline on emergent rock and not in

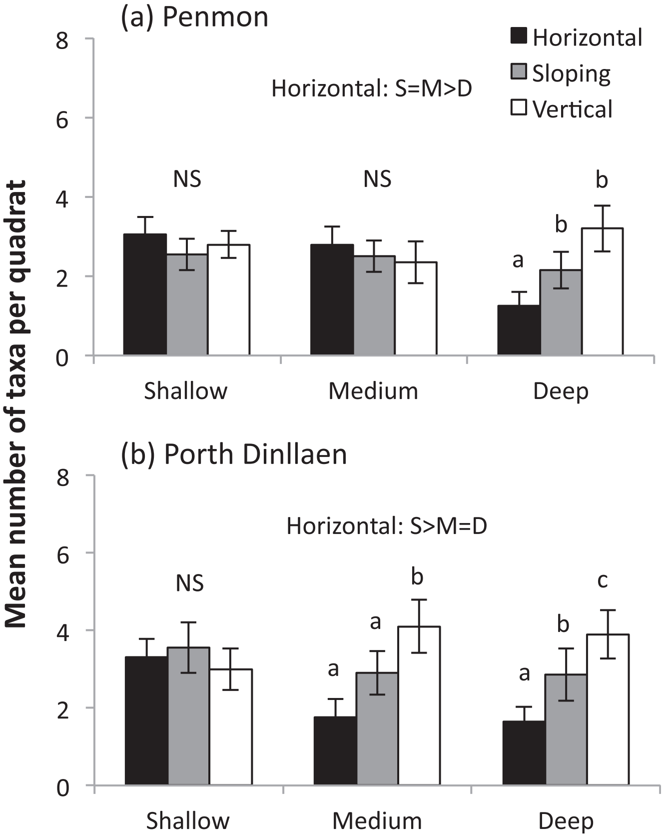

Fig. 4. Mean canopy and subcanopy taxon richness across tidal heights (±SE) on horizontal (0–20°, black bars), sloping (40–60°, grey bars) and vertical rock faces (70–90°, white bars) in shallow (<10 cm), medium (10–20 cm) and deep (>20 cm) rock pool habitats at Penmon (a) and Porth Dinllaen (b). (*n* = 20; lettering denotes instances where results were significant).

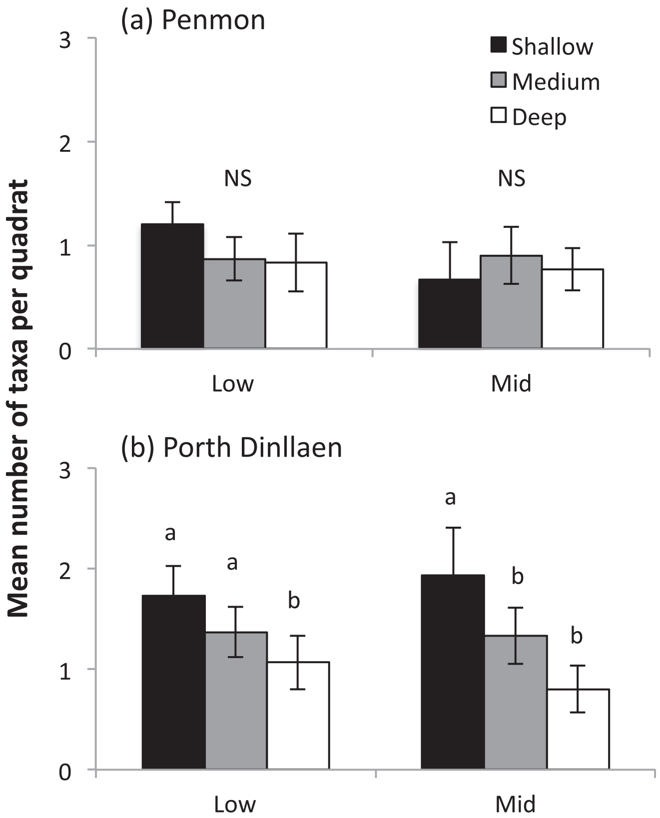

Fig. 5. Mean turf algal taxon richness (±SE) across all inclines in shallow (<10 cm, black bars), medium (10–20 cm, grey bars) and deep (>20 cm, white bars) rock pool habitats on the low and mid shore at Penmon (a) and Porth Dinllaen (b). (*n* = 30; NS = Not significant; lettering denotes instances where results were significant).

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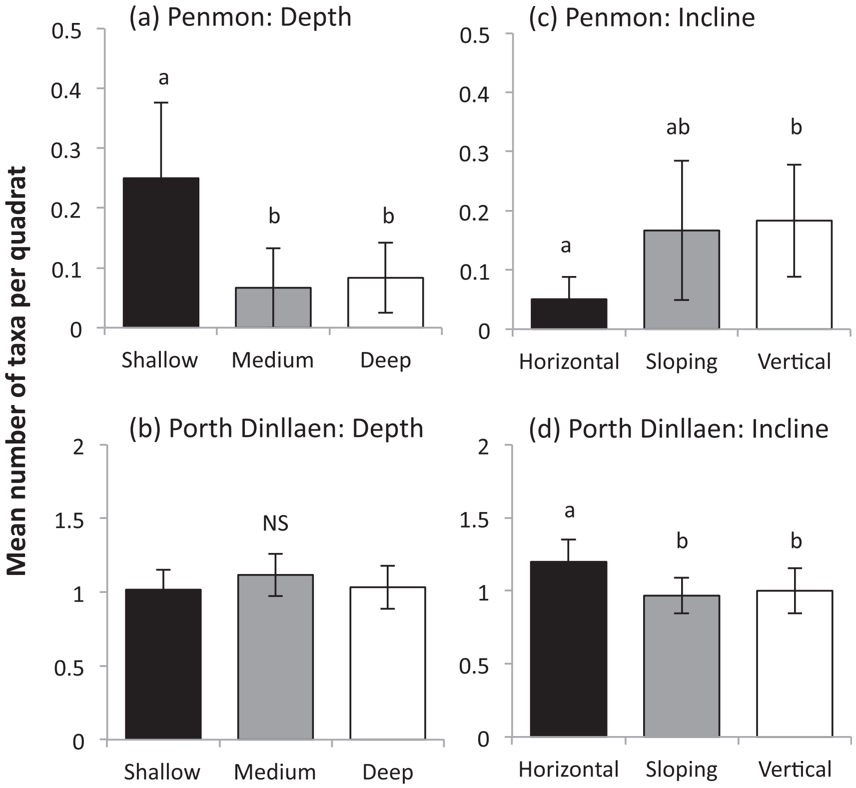

Fig. 6. Mean encrusting algal taxon richness (±SE) in shallow (<10 cm, black bars), medium (10–20 cm, grey bars) and deep (>20 cm, white bars) across all tidal heights and inclines at Penmon (a) and Porth Dinllaen (b). Mean encrusting algal taxon richness (±SE) on horizontal (0–20°, black bars), sloping (40–60°, grey bars) and vertical rock faces (70–90°, white bars) across all tidal heights and inclines at Penmon (c) and Porth Dinllaen (d). ($n = 90$; NS = Not significant; lettering denotes instances where results were significant).

pools (e.g. Knott et al., 2004) and results varied depending on the response variable being measured. For example, in a study examining algal mat communities, Whorff et al. (1995) found that horizontal surfaces supported higher biomass than vertical surfaces, whilst other studies found species more positively associated with vertical habitats (e.g. gastropods (Garrity, 1984), and coralline algae (Johnson and Skutch, 1928)) and others found no relationship (e.g. the mussel, *Mytilus edulis* (Lintas and Seed, 1994)). Furthermore, Chapman and Underwood (2011) investigated the role of both horizontal and vertical surfaces on stepped artificial blocks in Sydney. Percentage cover of sessile animals was significantly greater on vertical than horizontal surfaces and the only mobile animal that was present (the limpet, *Siphonaria denticulata*) was more abundant on vertical surfaces than on horizontal surfaces.

Solar radiation could be one factor influencing the distribution of organisms. Vertical habitats are more likely to be shaded and therefore protected from solar radiation than horizontal habitats. Many algal species are sensitive to solar radiation (Figueroa et al., 1997; Aguilera et al., 1999) which may explain why the canopy and subcanopy algae were more positively associated with vertical surfaces than horizontal surfaces (in deep habitats). Alternatively, grazing activity of gastropods is known to vary with substratum incline, tidal activity and location (Williams et al., 1999) and it is possible that grazing activity is greater on horizontal surfaces at the locations investigated in the present study, thus limiting the establishment and growth of canopy and subcanopy algae on horizontal surfaces (Noël et al., 2009).

5. Conclusion

The hardening of the coast with artificial structures is likely to continue with current population increases and climate change predictions. The placement of such structures in both intertidal and subtidal marine habitats provides substrate for attachment, and potential habitat for a wide range of marine organisms, from native and non-native to those of conservation importance (Bulleri and Airoldi, 2005; Vaselli et al., 2008; Martins et al., 2010; Perkol-Finkel and Airoldi, 2010; Firth et al., 2011; Mineur et al., 2012; Perkol-Finkel et al., 2012; Bracewell et al., 2012, 2013; Firth et al., 2013b). Despite the potential for these structures to provide habitat, they generally support lower biodiversity than adjacent natural rocky habitats (Chapman and Bulleri, 2003; Moschella et al., 2005; Pister, 2009; Firth et al., 2013a). Recent work investigating the efficacy of engineering novel habitats on these structures has found that the incorporation of pits and crevices can have a significant positive effect on biodiversity (Martins et al., 2010; Borsje et al., 2011; Witt et al., 2012; Firth et al., 2014) with the incorporation of rock pools having a very dramatic positive effect on biodiversity (Chapman and Blockley, 2009; Browne and Chapman, 2011, 2014; Firth et al., 2014).

The results obtained from the present study show that rock pools support more diverse and different assemblages compared to emergent rock habitats and are important habitats in intertidal environments (Metaxas and Scheibling, 1994; Firth et al., 2013a, 2014). Some relatively clear results were evident for depth and incline for some functional groups (particularly algae) with shallow and vertical habitats generally supporting higher numbers of species than deeper and horizontal habitats respectively. Despite these patterns, it is clear that the greater the number of habitat types that are available, the more species that will be able to colonize any given environment (Huston, 1979; Firth et al., 2014). With increasing pressure to improve the habitat value of built environments, our work demonstrates that there is no simple solution in the marine environment. Functional groups and species respond

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differently to different physical conditions. The creation of pools is an effective way of providing important habitat for intertidal organisms in artificial environments (Chapman and Blockley, 2009; Browne and Chapman, 2011, 2014), but the creation of rock pools with a variety of depths and slopes (such as the multi-habitat enhancement unit called the BIOBLOCK (Firth et al. 2014)) at a range of different shore heights will ultimately increase the availability of potential habitat types and thus promote the maintenance of biodiversity.

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