Aberystwyth University

The population structure, sex ratio and reproductive potential of limpets (*Patella* spp.) on natural shores and artificial structures in the Irish Sea

Hannah S. Earp [a,b,*,1], Ruby George [a,1], Paul R. Brooks [c], Veronica Farrugia Drakard [c], Bryan J. Thompson [c], Benjamin Fisher [a], Róisín Hayden [c,d], Tasman P. Crowe [c], Pippa J. Moore [a,b]

[a] *Institute of Biological Environmental and Rural Sciences (IBERS), Aberystwyth University, Aberystwyth, SY23 3DA, UK*
[b] *The Dove Marine Laboratory, School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, NE1 7RU, UK*
[c] *UCD Earth Institute and School of Biology and Environmental Science, Science Centre West, University College Dublin, Belfield, Dublin 4, Ireland*
[d] *The Swire Institute of Marine Science, University of Hong Kong, Cape D'Aguilar, Hong Kong*

ABSTRACT

Artificial structures often support depauperate communities compared to natural rocky shores. Understanding variation in ecological success across shore types, particularly regarding habitat-forming species or those with structuring roles, is important to determine how artificial structure proliferation may influence ecosystem functioning and services. We investigated the population structure, sex ratio and reproductive potential of limpets on natural shores and artificial structures on Irish Sea coasts. Limpets were generally less abundant and *Patella vulgata* populations were often male dominated on artificial structures compared to natural shores, suggesting that shore type may influence these factors. *P. vulgata* length varied across sites within the Irish Sea (nested in coast and shore type) in autumn/winter, as well as temporally across sites along the Welsh coast. There was no difference in the proportion of *P. vulgata* in advanced stages of gonad development across shore types. The results suggest that rip-rap artificial structures may provide a habitat comparable to natural shores, however, the addition of ecological engineering interventions on artificial structures may allow limpet populations to better approximate those on natural shores.

1. Introduction

Marine artificial structures, of which a significant proportion are hard-substrate coastal defence constructs (i.e., seawalls, breakwaters, groynes) (Hall, 2017; Moschella et al., 2005), are proliferating worldwide in a process termed 'ocean sprawl' (Duarte et al., 2013; Evans et al., 2019; Firth et al., 2016a; Hall, 2017; Heery et al., 2017). For example, 50% of Italian shores of the northern Adriatic Sea are armoured (Airoldi and Bulleri, 2011), 27% of the Japanese coast is protected (Koike, 1996), and 10.2% of coastline of Wales and Ireland is covered by coastal defence structures (11.5% and 9.1% respectively) (Thompson, 2022). Such structures are expected to become more widespread in coming years in response to rising sea levels, increasing storm frequencies and intensities, and increasing coastal populations (Firth et al., 2016a; Mayer-Pinto et al., 2019; Moschella et al., 2005).

While artificial structures themselves represent ecological habitats that can be colonised by marine life, the biological assemblages they support are considered depauperate, with reduced biodiversity and abundances compared to assemblages on natural rocky shores (Aguilera et al., 2014; Bulleri and Chapman, 2004; Chapman, 2003; Firth et al., 2013b; Moschella et al., 2005). This may be attributed to the location and design of artificial structures. Artificial structures are often constructed in soft-sediment environments (Firth et al., 2013a) that may restrict colonisation by rocky shore species with limited dispersal capacities (Dethier et al., 2003). These structures, particularly those constructed for coastal protection, are often located in areas that experience significant wave action leading to sediment scouring/deposition, meaning they represent more stressful environments for colonizing species (Moschella et al., 2005). Furthermore, the limited availability of microhabitats and water retaining features (e.g., grooves and pools), the lower topographic complexity, and the use of materials such as concrete, the chemistry of which can impact settlement, present further challenges for organisms colonising artificial structures (Aguilera et al., 2014; Chapman, 1994; Firth et al., 2013b; Natanzi et al., 2021; Sella et al.,
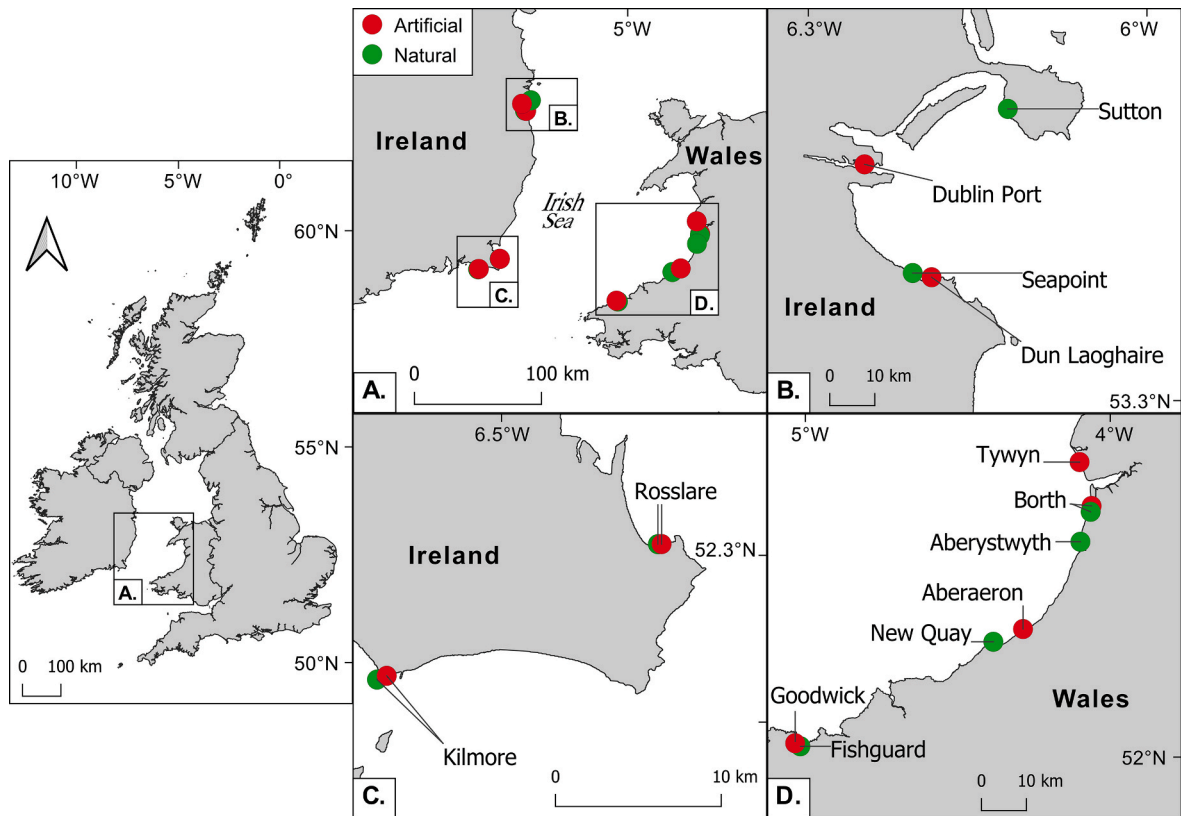

Fig. 1. Map showing the location of the natural rocky shores (green) and artificial structures (red) selected for investigation.

2018).

To date, the majority of studies comparing communities across artificial structures and natural rocky shores have focussed on differences in richness, abundance and assemblage structure (Aguilera et al., 2014; Bulleri, 2005; Bulleri and Chapman, 2004; Chapman and Bulleri, 2003; Firth et al., 2013b; Lopez, 2019; Pister, 2009), with less attention given to the population structure or performance of individual species (but see Díaz-Agras et al., 2010; Farrugia Drakard et al., 2021; Drexler et al., 2014; Moreira et al., 2006). Given that artificial structures are subject to greater levels of disturbance, and competition between individuals for limited resources (e.g., food and shelter) is believed to be greater than on natural rocky shores (Iveša et al., 2010), colonizing species likely experience increased physiological stress, which may affect the allocation of resources and in turn the productivity and viability of populations (Moreira et al., 2006). For example, in the Irish Sea, the canopy-forming macroalga, *Fucus vesiculosus,* is dislodged from artificial structures before it reaches its full reproductive potential, and while this did not appear to influence coverage, it could do so in future years should source populations, likely on surrounding natural rocky shores, be replaced with artificial structures (Farrugia Drakard et al., 2021). Understanding variation in, and the drivers of ecological success across shore types, particularly in terms of habitat-forming species or those with structuring roles, is important to determine how the proliferation of artificial structures may influence ecosystem functioning and services (Aguilera, 2018). Such information can inform coastal management strategies and enhance ecological engineering interventions that aim to modify elements of artificial structures so they may support assemblages more analogous to natural rocky shores (Evans et al., 2016; Morris et al., 2017; Strain et al., 2018).

Limpets are gastropod molluscs that play an important role in structuring natural rocky shore communities where they influence the abundance of algae and small sessile organisms through grazing and bulldozing (Chapman, 2006; Coleman et al., 2006b; Moore et al., 2007b;

Safriel et al., 1994). Limpets have also successfully colonised a range of artificial structures (Chapman, 2006), although patterns in their abundance appear to be species and context dependent (Bulleri et al., 2005; Bulleri and Chapman, 2004; Chapman, 2006; Díaz-Agras et al., 2010; Moreira et al., 2006). Investigations into their population structure and reproductive potential across natural and artificial environments remain limited, although initial research suggests that individuals on seawalls are generally smaller (Díaz-Agras et al., 2010) and are more likely to be juveniles (Moreira et al., 2006). It has also been suggested that the reproductive output of limpets on seawalls may be lower (Moreira et al., 2006). As such, the proliferation of artificial structures could have significant effects on limpet populations, their associated communities, and the ecological processes they underpin.

Along the coastlines of the United Kingdom and Ireland, patellid limpets represent an important component of intertidal communities. The most widespread species, *Patella vulgata* Linnaeus 1758, has a range extending from Norway to Portugal, while *Patella depressa* Pennant 1777, is distributed from Senegal to north Wales and is absent from Ireland (Moore et al., 2007a; Southward and Crisp, 1954). Both species inhabit stable rocky substratum, including artificial structures, between the mid-shore to the shallow sublittoral (Blackmore, 1969; Firth et al., 2016b; Skewes, 2003).

P. vulgata can reach lengths of ~60 mm and females are usually larger than males (Hill, 2008). As sequential protandric hermaphrodites, they switch from male to female with increasing size, usually after 2–6 years (Ballantine, 1961; Hill, 2008; Orton, 1919; Sundelöf et al., 2010). They are broadcast spawners, spawning annually between October and January, induced by strong wind and wave action and reductions in sea temperature (Blackmore, 1969; Bowman and Lewis, 1977, 1986; Coleman et al., 2006a; Moore et al., 2011; Orton et al., 1956). By contrast, *P. depressa* is smaller, reaching approximately 35 mm, and is believed to be a gonochoric species (i.e., it does not change sex during its life) with spawning occurring between July and September (Borges et al., 2015;

Bowman, 1981; Orton and Southward, 1961). The short-lived, free-swimming planktonic larvae of both species settles in damp areas on rocky substratum (Brazao et al., 2003; Seabra et al., 2020). However, the population dynamics and reproductive cycles of both species have been found to vary across the UK and Ireland in response to a complex array of biotic and abiotic factors (e.g., intra-specific interactions, wave exposure, latitude, temperature) (Baxter, 1983; Borges et al., 2015; Bowman and Lewis, 1977; McCarthy et al., 2008; Moore et al., 2011; Morais et al., 2003).

Given that environmental conditions on artificial structures are not analogous to conditions on natural rocky shores, differences in limpet populations across the different shore types are expected. Here we aimed to characterise and compare the population structure and reproductive potential of patellid limpets on artificial structures and natural rocky shores across Irish Sea coastlines. Specifically, we hypothesise that:

(1) The abundance of *P. vulgata* and *P. depressa* is reduced on artificial structures compared to natural rocky shores;
(2) The length of *P. vulgata* is reduced on artificial structures compared on natural rocky shores;
(3) *P. vulgata* populations on artificial structures are more male dominated on artificial structures compared to natural rocky shores; and
(4) There is a reduced proportion of *P. vulgata* with 'mature' gonads on artificial structures compared to natural rocky shores.

Hypotheses 2 to 4 focussed on *P. vulgata* alone because *P. depressa* is not present along the Irish coast and it is only found in low abundances at the sites in Wales, therefore we were unable to measure sufficient individuals for length analyses, and we did not want the removal of individuals for determining reproductive state to negatively influence local populations.

2. Materials and methods

2.1. Study location

Field surveys were conducted from late-2018 to mid-2019 at sixteen moderately exposed to exposed sites along the Irish Sea coastlines of Wales and Ireland (Fig. 1). Exposure was determined based on wave fetch values extracted from Burrows (2020), with exposure generally greater at sites along the Welsh coast compared to the Irish coast (Appendix A). The sites comprised eight natural rocky shores and eight artificial structures. Sites were selected in loose pairs consisting of one natural shore and one artificial structure based on geographical proximity and similarity of environmental conditions (e.g., wave exposure, aspect; Appendix A). Artificial structures were all >5 years of age and were rip-rap coastal defences (i.e., groynes or breakwaters) composed of granite boulders, except for Dublin and Dun Laoghaire that were concrete seawalls. For all artificial structures, a source population of limpets was present within 10 kilometers, which represents the estimated larval dispersal capacity of *P. vulgata* (Hill, 2008). Surveys were undertaken on the lower mid-shore, defined as the area between mid-tide line and the top of the low shore (i.e., zone of occurrence of *Fucus serratus*).

2.2. Population structure

Limpet density was determined once in Autumn/Winter 2018 (October–February) and once in Spring (April–May) 2019. Ten 0.25 m^2 quadrats were haphazardly placed on relatively flat (0–45°) rocky substrate. On seawalls, quadrats were placed in more vertical positions (~90°), and this was mirrored at their corresponding natural sites (Appendix A). In each quadrat, limpets were counted and in Wales identified as either *P. vulgata* or *P. depressa* (note: *P. depressa* is absent in Ireland). The anterior to posterior length of 100 *P. vulgata*, present in the density quadrats and additional haphazardly placed quadrats until the required sample number had been achieved, was taken using Vernier callipers (to the nearest mm).

2.3. Sex ratios and reproductive potential

At each site, ~30 *P. vulgata* between 25 and 40 mm in length were haphazardly collected each month during the reproductive season, from October 2018 until February 2019. *P. vulgata* were deemed to scarce at Aberaeron in October/November and December and thus ~20 individuals were collected to prevent exhaustion of the population. The size range selected represents the approximate size range of adult *P. vulgata* whereby gonad development is distinguishable (Moore et al., 2011). Removed individuals were frozen until processed. To determine sex and stage the gonads, individuals were dissected by removing the foot to revel the visceral mass. Sex was determined based on gonad pigmentation and in cases where it was indeterminable, the individual was considered neuter. The gonads of each individual were staged based on Orton et al. (1956) and photographed. The anterior to posterior length of dissected individual was recorded using Vernier callipers (to the nearest mm). Sex and gonad stage was quality assured by two qualified marine scientists who independently analysed the dissection photographs. Their findings were compared to the laboratory data and where discrepancies were identified, data from the photograph analysis was used.

2.4. Gaps in the data sets

Various circumstances led to partial gaps in the data sets from Ireland. Firstly, density data were collected from only three artificial structures in Spring 2019. Secondly, *P. vulgata* length data were not collected in Spring 2019. Finally, *P. vulgata* sex ratio data were not collected beyond January 2019.

2.5. Data analyses

Population structure and reproductive potential data were analysed using univariate permutational analysis of variance (PERMANOVA) in PRIMER [v.7.0.13] with PERMANOVA+ (PRIMER-E Ltd, Plymouth, UK) (Anderson et al., 2008) and were based on the Euclidean distance of untransformed data. To test for differences in the density of *P. vulgata*, a four-way PERMANOVAs (with 9999 unrestricted permutations of raw data) was conducted with Coast (fixed; Wales or Ireland), Type (fixed; natural or artificial), Time (fixed; autumn/winter or spring), Site (random; nested in Coast and Type) and their interactions as factors. To test for differences in the density of *P. depressa* in Wales, a three-way PERMANOVA (with 9999 unrestricted permutations of raw data) was conducted, with Type (fixed; artificial or natural), Time (fixed; autumn/winter or spring), Site (random; nested in Type) and their interactions as factors. To test for differences in the length of *P. vulgata*, two three-way PERMANOVAs (with 9999 unrestricted permutations of raw data) were conducted to ensure a balanced design. Firstly, the length of *P. vulgata* between natural rocky shores and artificial structures across the Irish Sea was assessed with Coast (fixed; Wales or Ireland), Type (fixed; natural or artificial), Site (random; nested in Coast and Type) and their interactions as factors. Secondly, the length of *P. vulgata* between natural and artificial structures along the Welsh coastline over time was assessed with Type (fixed; natural or artificial), Time (fixed; autumn/winter or spring), Site (random; nested in Coast and Type) and their interactions as factors. To investigate differences in the number of *P. vulgata* in advanced stages of gonad development (i.e., gonad stage 4 and 5), a four-way PERMANOVA was conducted with Coast (fixed; Wales or Ireland), Type (fixed; natural or artificial), Month (fixed; October/November, December, January), Site (random; nested in Coast and Type) and their interactions as factors.

Table 1

PERMANOVA for the density of *Patella vulgata* between natural rocky shores and artificial structures along Irish Sea coasts. Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion.

Source of variation	df	Pseudo-F	p	Unique permutations
Coast = C	1	3.4594	0.0906	9813
Type = Ty	1	5.2695	**0.0432**	9863
Time = Ti	1	0.1502	0.7151	9838
C x Ty	1	2.0377	0.1796	9830
C x Ti	1	8.7055	**0.0122**	9816
Ty x Ti	1	0.7164	0.4189	9842
Site (C x Ty)	12	12.647	<u>**0.0001**</u>	9921
C x Ty x Ti	1	7.5342	**0.0191**	9843
Ti x Site (C x Ty)	11	1.9178	**0.0393**	9914
Res	279			
Total	309			

Analyses of *P. vulgata* density were repeated excluding Dublin to better balance the design, and analyses of *P. vulgata* density, length, and the number of individuals in mature stages of gonad development were repeated excluding vertical quadrats (i.e., seawalls at Dublin and Dun Laoghaire and the corresponding natural rocky shores at Sutton and Seapoint) to account for the influence of gradient. Due to the similarity of the findings, results including Dublin and other vertical quadrats are provided in the main text and results of analyses on the reduced data sets are given in Appendix B-D. For each PERMANOVA, type III sum of squares were calculated. The PERMDISP routine was used to assess the

homogeneity of dispersion around the centroid for each main factor. In the case of significant differences in dispersion, the significance threshold of the factor was assessed at a more conservative level ($p < 0.01$). Where this did not occur, significance was considered at $p < 0.05$. Where the number of unique permutations in the PERMANOVA was considered low (i.e., <5000), the reported p-values represent those from Monte Carlo tests. Pairwise post hoc PERMANOVAs were performed where significant effects were detected.

To investigate differences in the sex ratio of *P. vulgata*, the statistical software R [v.3.6.0] (R Core Team, 2021) was used. A binomial generalized linear model (GLM) was applied using the 'glm' function of the 'stats' package to the proportion of male to female individuals. Coast (Wales or Ireland), Type (natural or artificial) and Month (October/November, December, January, or February), and their interactions were factors included in the model. It was not possible to include Site as a factor in the GLM due to model overparameterization, however a generalized linear mixed-effects model (GLMM) was run using the 'glmer' function of the 'lme4' package (Bates et al., 2015) on a reduced data set (February data were excluded to balance the design across the Irish Sea) including all initial factors plus a random intercept for Site to determine whether Site influenced the results. The GLMM was repeated excluding vertical quadrats (i.e., seawalls at Dublin and Dun Laoghaire and the corresponding natural rocky shores at Sutton and Seapoint) to account for the influence of gradient, however due to the similarity of the findings, results including vertical quadrats are provided in the main text and results of the analysis on the reduced data set is provided in Appendix E. To test for differences in the length of *P. vulgata* involved in the sex ratio analysis, a linear mixed-effects model (LMER) was applied using the 'lmer' function of the 'lme4' package (Bates et al., 2015). Sex
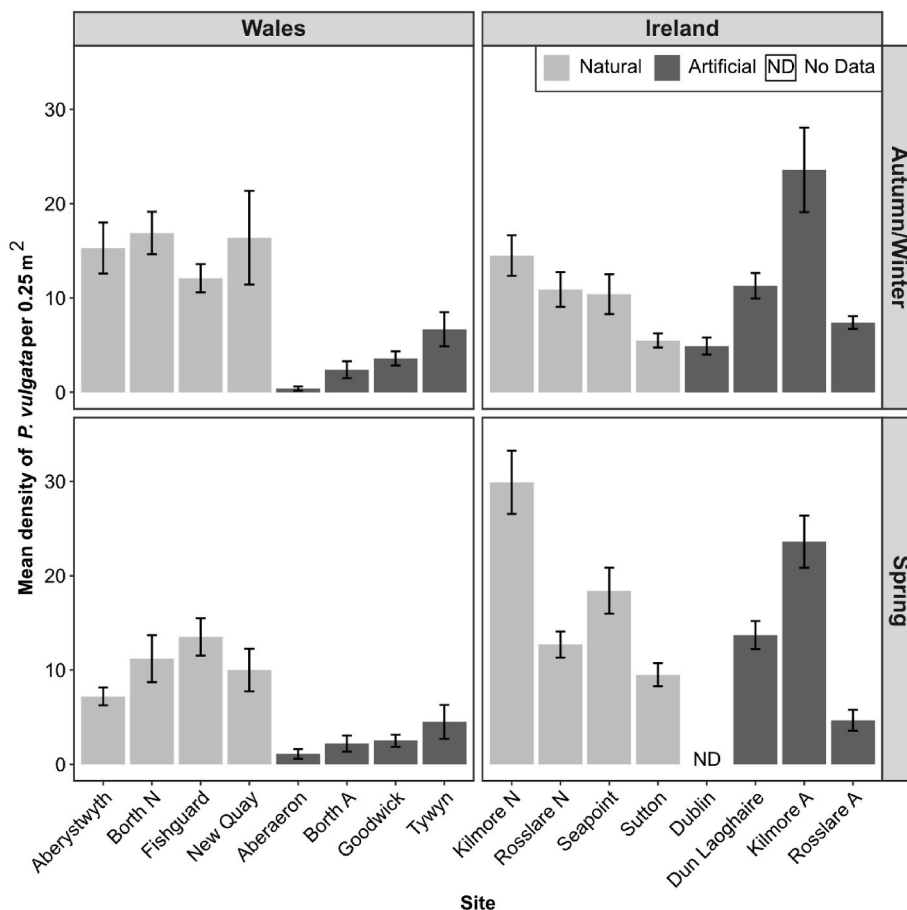

Fig. 2. Mean density of *Patella vulgata* (± 1 standard error) in autumn/winter and spring on natural rocky shores (light grey) and artificial structures (dark grey) along Irish Sea coasts. $n = 10 \times 0.25 \ \mathrm{m}^2$ quadrats per site per time period.
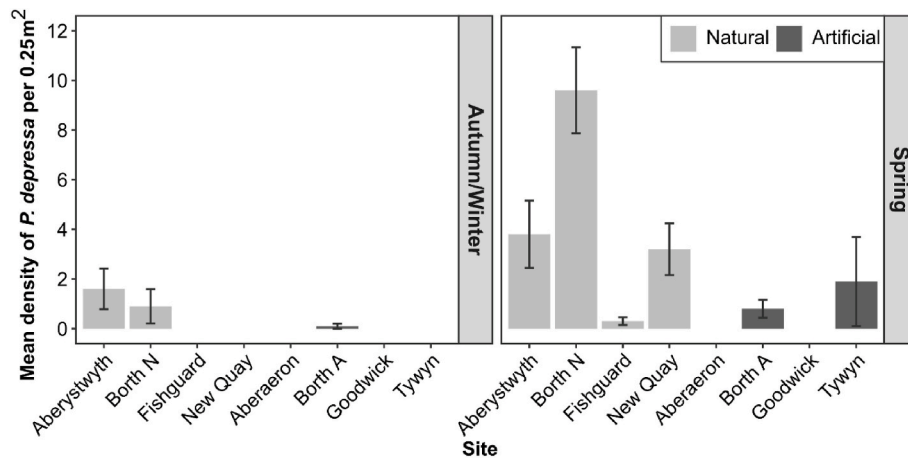
Fig. 3. Mean density of *Patella depressa* (± 1 standard error) in autumn/winter and spring on natural rocky shores (light grey) and artificial structures (dark grey) along the Welsh coast of the Irish Sea. $n = 10 \times 0.25$ m^2 quadrats per site per time period. Zero values represent an absence of *P. depressa*, not an absence of data.

Table 2
PERMANOVA for the density of *Patella depressa* between natural rocky shores and artificial structures along the Welsh coast of the Irish Sea. Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion. MC represents where the reported p-value relates to a Monte Carlo test due to a low number of unique permutations.

Source of variation	df	Pseudo-F	p	Unique permutations
Type = Ty	1	3.5565	<u>0.1105 (MC)</u>	23
Time = Ti	1	5.2317	<u>0.0136</u>	9774
Site (Ty)	6	7.4151	<u>**0.0001**</u>	9949
Ty x Ti	1	2.5206	0.1312	9728
Ti x Site (Ty)	6	5.2865	**0.0001**	9958
Res	144			
Total	159			

was given as a factor and random intercepts were given for Coast, Type, Month and Site. The fit of each model was assessed by examining Quantile-Quantile (QQ) plots of residual values. For all models, type II sums of squares were calculated using the 'Anova' function of the 'car' package (Fox and Weisberg, 2019). Post hoc Tukey adjusted comparisons were generated using the 'lsmeans' function of the 'emmeans' package (Lenth, 2020) when significant effects were detected. All graphs were produced using the 'ggplot2' package (Wickham, 2016).

3. Results

3.1. Population structure

Patella vulgata density exhibited small-scale variability with significant temporal variation across the sites (nested in coast and shore type; Fig. 2; Table 1). Pairwise post hoc comparisons revealed that temporal differences were most pronounced at five sites (Aberystwyth, Kilmore Natural, Seapoint, Sutton, Rosslare Artificial), of which the majority were natural rocky shores along the Irish coast. There was also significant temporal variation in density between shore types across Irish Sea coasts (Fig. 2; Table 1). These differences were most pronounced in Wales where irrespective of the time period, densities were greater on natural rocky shores (12.8 $\pm$ 1.0 individuals per 0.25 m^2) compared to artificial structures (2.9 $\pm$ 0.4 individuals per 0.25 m^2; Fig. 2). The same pattern, however, was not mirrored along Irish coasts, where irrespective of the time period, densities on natural rocky shores were comparable to those on artificial structures (14 $\pm$ 1.1 and 12.9 $\pm$ 1.2 individuals per 0.25 m^2 respectively; Fig. 2). Differences across shore

types as a main factor, however, were only significant when vertical quadrats were included in the analysis (Table 1; Appendix B).

Patella depressa occurred at lower densities than *P. vulgata* along the Welsh coast of the Irish Sea (Fig. 2; Fig. 3). While a tendency for greater densities on natural rocky shores (2.4 $\pm$ 0.5 individuals per 0.25 m^2) compared to artificial structures (0.4 $\pm$ 0.2 individuals per 0.25 m^2) was observed (Fig. 3), this was not statistically significant (Table 2). Instead, *P. depressa* density showed significant temporal variation across the sites (nested in shore type; Table 2). Greatest densities were observed at all sites (where present) in spring (2.5 $\pm$ 0.5 individuals per 0.25 m^2) compared to autumn/winter (0.3 $\pm$ 0.1 individuals per 0.25 m^2; Fig. 3) and pairwise post hoc comparisons revealed the most pronounced temporal differences occurred at the natural shores of Borth Natural and New Quay.

The length of *P. vulgata* varied across sites within the Irish Sea (nested in coast and type), and temporally across sites along the Welsh coast (Fig. 4; Table 3). At the majority of Welsh sites (6 of 8), length was greater in spring compared to autumn/winter (Fig. 4), however pairwise post hoc comparisons revealed that temporal differences in length were only significant at five sites (of which three were natural shores). Despite a tendency, particularly in autumn/winter, for larger individuals on artificial structures in Wales, there was no significant difference in the length of *P. vulgata* across shore types in Wales (Fig. 4; Table 3b). During autumn/winter, the length of *P. vulgata* appeared to be greater at sites along the Irish coast compared to the Welsh coast, particularly in respect to artificial structures, however, there were no significant difference in length between shore types across Irish Sea coasts (Fig. 4; Table 3a). Differences in length across shore type as a main factor, were not significant over time along the Welsh coastline, nor were they significant across the Irish Sea in autumn/winter when vertical quadrats were excluded from the analysis (Table 3; Appendix C).

3.2. Sex ratio and reproductive potential

The proportion of male to female *P. vulgata* varied significantly between artificial and natural shores as the reproductive season progressed, with variation most apparent on natural shores (Fig. 5; Table 4). The variation across shore types remained significant when vertical quadrats were excluded from the analysis (Appendix E). Pairwise post hoc comparisons revealed that in all months in Ireland, the male to female ratio was significantly greater on artificial structures compared to natural shores. In addition, irrespective of shore type, the proportion of males was always greater in Ireland compared to Wales (Fig. 5). In Wales however, sex ratios exhibited a more complex pattern, with little difference in the male to female ratio observed in October/November and February. While in December the male to female ratio was significantly
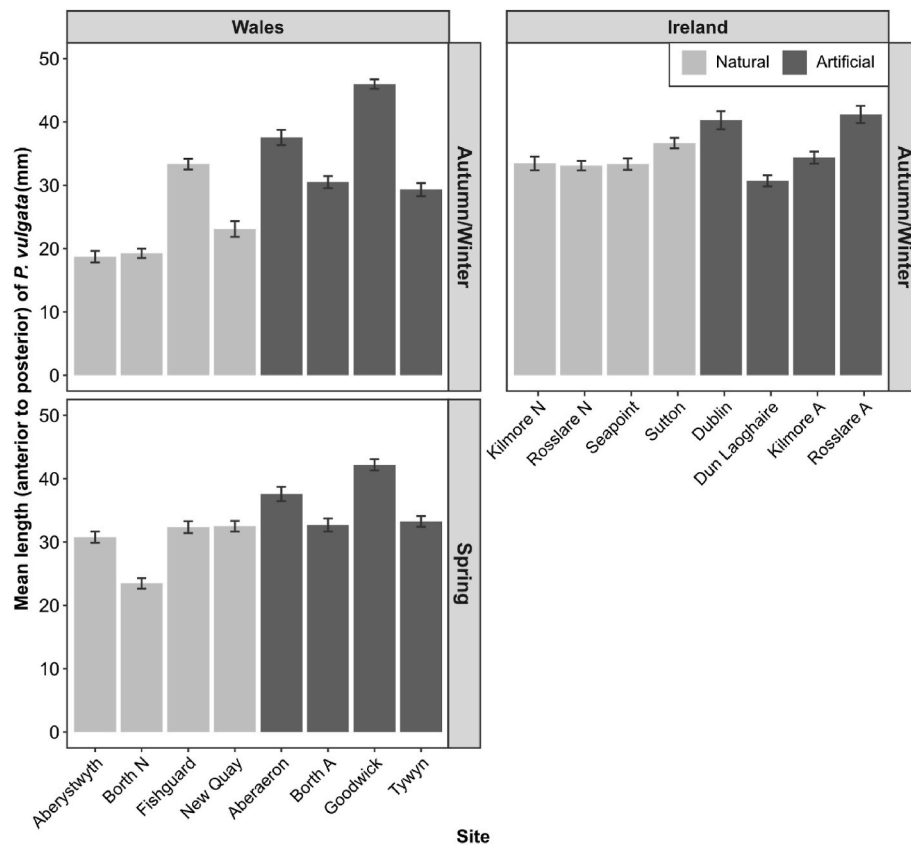
Fig. 4. Mean length of *Patella vulgata* (±1 standard error) in autumn/winter and spring on natural rocky shores (light grey) and artificial structures (dark grey) along Irish Sea coasts. *n* = 100 individuals per site per time period.

Table 3

PERMANOVA for the length of *Patella vulgata* between natural rocky shores and artificial structures across the Irish Sea (**a.**) and between timepoints along the along the Welsh coast of the Irish Sea (**b.**). Significance was assessed as *p* < 0.05 except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as *p* < 0.01. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion.

	Source of variation	df	Pseudo-F	p	Unique permutations
a.	Coast = C	1	3.8790	<u>0.0793</u>	9805
	Type = Ty	1	6.5681	<u>**0.0249**</u>	9838
	C x Ty	1	2.8670	0.1081	9932
	Site (C x Ty)	12	32.191	<u>**0.0001**</u>	9917
	Res	1584			
	Total	1599			
b.	Type = Ty	1	5.9209	0.0510 (MC)	35
	Time = Ti	1	4.1387	<u>0.0898</u>	9776
	Site (Ty)	6	66.362	<u>**0.0001**</u>	9931
	Ty x Ti	1	2.8125	0.1409	9803
	Ti x Site (Ty)	6	12.212	**0.0001**	9933
	Res	1584			
	Total	1599			

greater on natural shores compared to artificial structures, and in January the reverse pattern was observed (Fig. 5). Irrespective of other factors, female *P. vulgata* were significantly larger than the males (38.49 ± 0.32 mm and 34.70 ± 0.24 respectively; $\chi^2_{(1)} = 36.738$, *p* < 0.001).

The proportion of *P. vulgata* in advanced stages of gonad development varied significantly across Irish Sea coasts and monthly sampling points (Table 5). Pairwise post hoc comparisons revealed that the greatest disparities between Welsh and Irish coasts occurred in October/November and January (Fig. 6). Gonad development peaked during October/November along Irish coasts where almost 50% of the population were in advanced states of gonad development (i.e., stage 4 and 5) (Fig. 5). A peak in gonad development was less apparent along the coastline of Wales, but likely occurred in either October/November or December (Fig. 6). However, the proportion of *P. vulgata* in advanced states of gonad development was consistently lower on Welsh coasts, where <10% of the *P. vulgata* population were in advanced stages at any point in time (Fig. 6). Despite mature individuals generally comprising a greater proportion of the population on artificial structures compared to natural rocky shores (19.4% and 11.3% respectively), shore type was not a significant driver of this difference, including when vertical quadrats were omitted from the analysis (Table 5; Appendix D).

4. Discussion

This study revealed significant spatio-temporal variation in the population structure, sex ratio and reproductive potential of limpets on natural shores and artificial structures within the Irish Sea, suggesting that local environmental conditions are important influencers on limpet assemblages. Differences between shore types in terms of the density, length and sex ratio of limpets suggests that the structure of populations is also influenced by whether limpets are located on natural rocky shores or artificial structures, although these patterns were not consistent between Irish Sea coastlines. Limited temporal variation in limpet density on artificial structures further suggests that the elements controlling these factors persist year-round. While a lack of difference in length and the proportion of individuals with mature gonads indicates that drivers other than the habitat in which they are located are important. Here we suggest potential drivers of the observed differences and highlight the
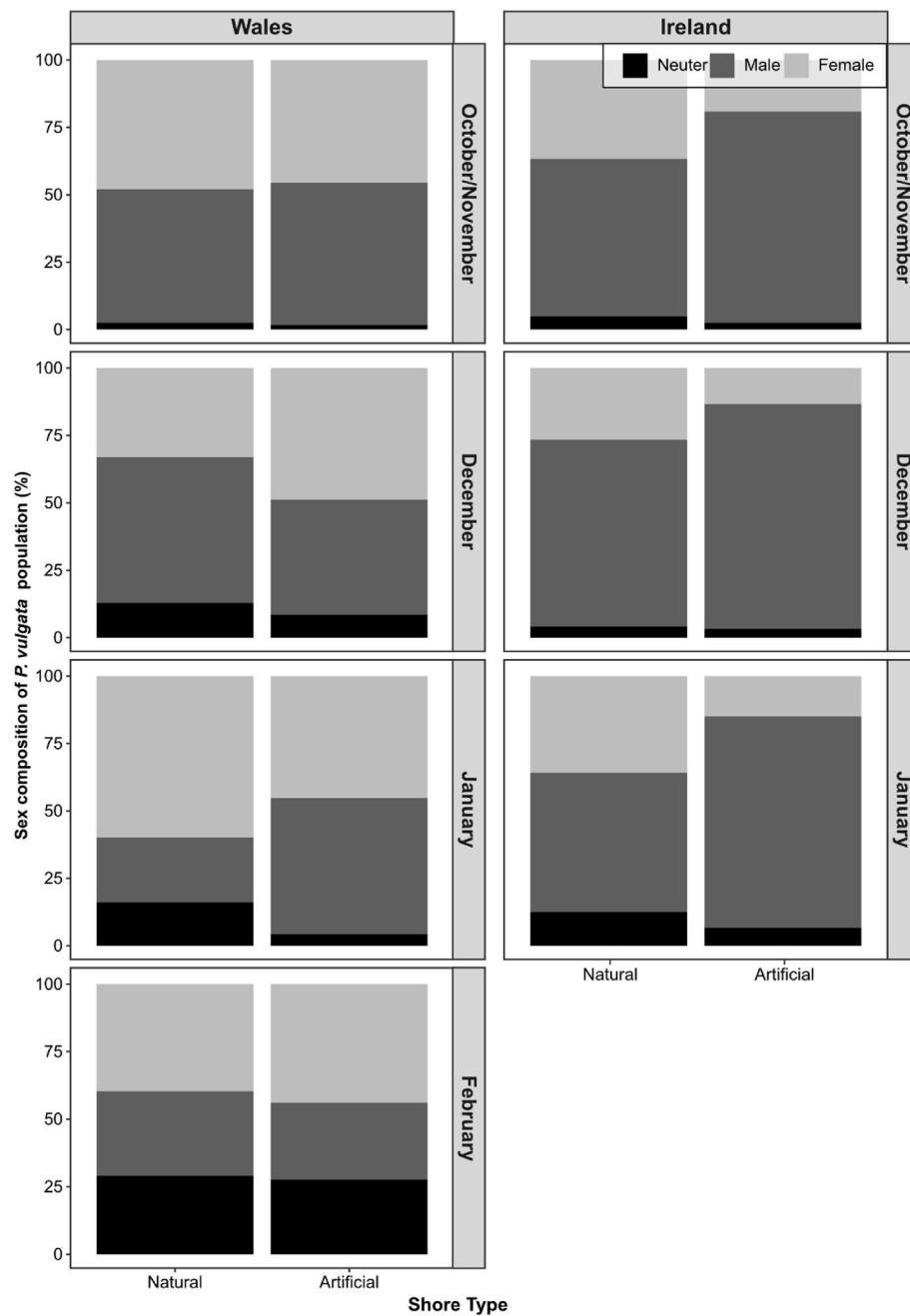
Fig. 5. Monthly sex ratios of *Patella vulgata* populations on natural shores and artificial structures along Irish Sea coasts (*n* sites = 8 per country). *n* of individuals sampled per site per month varied between 18 and 38 in Wales and was always 30 in Ireland.

Table 4
Analysis of deviance (Type II) for the proportion of male to female *Patella vulgata* determined through (**a.**) GLM and (**b.**) GLMER (i.e., site as random intercept) models. Significant values (*p* < 0.05) indicated in bold.

	a. Likelihood-ratio chi-square test			b. Wald chi-square test		
Source of variation	df	χ^2	p	df	χ^2	p
Coast (C)	1	94.16	**< 0.001**	1	39.91	**< 0.001**
Type (Ty)	1	16.72	**< 0.001**	1	9.84	**0.0017**
Month (M)	3	14.14	**0.0027**	2	9.92	**0.0069**
C x Ty	1	12.94	**< 0.001**	1	6.50	**0.0107**
C x M	2	4.26	0.12	2	3.79	0.15
Ty x M	3	16.95	**< 0.001**	2	15.83	**< 0.001**
C x Ty x M	2	4.18	0.12	2	4.61	0.09

importance of further research to fully understand the mechanisms responsible for differences in limpet population structure and functioning, particularly between artificial structures and natural rocky shores. Such information can benefit marine management strategies and inform eco-engineering interventions.

4.1. Population structure

In general, artificial structures support communities with lower abundances of individuals (Aguilera et al., 2014; Bulleri and Chapman, 2004; Chapman and Bulleri, 2003; Gacia et al., 2007), which is particularly important in regards to organisms such as limpets that have important structuring and functioning roles (Chapman, 2006; Coleman et al., 2006b; Safriel et al., 1994). As expected, and in line with findings for other gastropods (*Nucella lapillus*; Thompson, 2022), limpet densities
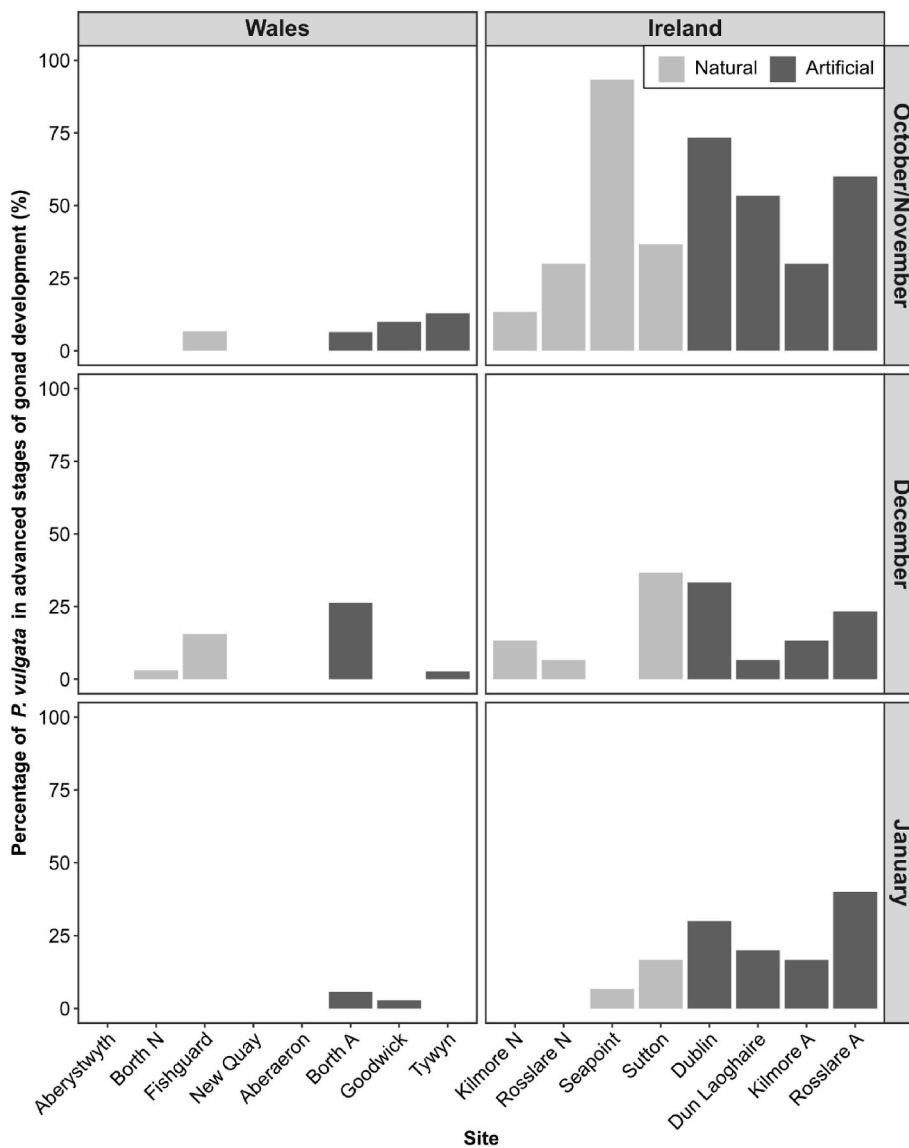
Fig. 6. Monthly variation in the proportion of *Patella vulgata* with gonads in advanced stages of development (i.e., stage 4 and 5) on natural rocky shores (light grey) and artificial structures (dark grey) along Irish Sea coasts. Zero values represent an absence of gonads in mature stages, not an absence of data. In February, there were no *P. vulgata* in advanced stages of gonad development along the Welsh coast and no data were available for the Irish coast. *n* of individuals sampled per site per month was between 18 and 38 in Wales and was always 30 in Ireland.

Table 5

PERMANOVA for percentage of *Patella vulgata* in advanced stages of gonad development on natural rocky shores and artificial structures along Irish Sea coasts. Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion.

Source of variation	df	Pseudo-F	p	Unique permutations
Coast = C	1	23.777	**<u>0.0012</u>**	9690
Type = Ty	1	3.0402	0.1096	9665
Month = M	2	8.265	**<u>0.0008</u>**	9966
C x Ty	1	0.7345	0.3994	9686
C x M	2	7.8055	**0.0014**	9953
Ty x M	2	0.28329	0.7665	9958
Site (C x Ty)	12	1.4948	<u>0.1816</u>	9939
C x Ty x M	2	0.47128	0.6427	9966
Res	24			
Total	47			

were generally lower on artificial structures compared to natural rocky shores within the Irish Sea, although this pattern was more clearly seen on shores along the Welsh coastline. This difference may be driven, in-part, by the lack of availability of microhabitats on artificial structures (Aguilera et al., 2014; Chapman, 1994; Firth et al., 2013b; Strain et al., 2018). For example, *P. depressa* preferentially settles in pools (Borja et al., 2004; Evans, 1947, 1957) that are often absent on artificial structures (Aguilera et al., 2014; Chapman, 1994; Firth et al., 2013b).

However, microhabitats can develop over time due to weathering, meaning the age of an artificial structure could influence the density of organisms observed, with older, potentially more heterogeneous structures, more likely to support densities comparable to natural shores (Bulleri and Chapman, 2010; Hall, 2017). While structure age was not considered within our analyses, it is important to note that all the artificial structures were >5 years of age, which is when most species have settled and begun to establish themselves (Pinn et al., 2005), and they had been colonised by perennial species with a similar size structure, which is indicative of natural shore succession (Chapman and

Underwood, 1998; Farrugia Drakard et al., 2021), making them relatively comparable to the adjacent rocky shores. However, future analyses would benefit from incorporating information on the age of artificial structures alongside quantifications of topographic complexity.

Limited microhabitat availability on artificial structures also means organisms may be exposed to greater wave action and predation, thus are at increased risk of dislodgement/mortality (Aguilera et al., 2014; Firth et al., 2013b). Similar work within the Irish Sea revealed that the macrophyte, *Fucus vesiculosus*, is dislodged at greater rates on artificial structures compared to natural rocky shores (Farrugia Drakard et al., 2021). It could be postulated that the lower densities of limpets on artificial structures may result from increased dislodgement rates in these environments. The exposure of the Welsh coast to the prevailing west and south-westerly winds (Mayes, 2013) is also likely to strengthen wave action and increase scour, particularly on artificial structures, further increasing dislodgement/mortality and enhancing differences in abundance across shore types. While the lack of clear difference between shore types along the Irish coast may relate to the more sheltered nature of these sites.

Another factor that may explain the lower density of limpets on artificial structures is the crevices separating rip-rap boulders which present a physical barrier to the movement of limpets (Díaz-Agras et al., 2010), with individuals confined to specific boulders potentially experiencing elevated competition for resources, which if scarce, could result in mortality and declines in abundance. Separating these competing hypotheses, however, requires further experimentation.

Comparably to density, the length of *P. vulgata* (in autumn/winter) varied significantly across shore types, with larger individuals often found on artificial structures. The challenging environmental conditions experienced on artificial structures are believed to increase the physiological stress of colonising organisms, potentially influencing their productivity and/or viability (Moreira et al., 2006). Our results suggest that this may be the case for *P. vulgata* in the Irish Sea, whereby individuals on artificial structures achieve greater lengths, potentially in order to achieve a larger foot size and reduce the risk of dislodgement in these more challenging environments (Vasconcelos et al., 2021; Vieira and Bueno, 2019). However, it is important to note that shore type as a main factor did not influence the length of *P. vulgata* in Wales (where all sites constituted rip-rap breakwaters), nor did it significantly influence *P. vulgata* density and length across the Irish Sea when sites where vertical quadrats were surveyed were excluded from the analysis. This suggests, like others (Glasby and Connell, 2001), that gradient may also influence the structure of marine assemblages, although further research is required to determine whether gradient, or potentially a lack of water retaining features on more vertical substrates, influences limpet populations.

The results also revealed significant temporal variation in *P. vulgata* length across sites along the Welsh coast, with the most pronounced differences occurring on natural shores. While it has not been possible to determine the underlying drivers of this variability, it could be due, in part, to migratory behaviour coupled with exposure to wave splash (Hobday, 1995), although further targeted research is required to support this.

4.2. Sex ratio and reproductive potential

Along the Irish coast, male *P. vulgata* outnumbered females on both natural shores and artificial structures which is not uncommon for this species, or limpets in general (Baxter, 1983; Blackmore, 1969; McCarthy et al., 2008; Sousa et al., 2017). Such a ratio can benefit broadcast spawning species such as *P. vulgata* by reducing the risk of sperm limitation and increasing fertilisation success (Hodgson et al., 2007; Metaxas et al., 2002). The greater proportion of males observed on artificial structures, particularly in Ireland, may be indicative of high dislodgement/mortality rates on artificial structures resulting in fewer individuals surviving the two to six years required to transition to females

(Ballantine, 1961; Hill, 2008; Sundelöf et al., 2010). Although this is not reflected in the data from Wales, where we postulate that wave action and thus dislodgement is greater than in Ireland.

Contrary to expectations, shore type did not influence the proportion of *P. vulgata* in advanced states of gonad development on artificial structures and natural rocky shores within the Irish Sea. Instead, Irish populations had a significantly higher percentage of the population in advanced states of gonad development across most of the months investigated, although there was considerable between site variability irrespective of shore type. An increase in the number of *P. vulgata* reproductive failure events have been observed in recent years, including at Welsh sites used in this study (Moore et al., 2011; Moore pers. obs.). This has been previously linked to ocean warming, but other factors may also be at play given the lack of consistency across Irish Sea coastlines.

5. Conclusion

This study provides an important contribution to the expanding knowledge on the influence of coastal artificial structures for the population structure and reproductive potential of species found on them. Patellid limpet populations were found to vary spatio-temporally across the Irish Sea, with differences between artificial structures and natural shores most apparent with regards to their density and sex ratio, however, there was lots of small-scale variability and no consistent difference in the average length and proportion of individuals in advanced stages of gonad development between different shore types. The limited differences observed may be due to the fact that our research primarily focussed on rip-rap coastal defences structures that may represent more analogous habitats to natural rocky shores than seawalls. As artificial structures are expected to proliferate in the coming years, further research is required to fill current data gaps and assess the impact of different structure types on the biology and ecology of marine species to determine whether they represent surrogate habitats or ecological sinks for ecologically important species. Such information can benefit policy and planning as well as eco-engineering solutions that aim to improve artificial structures for nature.

Author contributions

HSE: Investigation, Validation, Formal Analysis, Visualization, Writing–Original Draft, Writing-Review & Editing.

RG: Investigation, Writing-Original Draft, Writing-Review & Editing.

PB: Investigation, Conceptualization, Methodology, Supervision, Writing-Review & Editing.

VFD: Investigation, Writing-Review & Editing.

BT: Investigation, Writing-Review & Editing.

BF: Investigation.

RH: Investigation.

TPC: Conceptualization, Methodology, Supervision, Writing – Review & Editing, Funding Acquisition.

PJM: Conceptualization, Methodology, Supervision, Writing – Review & Editing, Funding Acquisition.

Data accessibility statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Data availability

Data will be made available on request.

Appendix A. Site pairings based on geographical proximity and similarity of environmental conditions, as well as the nature of the artificial structure and the corresponding latitude and longitude. Exposure was determined based on wave fetch values extracted from Burrows (2020), with sheltered sites having wave fetch values of <2, moderately exposed sites between 2 and 3.5, and exposed >3.5 (Burrows, 2012)

Site Pair	Site Name	Site Type	Latitude & Longitude	Wave Fetch
W1	Tywyn	Artificial rip-rap	52.57726°N, −4.09621°W	4.13
	Aberystwyth	Natural	52.41985°N, −4.08595°W	4.14
W2	Borth A	Artificial rip-rap	52.49115°N, −4.05279°W	4.11
	Borth B	Natural	52.47957°N, −4.05530°W	4.02
W3	Aberaeron	Artificial rip-rap	52.24397°N, −4.26452°W	4.15
	New Quay	Natural	52.21691°N, −4.35970°W	4.01
W4	Goodwick	Artificial rip-rap	52.00202°N, −4.98997°W	3.54
	Fishguard	Natural	51.99643°N, −4.97284°W	3.82
I1	Dublin	Artificial seawall	53.345119°N, −6.201861°W	NA
	Sutton	Natural	53.373013°N, −6.098573°W	3.57
I2	Dun Laoghaire	Artificial seawall	53.297553°N, −6.147643°W	3.16
	Seapoint	Natural	53.298915°N, −6.161725°W	3.76
I3	Rosslare A	Artificial rip-rap	52.252592°N, −6.351773°W	3.97
	Rosslare B	Natural	52.252420°N, −6.355033°W	3.96
I4	Kilmore A	Artificial rip-rap	52.172794°N, −6.587012°W	4.30
	Kilmore B	Natural	52.170424°N, −6.595372°W	4.35

Appendix B. PERMANOVA for the density of *Patella vulgata* between natural rocky shores and artificial structures along Irish Sea coasts. (a.) Data set excluding Dublin and (b.) Data set excluding vertical quadrats (i.e., seawalls at Dublin and Dun Laoghaire and the corresponding natural rocky shores at Sutton and Seapoint). Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion

	Source of variation	df	Pseudo-F	p	Unique permutations
a.	Coast = C	1	5.1589	**0.0376**	9811
	Type = Ty	1	3.4075	0.0883	9838
	Time = Ti	1	0.1502	0.7019	9825
	C x Ty	1	3.3960	0.0892	9842
	C x Ti	1	8.7055	**0.0142**	9828
	Ty x Ti	1	0.7164	0.4233	9844
	Site (C x Ty)	11	12.119	**<u>0.0001</u>**	9926
	C x Ty x Ti	1	7.5342	**0.0200**	9824
	Ti x Site (C x Ty)	11	1.8674	**0.0392**	9932
	Res	270			
	Total	299			
b.	Coast = C	1	5.9271	<u>0.0477</u>	8746
	Type = Ty	1	3.4677	0.1063	9336
	Time = Ti	1	0.0882	0.7759	9853
	C x Ty	1	1.3457	0.2740	9328
	C x Ti	1	5.2948	**0.0500**	9848
	Ty x Ti	1	1.3237	0.2815	9831
	Site (C x Ty)	8	11.923	**<u>0.0001</u>**	9936
	C x Ty x Ti	1	6.9435	**0.0310**	9835
	Ti x Site (C x Ty)	8	2.0167	**0.0443**	9941
	Res	216			
	Total	239			

Appendix C. PERMANOVA for the length of *Patella vulgata* between natural rocky shores and artificial structures across the Irish Sea excluding vertical quadrats (i.e., seawalls at Dublin and Dun Laoghaire and the corresponding natural rocky shores at Sutton and Seapoint). Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion

Source of variation	df	Pseudo-F	p	Unique permutations
Coast = C	1	2.1297	<u>0.1770</u>	8888
Type = Ty	1	4.4230	0.0710	9349
C x Ty	1	0.9468	0.3545	9359
Site (C x Ty)	8	41.825	**<u>0.0001</u>**	9932
Res	1188			
Total	1199			

Appendix D. PERMANOVA for percentage of *Patella vulgata* in advanced stages of gonad development on natural rocky shores and artificial structures along Irish Sea coasts excluding vertical quadrats (i.e., seawalls at Dublin and Dun Laoghaire and the corresponding natural rocky shores at Sutton and Seapoint). Significance was assessed as $p < 0.05$ except when PERMDISP revealed significant differences in within-group dispersion between levels of a particular factor, in which case significance was conservatively assessed as $p < 0.01$. Significant values are indicated in bold. Underlined values identify main factors with significant differences in within group dispersion

Source of variation	df	Pseudo-F	p	Unique permutations
Coast = C	1	14.094	**<u>0.0077</u>**	8019
Type = Ty	1	7.7931	**<u>0.0312</u>**	8839
Month = M	2	6.6837	**0.0079**	9957
C x Ty	1	3.3452	0.1082	8781
C x M	2	6.1617	**0.0089**	9951
Ty x M	2	1.2596	0.3173	9948
Site (C x Ty)	8	2.7553	**0.0338**	9943
C x Ty x M	2	1.4638	0.2531	9959
Res	16			
Total	35			

Appendix E. Analysis of deviance (Type II) for the proportion of male to female *Patella vulgata* determined through a GLMER (i.e., site as random intercept) model. Significant values ($p < 0.05$) indicated in bold

Source of variation	Wald chi-square test		
	df	χ^2	p
Coast (C)	1	49.37	**< 0.001**
Type (Ty)	1	9.70	**0.0019**
Month (M)	2	6.88	**0.0321**
C x Ty	1	13.45	**< 0.001**
C x M	2	3.83	0.14
Ty x M	2	15.30	**< 0.001**
C x Ty x M	2	3.48	0.18

References

Aguilera, M.A., 2018. Artificial defences in coastal marine ecosystems in Chile: opportunities for spatial planning to mitigate habitat loss and alteration of the marine community structure. Ecol. Eng. 120, 601–610. https://doi.org/10.1016/j.ecoleng.2017.04.021.

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

Airoldi, L., Bulleri, F., 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. PLoS One 6. https://doi.org/10.1371/journal.pone.0022985.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for Primer: Guide to Software and Statistical Methods.

Ballantine, W.J., 1961. The Population Dynamics of Patella Vulgata and Other Limpets, vol. 236. Ph.D. thesis, Queen Mary Coll. Univ. London.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Baxter, J.M., 1983. Annual variations in soft-body dry weight, reporductive cycle and sex ratios in populations of Patella vulgata at adjacent sites in the Orkney Islands. Mar. Biol. 76, 149–157. https://doi.org/10.1007/BF00392731.

Blackmore, D.T., 1969. Studies of patella vulgata L. I. Growth, reporduction and zonal distribution. J. Exp. Mar. Biol. Ecol. 3, 200–213. https://doi.org/10.1016/0022-0981(69)90018-5.

Borges, C.D.G., Doncaster, C.P., Maclean, M.A., Hawkins, S.J., 2015. Broad-scale patterns of sex ratios in Patella spp.: a comparison of range edge and central range populations in the British Isles and Portugal. J. Mar. Biol. Assoc. U. K. 95, 1141–1153. https://doi.org/10.1017/S0025315415000417.

Borja, A., Aguirrezabalaga, F., Martínez, J., Sola, J.C., García-Arberas, L., Gorostiaga, J. M., 2004. Benthic communities, biogeography and resources management. Oceanogr. Mar. Environ. Basqu. Ctry. 70, 455–492.

Bowman, R.S., 1981. The morphology of patella SPP. Juveniles in Britain, and some phylogenetic inferences. J. Mar. Biol. Assoc. U. K. 61, 647–666. https://doi.org/10.1017/S0025315400048104.

Bowman, R.S., Lewis, J.R., 1986. Geographical variation in the breeding cycles and recruitment of Patella spp. Hydrobiologia 142, 41–56. https://doi.org/10.1007/BF00026746.

Bowman, R.S., Lewis, J.R., 1977. Annual fluctuations in the recruitment of patella vulgata l. J. Mar. Biol. Assoc. U. K. 57, 793–815. https://doi.org/10.1017/S0025315400025169.

Brazao, S., Boaventura, D., Morais, S., Narciso, L., Ré, P., 2003. Population structure, recruitment and distribution patterns of Patella depressa Pennant, 1777 on the central Portuguese coast. Bol. Inst. Esp. Oceanogr. 19, 453–460.

Bulleri, F., 2005. Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Mar. Ecol. Prog. Ser. 287, 53–64. https://doi.org/10.3354/meps287053.

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

Bulleri, F., Chapman, M.G., 2004. Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. Mar. Biol. 145, 381–391. https://doi.org/10.1007/s00227-004-1316-8.

Bulleri, F., Chapman, M.G., Underwood, A.J., 2005. Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. Austral Ecol. 30, 655–667. https://doi.org/10.1111/j.1442-9993.2005.01507.x.

Burrows, M.T., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. Mar. Ecol. Prog. Ser. 445, 193–207. https://doi.org/10.3354/meps09422.

Burrows, M.T., 2020. Wave fetch GIS layers for Europe at 100m scale. Figshare Dataset. https://doi.org/10.6084/m9.figshare.8668127.

Chapman, M.G., 2006. Intertidal seawalls as habitats for molluscs. J. Molluscan Stud. 72, 247–257. https://doi.org/10.1093/mollus/eyi069.

Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Mar. Ecol. Prog. Ser. 264, 21–29. https://doi.org/10.3354/meps264021.

Chapman, M.G., 1994. Small- and broad-scale patterns of distribution of the upper-shore littorinid Nodilittorina pyramidalis in New South Wales. Aust. J. Ecol. 19, 83–95. https://doi.org/10.1111/j.1442-9993.1994.tb01547.x.

Chapman, M.G., Bulleri, F., 2003. Intertidal seawalls - New features of landscape in intertidal environments. Landsc. Urban Plann. 62, 159–172. https://doi.org/10.1016/S0169-2046(02)00148-2.

Chapman, M.G., Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. J. Exp. Mar. Biol. Ecol. 224, 265–289. https://doi.org/10.1016/S0022-0981(97)00202-5.

Coleman, R.A., Hawkins, S.J., Wood, H.L., 2006a. Testing the reproductive benefits of aggregation: the limpet Patella vulgata shows no evidence of synchrony in gonad development. Mar. Ecol. Prog. Ser. 306, 201–207. https://doi.org/10.3354/meps306201.

Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Åberg, P., Arenas, F., Arrontes, J., Castro, J., Hartnoll, R.G., Jenkins, S.R., Paula, J., Santina, P., Hawkins, S.J., 2006b. A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147, 556–564. https://doi.org/10.1007/s00442-005-0296-9.

Dethier, M.N., McDonald, K., Strathmann, R.R., 2003. Colonization and connectivity of habitat patches for coastal marine species distant from source populations. Conserv. Biol. 17, 1024–1035. https://doi.org/10.1046/j.1523-1739.2003.01606.x.

Díaz-Agras, G., Moreira, J., Tato, R., García-Regueira, X., Urgorri, V., 2010. Distribution and population structure of Patella vulgata linnaeus, 1758 (Gastropoda: Patellidae) on intertidal seawalls and rocky shores in the ría de ferrol (galicia, NW iberian peninsula). Thalassas 26, 79–91.

Drexler, M., Parker, M.L., Geiger, S.P., Arnold, W.S., Hallock, P., 2014. Biological assessment of eastern oysters (Crassostrea virginica) inhabiting reef, mangrove, seawall, and restoration substrates. Estuar. Coast 37, 962–972. https://doi.org/10.1007/s12237-013-9727-8.

Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., Mianzan, H., Gili, J.-M., Fuentes, V., Atienza, D., Pages, F., Breitburg, D., Malek, J., Graham, W.M., Condon, R.H., 2013. Is global ocean sprawl a cause of jellyfish blooms? Front. Ecol. Environ. 11, 91–97. https://doi.org/10.1890/110246.

Evans, A.J., Firth, L.B., Hawkins, S.J., Hall, A.E., Ironside, J.E., Thompson, R.C., Moore, P.J., 2019. From ocean sprawl to blue-green infrastructure – a UK perspective on an issue of global significance. Environ. Sci. Pol. 91, 60–69. https://doi.org/10.1016/j.envsci.2018.09.008.

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

Evans, R.G., 1947. The intertidal ecology of cardigan bay. J. Ecol. 34, 273–309. https://doi.org/10.2307/2256720.

Evans, R.G., 1957. The intertidal ecology of some localities on the atlantic coast of France. J. Ecol. 45, 245. https://doi.org/10.2307/2257088.

Farrugia Drakard, V., Brooks, P., Crowe, T.P., Earp, H.S., Thompson, B., Bourke, N., George, R., Piper, C., Moore, P.J., 2021. Fucus vesiculosus populations on artificial structures have potentially reduced fecundity and are dislodged at greater rates than on natural shores. Mar. Environ. Res. 168, 105324 https://doi.org/10.1016/j.marenvres.2021.105324.

Firth, L.B., Knights, A.M., Bridger, D., Evans, A.J., Mieszkowska, N., Moore, P.J., O'connor, N.E., Sheehan, E.V., Thompson, R.C., Hawkins, S.J., 2016a. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. Oceanogr. Mar. Biol. Annu. Rev. https://doi.org/10.1201/9781315368597.

Firth, L.B., Mieszkowska, N., Thompson, R.C., Hawkins, S.J., 2013a. Climate change and adaptational impacts in coastal systems: the case of sea defences. Environ. Sci. Process. Impacts 15, 1665–1670. https://doi.org/10.1039/c3em00313b.

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

Firth, L.B., White, F.J., Schofield, M., Hanley, M.E., Burrows, M.T., Thompson, R.C., Skov, M.W., Evans, A.J., Moore, P.J., Hawkins, S.J., 2016b. Facing the future: the importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. Mar. Freshw. Res. 67, 131–143. https://doi.org/10.1071/MF14163.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, third ed. Sage, Thousand Oaks, CA.

Gacia, E., Satta, M.P., Martin, D., 2007. Low crested coastal defence structures on the Catalan coast of the Mediterranean Sea: how they compare with natural rocky shores. Sci. Mar. 71, 259–267. https://doi.org/10.3989/scimar.2007.71n2259.

Glasby, T.M., Connell, S.D., 2001. Orientation and position of substrata have large effects on epibiotic assemblages. Mar. Ecol. Prog. Ser. 214, 127–135. https://doi.org/10.3354/meps214127.

Hall, A.E., 2017. The Ecology and Ecological Enhancement of Artificial Coastal Structures. PhD Thesis. Bournemouth University.

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

Hill, J.M., 2008. Patella vulgata common limpet. In: Tyler-Walters, H., Hiscock, K. (Eds.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews. Marine Biological Association of the United Kingdom, Plymouth, UK.

Hobday, A., 1995. Body-size variation exhibited by an intertidal limpet: influence of wave exposure, tidal height and migratory behavior. J. Exp. Mar. Biol. Ecol. 189, 29–45. https://doi.org/10.1016/0022-0981(95)00009-G.

Hodgson, A.N., Le Quesne, W.J.F., Hawkins, S.J., Bishop, J.D.D., 2007. Factors affecting fertilization success in two species of patellid limpet (Mollusca: Gastropoda) and development of fertilization kinetics models. Mar. Biol. 150, 415–426. https://doi.org/10.1007/s00227-006-0354-9.

Iveša, L., Chapman, M.G., Underwood, A.J., Murphy, R.J., 2010. Differential patterns of distribution of limpets on intertidal seawalls: experimental investigation of the roles of recruitment, survival and Competition. Mar. Ecol. Prog. Ser. 407, 55–69. https://doi.org/10.3354/meps08539.

Koike, K., 1996. The countermeasures against coastal hazards in Japan. Geojournal 38, 301–312. https://doi.org/10.1007/BF00204722.

Lenth, R., 2020. Emmeans: Estimated Marginal Means, Aka Least-Squares Means.

Lopez, E., 2019. Annelid assemblages on artificial and natural hard substrata differ decades after building: a case study on a one-century old seawall. Estuar. Coast Shelf Sci. 227, 106309 https://doi.org/10.1016/j.ecss.2019.106309.

Mayer-Pinto, M., Dafforn, K.A., Johnston, E.L., 2019. A decision framework for coastal infrastructure to optimize biotic resistance and resilience in a changing climate. Bioscience 69, 833–843. https://doi.org/10.1093/biosci/biz092.

Mayes, J., 2013. Regional weather and climates of the British Isles - Part 5: Wales. Weather 68, 227–232. https://doi.org/10.1002/wea.2149.

McCarthy, M., Woosnam, P., Culloty, S.C., 2008. Histological investigation of the reproductive cycles of the limpets Patella vulgata and Patella ulyssiponensis. Mar. Biol. 153, 871–877. https://doi.org/10.1007/s00227-007-0859-x.

Metaxas, A., Scheibling, R.E., Young, C.M., 2002. Estimating fertilization success in marine benthic invertebrates: a case study with the tropical sea star Oreaster reticulatus. Mar. Ecol. Prog. Ser. 226, 87–101. https://doi.org/10.3354/meps226087.

Moore, P., Hawkins, S.J., Thompson, R.C., 2007a. Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. Mar. Ecol. Prog. Ser. 334, 11–19. https://doi.org/10.3354/meps334011.

Moore, P., Thompson, R.C., Hawkins, S.J., 2007b. Effects of grazer identity on the probability of escapes by a canopy-forming macroalga. J. Exp. Mar. Biol. Ecol. 344, 170–180. https://doi.org/10.1016/j.jembe.2012.012.

Moore, P.J., Thompson, R.C., Hawkins, S.J., 2011. Phenological changes in intertidal con-specific gastropods in response to climate warming. Global Change Biol. 17, 709–719. https://doi.org/10.1111/j.1365-2486.2010.02270.x.

Morais, S., Boaventura, D., Narciso, L., Re, P., Hawkins, S.J., 2003. Gonad development and fatty acid composition of Patella depressa Pennant (Gastropoda: Prosobranchia) populations with different patterns of spatial distribution, in exposed and sheltered sites. J. Exp. Mar. Biol. Ecol. 294, 61–80. https://doi.org/10.1016/S0022-0981(03)00258-2.

Moreira, J., Chapman, M.G., Underwood, A.J., 2006. Seawalls do not sustain viable populations of limpets. Mar. Ecol. Prog. Ser. 322, 179–188. https://doi.org/10.3354/meps322179.

Morris, R.L., Chapman, M.G., Firth, L.B., Coleman, R.A., 2017. Increasing habitat complexity on seawalls: investigating large- and small-scale effects on fish assemblages. Ecol. Evol. 7, 9567–9579. https://doi.org/10.1002/ece3.3475.

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

Natanzi, A.S., Thompson, B.J., Brooks, P.R., Crowe, T.P., McNally, C., 2021. Influence of concrete properties on the initial biological colonisation of marine artificial structures. Ecol. Eng. 159 https://doi.org/10.1016/j.ecoleng.2020.106104.

Orton, J.H., 1919. Sex-phenomena in the common limpet (Patella vulgata). Nature 104, 373–374. https://doi.org/10.1038/104373a0.

Orton, J.H., Southward, A.J., 1961. Studies on the biology of limpets IV. The breeding of patella depressa pennant on the north Cornish coast. J. Mar. Biol. Assoc. U. K. 41, 653–662. https://doi.org/10.1007/978-3-642-67028-2_47.

Orton, J.H., Southward, A.J., Dodd, J.M., 1956. Studies on the biology of limpets. II. The breeding of Patella vulgata in Britain. J. Mar. Biol. Assoc. U. K. 35, 149–176. https://doi.org/10.1017/S0025315400009036.

Pinn, E.H., Mitchell, K., Corkill, J., 2005. The assemblages of groynes in relation to substratum age, aspect and microhabitat. Estuar. Coast Shelf Sci. 62, 271–282. https://doi.org/10.1016/j.ecss.2004.09.002.

Pister, B., 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Mar. Biol. 156, 861–873. https://doi.org/10.1007/s00227-009-1130-4.

R Core Team, 2021. R: a language and environment for statistical computing. R Found. Stat. Comput.

Safriel, U.N., Erez, N., Keasar, T., 1994. How do limpets maintain barnacle-free submerged artificial surfaces? Bull. Mar. Sci. 54, 17–23.

Seabra, M.I., Hawkins, S.J., Espírito-Santo, C., Castro, J.J., Cruz, T., 2020. Rock-pools as nurseries for co-existing limpets: spatial and temporal patterns of limpet recruitment. Reg. Stud. Mar. Sci. 37, 101339 https://doi.org/10.1016/j.rsma.2020.101339.

Sella, I., Perkol-Finkel, S., Rella, A., 2018. ECOncrete technologies: bio-enhanced concrete for coastal and marine infrastructure. In: Burgess, K. (Ed.), Coasts, Marine Structures and Breakwaters 2017. ICE Publishing, pp. 549–552. https://doi.org/10.1680/cmsb.63174.0549.

Skewes, M., 2003. Patella depressa Black-footed limpet. In: Tyler-Walters, H., Hiscock, K. (Eds.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews. Marine Biological Association of the United Kingdom, Plymouth, UK.

Sousa, R., Delgado, J., Pinto, A.R., Henriques, P., 2017. Growth and reproduction of the north-eastern Atlantic keystone species Patella aspera (Mollusca: Patellogastropoda). Helgol. Mar. Res. 71 https://doi.org/10.1186/s10152-017-0488-9.

Southward, A.J., Crisp, D.J., 1954. The distribution of certain intertidal animals around the Irish coast. Proc. R. Ir. Acad. B. 57, 1–29.

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

Sundelöf, A., Jenkins, S.R., Svensson, C.J., Delany, J., Hawkins, S.J., Åberg, P., 2010. Determinants of reproductive potential and population size in open populations of Patella vulgata. Mar. Biol. 157, 779–789. https://doi.org/10.1007/s00227-009-1361-4.

Thompson, B.J., 2022. The Distribution, Ecology and Ecological Enhancement of Marine Artificial Structures on Irish Sea Coasts. PhD Thesis. University College Dublin.

Vasconcelos, J., Caamaño, D., Tuset, V.M., Sousa, R., Riera, R., 2021. The shell phenotypic variability of the keyhole limpet Fissurella latimarginata: insights from an experimental approach using a water flow flume. J. Molluscan Stud. 87 https://doi.org/10.1093/mollus/eyab043.

Vieira, E.A., Bueno, M., 2019. Small spatial scale effects of wave action exposure on morphological traits of the limpet Lottia subrugosa. J. Mar. Biol. Assoc. U. K. 99, 1309–1315. https://doi.org/10.1017/S0025315419000195.

Wickham, H., 2016. Elegant Graphics for Data Analysis. Springer-Verlag, New York.