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# Spatial variation in epibiont communities on the shells of *Patella vulgata* along an estuarine gradient

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## Abstract

In space limited intertidal habitats, non-specific substratum generalists can be observed to increase their survival and settlement opportunities by growing upon other living organisms. To date, few studies have assessed the influence of multiple environmental factors in determining patterns of epibiont diversity and community structure upon gastropod shells, across spatial scales. This study investigated the significance of surface salinity range, wave exposure and shell metrics in determining the composition and diversity of epibionts found upon shells of *Patella vulgata* (Common Limpet), throughout the Plymouth Sound and lower reaches of the Tamar Estuary, United Kingdom (UK). A total of 292 shells were sampled, identifying 26 epibiont species amongst 9 phyla. Species richness and diversity ( $H'$ ) were greatest upon shells at exposed marine sites (where salinity variation was lower), decreasing as surface salinity range increased towards the Lynher River. Multivariate analysis revealed epibiont community composition to differ significantly between sites, being influenced mainly by surface salinity range and, to a lesser extent, wave exposure. Species contributing to community dissimilarities were identified to reflect the dominant species between sites, with observed community shifts attributed mainly to a species physiological tolerance to environmental conditions. This study is the first to describe epibiont community variation upon shells of *P. vulgata* along an estuarine-exposure gradient in the UK. Although salinity variation and wave exposure explained most of the observed community composition patterns, further investigation including exploration of additional environmental factors, is required to fully explain the distribution and diversity patterns of epibionts upon shells of *P. vulgata*.

**Keywords:** Epibiont diversity, Facilitation, Intertidal, *Patella vulgata*, Biogenic Habitat, Biodiversity, Intertidal ecology, Ecosystem engineer, Community composition, Ecology

## **Introduction**

Intertidal rocky shores are regarded by numerous authors to be one of the most highly dynamic and stressful environments within marine systems, experiencing spatial and temporal environmental heterogeneity, across both vertical (i.e. tidal, temperature) and horizontal (i.e. wave exposure, salinity; Denny & Wetthey, 2001) gradients (Underwood & Chapman, 1996, Harley, 2008, Moisez et al. 2020). When combined with negative biotic interactions (i.e. competition, predation, biological disturbance; see Menge, 1976, Terbough, 2015), these factors greatly influence community composition and diversity patterns across various scales (Scrosati et al. 2011, Catalan et al. 2020). Historically, the ability of ecologists to understand the mechanisms driving community composition and diversity has been a major research objective within the field of ecology (Brown, 1995, Connell, 1961, Paine, 1966). However to date, some ecologists investigating intertidal community composition have directed their interest upon understanding the effects of negative biotic interactions that act between intertidal epibionts and basibionts among a multitude of differential contexts, ranging from: the mechanistic implications of epibionts (i.e. Seaborn, 2014, Garner & Litvaitis, 2017) and predation (i.e. Laudien & Wahl, 2004, Thangarathinam & Chattopadhyay, 2020), to the ability of basibionts to harbour invasive species (i.e. Normant et al. 2013, Firth et al. 2020); somewhat eluding the impacts of positive biotic interactions, such as the facilitation of micro-habitat (i.e. epibiosis) (Bruno et al. 2003; MCGowan & Lyengar, 2017).

The fundamental ability of sessile marine organisms of numerous phyla, to disperse and settle upon stable substratum, is crucial, in order to promote an organism's growth and fitness (Menge, 1991, Olivier et al. 2000, Blockly & Chapman, 2006). However, within the eulittoral zone of intertidal rocky shores, space is often limited, being characterised by intense intra/interspecific competition (Connell, 1961, Dayton, 1971). In order to overcome this limiting resource, some sessile intertidal species- generally non-specific substratum generalists (Wahl and Mark, 1999)- can be observed to increase their survival and settlement opportunities by growing, epiphytically upon other living organisms (the basibiont/host); via a phenomenon known as epibiosis (Harder, 2009, Wahl, 2009). Epibiotic associations have been documented for numerous sessile taxa including barnacles (Chan & Chan, 2005), macroalgae (Ballantine et. 2001), polychaetes (Warner, 1997) and bryozoans (Stachowicz & Whitlatch, 2005, Lopez-Gappa & Zelaya, 2021). Marine basibionts that provide additional hard substratum for epibionts, are generally found to be large long-lived species, that are either slow-moving or sessile in nature (Wahl & Mark, 1999, Martins, 2014). Research has identified that the presence of epibionts can cause both positive and negative consequences upon gastropod hosts (Wahl, 1989). For example, epibionts can positively benefit its associated host via reducing predation susceptibility (Wahl & Hay, 1995, Marin & Belluga, 2005, Thornber, 2007), or by reducing the rate of desiccation (Penhale & Smith, 1977). Alternatively, some epibionts can negatively affect their host through increasing energy expenditure via drag (Donovan et al. 2003), which can subsequently increase the risk of dislodgement (Witman et al. 1984, O' Connor et al. 2006). However, the strength and presence of these interactions can vary, being somewhat dependent upon the intensity of local abiotic disturbances, as well as the density of epi-fauna and flora (O'Connor, 2010, Seaborn, 2014).

Across all coastlines of North-West Europe and the British Isles, the gastropod *Patella vulgata* (Common Limpet) is an abundant “keystone” grazer within the mid-intertidal zone, that regulates the distribution and abundance of micro and macroalgal species (Jenkins & Hartnoll, 2001, Jenkins et al. 2005, Coleman et al. 2006). Indirectly, they influence the composition and functioning of intertidal communities, through inhibiting and/or enhancing the establishment of organisms upon intertidal substratum (Poore et al. 2012, Notman et al. 2016). Individuals of *P. vulgata*, have been evidenced to tolerate salinities down to 20 psu and as a result, populations can commonly be found to inhabit the lower reaches of estuarine systems (Arnold, 1957, Fish & Fish, 2011). Alike other large, slow-moving intertidal gastropod species, opportunistic epi-fauna and flora can be observed to form fouling communities upon the shells of *P. vulgata* (Wahl & Mark, 1999, O’Connor, 2010, Seaborn, 2014). However, surprisingly few detailed recordings of epibiont community composition upon shells of *P. vulgata* have been recorded within the literature, with most studies focusing upon the importance of limpets structuring rocky shore communities (Jonsson et al. 2006, Burgos-Rubio et al. 2015). Thus, as a result of the widespread distribution and tolerance of *P. vulgata* to environmental stressors, it is likely that sessile epibiont communities fouled upon shells will be somewhat influenced by the external variation of abiotic and biotic factors exhibited throughout marine and estuarine systems (Wernberg et al. 2010, Thyrring et al. 2015).

Throughout estuarine systems the effects of physio-chemical gradients (e.g Salinity and wave exposure) upon intertidal communities is well documented, with studies commonly evidencing spatially fluctuating patterns of community composition and diversity, as a result of environmental filtering (Loneragan et al. 1987, Atrill, 2002, Gascon et al. 2016, Namba et al. 2020). The Tamar Estuary, located within the Southwest of the UK, is like other temperate estuaries, with its mid-lower reaches characterised by highly dynamic physio-chemical gradients (Uncles et al. 1983, Miller, 1999, Ducrotoy et al. 2019). Therefore, the lower reaches of the Tamar Estuary, in addition to marine sites situated throughout the Plymouth Sound, provides an ideal model system to spatially investigate the relative effect of multiple physio-chemical factors on the composition and diversity of epibiont communities found upon shells of *P. vulgata*.

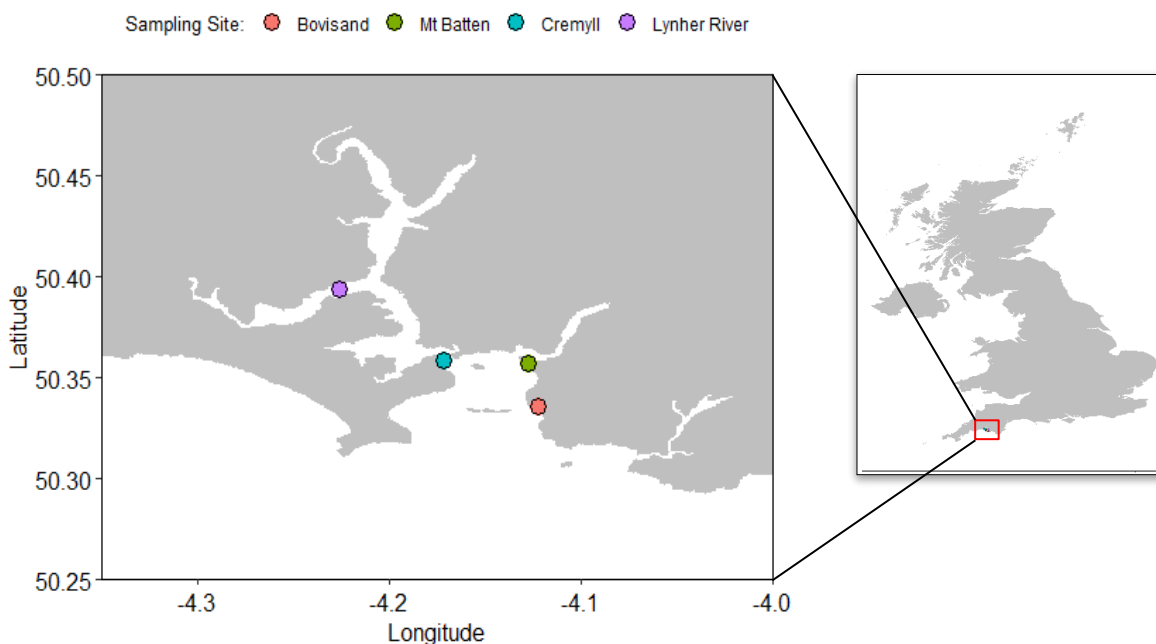
Rarely have studies investigated and compared the spatial effect of vertical and horizontal gradients upon epibiont community composition and diversity on gastropod shells (Hardwick-Witman and Mathieson, 1983, Martins, 2014, Thyrring et al. 2015, McGowen & Iyengar, 2017). Until now, no specific studies within the UK have been carried out to describe the spatial variation of epibiont diversity and community composition upon limpet shells. This present study was aimed to fill this gap within literature, specifically describing whether there is a spatial differentiation of epibiont diversity and community composition upon shells of *P. vulgata*, along an estuarine gradient. Data was additionally explored to reveal evidence for the processes primarily responsible for the composition of shell communities.

## Methodology

### Sampling Methodology

Between the 8<sup>th</sup> of October and 4<sup>th</sup> November 2020, a total of 292 *Patella vulgata* individuals were collected at low tide, from four sampling sites located throughout the Plymouth Sound and the lower reaches of the Tamar Estuary (Fig.1; Table 1). At

each site, within the mid-intertidal zone, a 20 m transect line was haphazardly placed parallel to the shore. Every 1 m, a 0.5 m x 0.5 m (0.25m<sup>2</sup>) quadrat was laid upon the transect, with all *P. vulgata* individuals present removed from the substratum. Cavity tissue was discarded, and shells collected. Where the density of *P. vulgata* differed between sites, replicate transects were conducted until N = 73 individuals were collected per site. Individuals were dorsally photographed, labelled and frozen prior to the identification of epibiont taxa.



**Figure 1:** Location of sites sampled within Plymouth Sound and Lower reaches of the Tamar Estuary, United Kingdom. Map data provided courtesy of GADM (no date).

All epibionts present were identified to species level, using a stereo microscope (Olympus SZ, x10). The shell metrics length, breadth and height were measured using dial callipers (accuracy 0.01mm). Individual dorsal photographs were processed using ImageJ (Schneider et al. 2012), in conjunction with known shell dimensions to scale and precisely measure an individual's exact shell area. Epi-faunal and floral, percentage cover (PC) was approximated through measuring the total area of occupancy for each epibiont species present upon each shell in ImageJ. Surface salinity ranges were sourced and extrapolated from Milne (1938), while wave exposure values for each site were obtained from the European Marine Observation Data Network habitats initiative (EMODnet, 2021).

**Table 1:** Location of sampling sites and associated site specific environmental parameters

Sampling Site:	Sampling Date:	GPS Coordinates:	Wave Exposure Value ( N.m <sup>2</sup> .s <sup>-1</sup> ):	Surface Salinity Range (psu):
Bovisand	08/10/2020	50°20'9.03"N, 4°7'18.91"W	1392	5
Mt Batten	4/11/2020	50°21'25.09"N, 4°7'37.79"W	139.28	5.4
Cremyll	15/10/2020	50°21'31.01"N, 4°10'17.16"W	6.64	9.5
Lynher River	22/10/2020	50°23'37.73"N, 4°13'33.02"W	1.72	16.4

### Statistical Methodology

Species richness and Shannon-Wiener's diversity (H') index were quantified for each shell using PC data. Where appropriate, data was square-root transformed to meet homoscedasticity and normality assumptions, with one-way ANOVA analysis used to test for differentiation of the  $\alpha$ -diversity metrics between sites. Where results were significant, post-hoc TukeyHSD tests were performed. A Bray-Curtis dissimilarity coefficient matrix was constructed using square-root transformed epibiont PC data. In order to visualise patterns of epibiont community composition between sites and individual shells, non-metric multidimensional scaling (nMDS) ordinations and hierarchical group-averaged clusters were generated based on the Bray-Curtis dissimilarity matrix. Permutational multivariate analysis of variance (PERMANOVA) was subsequently conducted utilising the Bray-Curtis matrix, to test for differentiation of epibiont community composition between sampling sites and/or abiotic (i.e. surface salinity range, wave exposure) and biotic parameters (i.e. Shell A and H). Prior to this analysis, multivariate homogeneity of group variances was checked by applying a betadisper routine. In order to identify the epibiont species mostly accountable for the observed dissimilarities of community composition between sampling sites, similarity percentage (SIMPER) analysis was conducted.

All statistical analysis was conducted using R v4.0.2 (R Core Team, 2020) in conjunction with the packages; vegan (Oksanen et al. 2019), car (Fox & Weisberg, 2019), dplyr (Wickham et al. 2020), gplots (Warnes et al. 2020), ggplot2 (Wickham, 2016), sp (Bivand et al. 2013), ggpubr (Kassambara, 2020), Clustsig (Whitaker & Christman, 2014), FSA (Ogle et al. 2021) and tidyr (Wickham, 2020).

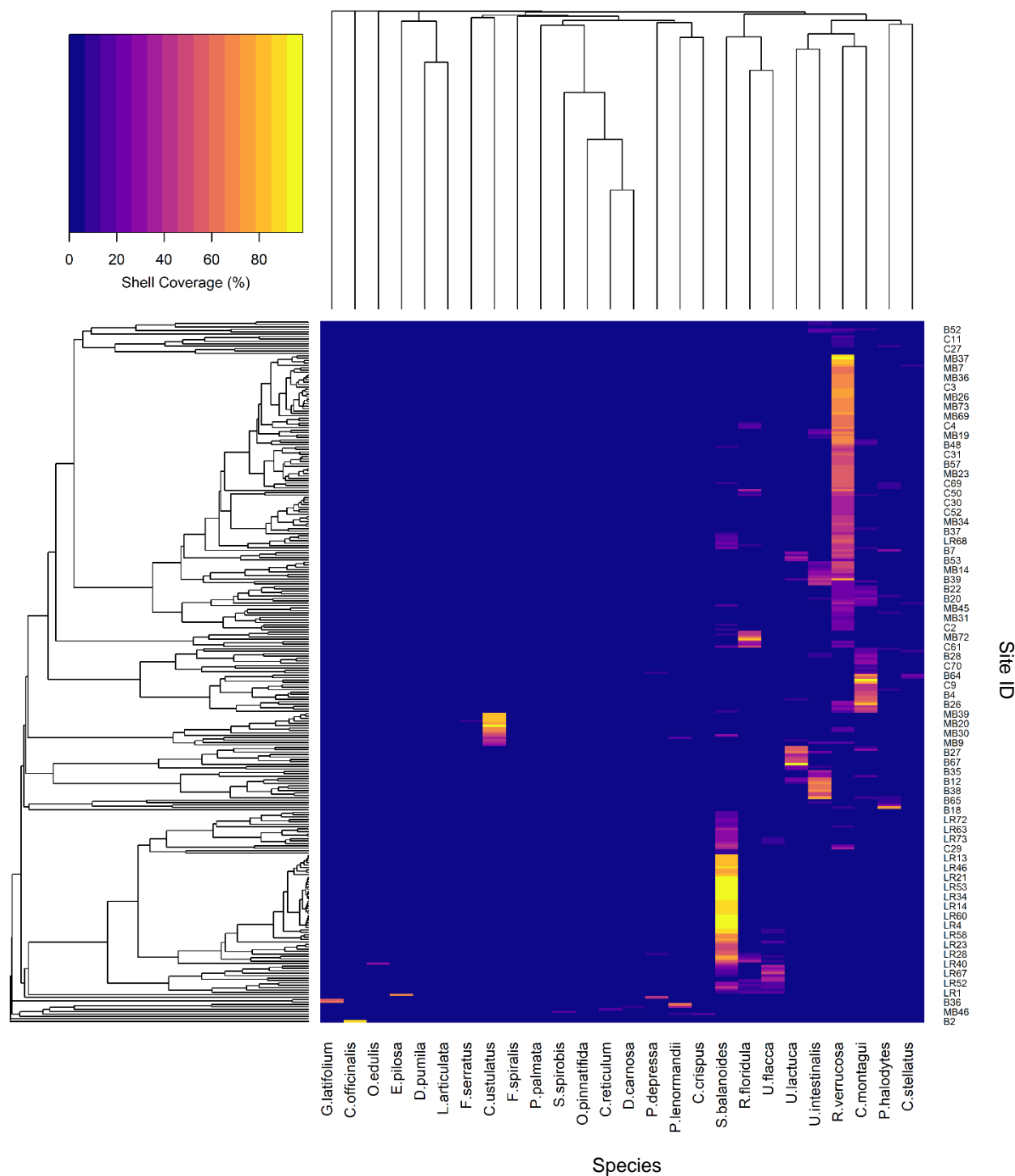
### Results

In total, 26 epibiont species belonging to 9 phyla, were recorded upon 292 shells of *Patella vulgata* (Table 2; Fig. 2). No shells were devoid of epibionts, provisioning habitat for at least one species. Epibiont composition was observed to be highly variable across individual shells (Fig. 2). Ochrophyta (84%) and Arthropoda (72%) were the two most frequently observed phyla upon all shells, both representing an average coverage of 11% (Table 2). Chlorophyta and RhydropHYta ranked third and fourth, occurring on 41% and 22% of shells, achieving an average shell coverage of 5% and 1% respectively (Table 2). Other phyla, such as Ascomycota, Mollusca,

Annelida, Cnidaria and Bryozoa, were only found to be present upon <10% of all shells sampled (Table 2). At lower taxonomic levels the encrusting seaweed *Ralfsia verrucosa* was identified to be the most abundant epibiont species present across all sites, occurring on 54% of all shells examined, achieving an average coverage of 32% (Table 2; Fig.2). A large proportion (69%) of all epibiont species identified were only found upon less than 10% of the total number of shells sampled (Fig. 2). At Bovisand, shells were observed to be mostly dominated by *Ulva intestinalis* (21%), *Ralfsia verrucosa* (22%), *Chthamalus montagui* (23%) and *Ulva lactuca* (15%) (Fig. 3). While, at Mt Batten and Cremyll, *Ralfsia verrucosa* (53%-48%), *Caulacanthus ustulatus* (0%-14%) and *Chthamalus montagui* (1%-15%) were identified to be the most dominant species upon shells, respectively (Fig.3). In contrast, at Lynher River, *Semibalanus balanoides* was solely identified to be the most dominant species, achieving an average coverage of 72% across all shells sampled at this site (Fig. 3).

**Table 2:** Epibiont phyla and species found upon shells of *Patella vulgata*, with indicated frequency and mean coverage (%) indicated.

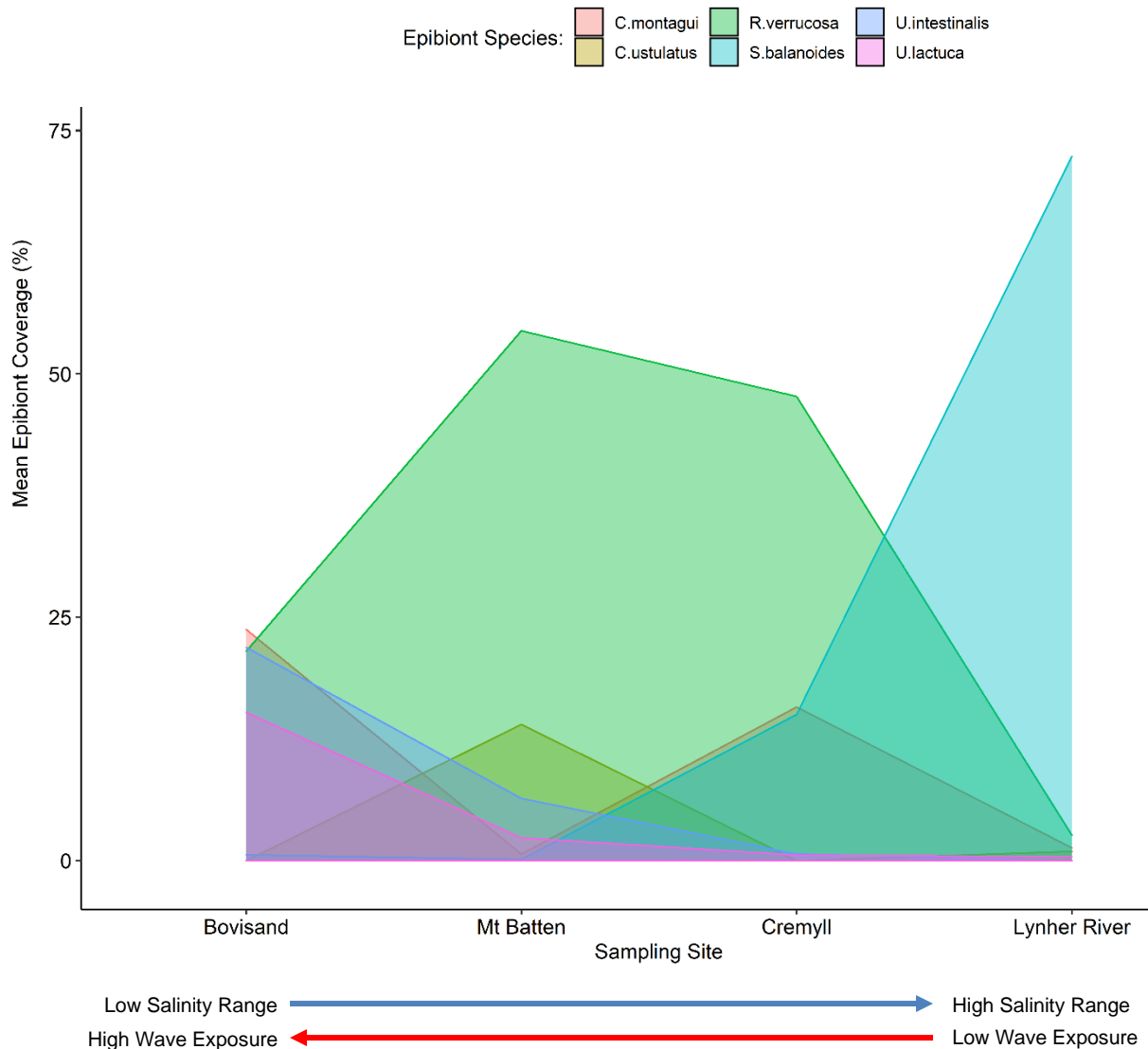
Epibiont Taxa	No. shells present upon (Frequency)	Average Coverage (%)
<b>OCHROPHYTA:</b>	<b>244 (84%)</b>	<b>11.2</b>
<i>Ralfsia verrucosa</i>	159	31.6
<i>Fucus serratus</i>	48	1.1
<i>Fucus spiralis</i>	37	0.8
<b>ARTHROPODA:</b>	<b>210 (72%)</b>	<b>11</b>
<i>Chthamalus montagui</i>	88	10.4
<i>Chthamalus stellatus</i>	9	1
<i>Semibalanus balanoides</i>	113	22.0
<b>CHLOROPHYTA:</b>	<b>120 (41%)</b>	<b>5</b>
<i>Ulva lactuca</i>	44	4.6
<i>Enteromorpha intestinalis</i>	53	7.2
<i>Ulothrix flacca</i>	23	3.1
<b>RHYDOPHYTA:</b>	<b>66 (22%)</b>	<b>1.1</b>
<i>Corallina officinalis</i>	2	0.3
<i>Gelidium latifolium</i>	2	0.5
<i>Rhodothamiella floridula</i>	28	4.3
<i>Phymatolithon lenormandii</i>	11	1
<i>Lomentaria articulata</i>	1	0.1
<i>Caulacanthus ustulatus</i>	14	3.7
<i>Osmundia pinnatifida</i>	1	0.1
<i>Palmaria palmata</i>	3	0.1
<i>Chondrus crispus</i>	2	0.2
<i>Dilsea carnosa</i>	2	0.2
<b>ASCOMYCOTA:</b>	<b>35 (12%)</b>	<b>2.8</b>
<i>Pyrenocellema halodytes</i>	35	2.8
<b>ANNELIDA</b>	<b>11 (4%)</b>	<b>0.1</b>
<i>Spirobis spirobis</i>	11	0.1
<b>MOLLUSCA</b>	<b>27 (9%)</b>	<b>0.9</b>
<i>Patella depressa</i>	26	1.5
<i>Ostrea edulis</i>	1	0.2
<b>CNIDARIA</b>	<b>3 (1%)</b>	<b>0.04</b>
<i>Dynamena pumila</i>	3	0.04
<b>BRYOZOA</b>	<b>3 (1%)</b>	<b>0.3</b>
<i>Electra pilosa</i>	1	0.3
<i>Conopeum reticulum</i>	2	0.2



**Figure 2:** Heatmap displaying the relative percentage cover (Coverage %) of epibiont species upon individual *Patella vulgata* shells between sites. Both cluster dendrograms (Left and top) were constructed utilising a Bray-Curtis dissimilarity matrix. The Left dendrogram, depicts the compositional similarity of epibiont species between the individual basibiont shells (N=73) at each site. The top dendrogram, clusters epibiont species by their

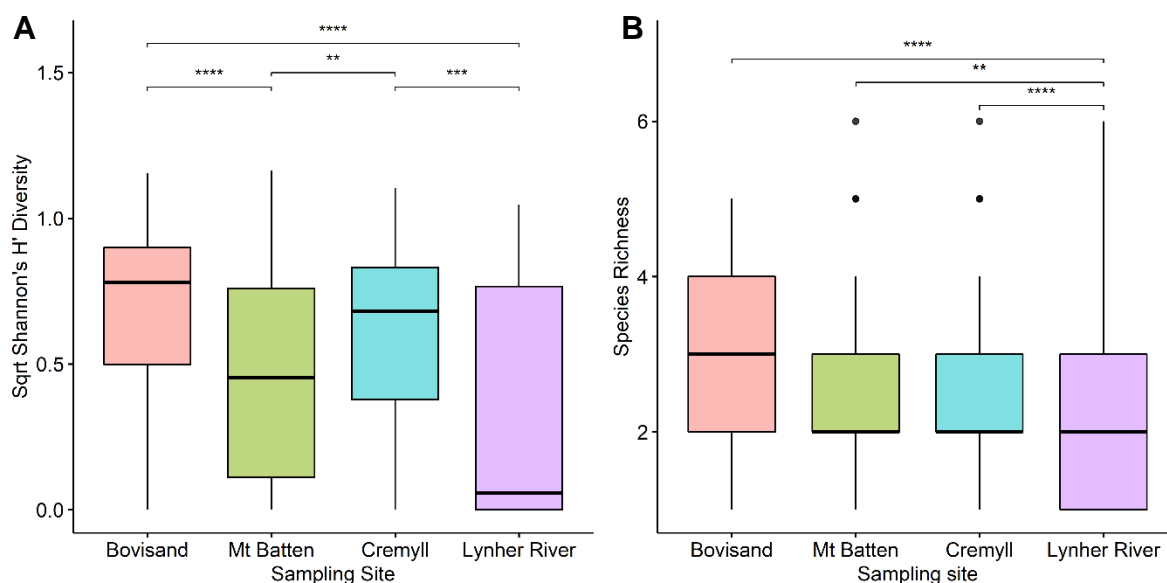


composition amongst samples. Site abbreviations: B = Bovisand, C = Cremyll, MB = Mt Batten, LR= Lynher River, with numbers (1-73) representing the ID number of individual shells collected at each site.



**Figure 3:** Mean percentage cover (Coverage %) of the six most dominant epibiont species present upon shells at different sampling sites. Direction of environmental stressors is indicated.

One-way ANOVA analysis identified a significant spatial differentiation of both epibiont diversity ( $H'$ ) ( $F_{3,288} = 10.4, P < 0.001$ ; Fig.4A) and species richness ( $F_{3,288} = 9.17, P < 0.001$ ; Fig. 4B) between sampling sites. For epibiont diversity ( $H'$ ), post-hoc TukeyHSD analysis identified four out of the seven pairwise comparisons to be significantly different from one another ( $P < 0.05$ ; Fig. 4A). In the case of species richness, post-hoc comparisons revealed richness to be similar throughout sites situated within the Plymouth Sound, being significantly lower at Lynher River ( $P < 0.05$ ; Fig. 4B).



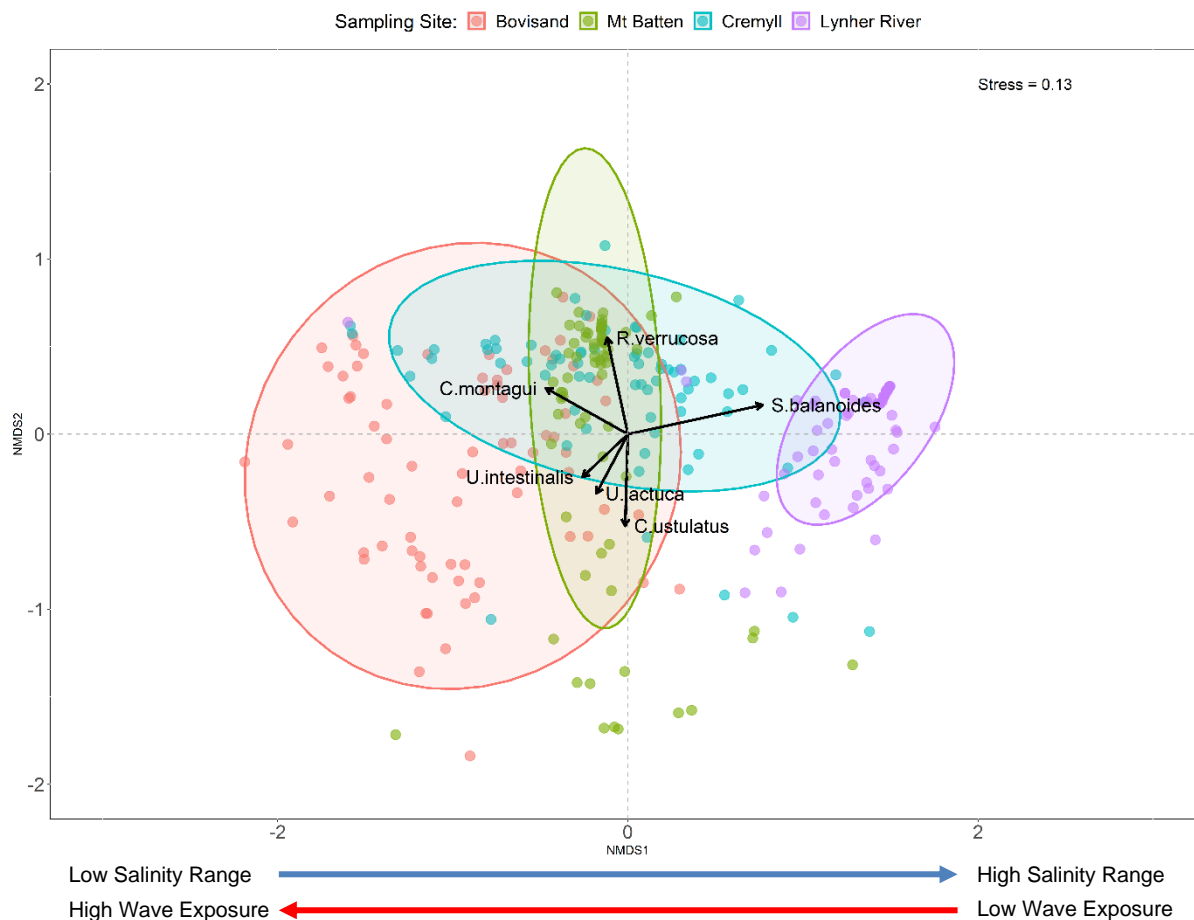
**Figure 4:** (A) Square rooted epibiont diversity (H') and (B) species richness upon shells of *Patella vulgata* across individual sampling sites. Differences in epibiont diversity between individual sites were assessed using TukeyHSD post-hoc tests (Top). \*\*P < 0.01, \*\*\*P < 0.001., \*\*\*\*P < 0.0001

Multivariate analysis revealed significant epibiont community composition differentiation between sampling sites (PERMANOVA:  $R^2 = 0.41$ ,  $F_{3,288} = 68.2$ ,  $P < 0.001$ ; Fig. 5). PERMANOVA analysis further confirmed that the environmental variables: wave exposure, surface salinity range and the shell metrics- height and area, all had a highly significant effect on epibiont community composition between sites; collectively explaining 40% of the variance (Table 3). Notably, surface salinity range was identified to contribute the most in the model, explaining 30% of the variance (Table 3).

**Table 3:** Results of PERMANOVA analysis, based upon a Bray-Curtis dissimilarity matrix of

Variable:	R2	F-Value:	d.f	P Value:
Surface Salinity Range	0.296	140.9	1,286	< 0.001 ***
Wave Exposure	0.087	42.1	1,286	< 0.001 ***
Shell Area	0.016	7.6	1,286	< 0.001 ***
Shell Height	0.010	4.7	1,286	< 0.05 **

square-root transformed data, testing for differences of epibiont community structure in response to abiotic and biotic parameters. \*\*P < 0.01, \*\*\*P < 0.001.



**Figure 5:** NMDS ordination among the four sampling sites (Colours ellipses), based on a Bray-Curtis dissimilarity matrix of epibiont percentage cover (%) upon shells of *Patella vulgata*. Additional overlaying arrows representing the strength and direction of species identified by SIMPER analysis to drive dissimilarities between sites (Black Arrows). MetaMDS Stress value is indicated. Direction of environmental stressors is indicated.

Having identified spatial differentiation of epibiont community composition between sites, SIMPER analysis revealed the main epibiont species accountable for the found compositional dissimilarity to reflect the most dominant species, expressing distribution patterns relating to differential environmental factors (Fig. 5). For instance, *Semibalanus balanoides* was found to be positively correlated with sites with reduced shore exposure, increased surface salinity range and shell height. Whereas *Chthamalus montagui*, *Ralfsia verrucosa*, *Caulacanthus ustulatus*, *Ulva intestinallis* and *Ulva lactuca* displayed a positive relationship with increased shore exposure levels, expressing a negative relationship with surface salinity range and shell height.

## Discussion

The results of this study demonstrates a clear spatial variation of epibiont diversity and community composition upon shells of *Patella vulgata*; along an estuarine-exposure gradient. The principal environmental factors responsible for epibiont community differences, were identified to be –surface salinity range and of lesser effect, wave exposure. These results correspond with other studies, which stress salinity variation to be the most important factor influencing the distribution and

composition of species within estuarine systems (Attrill et al. 2002, Ysebaert et al. 2003, Mclusky and Elliot, 2004).

Patterns of both epibiont diversity ( $H'$ ) and richness were observed to decline throughout marine sites, being lowest at Lynher River where surface salinity variation was greatest. Such patterns are typical of estuarine systems, of which declines similarly have been documented within studies that have investigated macro-benthic and epibiont communities (e.g. Attrill 2002, Thyring et al. 2015, Hossain et al. 2019). For instance, Thyring et al. (2015) identified epibiont diversity and abundance upon shells of the gastropods- *Batillaria australis*, *Nassarius pauperatus*, *Bedeva paiva*, to decline with distance away from marine sites as salinity variability increased throughout the Swan River Estuary (Western Australia). It can be speculated that the observed results are indicative of the concomitant replacement of dominant stenohaline species at the edge of their physiological range, by competitively dominant euryhaline adapted species- in response to increased salinity variability (Remane & Schlieper, 1971, Attrill, 2002, Gascon et al. 2016). In accordance with this hypothesis, the euryhaline adapted barnacle- *Semibalanus balanoides*, was identified to dominate shell communities at Lynher River (73%), exhibiting a positive correlation with surface salinity range. Notably, dominance exhibited by *S. balanoides* within the lower to mid reaches of temperate estuaries is not an uncommon occurrence (Hardwick-Witman & Mathieson, 1983, Gomes-Filho et al. 2010). Barnacles, such as *S. balanoides* are physiologically adapted to tolerate periodic environmental stressors during submersion and emersion, via the closure of opercular plates (Foster, 1970). Thus, where salinity variation is known to be the primary determinant of species distributions in estuarine systems, it is likely that this physiological tolerance enables *S. balanoides* to be competitively advantageous post-settlement, over other stenohaline adapted species for space; potentially explaining the dominance and subsequent low diversity patterns observed upon shells sampled at Lynher River (Remane & Schlieper, 1971, Attrill et al. 2002, Mclusky and Elliot, 2004, Sundell et al. 2019).

Intriguingly, both shell height and area were evidenced to display a positive correlation towards Lynher River, marginally contributing to community dissimilarities between sites. This result is interesting, in light of studies that have evidenced positive relationships between species richness and a basbionts shell size (Wernberg, 2010, Martins, 2014). The results of this study, however, do not agree with previous studies, as both epibiont diversity ( $H'$ ) and richness were observed to be lowest at Lynher River where shells were largest. Therefore, this result indicates that surface salinity range is the primary factor responsible for the patterns of community composition and diversity found at Lynher River.

Although salinity variation is likely to explain the observed patterns of diversity and community composition at Lynher River and Cremyll, it is unlikely to explain patterns of diversity and composition at more exposed sites such as Bovisand- where salinity variation is less. In intertidal marine systems, abiotic disturbances have been demonstrated to mediate biotic interactions, strongly influencing the composition, abundance and distribution of taxa (Denny 1987, Wernberg & Connell, 2008). Hence, a plausible explanation for the patterns of epibiont diversity and community composition found at exposed marine sites- such as Bovisand, where the influence of salinity variability was lesser, is likely to be explained by increased levels of wave action- a physical disturbance, stimulating the periodical dislodgement of dominant

sessile species upon shells; promoting the continual recruitment, succession and co-existence of competitively subdominant or opportunistic taxa (Dayton, 1971, Norderhaug et al. 2012). Nevertheless, it cannot be assumed that wave action alone, fully explains the patterns of epibiont diversity and community composition found upon shells at Bovisand. For instance, studies (see Leigh et al. 1987, Worm & Lotze, 2006) have shown that at intertidal locales, increased wave exposure can also indirectly increase the concentration and transport of nutrients, stimulating the growth and dominance of opportunistic ephemeral macroalgal species (Kraufvelin et al. 2010, Martinez et al. 2012). Although nutrient concentrations were not recorded in this study, filamentous macroalgal species were predominantly observed to be the most dominant epibiont taxa observed upon shells at Bovisand. In particular, ephemeral Chlorophytes- such as *Ulva lactuca* and *Ulva intestinalis* were found only to dominate shells at this site, indicating that increased nutrient concentrations may have been an additional factor influencing community composition (Kraufvelin et al. 2010). Although further investigation would be required, it can be concluded that increased levels of wave action, in addition with other untested physio-chemical factors (e.g. nutrient concentrations), provides a rational explanation for the observed patterns of epibiont diversity and community composition found upon shells at exposed marine sites such as Bovisand (Kraufvelin et al. 2010).

Unexpectedly, patterns of epibiont diversity ( $H'$ ) were found to be lower at Mt Batten than that of both Bovisand and Cremyll, being most similar to levels at Lynher river. This discontinuity, in an area where the influence of both salinity variation and wave exposure is low, indicates that other environmental factors are influencing the recruitment and survival of epibiont taxa upon shells (Menge, 1976, Scrosati et al. 2011). In this study the encrusting algae *Ralfsia verrucosa*, was observed to be the most abundant species upon shells at Mt Batten. Studies have demonstrated that the growth of *R. verrucosa* can be stimulated by herbivorous grazing (McQuaid & Froneman, 1993), with epibiont species found to grow and persist upon algal crusts in the absence of abiotic and biotic disturbances (Dethier, 1994). Thus, indicative of the lower levels of shell diversity and low coverage of other epibiont species observed upon shells at Mt Batten, it can be postulated that biotic disturbances such as algal whiplash and predation may alternatively be driving the found patterns of diversity ( $H'$ ) and community composition upon shells- through limiting the recruitment and succession of epibionts (Steneck 1986, Wernberg et al, 2020). However, this remains speculative with further investigation, explicitly surveys and comparisons of the external rocky shore communities surrounding *in situ* *P. vulgata* shells required, in order to conclusively explain the observed patterns at Mt Batten.

## Conclusion

This present study has addressed its aims, being the first study within the UK to describe epibiont community structure and diversity upon the shells of *Patella vulgata* along a estuarine gradient. Epibiont diversity was found to be greatest at marine sites with increased wave exposure, decreasing as surface salinity range increased towards Lynher River. Multivariate analysis revealed epibiont community composition to differ between sites, being influenced mainly by the variation of surface salinity range and to a lesser extent wave exposure; of which, observed community shifts and shell dominance were attributed to a species specific physiological tolerance to differential environmental conditions. Although, its clear

that salinity variation and wave exposure both influence epibiont community composition, further investigation including additional explanatory environmental factors in models, is required in order to conclusively explain the observed patterns of epibiont diversity and composition upon shells of gastropods such as *P. vulgata*.

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