



Intertidal biodiversity and physical habitat complexity on historic masonry walls: A comparison with modern concrete infrastructure and natural rocky cliffs

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ABSTRACT

Maritime built heritage (e.g., historic seawalls) represents an important component of coastal infrastructure around the world. Despite this, the ecological communities supported by these structures are poorly understood. At seven locations across the UK, we compared the biodiversity and physical habitat characteristics of (1) historic (pre-1900s) masonry walls, (2) concrete walls, and (3) natural rocky cliffs.

Historic masonry walls were found to support significantly more species than concrete walls, and in some locations, more diverse communities than nearby rocky cliffs. Nevertheless, community composition remained distinct between the three habitat types at each location. We also found that historic masonry walls provided substantially more cryptic space (i.e., crevices) than both concrete walls and rocky cliffs, and this is positively associated with the ecological value of these structures. Overall, our results suggest that the unique physical properties of historic masonry walls make them an important component of habitat diversity along developed coastlines.

1. Introduction

Compared to natural rocky shores, artificial structures are generally considered to be ecologically poor (Aguilera et al., 2014; Chapman and Bulleri, 2003; Moschella et al., 2005; Pister, 2009). With a few exceptions (e.g., Hill et al., 2021; Holmes et al., 2020; López, 2019; Patrick et al., 2022), research examining the effects of artificial structures on marine wildlife has almost exclusively focused on determining the ecological impacts of modern infrastructure built from concrete and other engineering materials (e.g., metal and natural rock armour) since the beginning of the 20th century (e.g., Airolidi et al., 2015; Bacchiocchi and Airolidi, 2003; Firth et al., 2015; Momota and Hosokawa, 2021; Vaselli et al., 2008). As such, there is relatively limited understanding of the ecological communities that are supported by older structures (i.e., those built pre 1900s), including those with traditional block-masonry designs, despite constituting a significant proportion of coastal infrastructure around the world (Baxter et al., 2022a; Chadwick and Catchpole, 2010; Luo et al., 2019). In Cornwall, UK, for example, historic masonry structures, including stonewalled piers, seawalls, and breakwaters, constitute >50 km of the intertidal shoreline (Fig. 1) including heavily urbanised sections of coast (e.g., Falmouth and Plymouth) and

those within areas of marine conservation (e.g., Whitsand and Looe Bay Marine Conservation Zone). Notably, research examining how biodiversity develops on rock armour over decadal timescales suggests that older structures might support more diverse ecological communities than newer structures (e.g., Pinn et al., 2005), and communities may become more similar to those found on nearby natural rocky shores with age (e.g., Burt et al., 2011; but also see Aguilera et al., 2022). It is surprising, therefore, that the ecological functions of historic maritime infrastructure have not been considered in greater detail, especially given their relative age, potentially unique construction features, and additional heritage value.

As first discussed by Baxter et al. (2022a), historic maritime structures may possess a number of characteristics relating to their traditional design (i.e., masonry configuration), material, age and decay mechanisms, maintenance regimes, and protected status that makes them favourable for marine wildlife colonisation (Fig. 2). This often contrasts with more recently built structures that have been shown to alter ecological connectivity (Bishop et al., 2017), attract and promote the spread of non-native and invasive species (Airolidi et al., 2015; Bulleri and Airolidi, 2005; Glasby et al., 2007; Mineur et al., 2012; Vaselli et al., 2008), and support younger, less diverse assemblages of marine

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organisms than natural shores (Connell and Glasby, 1999; Moschella et al., 2005). Notably, historic structures are typically constructed of the same or similar materials to the local geology, such as locally quarried stone, which contrasts with the abundance of concrete and imported stone used in modern engineering (Bijen, 1996; Kampa and Laaser, 2009). Furthermore, textured surfaces and fine-scale topographic features typical of natural rock and quarried stone are generally considered beneficial for marine colonisation, unlike the smooth surfaces characteristic of metal and cast concrete (Coombes et al., 2011; Dodds et al., 2022; Firth et al., 2023; MacArthur et al., 2019; Sempere-Valverde et al., 2018).

Due to years of progressive degradation by weathering and erosion, the availability of fine- (<1 cm) and meso-scale (>1 cm) surface features is expected to be higher on historic masonry structures (Fig. 2). For example, surface pitting from salt weathering and the development of fine cracks via the enlargement of discontinuities in natural stone may provide functional habitat space for benthic organisms (e.g., Chapman and Underwood, 2011; Moreira et al., 2007). In the particular case of old waterfront walls built from dimension stone (i.e., quarried stone selected and/or shaped for use in construction), horizontal and vertical crevices of varying sizes and shapes occur between adjacent stones both in mortared and traditional drystone configurations (i.e., free-draining structures without mortared joints), which may provide cryptic habitat space and refugia (in association with porous designs and internal void space; see Sherrard et al., 2016) for a range of sessile and mobile species (e.g., Chapman and Blockley, 2009; Dugan et al., 2011; Johnson et al., 1998; Moreira et al., 2007). Many historic structures also provide larger-scale physical habitat features that make them more similar to natural rocky shores than simpler, modern structures, including overhangs and ledges that resemble ecologically important water-retaining features like rockpools (Firth et al., 2013; MacArthur et al., 2020; Fig. 2). The progressive loss of core materials and the

dislodgement of individual stones may also create novel habitat space in older walls (Chapman and Blockley, 2009; Sherrard et al., 2016). Fine- and meso-scale topographic features are known to mitigate thermal stress on both natural rock shores and artificial structures (Aguilera et al., 2019; Cox and Smith, 2011; Williams and Morritt, 1995; Garrity, 1984), especially during summer and heatwave conditions. As such, the presence of these features on historic structures (whether by design or not) might facilitate more diverse assemblages compared to modern infrastructure typically lacking in topographic complexity. As of yet, however, few studies have quantified differences in the provision and biodiversity of microhabitat features between built heritage, modern infrastructure, and natural rock surfaces.

Due to their age, unique architectural features, and/or historical and cultural significance, the protected status of many historic structures (e.g., listed buildings and Scheduled Monuments) means that original materials or those with compatible technical and aesthetic properties are considered most suitable for maintenance and repair works (Historic England, 2016a, 2016b). As such, pre-weathered stone or original materials are favoured for minor repairs to historic masonry walls (Historic England, 2016c), particularly when stonework can be salvaged from nearby (e.g., DeSilvey, 2017). This adds to the complex history of traditional construction, maintenance, repair, and replacement of old maritime walls that often gives rise to a unique mosaic of topographic features (Fig. 2). The age of historic masonry walls also means that, over time, ecological succession and interactions among colonising organisms (e.g., predation, competition, symbiosis, etc.), might give rise to more complex and diverse communities relative to those built more recently (Burt et al., 2011; Butler and Connolly, 1999; Perkol-Finkel et al., 2005; Pinn et al., 2005). For instance, while key ecosystem engineers, such as canopy-forming macroalgae known to facilitate a range of understory species (Bertness et al., 1999; Burnaford, 2004; Umanzor et al., 2017, 2019; Watt and Scrosati, 2013), are typically absent from

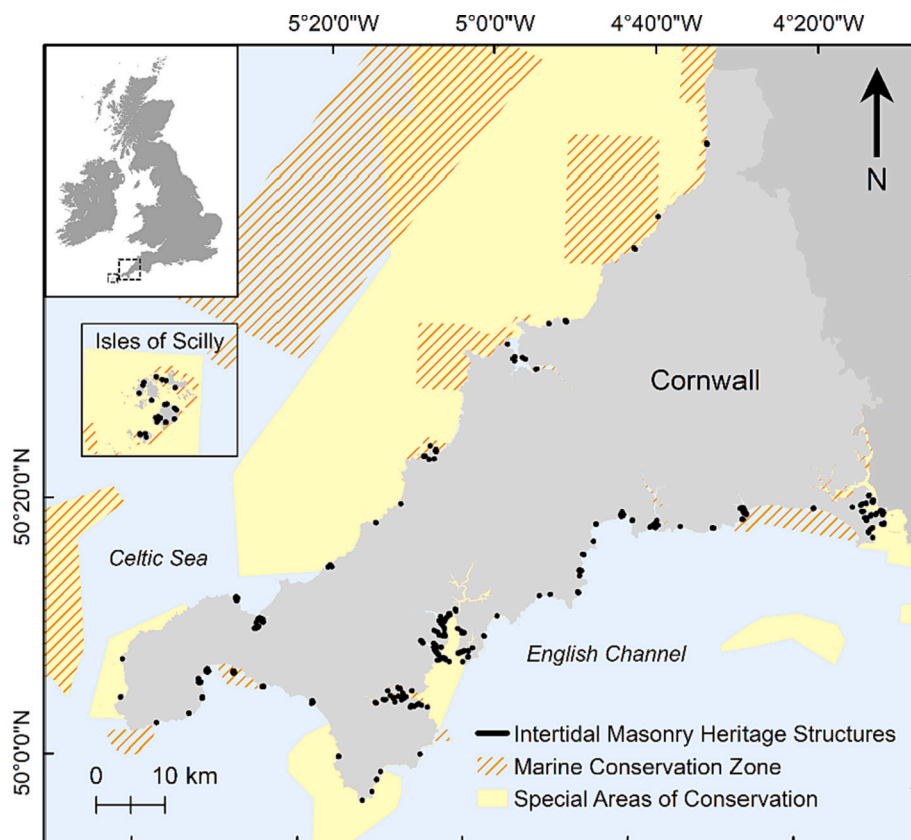


Fig. 1. Built heritage constructed of masonry within the intertidal zone of Cornwall, UK. This includes approximately 260 structures recorded in either the National Heritage List for England or Cornwall's Historic Environment Record. Marine Conservation Zones (MCZs) and Special Areas of Conservation (SACs) are also shown.

new and flat concrete walls, historic walls often support a greater range and abundance of these species (Fig. 2), although this remains largely untested.

In this study, we sought to provide a detailed assessment of the ecological communities (surface and cryptic) found on historic masonry walls at several locations across the UK in comparison to nearby concrete walls and natural rocky cliffs. By specifically comparing vertical surfaces, we build on a growing number of comparisons between rock armour, vertical/steeply sloping structures, and semi-horizontal rocky shores (e.g., Aguilera et al., 2014, 2019, 2022; Bulleri, 2006; Cacabelos et al., 2018; Holloway and Field, 2020; Lam et al., 2009; Pister, 2009). We compared the (1) diversity and composition of surface ecological communities, (2) fine-scale surface topographic complexity, and (3) the provision and species richness of cryptic microhabitats (i.e., internal void space) between the three studied habitat types. We show that historic masonry walls support more diverse communities than modern concrete walls, but that these communities differ to those found on nearby natural rocky cliffs. Importantly, for the first time, we highlight the ecological importance of the provision of cryptic microhabitats on traditional masonry walls. Based on these findings, we argue that historic masonry walls should be considered important multifunctional assets valued not only for their functional uses and historical significance, but also the unique habitats they provide and the diverse ecological communities they can support.

2. Methods

2.1. Field sites

was >180 years old and had either a mortared or drystone configuration; (2) a concrete wall constructed or significantly repaired within the last 100 years; and (3) a rocky cliff habitat consisting of an area of vertical natural rock substrate (Table 1). At all but one location (Cockenzie), the historic masonry wall and the rocky cliff habitat consisted of a similar rock type. The locations for the field surveys were selected because the three habitats at each site were <200 m apart and broadly comparable in terms of gradient (steep/vertical, 60–90°), aspect, position within the tidal zone (mid-to-high intertidal), MarLIN wave exposure category,¹ and surrounding habitat (i.e., rocky, sandy, or mixed).

To gain a holistic understanding of the biodiversity and physical complexity of the three habitat types, data were collected from two distinct environments on each wall/cliff: (1) the outer, seaward-facing surface, and (2) within cryptic microhabitat features (i.e., internal void space connected to the surface, such as crevices and holes). As discussed in the following sections, due to fundamental differences in the morphology (flat surfaces vs. crevices) and accessibility of the two environments, different sampling techniques were used to collect biodiversity and habitat complexity data from each. As such, the data from these two environments were analysed separately, although overall biodiversity was also compared qualitatively. Near-surface temperature data were also collected at one location (Aberdour) using an infra-red camera to provide preliminary evidence of differences in the thermal behaviours of surface and cryptic microhabitats (Supplementary material, Fig. A1).

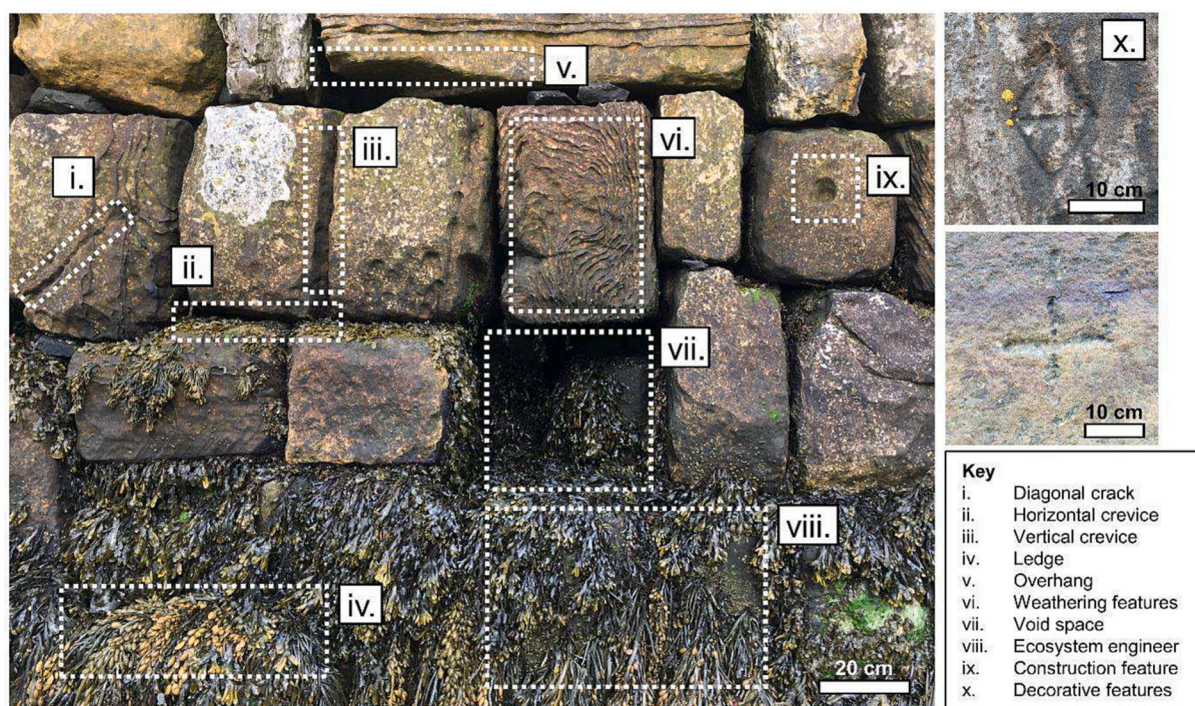


Fig. 2. Eighteenth century sandstone breakwater at St Andrews harbour, Scotland, with examples of microhabitat features typically found on historic masonry walls including (i) surface cracks, (ii) horizontal and (iii) vertical crevices in the stonework or between the joints, (iv) ledges and (v) overhangs, (vi) mm-scale topographic features caused by years of weathering processes (e.g., salt weathering), (vii) void space created by missing stonework, (viii) biotic covers formed by ‘ecosystem engineer’ species (e.g., seaweeds), (ix) features from historic construction, such as indented grips and holes used to manoeuvre stone into place, and (x) legacy features from the prior use of materials (in this case, parts of St Andrews harbour were rebuilt with stone from the nearby ruined castle dating to 1656).

Field surveys were conducted at seven locations across the UK during the summer of 2021 (Fig. 3). At each location, three types of habitat were surveyed: (1) a historic masonry wall listed as a heritage asset that

¹ Available at: <https://www.marlin.ac.uk/glossarydefinition/waveexposure>.

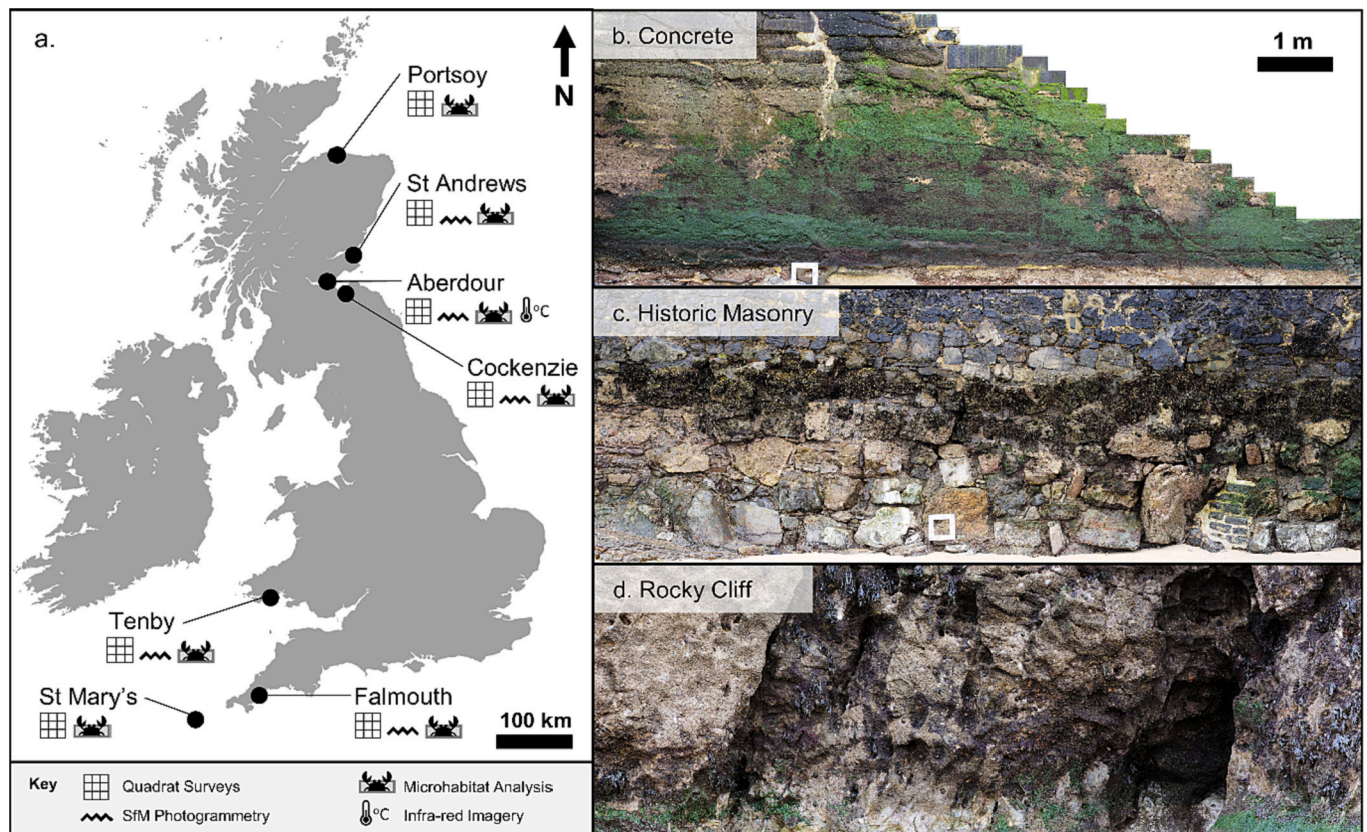


Fig. 3. (a) Locations of field surveys around the UK and the methods used at each site. Examples, from Tenby, Wales, of the different types of habitats surveyed at each location are shown, including (b) a concrete seawall, (c) a historic masonry breakwater, and (d) a near-vertical natural cliff.

Table 1

Locations of ecology surveys conducted on three types of coastal structure (masonry walls, concrete walls, and rocky cliffs) at seven sites across the UK (also see Fig. 3).

Location	Structure	Coordinates	Age	Material	Orientation	Listed status ^b
Portsoy (Scotland)	Drystone breakwater	57.685, -2.691	1692	Igneous rubble	North-east	Category A
	Concrete breakwater	57.686, -2.688	1883	Concrete	North	–
	Rocky cliff	57.686, -2.691	–	Olivine-gabbro	North-east	–
St Andrews (Scotland)	Drystone breakwater	56.339, -2.783	1700–27 ^a	Sandstone	South-east	Category A
	Concrete breakwater	56.339, -2.782	1910–1920 ^a	Concrete	South	–
	Rocky cliff	56.340, -2.784	–	Sandstone	South-east	–
Aberdour (Scotland)	Drystone breakwater	56.052, -3.295	1703	Sandstone	South	Category B
	Concrete slipway	56.052, -3.295	Post-1850s	Concrete	South	–
	Rocky cliff	56.051, -3.297	–	Sandstone	South	–
Cockenzie (Scotland)	Masonry (mortared) breakwater	55.970, -2.967	1835	Sandstone	North	Category B
	Concrete seawall	55.970, -2.969	~1967 ^a	Concrete	North-west	–
	Rocky cliff	55.970, -2.968	–	Quartz-dolerite	North	–
Tenby (Wales)	Masonry (mortared) breakwater	51.673, -4.697	1328, 1842	Limestone	North-east	Grade II
	Concrete seawall	51.673, -4.697	Pre-1890	Concrete	North-east	–
	Rocky cliff	51.673, -4.696	–	Limestone	North	–
Falmouth (S. England)	Masonry (mortared) pier	50.162, -5.060	1700–1839 ^a	Shale	West	Grade II
	Concrete seawall	50.154, -5.067	1960–1970 ^a	Concrete	North-west	–
	Rocky cliff	50.162, -5.062	–	Slate, Siltstone	North-west	–
St Mary's (Isles of Scilly)	Drystone breakwater	49.916, -6.317	1751	Granite	South	Grade II
	Concrete outflow	49.916, -6.317	1900–89 ^a	Concrete	South	–
	Rocky cliff	49.917, -6.312	–	Granite	South	–

^a Estimated age of construction based on historic maps and/or heritage records.

^b Listed status as reported by Historic England in the National Heritage List for England (Grade II = buildings of special interest) or by Historic Environment Scotland (Category A = buildings of national or international importance; Category B = buildings of regional or more than local importance).

2.2. External surface surveys

2.2.1. Surface biodiversity

The biological communities on the outer, seaward-facing surfaces of each habitat type were sampled at the seven locations using ten 20 × 20 cm quadrats placed at least 1 m apart at mid-tide level, as determined

using local tide tables. The percent cover of sessile organisms (e.g., barnacles and algae) and counts of mobile fauna were recorded within the quadrats (Evans et al., 2021). Using a similar method to Baxter et al. (2022a), individual count records were subsequently converted to percent cover depending on organism size (i.e., 0–20 mm = 1 %, 20–40 mm = 2 %, >40 mm = 4 %) to aid further analysis and comparison

between each habitat type. Mobile organisms observed within quadrats that were too small to count by eye (i.e., <2 mm, e.g., *Anurida maritima*) were given a nominal cover value of 1 %. Taxa were recorded to species level or, where this was not possible, by genus or family. A record was also made of whether the taxa were native or non-native according to the GB Non-native Species Secretariat (NNSS)² and National Biodiversity Network (NBN)³ websites (Baxter et al., 2022a).

2.2.2. Surface topography

To identify potential associations between surface topographic complexity and ecological communities present on each of the habitat types, at five of the study sites (Falmouth, Tenby, Cockenzie, Aberdour, and St Andrews), we used structure-from-motion (SfM) photogrammetry to record the surface topography of the substrates beneath the ecological communities surveyed using the 20 × 20 cm quadrats (Evans et al., 2021; Grasselli and Airoldi, 2021). Surface topography was not recorded at Portsoy and St Mary's due to practical constraints. At the other five sites, a wire brush was used to remove all colonising organisms from within the quadrat areas; care was taken to ensure the underlying substrate was not damaged during this procedure. A 23 × 23 cm frame with six control points was then placed centrally on each cleared area. A Sony Alpha a6600 APS-C Mirrorless Camera with an E 20 mm F2.8 lens was then used to take 19 photographs of the substrate surface: four photographs were taken from each corner angled 45° towards the centre, and then three sets of five overlapping perpendicular photographs (i.e., 15 in total) were taken below, above, and in line with the centre of each quadrat. Using Darktable v4.0, the raw images were checked to ensure they were well exposed, and no photometric correction was required before conversion to tiff format (Verma and Bourke, 2019). Accurately scaled (1 mm) digital elevation models (DEMs) with Cartesian coordinates were then generated using Agisoft Metashape Professional v1.6.5 and CloudCompare v2.11.3. For each model, the central 20 × 20 cm area was clipped so that the final topographic model represented the substrate directly beneath the surveyed biological community (Evans et al., 2021). The slope (i.e., the maximum rate of change in height from one 1-mm² cell to its neighbouring cells) in each topographic model (n = 40,000 cells per model) was then calculated using the Benthic Terrain Modeller (BTM) v3.0 add-on in ArcMap v10.8 (Walbridge et al., 2018). Mean slope values (S, deg.) were then determined for each area surveyed, with higher values indicating greater variability in mm-scale surface topography and lower values indicating flatter surfaces. Slope (mm-scale) has previously been identified as an important topographic variable that influences the biodiversity of substrates in marine environments (e.g., Evans et al., 2021).

2.3. Cryptic microhabitat provision and biodiversity surveys

To determine whether the provision and biodiversity of cryptic microhabitats (i.e., internal void space) varied between habitat type, the presence/absence of taxa within microhabitat features in a 15-cm area around each surveyed quadrat (i.e., 0.21 m² survey area) was recorded along with the dimensions (length, width, and approximate depth) of each feature. The approximate (internal) 3D surface area of each microhabitat feature was then calculated as follows:

$$\text{Surface area} = (\text{width} \times \text{depth} \times 2) + (\text{length} \times \text{depth} \times 2) + (\text{width} \times \text{length})$$

where length represents the longest distance between two points at the (surface) opening of a microhabitat feature, width represents the dimension perpendicular to length at the opening of a microhabitat feature, and depth represents the internal dimension of a microhabitat feature (i.e., how far the void associated with a feature penetrates into a

wall/cliff). The cryptic microhabitats were then grouped into one of six categories (crack, crevice, chasm, pit, hole, and hollow) based on size and shape using a classification system that corresponds to previous attempts to categorise topographic features on natural and artificial substrate in marine and coastal environments (e.g., MacArthur et al., 2020; Strain et al., 2018; Table 2). The frequency, total surface area, and total species richness (R_C) of the cryptic microhabitats per 2.1 m² of surveyed area (i.e., 0.21 m² × 10 areas) were then compared between each habitat type (masonry wall, concrete wall, and natural cliff) at each location.

2.4. Statistical analysis

To compare the surface communities across the three habitat types, species richness was first calculated for each quadrat (R_Q) using the DIVERSE function in PRIMER-e v.7 (Anderson et al., 2008; Clarke, 1993; Clarke et al., 2014; Clarke and Gorley, 2015). To model R_Q as a function of habitat type, a Poisson Generalised Linear Mixed Effects Model (GLMM) with a log link function was used (Zuur and Leno, 2016; Zuur et al., 2009). The log link function ensures positive fitted values, and the Poisson distribution is typically used for count data. 'Habitat type' was treated as a fixed factor (categorical with three levels: Concrete, Masonry, and Rocky cliff). To incorporate the dependency among observations of the same location, 'location' was used as a random intercept.

Differences in the composition of the ecological communities on the surfaces of each habitat type were also compared using PRIMER-E v.7 and PERMANOVA+ statistical software (Anderson et al., 2008; Clarke, 1993; Clarke et al., 2014). After examining shade plots, percentage abundance data were square-root-transformed to reduce the dominance of abundant species on similarity computations (Clarke and Gorley, 2015). A Bray–Curtis similarity matrix (Bray and Curtis, 1957) was then created for the statistical tests. Non-metric multidimensional scaling (nMDS) plots were created to visualise patterns using rank similarities and hierarchical clustering in the multivariate output (Clarke, 1993; Clarke et al., 2014). Permutational multivariate analysis of variance (PERMANOVA, McArdle and Anderson, 2001; Anderson, 2005) was also performed to test for differences in the assemblages, based on 9999 unrestricted random permutations of residuals (Anderson et al., 2008). Factors used in the analysis were 'habitat' (fixed, three levels: concrete, masonry, and rocky cliff) and 'location' (random, seven levels: see

Table 2

Categories of cryptic microhabitat features recorded on walls and cliffs at seven sites across the UK. The dimension ratios are based on those used in a classification system developed by Strain et al. (2018).

Type	Definition	Dimensions	Length ^a	Width ^b	Depth ^c
Crack	Narrow space of any length between two surfaces	Length:width ratio > 3:1	Any	$h \leq 1$ cm	≥ 0.5 cm
Crevice	Small, linear gap of any length between two surfaces	Length:width ratio > 3:1	Any	5 cm $\geq h > 1$ cm	≥ 1 cm
Chasm	Large, linear gap of any length between two surfaces	Length:width ratio > 3:1	Any	$h > 5$ cm	≥ 5 cm
Pit	Small, round hole	Length:width ratio $\leq 3:1$	$L \leq 3$ cm	$h \leq 3$ cm	≥ 0.5 cm
Hole	Medium, round hole	Length:width ratio $\leq 3:1$	15 cm $\leq L < 3$ cm	15 cm $\leq h < 3$ cm	≥ 1 cm
Hollow	Large, round hole	Length:width ratio $\leq 3:1$	$L > 15$ cm	$h > 5$ cm	≥ 5 cm

^a Longest distance between two points at the opening of a microhabitat feature.

^b Dimension perpendicular to length at the opening of a microhabitat feature.

^c Internal dimension.

² Accessed at: <https://www.nonnativespecies.org/>.

³ Accessed at: <https://nbnatlas.org/>.

Table 1 and Fig. 3). Pairwise comparisons were used to test differences in overall community structure between the three habitat types at each location. An analysis of similarity percentages (SIMPER) was then used to identify the percentage contributions of individual species to the dissimilarities between the habitat levels (Anderson et al., 2008; Clarke, 1993; Clarke et al., 2014; Sherrard et al., 2016).

To evaluate the surface topography data obtained from the SfM models, slope was modelled as a function of habitat type using a Linear Mixed Effects Model (LMM). To allow assumptions of normality and equal variance, the mean slope data (S) were square-root transformed. As with the GLMM, 'Habitat type' was treated as a fixed factor (categorical with three levels: Concrete, Masonry, and Rocky cliff), while 'location' was used as a random intercept. Both the GLMM and LMM were run using R v4.0.3 (R Core Team, 2021) and the package "lme4" version 1.1-30. Model assumptions were verified by plotting residuals against the fitted values and covariates in each model (Zuur and Leno, 2016).

3. Results

3.1. External surfaces

3.1.1. Surface species richness

Across all seven locations, a total of 56 taxa were recorded on the outer, seaward-facing surfaces of the three habitats surveyed (i.e., concrete walls, historic masonry walls, and rocky cliffs). Of these, 31 were recorded on concrete walls, 40 on historic masonry walls, and 48 on rocky cliffs (Supplementary material, Table A1). Three taxa were uniquely observed on the concrete walls, one on the historic masonry walls, and nine on the rocky cliff faces. Across all locations, only native species were observed on the outer surfaces of these habitats.

Significant differences in the number of surface-colonising species (R_Q) were found between the habitat types (Table 3). Compared to historic masonry walls, R_Q was significantly lower on concrete walls ($\beta = -0.46476$, $z = -6.429$, $p < 0.001$), and significantly higher on rocky cliff habitats ($\beta = 0.12516$, $z = 2.032$, $p < 0.05$). Concrete walls were found to have the lowest average R_Q at each of the study locations, apart from Portsoy (Fig. 4). In contrast, rocky cliff habitats had the highest average R_Q at four locations (Falmouth, St Andrews, St Mary's, and Tenby), while masonry walls had the highest values at three locations (Aberdour, Cockenzie, and Portsoy). When averaged across all seven locations, mean R_Q values for concrete, historic masonry, and rocky cliff habitats were 4.44, 7.07, and 8.01, respectively.

3.1.2. Surface community composition

There was significant interaction between habitat type and location in the community analysis ($Pseudo-F = 17.412$, $p \leq 0.0001$; Table 4), with the post-hoc pair-wise comparisons revealing significant differences between the three habitat types at each location ($p \leq 0.01$). These

Table 3

Estimated regression parameters, standard errors, z-values, and p-values for the Poisson GLMM used to model the number of surface-colonising species (R_Q) as a function of habitat type (* $p < 0.05$, *** $p < 0.001$).

Fixed effects	Estimate	Std. error	z value	p-Value
Intercept	1.93964	0.08244	23.527	<2e-16***
Habitat type concrete (relative to masonry)	-0.46478	0.07229	-6.429	1.28e-10***
Habitat type rocky cliff (relative to masonry)	0.12516	0.06161	2.032	0.0422*
Random effects	Variance	Std. dev.		
Location	0.03328	0.1824		

differences are evident in the nMDS ordination plots (Fig. 5). The SIMPER analysis revealed that dissimilarities between the habitat types at each location were driven by different species. For example, although barnacles (e.g., *Semibalanus balanoides*) were typically most abundant on the concrete walls at St Andrews, Portsoy, Falmouth, and Cockenzie, they were least abundant on the concrete walls and most abundant on the rocky cliffs at Tenby, St Mary's, and Aberdour. In general, historic masonry walls and rocky cliff habitats supported greater abundances of canopy-forming ecosystem engineers (e.g., seaweeds and mussels) and associated understory species, while concrete walls were typically dominated by a few, opportunistic species (e.g., *S. balanoides*, *Ulva* spp., etc.).

3.1.3. Surface topographic complexity

As a measure of topographic complexity, significant differences in square-root transformed mean slope (S_{sqr}) were found between the three habitat types (Table 5). Compared to the historic masonry walls, S_{sqr} was significantly lower on the concrete walls ($\beta = -1.157568$, $t = -8.126218$, $p < 0.001$) while the rocky cliff surfaces were no different ($\beta = 0.126654$, $t = 0.910160$, $p < 0.3643$). At all seven locations, concrete walls had the lowest average S_{sqr} (Fig. 6); when averaged across all seven locations, mean S_{sqr} values for concrete, historic masonry, and rocky cliff habitats were 2.96°, 4.01°, and 4.23°, respectively.

3.2. Cryptic microhabitats

3.2.1. Microhabitat frequency and surface area

At all locations, the historic masonry walls had the greatest number of microhabitat features (i.e., internal void space connected to the surface), while concrete walls had the least (Fig. 7). On average, the number of microhabitat features recorded on concrete, historic masonry, and rocky cliff habitats per m² area of wall/cliff surveyed was 0.75, 11.56, 4.49, respectively. Microhabitat features were particularly prevalent on free-draining masonry walls (i.e., without mortared joints), such as those at Aberdour, Portsoy, St Andrews, and St Mary's. In contrast, no microhabitat features were found on three of the seven concrete walls surveyed (Cockenzie, Falmouth, and St Mary's). Crevices were the most common cryptic feature type on masonry and concrete walls, while holes were most common on the rocky cliff habitats. However, microhabitat features of every type (Table 2) were on average most frequently observed on the historic masonry walls (Fig. 7).

Corresponding to the frequency data, with the exception of Tenby, the combined surface area of microhabitat features was typically greatest on the historic masonry walls and lowest on the concrete walls (Fig. 7). When averaged across all locations, the mean total (internal) 3D surface area of cryptic microhabitats on the concrete wall, historic masonry wall, and rocky cliff habitats per m² of surveyed area was 0.02, 1.63, and 0.35 m², respectively.

3.2.2. Cryptic microhabitat species richness

The total number of species observed within the cryptic microhabitat features at each location (R_C) was typically greatest for the masonry walls and lowest for the concrete walls (Fig. 7). With the exception of Tenby, the masonry walls also supported the greatest number of species found uniquely within the cryptic microhabitats. At Tenby, most cryptic species were found on the rocky cliff, which also supported the greatest proportion of species unique to these microhabitats. When averaged across all locations, R_C for the concrete, historic masonry, and rocky cliff habitats was 2.9, 21.3, and 15.0, respectively, of which 25 %, 48 %, and 34 % were only found in these microhabitat features and not on the surfaces of the walls/cliffs. In general, species richness increased in association with the number and total surface area of microhabitat features, both of which were generally highest on the historic masonry walls (Fig. 8). Only one non-native and invasive species (*Watersipora subatra*) was identified while surveying the cryptic microhabitats, which was found at low abundances within crevices on the historic masonry

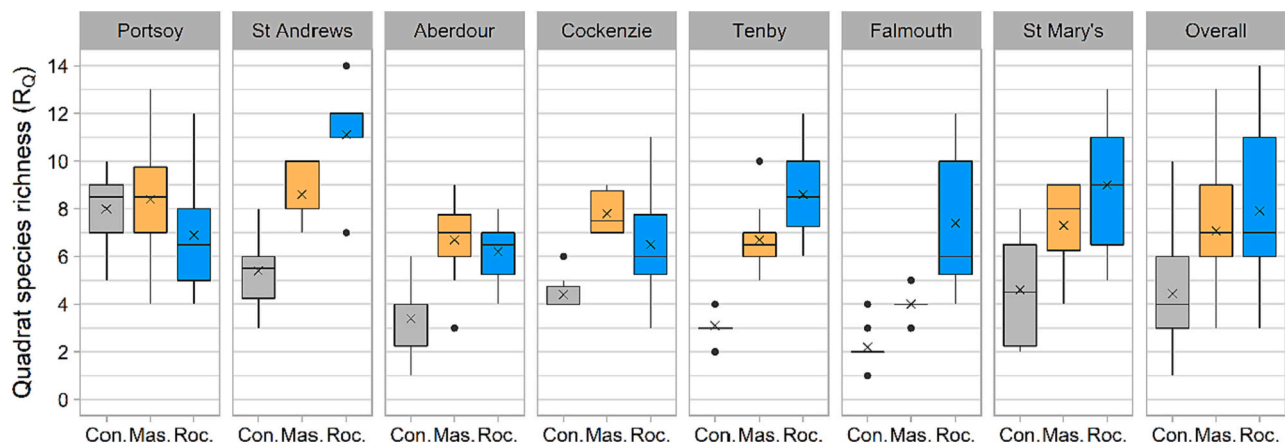


Fig. 4. Numbers of species observed within 20×20 cm quadrats (R_Q , $n = 10$) on the external, seaward-facing surfaces of concrete (grey, 'Con.'), historic masonry (orange, 'Mas.'), and rocky cliff habitats (blue, 'Roc.') at seven locations in the UK (see Fig. 3a). Pooled R_Q data across all locations ($n = 70$, 'overall') are also shown. Interquartile range (IQR) = boxes; median = horizontal line within boxes; mean = 'x'; whiskers = "minimum" ($Q1 - 1.5 \times IQR$) and "maximum" ($Q3 + 1.5 \times IQR$); outliers = dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Comparison of community composition (PERMANOVA) among concrete walls, historic masonry walls, and rocky cliff habitats. Analyses were based on Bray-Curtis similarities. All tests used 9999 permutations under a reduced model ($***p < 0.001$).

Source	df	MS	Pseudo-F	p-Value
Location	6	41,657	57.218	0.0001***
Habitat	2	14,289	1.1272	0.3591
Location \times Habitat	12	12,676	17.412	0.0001***
Residual	189	728.03		

wall on St Mary's, the southernmost site surveyed.

3.3. Overall species richness

While recognising the limitations of jointly analysing biodiversity data collected using different sampling techniques, overall species richness (R_T) for each habitat type at each location was determined by combining the number of species observed on the surfaces of each wall/cliff with those observed uniquely within the microhabitat features (Supplementary material, Fig. A2). At four locations (Portsoy, Aberdour, Cockenzie, and St Mary's), the historic masonry walls had the highest R_T values, while rocky cliff habitats had the highest values at three locations (St Andrews, Tenby, and Falmouth). In contrast, the concrete walls had the lowest R_T values at every location. When averaged across all locations, the most species were present on the historic masonry walls while fewest were present on the concrete walls.

4. Discussion

4.1. Surface biodiversity

We found significant differences between the biodiversity and community composition of ecological assemblages present on the external, seaward-facing surfaces of concrete walls, historic masonry walls, and rocky cliff habitats. In general, species richness was greatest on the external surfaces of rocky cliff habitats and least on concrete walls. However, the strength and direction of this trend varied with location, indicating the potential importance of other ecological (e.g., larval recruitment regime), environmental (e.g., wave exposure, salinity, climate, light, etc.), and anthropogenic factors (e.g., trampling, harvesting, pollution, etc.) in determining community structure beyond habitat type (Amstutz et al., 2021; Bracewell et al., 2018; Bulleri, 2005;

Cacabelos et al., 2016; Crowe et al., 2000; Southward and Orton, 1954).

Notably, at three of the seven locations surveyed (Aberdour, Cockenzie, and Portsoy), the historic masonry habitats were found to support the greatest diversity of surface-colonising organisms. Furthermore, across all locations, species richness was consistently higher on the surfaces of the historic masonry walls than on the concrete walls, supporting results reported elsewhere in the UK, including the Isles of Scilly (e.g., Baxter et al., 2022a). Together, these findings indicate that not all artificial structures should be considered ecologically poor and, in some cases, historic masonry walls can support comparable numbers of species to natural rocky cliffs. We also found no evidence that the historic masonry walls supported significantly more non-native or invasive species. However, based on composition, the communities supported by the artificial structures were distinct from the natural rocky cliff habitats, even after hundreds of years of colonisation in the case of the historic masonry walls. As with previous research examining ecological communities on rock armour defences, our results suggest that communities on artificial structures become more diverse with age (Burt et al., 2011; Pinn et al., 2005) yet remain distinct from those found on rocky shores (Gacia et al., 2007; López, 2019).

Differences in topographic complexity may explain some of the observed patterns in species richness (Evans et al., 2021). As well as influencing the attachment strength of colonising organisms, topographic variability benefits marine species by providing predatory and environmental refuge during low-tide periods (Aguilera et al., 2014, 2019; Coombes et al., 2015; Fletcher and Callow, 1992). For instance, a lack of physical refuges on smooth seawalls has been shown to facilitate the grazing activity of limpets, in some cases, resulting in the exclusion of almost all other types of colonising wildlife (Firth et al., 2023). In this study, topographic variability (quantified as slope) was significantly lower on the concrete walls, while there was no difference between the masonry walls and rocky cliffs at the measured scale. This supports previous research showing that concrete structures often lack surface heterogeneity compared to quarried stone and natural rock (e.g., Lawrence et al., 2021). This primarily relates to differences in construction design and engineering standards between cast concrete and masonry structures, but also possible differences in structure age, material type, and the formation of ecologically relevant surface features from progressive deterioration in the marine environment (e.g., Coombes, 2011; Coombes et al., 2011). Furthermore, given the vulnerability of reinforced concrete to corrosion and salt ingress, concrete walls might be more regularly maintained (e.g., patch repairs) than masonry walls to avoid more serious damage (Cork and Chamberlain, 2015). In the case of older concrete structures, topographic variability may increase if use

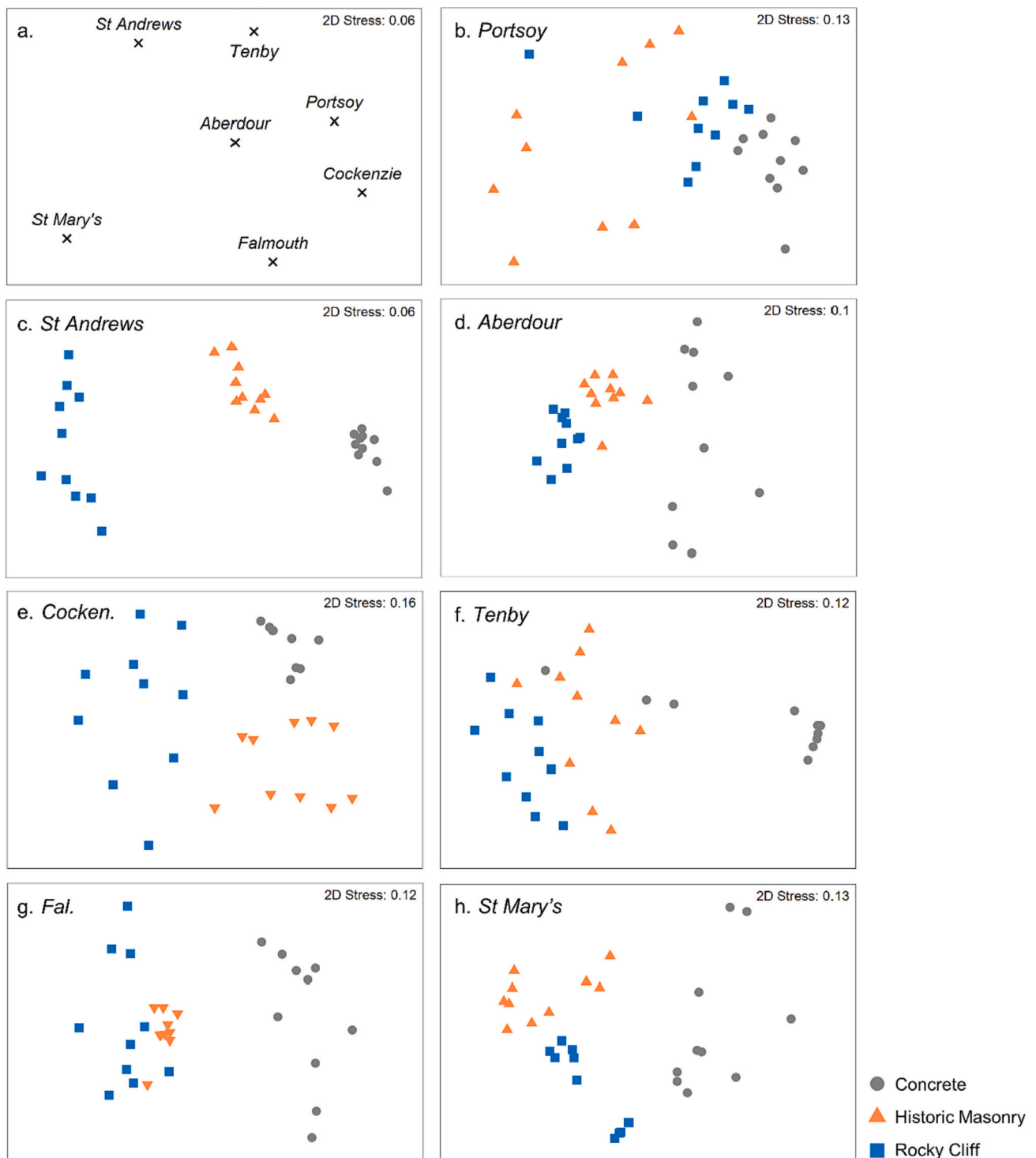


Fig. 5. Non-metric multidimensional scaling (nMDS) ordination of intertidal assemblage composition recorded at (a) the seven study locations (black crosses), and on the outer, seaward-facing surfaces of concrete walls (grey circles), historic masonry walls (orange triangles), and rocky cliff habitats (blue squares) at (b) Portsoy, Scotland, (c) St Andrews, Scotland, (d) Aberdour, Scotland, (e) Cockenzie, Scotland, (f) Tenby, Wales, (g) Falmouth, South England, and (h) St Mary's, Isles of Scilly. In part a, each point represents the average of 30 quadrats (i.e., 10 × concrete, 10 × historic masonry, and 10 × rocky cliff), whereas in parts b–h, each point represents one replicate quadrat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and maintenance have declined. For example, at St Andrews and Aberdour, the ~100-year-old concrete walls had the highest range and maximum S_{sqrt} values of the five concrete walls surveyed. These walls consist of relatively smooth areas of intact concrete as well as significantly deteriorated areas where spalling (i.e., surface breakdown, such as cracking or delamination) has exposed more topographically complex

internal aggregates. As with natural rock, this indicates that the surface complexity of concrete structures—and especially older ones—is intrinsically linked to decay mechanisms acting upon their surfaces. Although the overall biodiversity of the concrete walls at St Andrews and Aberdour was relatively low, these deteriorated surfaces tended to support more species than adjacent areas of smooth intact concrete.

Table 5

Estimated regression parameters, standard errors, t-values, and *p*-values for the LMM used to model square-root-transformed mean slope (S_{sqrt}) as a measure of surface topographic complexity, as a function of habitat type (***p* < 0.001).

Fixed effects	Estimate	Std. error	t value	<i>p</i> -Value
Intercept	4.099988	0.148576	27.595123	<0.001***
Habitat type concrete (relative to masonry)	−1.157568	0.1424486	−8.126218	<0.001***
Habitat type rocky cliff (relative to masonry)	0.126654	0.1391560	0.910160	0.3643

While colonisation might be favoured on deteriorating assets (with greater surface complexity), this will clearly not be desirable if structures are vulnerable to further biodeterioration; on the other hand, there may be situations where colonising organisms provide some degree of protection, with research on these issues gradually gathering pace (e.g., Baxter et al., 2022b; Bone et al., 2022a; Chlayon et al., 2018; Coombes et al., 2017).

In addition to differences in topographic complexity, variations in ecological processes and dynamics may explain some of the observed patterns of species richness on the surfaces of the three habitat types. Previous studies have shown greater rates of dislodgement/disturbance and reduced fecundity for ecosystem engineer species, such as seaweeds (e.g., *Fucus vesiculosus*), on artificial structures compared to natural shores (Drakard et al., 2021). In this study, the historic masonry walls and rocky cliff habitats were found to support greater abundances of canopy-forming seaweeds and mussels than the concrete walls. In addition to contributing to overall biodiversity, these species support epiphytic organisms, such as bryozoans (e.g., *Flustrellidra hispida*, *Electra pilosa*, etc.) and hydroids (e.g., *Dynamena pumila*), and also provide habitat space and refuge for understory species (Bertness et al., 1999; Burnaford, 2004; Umanzor et al., 2019; Watt and Scrosati, 2013). By supporting more ecosystem engineer species, abiotic stresses on the colonised sections of the historic masonry walls and rocky cliffs are likely reduced compared to the, often, less colonised concrete walls (Aguilera et al., 2019). This is supported by our preliminary temperature data, which indicate that at Aberdour in Scotland, the colonised surfaces of the masonry wall and natural cliff remained relatively cool during low-tide periods compared to bare areas of the nearby concrete wall (Supplementary material, Fig. 1A). As few studies have yet compared the thermal characteristics of biotic canopies and abiotic microhabitats (e.g., crevices and other cryptic features) between vertical rocky substrate and different types of coastal engineering assets, including heritage buildings and modern infrastructure, this represents a potential

avenue for future research.

4.2. Cryptic microhabitat provision and biodiversity

In contrast to previous studies that have analysed and compared the provision of microhabitats on natural shores and artificial structures across latitudinal gradients (e.g., Aguilera et al., 2022), no meaningful association was identified between latitude and microhabitat availability and associated biodiversity in this study. Instead, microhabitat availability varied between the three habitat types, with historic masonry walls providing substantially more cryptic space than both concrete walls and rocky cliff habitats at every location surveyed. This finding contributes to a growing field of research comparing the physical structure of coastal infrastructure and natural shores (e.g., Aguilera et al., 2014, 2022; Grasselli and Airolidi, 2021; Lawrence et al., 2021), and in terms of vertically orientated substrate, indicates that historic masonry walls may represent some of the most physically complex habitats along many developed coastlines. Microhabitat features on historic masonry walls not only provide unique habitat conditions, but also increase the available surface area for colonisation. It is unsurprising, therefore, that microhabitats on the historic masonry walls generally supported more species than the concrete walls and rocky cliff habitats. The cryptic microhabitats provided by free-draining masonry walls, such as those at Aberdour, Portsoy, St Andrews, and St Mary's, were found to be particularly valuable for marine wildlife; of all the habitats surveyed, these structures had the highest densities of cryptic microhabitats and, concurrently, supported the greatest numbers of species. This included unique species not found on the surfaces of these walls, including sea anemones (e.g., *Actinia equina*), blennies (e.g., *Lipophrys pholis*), and sponges. As with porous rock armour, habitat space between unmortared stonework likely provides valuable refuge for a range of species (Sherrard et al., 2016). For example, temperatures within cryptic microhabitats on the historic masonry wall at Aberdour were consistently cooler (and presumably wetter) than their surfaces during low-tide periods (Supplementary material, Fig. 1A). Thus, when considered together, the surface and cryptic habitats provided by historic masonry walls (particularly free-draining/drystone constructions) can support some of the most diverse assemblages of comparable vertical habitat in the coastal environment (Supplementary material, Fig. 2A).

4.3. Implications

Maritime built heritage is valued for its functional uses (e.g., flood

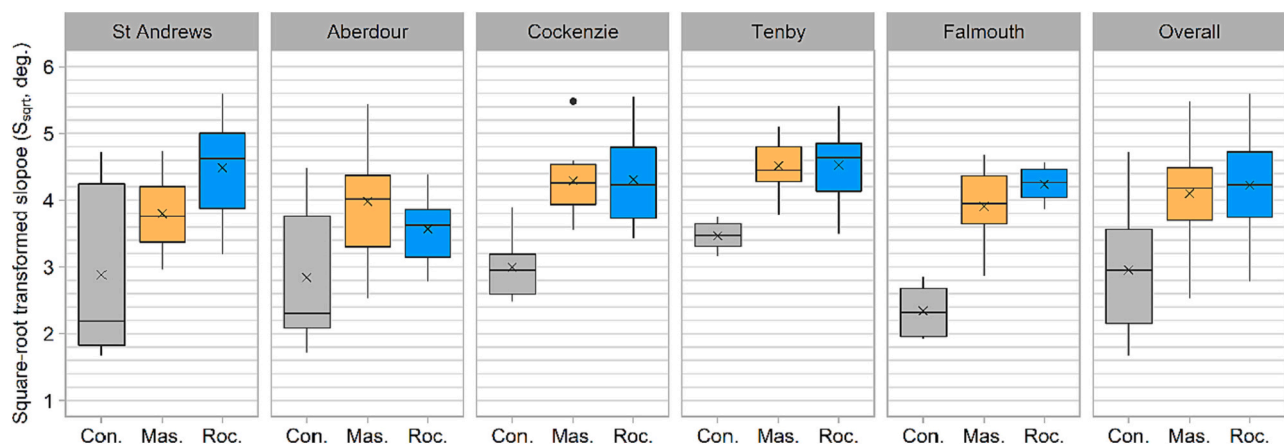


Fig. 6. Square-root-transformed mean slope (deg., S_{sqrt}) on the external, seaward-facing surfaces of concrete (grey, 'Con.'), historic masonry (orange, 'Mas.'), and rocky cliff habitats (blue, 'Roc.') at seven locations in the UK. Pooled S_{sqrt} data across all locations (i.e., $n = 50$) is also shown. Interquartile range (IQR) = boxes; median = horizontal line within boxes; mean = 'x'; whiskers = "minimum" ($Q1 - 1.5 * IQR$) and "maximum" ($Q3 + 1.5 * IQR$); outliers = dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

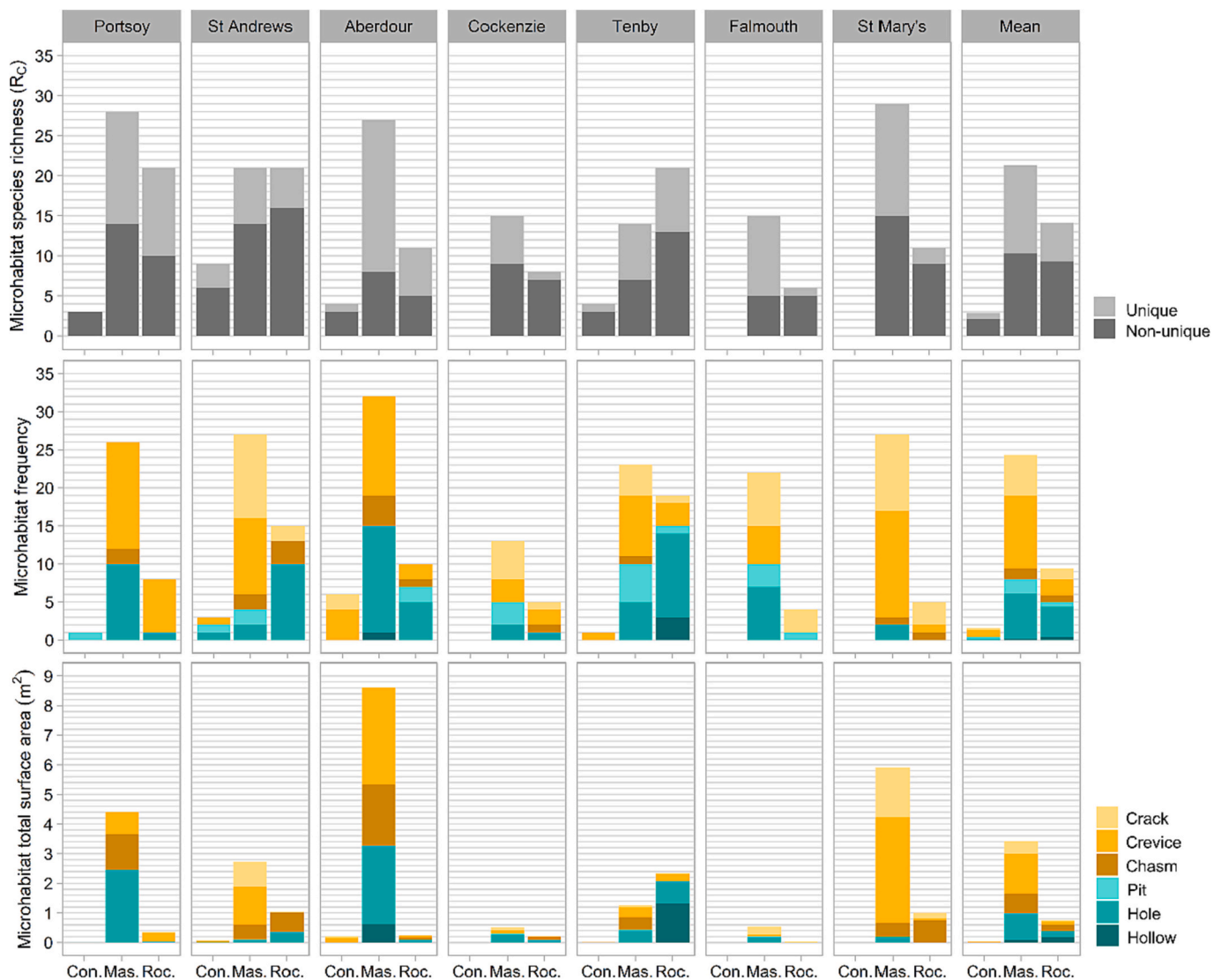


Fig. 7. Top row: Total number of species found within cryptic microhabitat features (R_c) per 2.1 m^2 of surveyed area on each habitat type (Con., concrete wall; Mas., historic masonry wall; Roc., natural rocky cliff) at seven locations in the UK. The number of species observed uniquely within the cryptic microhabitat features are shown in light grey, while those also observed on the outer surfaces of the walls/cliffs are shown in dark grey. Middle Row: Frequency of different types of microhabitat features per 2.1 m^2 of surveyed area on each habitat type at each location. Bottom Row: Total surface area (m^2) of microhabitat features per 2.1 m^2 of surveyed area on each habitat type at each location. Mean values across all locations are also shown.

protection, access to the sea, etc.) as well as its historical and cultural significance (Fulford et al., 1997). Increasingly, wrecks and other submerged aspects of built heritage are recognised for the diverse ecological communities they support (Castelló y Tickell et al., 2019; Gravina et al., 2021; Lengkeek et al., 2013; Meyer-Kaiser and Mires, 2022). Our results suggest that the ecological value of built heritage is not limited to underwater structures. Rather, based on seven sites across the UK, historic masonry walls within the intertidal zone support assemblages of marine wildlife that are significantly more diverse than those found on nearby concrete walls and, in some cases, adjacent vertical rocky cliffs. Crucially, for the first time, our results highlight the provision and ecological importance of cryptic habitat on seaward-facing traditional masonry walls and, as such, their multi-functional value as heritage assets and for ecosystem service provision, including supporting biodiversity. This typically contrasts with modern coastal infrastructure that can lack secondary benefits beyond its primary purpose (e.g., flood protection; Evans et al., 2017). By highlighting the ecological potential of historic masonry walls, this study contributes to a small but growing field of research examining the ecological communities supported by

intertidal stone-built heritage, including centuries-old rock-walled terraces used to enhance shellfish production in North America (i.e., 'clam gardens'; Cox et al., 2019; Holmes et al., 2020), and ancient stone fish traps found along coastlines around the world (e.g., Favier Dubois et al., 2018; Patrick et al., 2022; Kemp, 2006; Kemp et al., 2009). Fundamentally, the ecological value of maritime built heritage should contribute to arguments for its continued protection and conservation in the face of multiple threats associated with climate change, increasing coastal urbanisation, and neglect.

As we have previously argued (Baxter et al., 2022a), an improved understanding of the ecological value of maritime built heritage presents mutually beneficial opportunities for the conservation of cultural heritage and marine biodiversity. For instance, our results highlight the importance of preserving traditional structures and construction features of historical or architectural interest that provide unique habitats for marine wildlife. This includes cryptic space between the stonework of free-draining masonry walls as well as older, weathered, and more topographically complex stone. The potential for cavities within historic masonry to function as refuge for marine wildlife also strengthens

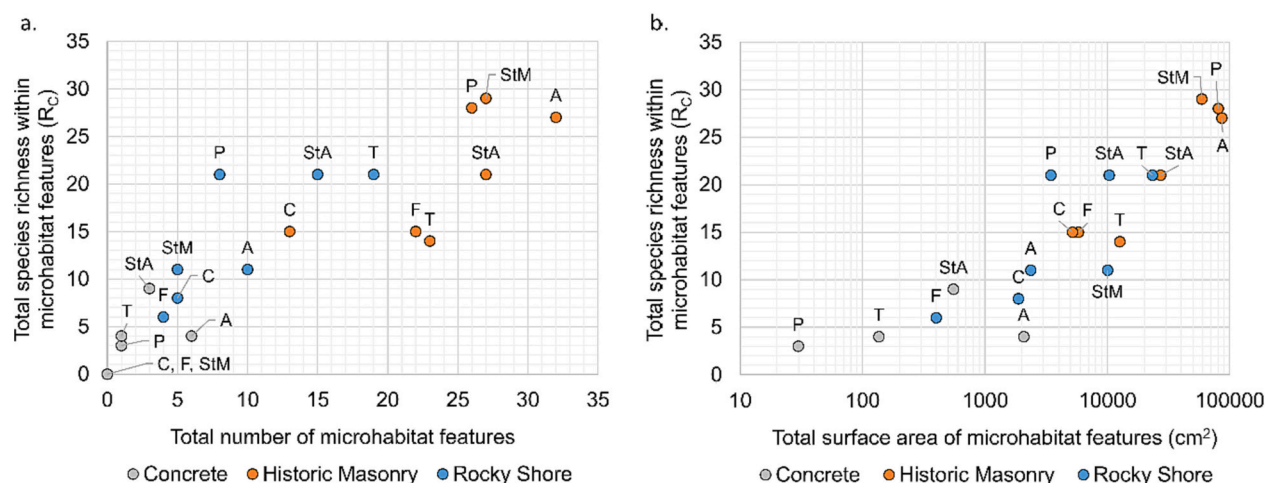


Fig. 8. The total number of species found within cryptic microhabitat features (R_c) against (a) the total number and (b) total surface area of microhabitat features (cm^2) found per 2.1 m^2 of surveyed area on concrete (grey), historic masonry (orange), and rocky cliff (blue) habitats at each location (A = Aberdour, C = Cockenzie, F = Falmouth, P = Portsoy, StA = St Andrews, StM = St Mary's, T = Tenby). Note that at three locations (Cockenzie, Falmouth, and St Mary's), no cryptic microhabitats were observed on the concrete walls surveyed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

arguments for using unintrusive repair methods that aim to preserve these features (e.g., Hine et al., 2015). This includes repurposing old stone to replace damaged or missing original stonework as well as using traditional maintenance techniques to secure dislodged material that retains rather than covers over or fills in novel habitat space (e.g., wooden pegs vs. pointing). Knowledge that historic masonry structures can support diverse ecological communities may also influence how managers of these sites perceive marine growth, in addition to the frequency and methods used to control and/or encourage colonisation by marine wildlife. For instance, based on a survey of >130 practitioners, we found that asset managers are more inclined to use eco-friendly cleaning techniques in historic harbours when they are aware of the biodiversity that maritime infrastructure can support (Baxter et al., 2022c).

Given that coastal development is predicted to increase over the next century in response to urbanisation and the threats associated with climate change (e.g., rising sea-levels, more frequent storm events), historic masonry structures may become increasingly important refuges for marine wildlife along with more recently constructed infrastructure designed or retrofitted to maximise ecological potential as well as any natural habitat left undisturbed or restored. This includes heavily urbanised coastlines dominated by vertical concrete infrastructure, where historic masonry walls might provide some of the only suitable habitat for marine organisms, particularly cryptic species (e.g., *L. pholis*).

Finally, features characteristic of historic masonry walls that we found to benefit marine wildlife may provide inspiration for the design of coastal eco-engineering solutions (Naylor et al., 2017a, 2017b; O'Shaughnessy et al., 2020). This could include: (1) using naturally or artificially pre-weathered materials or those that are more prone to weathering (e.g., limestone and sandstone) and the formation of complex surface texture (e.g., honeycomb weathering, pits, etc.) on their seaward-exposed sides (Coombes et al., 2011); (2) using materials that are the same or have similar physical, chemical, and aesthetic (e.g., colour) properties to the local geology (Firth et al., 2014; Naylor et al., 2012); (3) selecting and positioning stonework so that complex surface features (both natural and artificial artefacts of quarrying and construction) face outwards (i.e., 'passive' ecological enhancement; MacArthur et al., 2020; Naylor et al., 2017a, 2017b); (4) deliberately indenting mortar joints to mimic cryptic microhabitats (e.g., Chapman and Underwood, 2011; Dugan et al., 2011; Firth et al., 2014; O'Shaughnessy et al., 2020); (5) eliminating the use of mortar completely to replicate the cavities between stonework in free-draining

masonry structures, and; (6) omitting blocks to replicate the habitat space created by missing stonework in historic masonry structures (e.g., Chapman and Blockley, 2009; Chapman and Underwood, 2011). In the case of concrete structures, similar retrofit options might be suitable to improve ecological potential (e.g., Hall et al., 2019; O'Shaughnessy et al., 2020; Paalvast et al., 2012; Strain et al., 2018), and for new-build assets, historic masonry walls can serve as inspiration for the design of physically complex surface textures produced using novel casting techniques (e.g., MacArthur et al., 2019; Bone et al., 2022b; Sheffield et al., 2022).

5. Conclusions

Until now, artificial coastal structures have generally been considered ecologically poor, acting as poor surrogates for natural shores due to a lack of surface heterogeneity and structural complexity. By comparing the ecological communities associated with both the surface and cryptic microhabitats of historic masonry walls, concrete walls, and vertical rocky cliff habitats at seven locations around the UK, we have shown that historic maritime walls not only support a greater range of species than nearby concrete assets but can also support communities with comparable species richness to adjacent vertical rocky habitats. In particular, our observations highlight the importance of cryptic microhabitat provision on traditional masonry walls (drystone and mortared types) relative to other types of engineering construction. Recognition of the importance of historic structures as potential hotspots of marine biodiversity along heavily urbanised coastlines supports arguments for built heritage to be conserved as valuable multi-functional assets. Going forward, the ecological value of other types of built heritage located within the marine environment, including those constructed of different materials (e.g., metal and wood) and with different functions or designs, warrants further research attention. More work is also needed to better understand species and community dynamics on historic masonry structures (e.g., colonisation rates, disturbance regimes and patch dynamics, trophic interactions, and community resilience in response to environmental change), especially in comparison to other asset types and natural rocky habitats. Finally, with coastal urbanisation predicted to increase into the 21st century, future studies should explore in greater detail how construction features associated with built heritage may help guide the future design of coastal infrastructure and ecological enhancement techniques.

CRediT authorship contribution statement

TB, MC, and HV contributed to the conception and design of the study. TB collected the data, conducted the analysis, and drafted the initial manuscript. MC and HV provided supervision. All authors discussed the results and reviewed and edited drafts of the manuscript.

Declaration of competing interest

All authors declare that they have no conflicts of interest.

Data availability statement

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2023.114617>.

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