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BIODIVERSITY RESEARCH

The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures

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ABSTRACT

Aim Artificial coastal defence structures are proliferating in response to rising and stormier seas. These structures provide habitat for many species but generally support lower biodiversity than natural habitats. This is primarily due to the absence of environmental heterogeneity and water-retaining features on artificial structures. We compared the epibiotic communities associated with artificial coastal defence structures and natural habitats to ask the following questions: (1) is species richness on emergent substrata greater in natural than artificial habitats and is the magnitude of this difference greater at mid than upper tidal levels; (2) is species richness greater in rock pools than emergent substrata and is the magnitude of this difference greater in artificial than natural habitats; and (3) in artificial habitats, is species richness in rock pools greater at mid than upper tidal levels?

Location British Isles.

Methods Standard non-destructive random sampling compared the effect of habitat type and tidal height on epibiota on natural rocky shores and artificial coastal defence structures.

Results Natural emergent substrata supported greater species richness than artificial substrata. Species richness was greater at mid than upper tidal levels, particularly in artificial habitats. Rock pools supported greater species richness than emergent substrata, and this difference was more pronounced in artificial than natural habitats. Rock pools in artificial habitats supported greater species richness at mid than upper tidal levels.

Main conclusions Artificial structures support lower biodiversity than natural habitats. This is primarily due to the lack of habitat heterogeneity in artificial habitats. Artificial structures can be modified to provide rock pools that promote biodiversity. The effect of rock pool creation will be more pronounced at mid than upper tidal levels. The challenge now is to establish at what tidal height the effect of pools becomes negligible and to determine the rock pool dimensions for optimum habitat enhancement.

Keywords

Artificial coastal defence structures, biodiversity, climate change, environmental heterogeneity, rock pool, tidal height.

INTRODUCTION

In response to the growing need to defend the coast, hard-substrata defence structures are becoming ubiquitous features of coastal landscapes in intertidal and shallow subtidal environments (Airoldi *et al.*, 2005; Moschella *et al.*, 2005; Bulleri & Chapman, 2010; Chapman & Underwood, 2011; Firth & Hawkins, 2011). These defence structures are designed to

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prevent or to reduce coastal erosion and flooding of adjacent land, in addition to stabilizing and retaining beaches and reclaimed land. World-wide, hard defence structures such as seawalls, jetties, breakwaters, groynes and dykes are being built at the expense of natural habitats, which can markedly affect the structure and functioning of marine ecosystems (Connell & Glasby, 1999; Bulleri & Chapman, 2004; Airoldi *et al.*, 2005; Chapman & Underwood, 2011).

The colonizing communities of artificial structures have been suggested to be analogous to, and function as simplified surrogates for natural rocky habitats (Southward & Orton, 1954; Thompson *et al.*, 2002; Martin *et al.*, 2005; Branch *et al.*, 2008). However, mounting evidence suggests the communities associated with artificial structures are generally less diverse than natural habitats (Chapman & Bulleri, 2003; Bulleri & Chapman, 2004; Gacia *et al.*, 2007; Vaselli *et al.*, 2008; Pister, 2009) and can support more invasive non-native species than natural habitats (Airoldi & Bulleri, 2011; Firth *et al.*, 2011; Mineur *et al.*, 2012). In addition to providing important habitat for epibiota, these artificial structures provide important refuge habitats for mobile species (including fish) during high water (Martin *et al.*, 2005), whilst during low water, a wide range of bird species can be observed feeding on and around the structures (E. Sharps, pers. comm.).

The lack of environmental heterogeneity is thought to be one factor accounting for lower epibiotic diversity on artificial structures (Moschella *et al.*, 2005). Rock pools are infrequent on artificial structures, but are ubiquitous features of natural rocky shores where they can support greater biodiversity and different communities than the surrounding emergent rock habitat (Goss-Custard *et al.*, 1979; Chapman & Johnson, 1990; Firth & Crowe, 2008, 2010; Firth *et al.*, 2009). Intertidal coastal defence structures are typically built at mid to upper tidal levels and consequently support lower biodiversity than those placed lower in the intertidal or in the subtidal zone (Burcharth *et al.*, 2007). Ecological engineering is an emerging field that integrates engineering criteria and ecological knowledge to create more environmentally friendly urban environments (Schulze, 1996; Bergen *et al.*, 2001; Chapman & Underwood, 2011). Recent work in Sydney has revealed that the incorporation of water-retaining features (mimicking rock pools) into seawalls can dramatically increase the diversity of colonizing epibiota (Chapman & Blockley, 2009; Browne & Chapman, 2011).

Some coastal defence structures have water-retaining features that effectively function as rock pools (Moschella *et al.*, 2005; Pinn *et al.*, 2005; Griffin *et al.*, 2010; Noël *et al.*, 2010). In the UK, for example, water is retained in the eroded limestone blocks on Plymouth Breakwater (Fig. 1a), in depressions around the base of some of the breakwaters at Elmer (Fig. 1b), between the pre-cast concrete 'reef units' at New Brighton (Fig. 1c) and in small depressions on top of the limestone boulders at Poole. These 'rock pools' provide a convenient opportunity for testing the importance of rock pools for species diversity on artificial coastal defence structures.

It is a common assumption in intertidal ecology that rock pools support higher biodiversity than emergent rock. Despite this widely accepted paradigm, there is relatively little empirical evidence to support this theory for natural shores (but see Metaxas & Scheibling, 1993; Araujo *et al.* 2006), and none for artificial structures. Furthermore, we

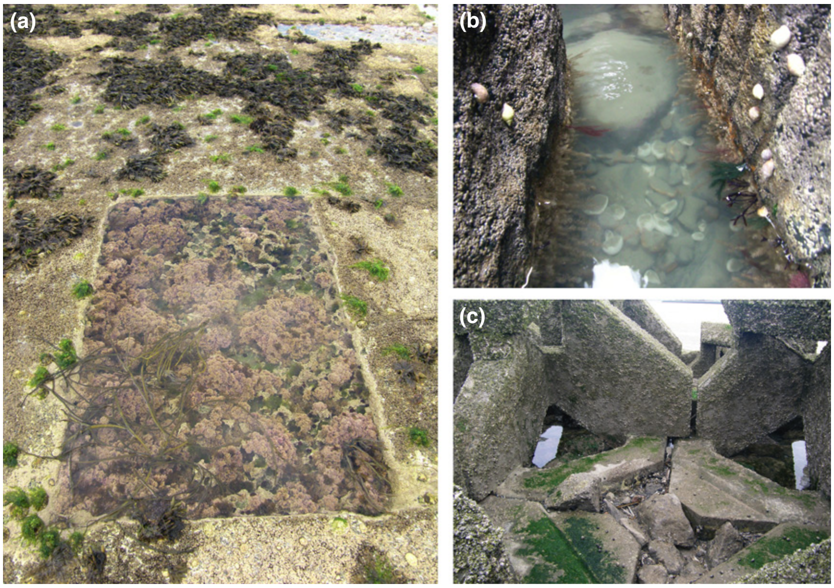

Figure 1 (a) Limestone and granite blocks on Plymouth Breakwater. The eroded limestone blocks form rock pools. (b) Pools at the base of breakwaters at Elmer. The depth in the pools at Elmer varied from 10 cm to 1 m and supported large numbers of the invasive non-native red alga *Grateloupia turuturu*. (c) Pools forming in the base of the pre-cast concrete 'reef units' at New Brighton – these pools supported large aggregations of anemones (*Diadumene cincta*).

know that tidal height has a significant effect on community structure and functioning in both natural and artificial habitats, but little is known about the interactive effects of habitat (natural/artificial and emergent substrata/rock pool) and tidal height. The present study investigated the diversity of intertidal assemblages associated with artificial coastal defence structures in the UK to test the following hypotheses:

1. Species richness on emergent substrata will be greater in natural than in artificial habitats, and the magnitude of this difference will be greater at mid than upper tidal levels.

2. Species richness will be greater in rock pools than emergent substrata, and the magnitude of this difference will be greater in artificial than natural habitats.

3. In artificial habitats, species richness in rock pools will be greater at mid than upper tidal levels.

METHODS

Study sites

Ten natural rocky shores (hereafter natural habitats) and 11 artificial coastal defence structures (hereafter artificial habitats) were sampled in the British Isles (Fig. 2, Table 1). The artificial habitats surveyed included rock groynes and shore-parallel breakwaters. Four artificial structures (New Brighton, Plymouth Breakwater, Poole, and Elmer) were specifically selected due to the presence of water-retaining features (Fig. 1, Table 1). Subsets of these locations were compared to address specific questions and are discussed in the relevant sections.

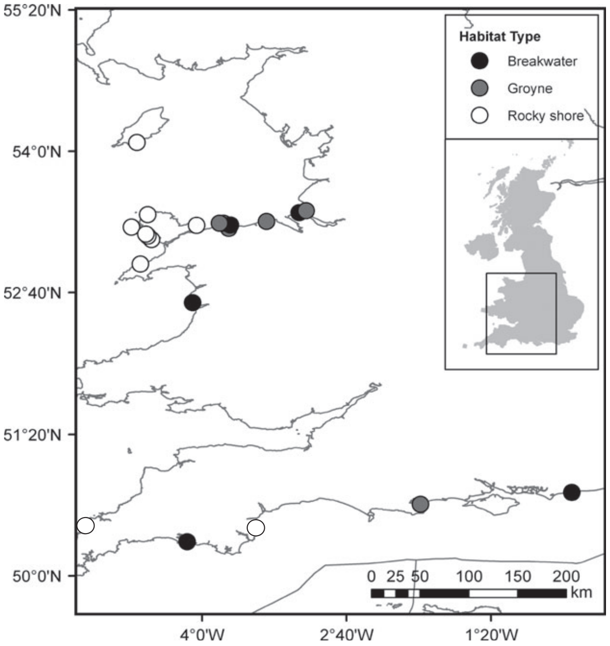

Figure 2 Study locations around the UK coast: natural rocky shores (open dots), groynes (grey dots) and breakwaters (black dots).

Sampling design

Study 1: Comparison of biodiversity on emergent substrata at different tidal heights among natural and artificial habitats

To investigate the differences in species richness between natural and artificial habitats, we surveyed eight natural habitats (Derbyhaven on the Isle of Man, and Aberffraw, Cable Bay, Penmon, Porth Dafarch, Porth Dinllaen, Rhosneigr and Cemlyn Bay in North Wales) and eight artificial habitats (Dinas Dinlle, Penrhyn Bay, Prestatyn, Rhos-on-Sea, West Shore and Tywyn in Wales, Elmer in West Sussex and Leasowe on the Wirral) (Fig. 2, Table 1). Only the seaward side of the artificial habitats was sampled to standardize exposure to wave action between natural and artificial habitats. At each location, 12 quadrats (25 cm × 25 cm) were haphazardly placed on emergent substrata at both mid and upper tidal levels. The majority of artificial coastal defence structures are typically built at mid-tidal levels (Burcharth *et al.*, 2007); therefore, only the mid and upper tidal levels of both natural and artificial habitats were investigated in this study.

Study 2: Comparison of biodiversity among rock pools and emergent substrata in natural and artificial habitats

To investigate the differences in species richness among rock pools and emergent substrata, we surveyed natural rocky shores at four locations (Penmon, Porth Dinllaen, Newquay and Torquay) and artificial structures at four locations

Table 1 Locations surveyed as part of the current study

Type	Location	Description	Position
Natural	Aberffraw*	Rocky shore	53°10′ N, 4°28′ W
	Cable Bay*	Rocky shore	53°12′ N, 4°30′ W
	Cemlyn Bay*	Rocky shore	53°24′ N, 4°30′ W
	Derbyhaven*	Rocky shore	54°05′ N, 4°36′ W
	Newquay†	Rocky shore	50°25′ N, 5°05′ W
	Penmon*,†	Rocky shore	53°18′ N, 4°03′ W
	Porth Dafarch*	Rocky shore	53°17′ N, 4°39′ W
	Porth Dinllaen*,†	Rocky shore	52°56′ N, 4°34′ W
	Rhosneigr*	Rocky shore	53°13′ N, 4°31′ W
	Torquay†	Rocky shore	53°27′ N, 3°30′ W
Artificial	Dinas Dinlle*	Groyne	53°05′ N, 4°20′ W
	Elmer*,†	Breakwater	50°47′ N, 0°35′ W
	Leasowe*	Breakwater	53°25′ N, 3°06′ W
	Penrhyn Bay*	Groyne	53°19′ N, 4°20′ W
	Prestatyn*	Groyne	53°20′ N, 3°24′ W
	Rhos-on-Sea*	Breakwater	53°18′ N, 3°44′ W
	West shore*	Groyne	53°19′ N, 3°50′ W
	Tywyn*	Groyne	53°19′ N, 3°50′ W
	Poole†	Groyne	52°34′ N, 4°05′ W
	New Brighton†	Groyne	53°26′ N, 3°02′ W
	Plymouth†	Breakwater	50°19′ N, 4°08′ W

*Used in Study 1.
†Used in Study 2.

Table 2 ANOVA results for comparison of species richness on emergent substrata in natural and artificial habitats

Source	Species richness d.f.	MS	*F*
Type = Ty	1	23.36	26.86***
Location = Lo (Ty)	14	0.86	6.29***
Height = He	1	7.07	22.37***
Ty × He	1	0.23	0.73
He × Lo (Ty)	14	0.32	2.29**
RES	352	0.14	

Student-Newman-Keuls comparisons
He × Lo (Ty)

Artificial	Mid vs. Upper	Natural	Mid vs. Upper
Dinas Dinlle	M > U	Aberffraw	M ≫ U
Elmer	M ≫ U	Cable Bay	M = U
Leasowe	M > U	Derbyhaven	M = U
Penrhyn	M = U	Penmon	M ≫ U
Prestatyn	M > U	Porth Dafarch	M = U
Rhos-on-sea	M ≫ U	Porth Dinllaen	M = U
West Shore	M = U	Rhosneigr	M = U
Tywyn	M = U	Cemlyn Bay	M = U

$^{**}P < 0.01$, $^{***}P < 0.001$.

(Elmer, Poole, New Brighton and Plymouth Breakwater). At each location, 10 quadrats (10 cm × 10 cm) were randomly placed on hard substrata in rock pools and on adjacent emergent substrata (*c.* 20 cm away).

A number of the groynes at Poole had water-retaining features at both the mid and upper tidal levels. Two of these groynes (*c.* 150 m apart) were selected based on sufficient abundance of shallow water-retaining features and adjacent emergent substrata to enable a formal comparison of mid and upper tidal levels. The water-retaining features on these groynes were comparable in terms of their tidal height and exposure to wave action. Five quadrats (10 cm × 10 cm) were randomly placed in each habitat type at both the mid and upper tidal levels on each groyne.

All surveys were made between July and September 2011 during low water spring tides. Epibiotic communities were observed in randomly placed quadrats and presence/absence recorded.

Statistical analyses

The total number of species present on: (1) natural and/or artificial habitats (study 1) and (2) in pools and/or on emergent substrata (study 2) were compared using chi-square (2 × 2) contingency tables.

Analysis of variance (ANOVA) was used for all other comparisons. To test hypotheses about the differences in species richness on emergent substrata at different tidal heights among artificial and natural habitats, three-factor ANOVA was used with factors: Type (two levels: artificial, natural; fixed), Location (eight levels: listed above; random and nested in Type) and Height (two levels: mid, upper; fixed and orthogonal).

To test hypotheses about the differences in species richness among rock pools and emergent substrata in artificial and natural habitats, three-factor ANOVA was used with factors: Type (two levels: artificial, natural; fixed), Location (four levels: listed above; random & nested in Type) and Habitat (two levels: pool, rock; fixed & orthogonal).

To test hypotheses about the differences in species richness among rock pools and emergent substrata at the mid and upper tidal levels at Poole, three-factor ANOVA was used with factors: Groyne (two levels: one, two; random), Height (two levels: mid, upper; fixed and orthogonal) and Habitat (two levels: pool, rock; fixed and orthogonal).

GMAV version 5 for Windows was used for ANOVA computations (Underwood & Chapman, 1998). Cochran's test was used to test for heterogeneity of variances, and Student–Newman–Keuls (SNK) procedure was used to make post hoc comparisons among levels of significant terms. In cases where variances were significant square root transformations were applied to the data.

RESULTS

Study 1: Comparison of biodiversity at different tidal heights on emergent substrata among natural and artificial habitats

There was a significant difference in total species richness among natural and artificial habitats. A total of 31 taxa were recorded across all locations and, of these, 31 were recorded in natural habitats, 18 in artificial habitats ($\chi^2 = 16.5$, $P < 0.01$), 13 of which were unique to natural habitats and none unique to artificial habitats (See Table S1 in Supporting Information). Rhodophyta contributed most to this diversity (10), followed by Mollusca (7), Phaeophyta (5), Chlorophyta (3), lichens (2), Arthropoda (2), Porifera (1) and Cnidaria (1).

Natural habitats supported significantly greater species richness than artificial habitats (main effect of factor Type, Fig. 3, Table 2, See Table S1). Artificial habitats supported an average of 2.7 species per quadrat, whilst natural habitats supported an average of 4.5 species per quadrat. There was a significant interaction between factors Height and Location (Fig. 4, Table 2). Species richness was consistently higher at mid than upper tidal levels at all locations, but this was not always significant, particularly in natural habitats (Fig. 4, Table 2).

Study 2: Comparison of biodiversity among rock pools and emergent substrata in natural and artificial habitats

There were significant differences in total species richness among rock pools and emergent substrata, both in natural

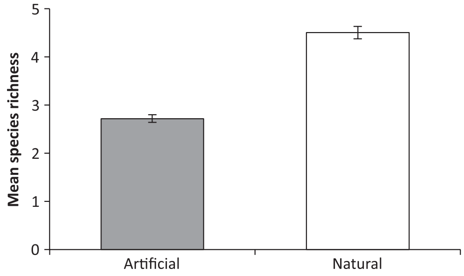

Figure 3 Mean species richness (± SE) on emergent substrata in artificial and natural habitats. Data shown were pooled for the mid and upper shore at eight locations for each of artificial and natural habitats [$\sum n$ = (8 locations × 2 heights × 12 quadrats = 192)]. Artificial locations sampled: Dinas Dinlle, Elmer, Leasowe, Penrhyn Bay, Prestatyn, Rhos-on-Sea, West Shore and Tywyn. Natural locations sampled: Aberffraw, Cable Bay, Derbyhaven, Penmon, Porth Dafarch, Porth Dinllaen, Rhosneigr and Cemlyn Bay.

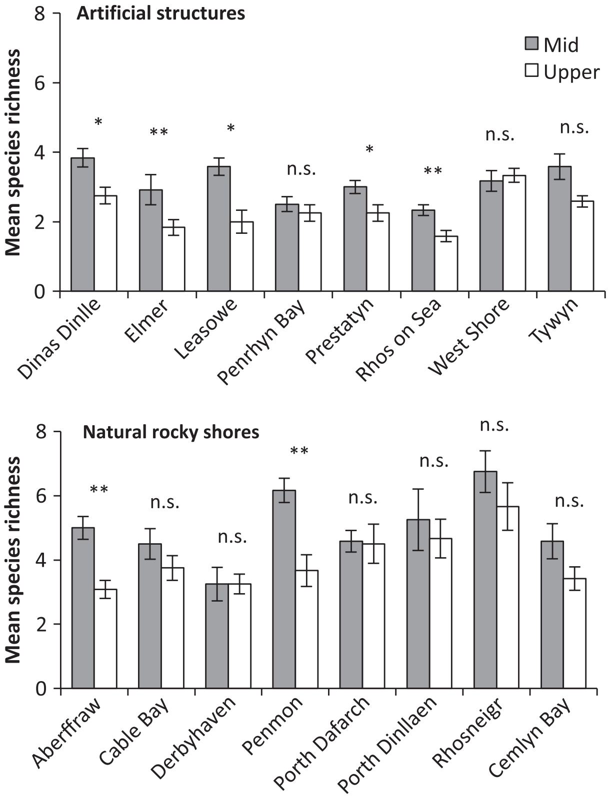

Figure 4 Mean species richness (± SE) on emergent substrata in the mid- (grey) and high (white) shore of artificial structures and natural habitats (n = 12 quadrats). Artificial locations sampled: Dinas Dinlle, Elmer, Leasowe, Penrhyn Bay, Prestatyn, Rhos-on-Sea, West Shore and Tywyn. Natural locations sampled: Aberffraw, Cable Bay, Derbyhaven, Penmon, Porth Dafarch, Porth Dinllaen, Rhosneigr and Cemlyn Bay. n.s.: $P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$.

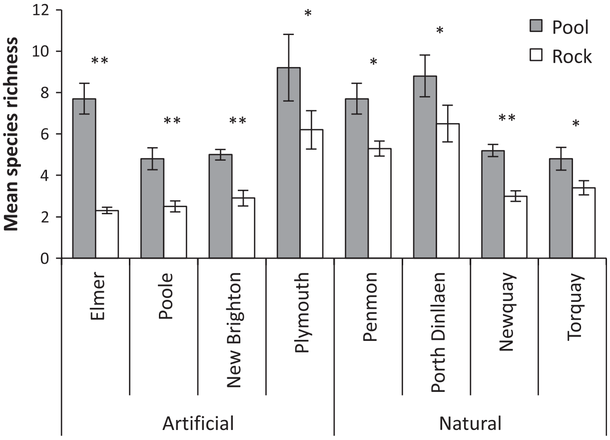

Figure 5 Mean species richness (± SE) in rock pools (grey bars) and emergent substrata (white bars) of artificial and natural habitats (n = 10 quadrats). $^*P < 0.05$; $^{**}P < 0.01$.

and artificial habitats. In artificial habitats, a total of 47 taxa were recorded across all locations and habitats. Of these taxa, 42 were recorded in pools and 14 on emergent substrata ($\chi^2 = 21.2$, $P < 0.01$). Thirty-two taxa were unique to rock pools, and four were unique to emergent substrata (See Table S2). Rhodophyta contributed most to this diversity (14), followed by Phaeophyta (10), Mollusca (9), Chlorophyta (4), Arthropoda (3), Porifera (2), Cnidaria (2), Tunicata (1), Annelida (1) and Pisces (1).

In natural habitats, a total of 66 taxa was recorded across all locations and habitats. Of these taxa, 56 were recorded in rock pools, and 30 on emergent substrata ($\chi^2 = 16.3$, $P < 0.01$). Thirty-six taxa were unique to rock pools, and nine were unique to emergent substrata (See Table S2). Rhodophyta contributed most to this diversity (26), followed by Phaeophyta (11), Mollusca (9), Chlorophyta (6), Arthropoda (3), Porifera (3), Echinodermata (2), Annelida (2), Cnidaria (1), Bryozoa (1), lichens (1) and Cyanobacteria (1).

Species richness was significantly greater in rock pools than on emergent substrata at all locations, irrespective of whether the habitat was natural or artificial (Fig. 5, Table 3). There was a significant interaction between Habitat and Location with pools consistently supporting greater species richness than emergent substrata at all locations, but the difference in magnitude was greater in artificial than natural habitats (Fig. 5, Table 3). Rock pools in artificial habitats supported proportionately more taxa compared with emergent substrata (48%) than those on natural rocky shores (32%), highlighting the differential importance of rock pools in artificial and natural environments. There was no significant difference in species richness in rock pools among natural and artificial habitats (Fig. 5, Table 3), but rock pools in natural habitats did support greater total species richness (56) than artificial habitats (42) (Table S2).

An additional survey was carried out comparing species richness among rock pools and emergent rock at mid- and upper tidal levels on the groynes at Poole. There were significant main effects of both Height and Habitat with greater species richness in rock pools than on emergent substrata and at mid than upper tidal levels (Fig. 6, Table 4). Despite

Table 3 ANOVA results for comparison of species richness between rock pools and emergent substrata in artificial and natural habitats

Source	Species richness d.f.	MS	*F*
Type = Ty	1	1.17	0.58
Location = Lo (Ty)	6	2.05	16.15***
Habitat = Ha	1	12.36	38.23***
Ty × Ha	1	1.03	3.17
Ha × Lo (Ty)	6	0.32	2.55*
RES	144	0.13	
Student-Newman-Keuls comparisons			
He × Lo (Ty)			

Artificial	Pool vs. Emergent	Natural	Pool vs. Emergent
Elmer	P ≫ R	Penmon	P > R
Poole	P ≫ R	Porth Dinllaen	P > R
New Brighton	P ≫ R	Newquay	P ≫ R
Plymouth	P > R	Torquay	P > R

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

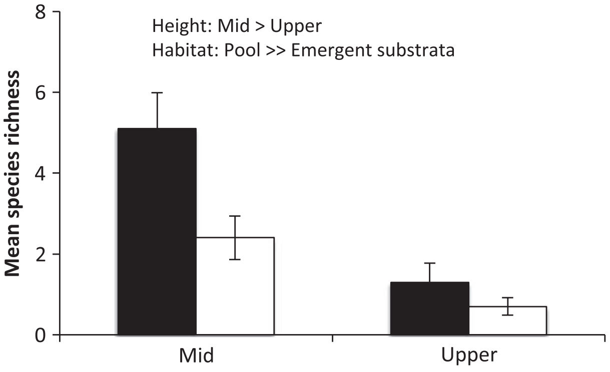

Figure 6 Mean species richness (± SE) in rock pools (black bars) and emergent substrata (white bars) at mid- and upper tidal levels on the artificial structures at Poole. Data shown were pooled for the two groynes surveyed [$\sum n$ = (2 groynes × 5 quadrats = 10)].

there being main effects of both Height and Habitat, the data in Fig. 6 have been kept separate for each factor to illustrate the differential effects of both factors on species richness.

Table 4 ANOVA results for comparison of species richness between rock pools and emergent substrata at the high and mid-tidal levels on the artificial structures at Poole (n = 5 quadrats). Data were square root transformed

Source	Species richness d.f.	MS	*F*
Groyne = Gr	1	0.03	0.17
Height = He	1	5.45	178.75*
Habitat = Ha	1	1.53	7.54**
Gr × He	1	0.03	0.15
Gr × Ha†	1	<0.0001	
He × Ha	1	0.46	25.05
Gr × He × Ha	1	0.02	0.09
RES	33	0.20	

*$P < 0.05$, **$P < 0.01$.

†Data are pooled (Underwood, 1997).

DISCUSSION

The hardening of the coast with artificial structures is likely to continue with current population increases and forecast climate changes. The construction of such structures in both intertidal and subtidal marine habitats provides substrata for attachment, and potential habitat for a wide range of marine organisms, from native and invasive non-native species to those of conservation importance (Bulleri & Airoldi, 2005; Vaselli *et al.*, 2008; Martins *et al.*, 2010; Perkol-Finkel & Airoldi, 2010; Firth *et al.*, 2011; Perkol-Finkel *et al.*, 2012). Despite the potential for these structures to provide habitat, they generally support lower biodiversity than adjacent natural rocky habitats (Chapman & Bulleri, 2003; Moschella *et al.*, 2005; Pister, 2009). The present study found species richness to be significantly lower in artificial than natural habitats. Despite sharing many species in common, natural habitats had almost twice as many species as artificial habitats (31 compared with 17 species). Species richness decreased with increasing shore height as hypothesized (Hawkins & Hartnoll, 1980; Little & Kitching, 1996; Raffaelli & Hawkins, 1996). The effect of tidal height was more pronounced in artificial than natural habitats with species richness being significantly greater at mid than upper tidal levels in 63% of artificial habitats compared with only 25% of natural habitats. The steeper aspect that is characteristic of artificial structures could lead to more significant changes in community structure and functioning over smaller spatial scales (Chapman & Underwood, 2011). Artificial structures also have less small-scale heterogeneity including surface roughness to ameliorate sharp intertidal gradients.

Species richness was significantly higher in rock pools than on adjacent emergent substrata in both natural and artificial habitats. However, the contribution of rock pools to species richness was more pronounced in artificial than natural habitats. The extent to which biodiversity of rock pools exceeded that of emergent substrata did not vary with tidal height. However, species richness in rock pools was much greater at mid than upper tidal levels in artificial habitats, mirroring trends for natural rocky shores (Raffaelli & Hawkins, 1996). It has long been known that diversity in rock pools is greater at lower than upper tidal levels on natural rocky shores (Raffaelli & Hawkins, 1996). Rock pools are relatively uncommon on artificial structures. The groynes at Poole comprise boulders of Portland limestone, which exhibit varying degrees of erosion and have many small depressions, creating environmental heterogeneity and important habitat for a range of organisms. When these depressions are located on the horizontal surface of the boulder, they retain water and mimic shallow rock pools. In contrast to other artificial structures that have rock pools at the base of the structures (e.g. New Brighton, concrete and Elmer, largely granite), these rock pools are present at all tidal heights on the groynes at Poole.

Many studies have compared the biodiversity of emergent substrata among natural and artificial habitats (e.g. Chapman & Bulleri, 2003; Moschella *et al.*, 2005; Pister, 2009). To our knowledge, this is the first time that species richness in rock pools in natural habitats has been compared with that in artificial habitats. Pools are relatively uncommon on artificial structures. The significant contribution of rock pools at mid-tidal levels to the species richness of artificial shores implies that the incorporation of water-retaining features will have a positive effect on the biodiversity of artificial habitats, particularly if added at mid rather than upper tidal levels.

The physical characteristics and positioning of rock pools on the artificial structures is likely to have a significant effect on epibiota. For example, the pools at Elmer and New Brighton were located at the base of the structures between boulders or reef units. Conversely, the pools on Plymouth Breakwater and the Poole groynes were all shallow and exposed on horizontal surfaces. Although rock pools can sometimes offer a refuge to physical stress, they can also become very stressful environments, with large fluctuations in temperature, salinity, carbon dioxide and dissolved oxygen and hence pH (Metaxas & Scheibling, 1994; Firth & Williams, 2009) especially at higher levels of the shore. Deeper pools are more stable environments and are sometimes considered to support more diverse assemblages than shallower pools (Moschella *et al.*, 2005).

CONCLUSIONS

Artificial structures do provide important habitat for marine species. In general, they are not as diverse as natural habitats, due to lack of environmental heterogeneity. Occasionally, these structures provide desirable habitats such as rock pools, as a consequence of natural erosion and weathering (Moschella *et al.*, 2005; Pinn *et al.*, 2005), unintentionally or as a by-product of the construction methods (e.g. Griffin *et al.*, 2010; Noël *et al.*, 2010). It is possible to retrospectively add water-retaining features and other desirable habitats (e.g. pits and crevices) to artificial structures by way of novel engineering interventions (Chapman & Blockley, 2009; Martins *et al.*, 2010; Borsje *et al.*, 2011; Browne & Chapman, 2011; Chapman & Underwood, 2011; Witt *et al.*, 2012).

The placement of rock pools at different tidal heights will have consequences for the colonizing assemblages, with results being more pronounced at mid than upper tidal levels. The challenge now is to establish at what tidal height the effect of rock pools becomes negligible and to determine the configuration of rock pool dimensions (i.e. depth, incline and diameter) for optimum habitat enhancement. The lessons learnt in the marine environment could also be applied to other environments; for example, techniques to enhance biodiversity of flood defence walls along urban rivers such as the Thames through London have been suggested with the focus on enhancing habitat heterogeneity for plants (Francis & Hoggart, 2009) and invertebrates (Hoggart *et al.*, 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 List of species recorded on natural rocky shores and on artificial coastal defence structures.

Table S2 List of species recorded in rock pools and on emergent surfaces.

BIOSKETCH

Louise B. Firth is a University Fellow at the National University of Ireland, Galway. Her research interests encompass community dynamics and global climate change in both natural and artificial environments. This study links with two projects: THESEUS (www.theseusproject.eu) and URBANE (www.urbaneproject.org) funded by EU-FP7 and Esmée Fairbairn, respectively.

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