

Facing up to climate change: community composition varies with aspect and surface temperature in the rocky intertidal

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John Spicer Validation, Writing – Review and Editing, Supervision

1 **Abstract**

2 Marine rocky intertidal organisms are amongst those most affected by climate change with
3 regional distributional changes observed for many species. Although often ascribed to
4 increased sea surface temperatures, precise assessment of the local habitat conditions
5 underpinning observed and predicted changes in community assembly is lacking. Here we
6 examine how aspect (i.e. north-south orientation) affects intertidal community composition and
7 how rock surface temperatures and stress responses of two dominant grazer species (*Patella*
8 spp.) elucidate emergent differences. We quantified year-round temperature variation and
9 surveyed intertidal community composition on paired natural rock gullies with Equator- (EF)
10 and Pole-facing (PF) surfaces. We also investigated variation in limpet (*Patella* spp.)
11 reproductive phenology and osmotic stress. Average annual temperatures were 0.8°C (1.6°C
12 at low tide) higher, with six-fold more frequent extremes (i.e. > 30°C) on EF than PF surfaces.
13 Intertidal community composition varied with aspect across trophic levels with greater overall
14 species richness, abundance of primary producers and grazers on PF-surfaces, and greater
15 barnacle abundance on EF-surfaces. Although species richness of organisms from different
16 biogeographical origins ('Boreal' or 'Lusitanian') did not vary, the Lusitanian limpet *Patella*
17 *depressa* exhibited earlier reproductive development on EF-surfaces and both limpet species
18 exhibited greater thermal stress on EF-surfaces. We argue that our study system provides a
19 good model for understanding how temperature variation at local scales can affect community
20 composition, as well as ecophysiological and ecological responses to climate change and so
21 better inform and predict regional range shifts over coming decades.

22 **Keywords:** Anthropogenic Climate Change; Community Composition; Extreme Events;
23 Limpets; Physiological Stress; Range Shifts, Rocky Shore; Surface Aspect

24

25

26 **1. Introduction**

27 There is overwhelming evidence that major geographical movements in animal and plant
28 populations are associated with anthropogenic climate change (ACC) (IPCC, 2014) and
29 growing evidence of community structure changes due to more frequent extreme events such
30 as heat waves (e.g. Weitzman et al. 2021). The ecological mechanisms underpinning
31 geographical range shifts remain unclear however, and our rather incomplete understanding
32 may explain why observation and prediction do not always agree (Parmesan and Hanley 2015;
33 Seabra et al. 2015; Parmesan et al. 2018). Many distribution models predicting species range
34 and population shifts are based on coarse-resolution ‘free-air’ temperatures, not considering
35 microhabitat variation on organismal ecophysiology (Seabra et al. 2015). Consequently, while
36 species-specific variation in response to regional temperature and precipitation is doubtless
37 important, it is now recognised that our ability to predict responses to ACC depends on
38 organismal response to environmental conditions at local scales (Gillingham et al. 2012; Barton
39 et al. 2019).

40 Fortunately, there is a long history of research into how habitat complexity shapes ecosystem
41 structure and functioning (MacArthur and MacArthur 1961; Kolar et al. 2019). This is
42 particularly true for the rocky intertidal where shoreline characteristics (tidal range, wave
43 action, surface topography, etc.) greatly affect organism abundance, distribution, and
44 behaviour (Johnson et al. 2008; Bracewell et al. 2018). These same environmental stressors,
45 coupled with daily, cyclical fluctuations in aerial and marine conditions, are one reason why
46 intertidal habitats and organisms are excellent indicators of climate change (see Southward et
47 al. 1995; Mieszkowska et al. 2014 for reviews). The impact of rising temperatures differs
48 however, among and even within intertidal species (Harley et al. 2006). Warm- and cold-
49 adapted species may for example, respond differently to thermal stresses associated with ACC
50 (Firth et al. 2009; Somero 2010) and be respectively more or less vulnerable to thermal maxima

51 and minima at their range edges due to limited ecophysiological acclimation (Somero 2010).
52 Populations at range edges are, therefore, often assumed to be more stressed and sensitive to
53 climate extremes (Guo et al. 2005) than those at the centre of range distribution where
54 individual fitness and population densities are often highest (Brown 1984, but see Sagarin and
55 Gaines, 2002).

56 In the context of gradual climate shifts and increased incidence and impact of extreme weather
57 events (IPCC 2014), the high topographic complexity of the rocky intertidal may become
58 increasingly important in providing organisms with refuge from extreme conditions
59 (Gillingham et al. 2012; Barton et al. 2019). Of the many local topographical and
60 environmental factors operating in the rocky intertidal, aspect (i.e. north-south directionality),
61 is perhaps one of the most important, but least well understood. In marine intertidal, as well as
62 terrestrial habitats there is, however, good reason to predict major variation in environmental
63 conditions, and thus, biological patterns and processes on, Pole-Facing (PF) versus Equator-
64 Facing (EF) surfaces. In a study spanning the Atlantic coast from Scotland to southern Portugal,
65 Seabra et al. (2015) demonstrated that within-site thermal differences between sun-exposed
66 and shaded habitats could be higher than experienced across seasons and 18° latitude, while
67 Denny and Gaines (2007) noted that exposed PF slopes were 10-15°C cooler than adjacent
68 unshaded habitat. Inevitably, sessile organisms exposed to incident radiation on EF slopes are
69 at greater risk of heat and desiccation stress and, thus, mortality, than mobile organisms, which
70 can exploit shaded microhabitats, or occupying nearby PF, shaded slopes (Seabra et al. 2011).

71 Despite these marked differences in environmental conditions, remarkably few studies have
72 systematically explored differences in community assembly on PF and EF surfaces in the
73 temperate rocky intertidal (see Wethey 1983, 1984). Firth et al. (2016) found greater species
74 richness and abundance on PF than EF surfaces in Britain. Five species were encountered more
75 frequently on PF surfaces, including the limpet *Patella vulgata*, while only one algae (*Porphyra*

76 spp.) was more common on EF aspects. Interestingly, in the second part of their study, Firth et
77 al. (2016) found more patellid limpets on EF slopes, a difference driven by a three-fold higher
78 representation of the Lusitanian warm-adapted *P. depressa*. The boreal (cold-adapted) limpet,
79 *P. vulgata* by contrast, showed no difference with aspect. These observations highlight an
80 important issue about the role of aspect in underpinning species distribution. Although those
81 closely-related species have similar upper lethal temperature limits (50% lethal point of 43.3°C
82 and 42.8°C for *P. depressa* and *P. vulgata*, respectively; Southward 1958), their differential
83 biogeographical origins may still influence other facets of their physiology or ecology.

84 Both limpet species have for instance, already adjusted their reproductive phenology
85 differently with increased sea surface temperatures (SSTs). Moore et al. (2011) demonstrated
86 that British populations of *P. depressa* showed advanced gonad development (~10.2
87 days/decade⁻¹ from 1940s-2000s), had a longer reproductive season, and higher proportions of
88 the population were reproductively active. In contrast, gonad development in *P. vulgata* was
89 delayed by ~3.3 days/decade⁻¹, with more reproductive failure years and a reduction in the
90 proportion of reproductively active individuals. Limpets, like all marine molluscs, are
91 osmoconformers; i.e. they do not regulate their extracellular osmolality and so, when
92 immersed, their body fluids are in equilibrium with surrounding seawater (Denny & Gaines
93 2007). The absence of osmotic regulation can place significant physiological strain on
94 individuals under thermal and salinity stress (Williams et al. 2011), although there is some
95 suggestion that this may be ameliorated by shell architecture (Branch and Branch 2018). On
96 this basis, variation in environmental conditions between PF and EF slopes is likely to influence
97 the osmotic concentrations of extracellular and extra-pallial fluids with possible consequences
98 for individual fitness and survival, with concomitant variation in local abundance with aspect.

99 In this study, we first explore how aspect affects patterns of community composition in the
100 temperate, rocky intertidal, specifically testing the following hypotheses:

- 101 (1) Rock surface temperature (averages and extremes) differs according to aspect;
- 102 (2) Community structure (i.e. species richness and relative abundance at taxonomic and
103 guild levels) differs with aspect;
- 104 (3) Distribution and abundance of boreal and Lusitanian species will vary with aspect.
- 105 We then focus on the limpets, *Patella depressa* and *Patella vulgata*, in order to investigate
106 whether variation in reproductive phenology and/or osmotic stress during emersion of these
107 important intertidal grazers contributes to observed (e.g. Firth et al. 2016) or emergent
108 variations in PF versus EF slope distribution.

109 **2. Methods**

110 2.1. Study sites

111 By virtue of its position at the nexus of range distributions for many boreal (cold-adapted) and
112 Lusitanian (warm-adapted) species (Mieszkowska et al. 2005), the seas around the British Isles
113 have witnessed numerous ACC-linked range shifts (Southward et al. 1995; Mieszkowska et al.
114 2014; but see Firth et al. 2021). We selected four natural rocky shores located in the Southwest
115 Peninsula of England. Bude (50°50'12"N, 04°33'25"W) and Croyde (51°08'02"N, 04°14'38"W)
116 on the north coast, and Bantham (50°16'37"N, 03°53'05"W) and South Milton Sands
117 (50°15'14"N, 03°51'43"W) on the south coast. All sites have broadly similar geology (inter-
118 bedded shales and sandstones) with strata tilted at 80°-90° (vertical dip) running perpendicular
119 (an east-west strike) to the shoreline. All sites are characterised by a series of 1-5m high almost-
120 vertical gullies with rock surfaces polar-facing (PF, north) or equator-facing (EF, south)
121 exposed to similar wave exposure. At each location, four gullies were selected because they
122 offered access to long sections of opposite PF and EF vertical rock surfaces at mid-shore height.

123 2.2. Aspect and temperature variation

124 Three data loggers (iButtons DS 1921G#F5, Maxim-Integrated, San Jose, CA, USA) were
125 deployed at mid shore level (i.e. ‘barnacle zone’) in two gullies per site (3 x 2 (aspect) x 2
126 (gullies) x 4 (sites) = 48 loggers total) to record (hourly for 12 months) temperature variation
127 on PF and EF surfaces. Prior to deployment, data loggers were waterproofed with plastic tool
128 dip (Plasti Dip, Plasti Dip International, Blaine, MN, USA) (Roznik and Alford, 2012). Data
129 loggers were attached to the rocks with marine epoxy (Veneziani Subcoat S, Nautimarket srl,
130 Carlino, Italy) and sprayed with waterproof matt grey paint (PlastiKote, Wolvega, Netherland)
131 to provide camouflage and imitate as much as possible the albedo of the natural rock.
132 Deployment started in September 2016, but due to losses at all sites, recording was suspended
133 in February 2017 and resumed in June 2017 with new loggers. This five-month calendar gap
134 was filled by deploying new data loggers during the same period the following year (2018).

135 Mean temperatures (average and maxima and minima), as well as the frequency of extreme
136 temperatures ($>40^{\circ}\text{C}$, $>30^{\circ}\text{C}$, $<0^{\circ}\text{C}$ and $<-10^{\circ}\text{C}$) were quantified on both aspects and compared
137 using a one-way Analysis of Variance (ANOVA) and 2-sample *t*-test respectively, after
138 checking for normality using Anderson-Darling test. We predicted higher mean temperatures
139 on EF than PF surfaces, and more frequent low ($<0^{\circ}\text{C}$ and $<-10^{\circ}\text{C}$) and high extremes ($>40^{\circ}\text{C}$
140 and $>30^{\circ}\text{C}$) on PF and EF surfaces, respectively. To ensure that temperatures were recorded
141 during periods of emersion and immersion, data were extracted one hour either side of low tide
142 (LW) and high tide (HW). Daily means were calculated and compared (one-way ANOVA) for
143 each season (i.e. winter (i.e. 01-Jan to 28-Feb), spring (i.e. 24-May to 20-Jun), summer (i.e.
144 27-Jun to 09-Aug) and autumn (01-Oct to 30-Nov)), but equipment failure resulted in dataset
145 gaps for Croyde (summer) and Bude (winter). We predicted limited variation with aspect
146 during HW, but major differences in daily means during LW, especially in warmer (i.e.
147 summer) conditions. All ANOVA and *t*-test analyses were performed using Minitab v. 17.

148 2.3. Aspect and intertidal community

149 In summer (June/July) 2016 and winter (January/February) 2017, twelve 0.5 x 0.5 m (0.25m²)
150 quadrats were randomly positioned along each of four gullies at each site, such that PF- and
151 EF-quadrats were opposite each other at the same relative shore height (192 quadrats total). All
152 quadrats were located on vertical, flat surfaces, avoiding crevices, pools and other
153 microhabitats. For mobile organisms, we quantified individual abundance; for sessile
154 invertebrates, lichen and algae, we recorded overall percentage cover. In order to sample
155 barnacles, four sub-quadrats (0.03 x 0.03 m) were photographed and all barnacles later
156 identified and counted on a computer using *imageJ* (Version 1.50, National Institute of Health,
157 Bethesda, MD, USA). *Semibalanus balanoides*, *Chthamalus stellatus* and *Chthamalus*
158 *montagui* are the dominant barnacles in the British intertidal (Southward et al. 1995), and as
159 their recruitment period in SW England occurs in spring and in summer respectively (Bowman
160 and Lewis 1986), analysis was undertaken for the winter survey only once cyprids had matured
161 into identifiable adults.

162 To investigate ‘overall community similarity’ between aspect, a non-Metric Multidimensional
163 Scaling (nMDS) was undertaken using the Bray-Curtis index of similarity on 4th-root
164 transformed abundance data of all taxa, to down-weight the influence of abundant species and
165 account for frequent zero counts (Clarke et al. 2014). The contributions of individual species
166 to dissimilarities between the two aspects were determined using similarity percentage analysis
167 (SIMPER). Differences in intertidal community structure and composition were investigated
168 using Permutational Multivariate Analysis of Variance (PERMANOVA). A four-factor design
169 was employed using distinct categories: ‘Aspect’ (fixed, two levels, PF and EF), ‘Coast’ (fixed
170 and orthogonal, two levels – north and south), ‘Season’ (fixed and orthogonal, two levels,
171 summer and winter), and ‘Site’ (random four and nested within ‘Coast’). All multivariate

172 analyses were carried out using the PRIMER 7 (Plymouth Routines in Multivariate Ecological
173 Research) package and the PERMANOVA add-on.

174 All species were subsequently assigned to one of three functional guilds, ‘primary producers’
175 ‘grazers’, ‘filter feeders’; terrestrial lichens and the sole carnivore, *Nucella lapillus*, were
176 considered separately. For these, and selected other species, aspect-linked variation in relative
177 abundance was examined using ANOVA (after checking for normality using Anderson-
178 Darling test).

179 2.4. Aspect and limpet reproductive phenology

180 Limpets were collected from March to October 2018 (*Patella depressa*) and September 2018
181 to February 2019 (*Patella vulgata*) in order to ensure capture of the full reproductive season
182 for both species (Bowman and Lewis 1986). Fifty individuals (25-45 mm diameter) of each
183 species were collected monthly from PF and EF slopes along all four gullies at two sites
184 (Bantham and South Milton Sands). Limpets were frozen (Moore et al. 2011) until processing
185 could be carried out. Dissection and assignation of gonad developmental stage followed Orton
186 et al. (1956) to quantify monthly variation in the proportion of reproductively active/advanced
187 limpets (i.e. stages 4 & 5).

188 2.5. Aspect and limpet water balance

189 Two gullies were selected from each of the four sites, and from each aspect, ten individuals
190 (20-35 mm diameter shell) of *P. depressa* and *P. vulgata* were carefully removed using an
191 oyster knife during spring tides in summer 2017 or 2018. Each site was sampled once.
192 Immediately upon removal, extrapallial water and then haemolymph (1 ml in each case) was
193 extracted from each limpet using a syringe fitted with a 14-gauge (14 G) needle (2.108 ± 0.025
194 diameter, colour coded pale green). Each sample was transferred to a microcentrifuge tube
195 (Eppendorf, vol. = 1.5 ml) and transported in a cool box to the laboratory within 4 hours of

196 harvest. Preliminary experiments with *P. vulgata* showed that freezing samples for one week
197 resulted in an increase in the osmolality of thawed, compared with fresh haemolymph samples
198 ($F_{1,13} = 8.66$, $P = 0.012$; based on 7 individuals) but not pallial water ($F_{1,16} = 0.29$, $P = 0.273$;
199 based on 10 individuals). All samples were therefore, processed on the day of collection.

200 The osmolality of haemolymph and pallial water (mOsm.kg^{-1}) subsamples (vol. = 8 μl) was
201 measured (where possible in duplicate) with a Vapour Pressure Osmometer (5600, Wescor,
202 USA). A measure of osmotic stress was produced by subtracting the values obtained from that
203 of the osmotic concentration of the inshore seawater. The osmometer was calibrated against
204 290 and 1000 mosM kg^{-1} NaCl standards (Wescor). Weather conditions at sampling were
205 categorised as ‘full sun’, ‘partially overcast’, ‘overcast’, or ‘rainy’.

206 As limpet size and shape can influence thermoregulation and osmolality in some species
207 (Williams et al. 2005; Branch and Branch 2018), a standardised size range (20-35 mm shell
208 diameter) was used. A preliminary comparison of shell architecture (following Cabral 2007)
209 confirmed that *P. vulgata* had greater shell surface area ($F_{1,518} = 36.63$, $P < 0.001$) and volume
210 (due to taller cone) ($F_{1,518} = 101$, $P < 0.001$) than *P. depressa* (Evans 1947; Bowman 1981). In
211 addition, *P. depressa* had greater shell volume on EF slopes ($F_{1,258} = 39.70$, $P < 0.001$), while
212 *P. vulgata* had a more conical shell on PF slopes ($F_{1,259} = 83.32$, $P < 0.001$). Both features
213 increase extravisceral space and may reduce the effects of desiccation on extrapallial water and
214 haemolymph osmolality (Marshall and McQuaid 1992).

215 **3. Results**

216 **3.1. Aspect and temperature variations**

217 Annual mean temperature was 0.9°C warmer on EF than PF surfaces (Appendix), a difference
218 that increased further (1.6°C) when we considered temperatures experienced during low tide

219 only (Table 1). Consistent seasonal differences were also noted (Appendix), with average
220 temperature 1.0°C, 0.9°C, and 0.4°C warmer on the EF than PF surfaces in autumn, both winter
221 and summer, and spring respectively.

222 Variation in temperature extremes also differed with aspect. Mean annual maxima across all
223 sites was 4.2°C warmer on EF aspects and the frequency of temperatures >30°C was on
224 average, six-fold higher than on PF surfaces (Table 1). Although the number of occasions
225 where temperatures fell below 0°C were similar for both aspects, all five occasions where
226 temperature exceeded 40°C were on EF surfaces. At the same time of day, organisms living on
227 different aspects in the same gully experienced very large temperature differences. For
228 instance, at Croyde on the 27-Jun-2018 at 14:20, EF-slopes experienced 42.5°C whilst the
229 corresponding PF surface was only 22.5°C.

230

231 **Table 1** Summary of daily average temperatures (\pm SE) during low and high tide, (min/max)
 232 extreme temperatures, daily average minima and maxima (\pm SE), and the average frequency of
 233 hot ($>40^{\circ}\text{C}$ and $>30^{\circ}\text{C}$) and cold ($<0^{\circ}\text{C}$ and $<-10^{\circ}\text{C}$) extreme temperature (\pm SE), on Pole-
 234 facing and Equator-facing surfaces. All measurements were collected hourly from the mid-
 235 intertidal at four sites in SW England using data loggers deployed from September 2016 to
 236 August 2017. Due to data loss between February and June 2017, spring values were
 237 supplemented with data collected from the same period in 2018. Significant differences
 238 between aspect ($P>0.05$) are denoted in bold.

Temperature conditions		Pole facing	Equator facing	ANOVA Results
Daily average	at Low tide	11.8°C \pm 0.1	13.0°C \pm 0.1	$F_{1,657} = 19.6 P < 0.001$
	at High tide	13.2°C \pm 0.1	13.3°C \pm 0.1	$F_{1,449} = 0.37 P = 0.544$
Minima temperatures	Extreme	-3°C	-3.5°C	$F_{1,679} = 0.04 P = 0.833$
	Daily average	9.3°C \pm 0.1	9.2°C \pm 0.1	
Maxima temperatures	Extreme	37.5°C	42.5°C	$F_{1,679} = 95.5 P < 0.001$
	Daily average	15.8°C \pm 0.2	20.0°C \pm 0.2	
Frequency of extreme temperatures	$> 40^{\circ}\text{C}$	0	1.5 \pm 1.5	$\chi^2 = 152.9_{(1)} P < 0.001$ $\chi^2 = 0.089_{(1)} P = 0.598$
	$> 30^{\circ}\text{C}$	10 \pm 6	63 \pm 20	
	$< 0^{\circ}\text{C}$	22 \pm 10	23 \pm 7	
	$< -10^{\circ}\text{C}$	0	0	

239

240 3.2. Aspect and the intertidal community

241 Overall community composition on PF aspects was significantly different from those observed
 242 on EF ('Aspect' effect in PERMANOVA, Table 2; and in nMDS plot, Figure 1a). Although
 243 there was a significant 'Site (Coast)' effect (Table 2), this most likely reflected the higher
 244 abundance of the polychaete *Sabellaria alveolata* (and species associated with this important
 245 biogenic habitat; e.g. *Eulalia viridis*, *Lineus ruber*, *Onchidella celtica*, and some algae), on PF
 246 surfaces at Bude and was unlikely to compromise the strong 'Aspect' effect identified in our

247 analysis. As the overall community assemblage did not vary between ‘Season’ and ‘Coast’
 248 (Table 2), unless stated, description of results applies to both winter and summer assemblages
 249 along both coasts.

250 **Table 2** PERMANOVA results comparing rocky intertidal community composition on
 251 poleward-and Equator-facing aspects in gullies (N=4) at four locations in SW England. Factors
 252 considered were ‘Aspect’ (PF, EF), ‘Season’ (winter, summer), ‘Coast’ (South, North), and
 253 ‘Site’ (two sites nested in ‘Coast’) and related interaction terms. Significant ($P < 0.05$) values
 254 are denoted by bold type.

Source	df	MS	Pseudo-F	P
Season	1	994.51	12.795	0.067
Coast	1	386.52	1.425	0.186
Aspect	7	1738.40	10.321	0.001
Site(Coast)	2	416.71	2.035	0.024
Season x Coast	1	129.68	0.807	0.488
Season x Aspect	6	183.77	2.430	0.137
Coast x Aspect	2	246.04	1.355	0.371
Season x Site(Coast)	2	59.15	0.289	0.991
Aspect x Site(Coast)	2	161.81	0.790	0.683
Season x Coast x Aspect	1	67.13	0.593	0.642
Season x Aspect x Site(Coast)	2	76.23	0.372	0.952
Residuals	31	204.81		

256
 257 In total 45 species were recorded across all locations. Species richness was higher on PF than
 258 EF surfaces during the summer ($F_{1,188} = 71.81, P < 0.001$; 45 vs. 30 species) and winter surveys
 259 ($F_{1,176} = 50.55, P < 0.001$; 42 vs. 24 species). Four species of primary producers, such as
 260 *Plumaria plumosa* and *Leathesia marina* were present on PF surfaces only during both seasons
 261 but at low abundance and limited to only one or two sites. However, SIMPER revealed that the
 262 relative abundance of 14 more common species accounted for over 72% of the observed
 263 dissimilarity according to aspect (i.e. ‘Aspect’ accounts for just under 39% of community
 264 dissimilarity) (Table 3). Abundance of primary producers and grazers was significantly higher

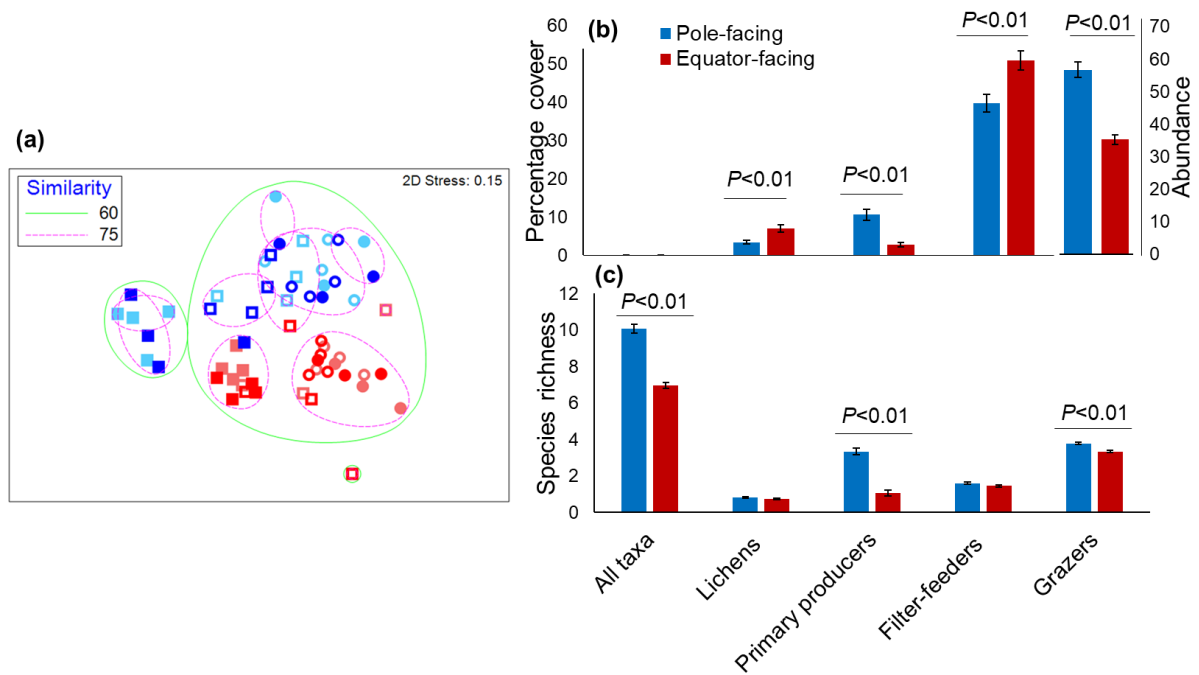
265 on PF than EF, whilst the opposite was true for lichens and filter feeders (Figure 1b).
 266 Additionally, the mobile predator *Nucella lapillus* was more abundant on PF-slopes ($F_{1,302} =$
 267 27.05, $P = 0.031$), which likely contributed to more than five times more eggs found on that
 268 aspect (89 on PF vs. 16 on EF surfaces). Taxon richness of ‘all taxa’, ‘primary producers’, and
 269 ‘grazers’ were higher on PF surfaces, but there was no difference for lichens or ‘filter feeders’
 270 (Figure 1c).

271 **Table 3** SIMPER analysis showing ranking of intertidal species according to their contribution
 272 to the overall 38.6% dissimilarity associated with aspect, with respect to average abundance
 273 (Av. Abund), average dissimilarity (Av. Diss), quotient of dissimilarity and standard deviation
 274 (Diss/SD), % contribution to differences (Contrib %) and cumulative percentage contribution
 275 to differences (Cum %). Bold font indicates the highest abundance of that species/group on the
 276 Equator-facing (EF) and Pole-facing PF) aspect. Note that average abundance is not necessarily
 277 statistically different, but considered sufficiently divergent to play an important role in
 278 community dissimilarity.

Species	PF	EF	Av. Diss	Diss/SD	Contrib %	Cum. %
	Group Av. Abund	Group Av. Abund				
<i>Lichina pygmaea</i>	0.07	0.80	3.08	1.1	7.98	7.98
<i>Verrucaria mucosa</i>	0.88	0.24	3.05	1.38	7.9	15.88
<i>Lithophyllum incrustans</i>	0.83	0.20	2.63	1.64	6.82	22.7
<i>Osmundea pinnatifida</i>	0.67	0.06	2.33	1.6	6.05	28.74
All barnacles	2.32	2.62	2.33	1.31	6.04	34.78
<i>Fucus sp.</i>	0.34	0.64	2.14	1.31	5.56	40.34
<i>Mytilus edulis</i>	0.37	0.41	2.06	1.01	5.33	45.67
<i>Patella vulgata</i>	1.98	1.68	1.95	1.35	5.06	50.73
<i>Sabellaria alveolata</i>	0.51	0.07	1.91	0.64	4.94	55.67
Unidentified juvenile <i>Patella sp.</i>	1.42	1.24	1.88	1.1	4.88	60.55
<i>Littorina saxatilis</i>	0.34	0.24	1.62	0.96	4.2	64.75
<i>Patella depressa</i>	2.12	1.93	1.58	1.35	4.1	68.85
<i>Actinia equina</i>	0.23	0.30	1.4	1.04	3.63	72.48

279

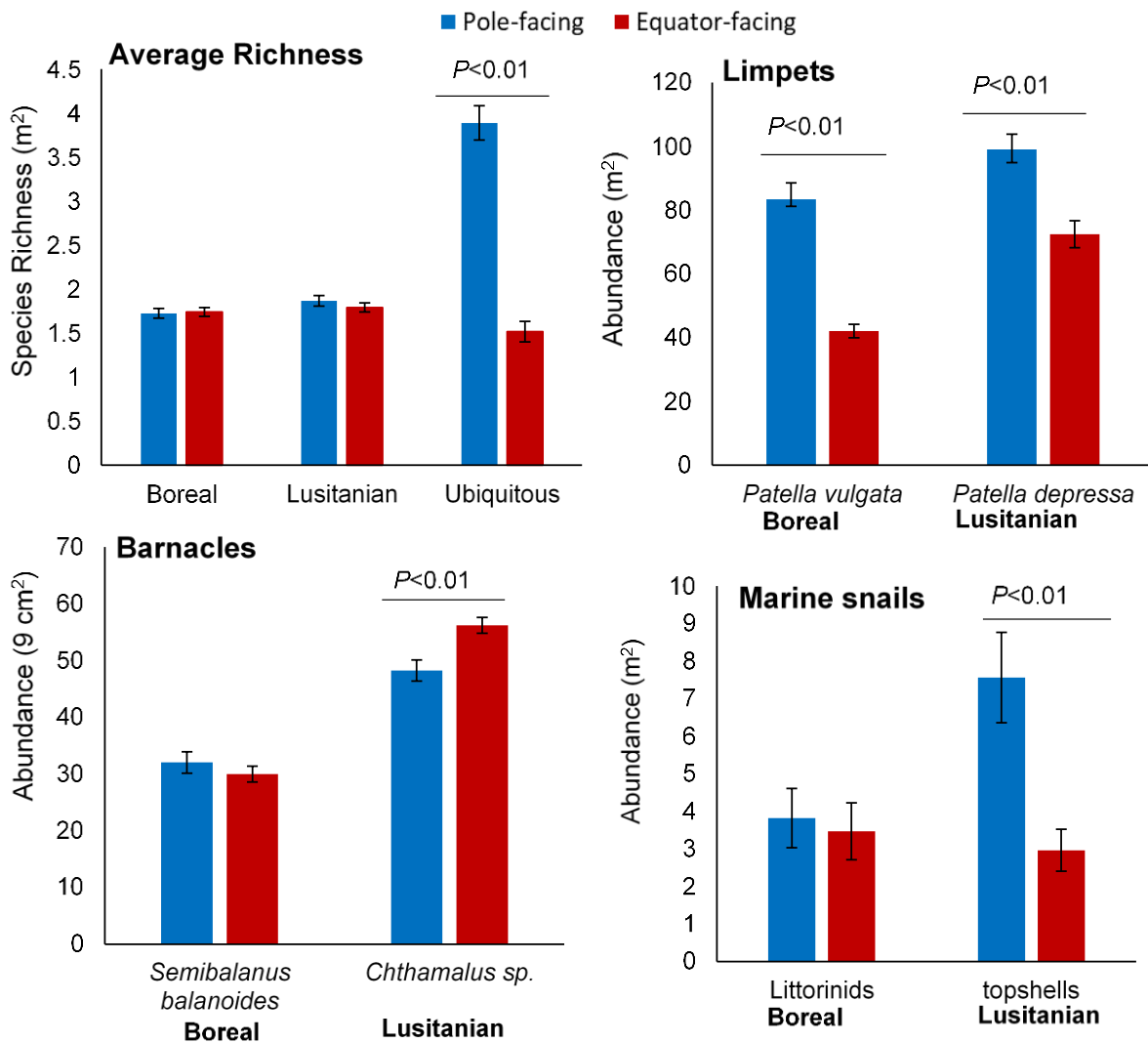
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281
 282 **Figure 1** Community, species richness and abundance differences with aspect. (a) Non-metric
 283 MDS ordination of Bray-Curtis resemblances between multivariate community compositions
 284 (Pole-Facing, in blue; Equator-Facing, in red). Each symbol represents the intertidal
 285 community on one side of one gully (aspect) at one location during either the summer (lighter
 286 colours; i.e. light blue and light red) or winter (darker colours; i.e. dark blue and dark red)
 287 sampling. Community composition was sampled from four sites across two coasts of the SW
 288 Peninsula of England over two seasons. The north coast, represented by the square symbol,
 289 includes the sites Croyde (open square) and Bude (full square), while the south coast of the SW
 290 England (circle symbol), includes the sites South Milton Sands (open circle) and Bantham (full
 291 circle). (b) Mean percentage cover (\pm SE) of sessile organisms and mean abundance (\pm SE) of
 292 mobile organisms. (c) species richness of the main functional and taxonomic groups, according
 293 to aspect.

294
 295 Although neither ‘Boreal’ nor ‘Lusitanian’ taxon richness differed with aspect, it was notable
 296 that the Lusitanian limpet (*Patella depressa*) and topshell (*Steromphala umbilicalis*), and the
 297 Boreal limpet (*Patella vulgata*) were more abundant on PF surfaces (Figure 2). Lusitanian
 298 barnacles (*Chthamalus* spp.) were the only taxon more abundant on EF surfaces.

299



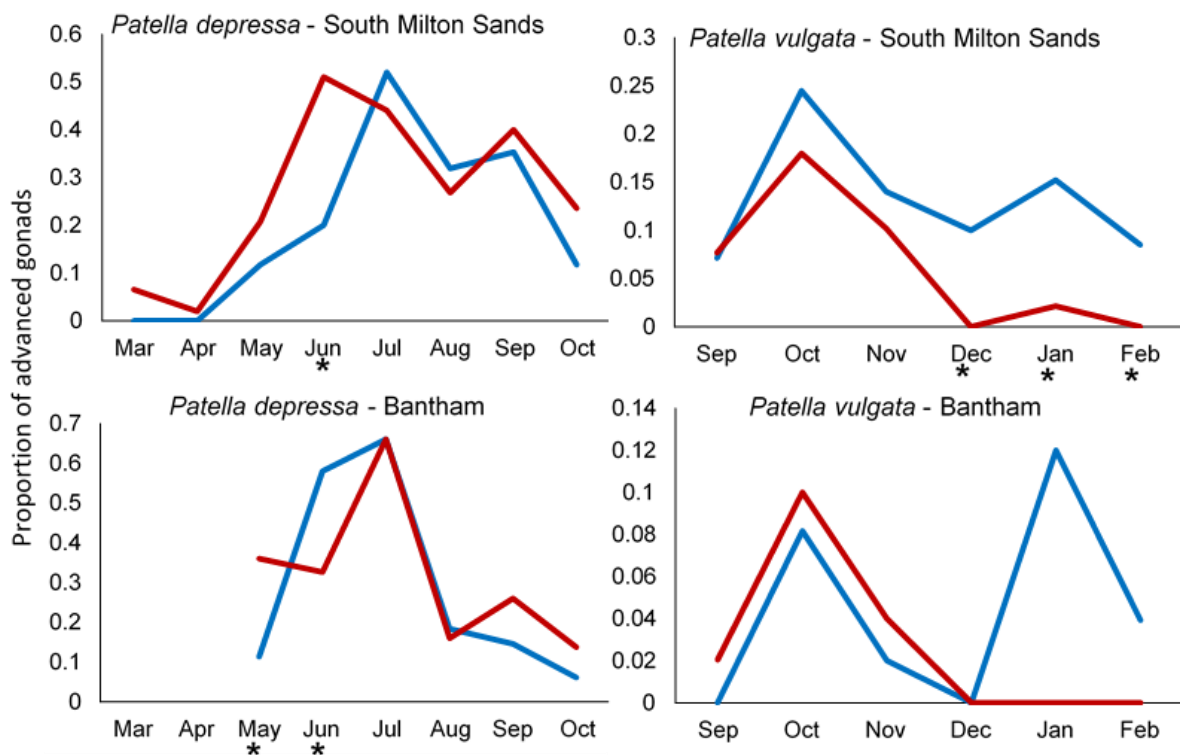
300 **Figure 2** Effects aspect on mean species richness (\pm SE) of intertidal ‘Boreal’, ‘Lusitanian’
 301 and ‘Ubiquitous’ species; mean abundance (\pm SE) of limpets (*Patella depressa* and *Patella*
 302 *vulgata*), barnacles (*Chthamalus sp.* and *Semibalanus balanoides*) and marine snails
 303 (‘Topshells’ and Littorinids). Abundance data were obtained from equator- and poleward-
 304 facing slopes from gullies at four different locations in SW England during summer and winter.
 305 *Chthamalus montagui* and *Chthamalus stellatus* were combined as *Chthamalus sp.*
 306

307

308 3.3. Aspect and limpet reproductive phenology

309 Reproduction in *Patella depressa* started earlier on EF surfaces at both sites (Figure 3) with
 310 evidence of advanced gonad maturation even before sampling started. Depending on aspect, *P.*
 311 *depressa* exhibited two distinct reproductive peaks in May and September on EF-, and July and

312 September on PF-surfaces. At Bantham, gonad maturity peaked on EF surfaces in July and
 313 September, but once only in July on PF surfaces (Figure 3). This second peak was almost twice
 314 as high at South Milton Sands than Bantham, before advanced gonad maturity began to decline
 315 and even out for both sites and aspects. Fewer *P. vulgata* individuals exhibited advanced gonad
 316 development than *P. depressa*. Indeed, maximum maturity was only 10% and 24% (in
 317 comparison to 50% and 60% for *P. depressa*) at Bantham and South Milton Sands respectively.



318

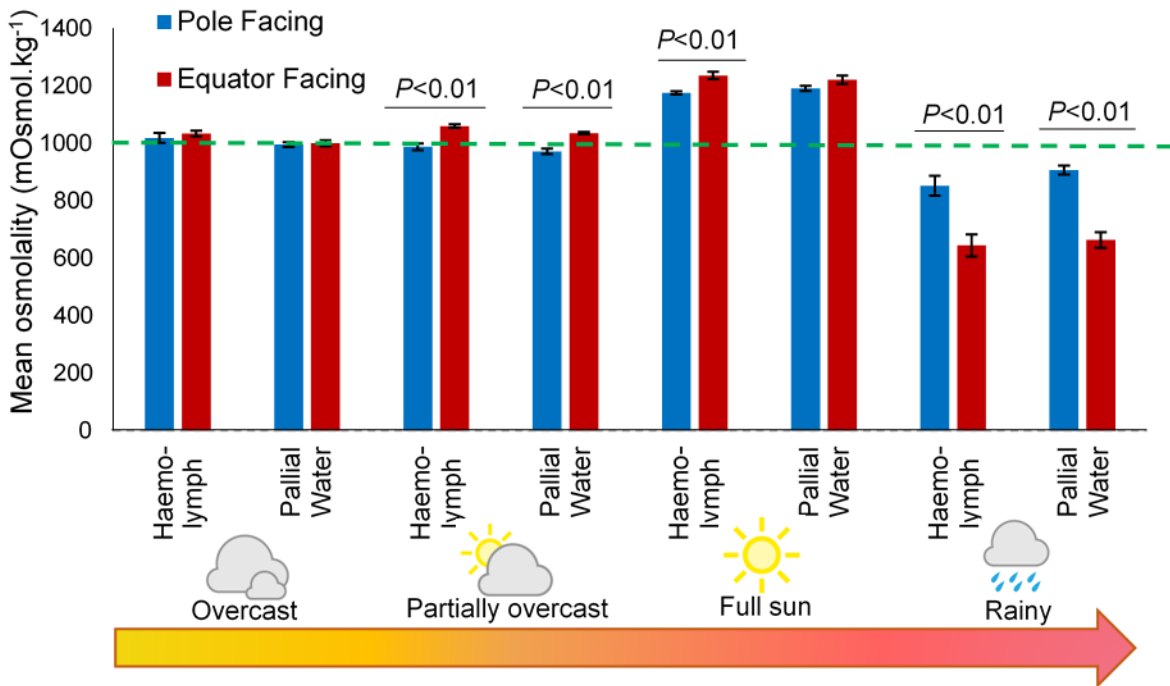
319 **Figure 3** The effect of aspect on the proportion of advanced stage gonads observed for *Patella*
 320 *depressa*, and *Patella vulgata* at two sites (South Milton Sands and Bantham) from SW
 321 England. Limpets were collected from Polar (blue) and Equator (red) facing surfaces during
 322 their respective reproductive season. Note – missing data for *P. depressa* from Bantham for
 323 March & April. Symbol * indicates a significant difference ($P \leq 0.05$) between aspect within
 324 the same month.

325

326 Both peaks were observed on PF surfaces with two small peaks in October and January at both
327 sites (Figure 3). Nonetheless, the second peak at Bantham was confined to PF surfaces only,
328 while at South Milton Sands it was markedly higher on PF surfaces (15% vs. 2% EF) (Figure
329 3).

330 3.4. Aspect and limpet water balance

331 As there was no significant species effect for either pallial water or haemolymph osmolality
332 ($F_{1,352} = 0.05$, $P = 0.823$ and $F_{1,355} = 0.60$, $P = 0.439$, respectively), data for both species were
333 pooled for subsequent analysis (Figure 4). During overcast conditions there was no significant
334 effect of aspect on either pallial water or haemolymph osmolality ($F_{1,79} = 0.13$, $P = 0.725$ and
335 $F_{1,80} = 0.59$, $P = 0.444$; respectively). There was however a significant ‘Aspect’ effect under
336 each of the remaining three climatic conditions: osmolality increased when it was sunny and
337 decreased when it was raining and to a greater extent in EF compared with PF individuals. The
338 same pattern was evident for extra-pallial water, except that there was no difference in ‘full
339 sun’.



341

342 **Figure 4** The effect of intertidal aspect (blue, Pole-Facing; and red, Equator-Facing) on mean
 343 osmolality (\pm SE) of limpet (*Patella vulgata* and *Patella depressa*) haemolymph and pallial
 344 water under four different climatic conditions (full sun, partially overcast, overcast and rainy).
 345 Limpets were sampled from four sites located in SW Peninsula of England during summer
 346 2017 and 2018, The dashed green line represents the inshore seawater osmolality (1000
 347 mOsmol.kg⁻¹), ‘baseline’ osmolality for an unstressed limpet immersed in sea water (Denny
 348 and Gaines, 2007).

349

350 4. Discussion

351 This is the first study to explore the association between local scale variation in aspect,
 352 temperature, community assembly, organismal physiology and reproductive phenology in the
 353 intertidal. Average daily temperatures for PF slopes across all four sites were 0.9°C cooler than
 354 corresponding EF surfaces, and when we exclude the buffering effect of immersion, the
 355 difference was 1.6°C. Given that, extreme weather events are potentially more critical to

356 understanding how organisms to respond to ACC than long-term changes in average conditions
357 (Wernberg et al. 2012; Parmesan and Hanley 2015) it is particularly notable that we also
358 observed marked variation in temperature extremes. Maximum temperatures in excess of 40°C
359 were only recorded on EF surfaces on five occasions, conditions approaching the upper thermal
360 tolerance for many intertidal species (Southward 1958), and extreme temperatures (i.e. above
361 30°C) occurred with considerably (i.e. six-fold) greater frequency compared to PF surfaces.

362 Although many studies focus on average SSTs (e.g. Piñeiro-Corbeira et al. 2018; Wilson et al.
363 2019), our study raises an important point about tracking variation in both air (during low tide)
364 and water temperatures (during high tide) (see Bates et al. 2018), as by definition, intertidal
365 organisms spend considerable time out of the water. Indeed, as Burrows et al. (2011) point out,
366 the median rate of warming since 1960 is more than three times greater on land than sea due to
367 greater latitudinal and topographical temperature differences on the former than the latter
368 (where large-scale currents moderate small-scale variability in SSTs). Moreover, a number of
369 studies have evidenced wide scale mortality events in intertidal organisms following short-term
370 exposure to extremely low or high air temperatures during low water (Crisp 1964; Wetthey et
371 al. 2011; Firth et al. 2021).

372 Despite its potential importance for algal distribution and/or growth (Blockley and Chapman
373 2006) and larval recruitment for some marine invertebrates (Miller and Etter 2008), we
374 recognise that we did not quantify light intensity. Nonetheless, in evidencing greater abundance
375 of ‘primary producers’ on PF-surfaces, our data strongly suggest that primary productivity was
376 not light limited on either aspect. Consequently, ecological interactions involving higher
377 trophic levels (e.g. the elevated abundance of *Chthamalus* on EF-surfaces but concomitant
378 preference their main predator, *Nucella lapillus*, had for PF-slopes) would parsimoniously
379 appear to be most strongly linked to the considerable variation in mean daily, and frequency of

380 extreme, temperatures between aspects. Moreover, desiccation and thermal stress are known
381 to have greater impact on species ecophysiology and distribution than light (Miller et al 2009;
382 Martone et al 2010; Chapperon et al 2016), while the process of barnacle settlement
383 (*Semibalanus* and *Chthamalus*) occurs independently from direct solar radiation (Wetthey
384 1986).

385 By demonstrating considerable variation in average and extreme temperature conditions over
386 a distance of just a few meters, we highlight the excellent potential the intertidal has for our
387 understanding of ACC on community pattern and process. Other than differences in incident
388 solar radiation, we see no *a priori* reason to expect other important physico-chemical factors
389 to vary across short distances as they do on land (e.g. soil nutrient status, moisture, etc. – see
390 Jasińska et al. 2019). Moreover, because the confounding influence of restricted propagule
391 movement (the majority of intertidal organisms disperse and recruit via the plankton) is
392 negligible, intertidal rocky gullies may offer a more robust ‘natural laboratory’ than, for
393 example, the ‘Evolution Canyon’ (EC) microscale model (Nevo 2012). Despite the proximity
394 (average 200m apart) of north- and south-facing aspects in the EC microscale model, very
395 different ecosystems have developed on opposing slopes. Undertaking manipulative
396 experiments on key ecological processes like recruitment, exploitation, and competition is
397 therefore considerably more feasible in marine rocky intertidal gullies where environmental
398 ‘initial conditions’ are more similar, and logistically easier to control or even reset.

399 The fact that we observed significant variation in physiology, reproductive phenology and
400 community patterns on PF and EF surfaces suggests that experiments focussed on associated
401 ecological processes is an important exercise. The role of putative interactions, alongside the
402 direct effect of temperature, highlights the importance of climate-linked variation in
403 distribution of several keystone organisms (Helmuth et al. 2006; Harley 2011). Like Firth et al.

404 (2016), we recorded more carnivorous whelks (*Nucella lapillus*), and grazers (littorinids and
405 the limpet *Patella vulgata*) on PF aspects; species known to play a major structuring role in
406 temperate rocky intertidal ecosystems (O'Connor and Crowe 2005; White et al. 2020). Cooler
407 PF slopes supported overall higher species richness and abundance, particularly for primary
408 producers and grazers, strongly suggesting that higher temperatures (and particularly the
409 incidence of extremes) experienced on EF slopes are likely underpinning these patterns by
410 driving mobile species to seek refuge in cooler habitats. Moreover, the abundance of
411 macroalgae on PF-slopes would likely reinforce local differences between aspects as their
412 canopies form dense, cool, moisture-retaining, conditions and provide sheltered microhabitats
413 for other organisms (Schmidt and Scheibling 2007).

414 Interestingly, there was limited support for the hypothesis that the distribution of organisms
415 from different biogeographical origins differs with aspect; only ubiquitous species showed any
416 consistent pattern (i.e. more species on PF slopes). We did however observe more Lusitanian
417 barnacles (*Chthamalus* spp.) on EF-slopes, most likely reflecting the fact that *Chthamalus* are
418 more tolerant of warmer, but less tolerant of colder, temperatures than their 'northern'
419 competitor, *Semibalanus balanoides* (Wetthey 1983). Although this observation corroborates
420 recent patterns of barnacle range shifts along UK shores (Southward 1958; Mieszkowska et al.
421 2005; Wetthey et al. 2011), we cannot, exclude the possibility that increased whelk abundance
422 and predation of *Chthamalus* spp., and/or relaxation of competition from *S. balanoides* also
423 contributes to emergent differences between PF and EF aspects.

424 In our most marked contrast with Firth et al. (2016), abundance of the Lusitanian limpet, *P.*
425 *depressa*, did not vary between PF and EF slopes (including one of their survey sites from
426 2003). This difference may simply represent stochastic, spatio-temporal, variation in
427 recruitment patterns and species turnover (Hawkins et al. 2008). It is an intriguing possibility

428 however, that 13 years after the original survey at Croyde, climate shift has facilitated the
429 spread of *P. depressa* onto PF slopes and the predicted replacement of *P. vulgata* by *P.*
430 *depressa* in UK waters (Hawkins et al. 2008; Firth et al. 2009). Not least because our data point
431 to major differences in mean and extreme temperatures on PF- and EF-slopes, range shifts, and
432 interactions between, these limpets may be linked to variation in reproductive behaviours and
433 ecophysiological responses. Our observation shows that *P. depressa* had delayed or reduced
434 gonad maturity on PF-slopes not only corroborates Moore et al. (2011), it also highlights how
435 aspect might facilitate range movements of intertidal organisms via an influence on
436 reproduction. Some terrestrial butterflies display higher oviposition, larval density, eclosion
437 body temperature and growth on EF slopes and these responses presumably explain therefore
438 why EF-slopes act as nuclei for observed range expansions in Lepidoptera (Weiss et al. 1988;
439 Bennie et al. 2013). It is also perhaps indicative of how climate change moderates distributional
440 shifts of intertidal organisms that the second reproductive spike in a species (*P. vulgata*) near
441 its trailing (southern) range edge was limited to PF-slopes.

442 That the osmolality of the exosomatic and extracellular fluids of limpets increased when it was
443 sunny (due to desiccation) and decreased when it was raining (due to dilution) is perhaps not
444 surprising; similar responses are apparent in other osmoconformers (Morritt et al. 2007; Suda
445 et al. 2015). What is noteworthy is that the desiccation-related increase and dilution-related
446 decrease in fluid osmolalities was greater in EF compared with PF individuals. Fraser et al.
447 (2016) found no difference in haemolymph osmolality between limpets in different
448 orientations, although they did not investigate different aspects. Also surprising was the
449 absence of a species-specific difference in osmotic response; given the different shell
450 architectures of *P. vulgata* and *P. depressa*, a difference might have been predicted (see
451 Williams et al. 2005; Branch and Branch 2018). Nonetheless, though similar in morphology,
452 EF limpets experienced greater osmotic stress than their PF counterparts. Greater exposure to

453 incident radiation on EF slopes imposes greater risk of heat and desiccation stress, but the
454 physiological and mechanistic basis of this difference remains unclear.

455 Taken together, our results indicate that the distribution of key intertidal species not only differs
456 markedly with aspect, but that variation in surface aspect at a local scale provides a relevant
457 field-system to study the effects of temperature variations on species assemblages, ecological
458 processes, phenological shifts and physiological stress. Moreover, by elucidating ‘local-scale’,
459 interactive effects, we might better predict organismal and ecosystem-level responses to ACC
460 (Gillingham et al. 2012; Barton et al. 2019). Notwithstanding observed variation in limpet
461 reproductive phenology, we cannot ascribe variation in the distributions of cold- and warm-
462 adapted organisms to temperature differences between EF and PF-aspects. Nonetheless, for a
463 region where numerous ACC-linked range shifts have already occurred (Southward et al. 1995;
464 Mieszkowska et al. 2005; Firth et al., 2009), this possibility seems likely and worthy of further
465 investigation.

466 **Acknowledgements**

467 The authors thank an anonymous referee for their comments on an earlier draft of this MS,
468 Professor Camille Parmesan for guidance with project design, and Dr Nick Berkley, Dr Nicola
469 Steer Mansfield, Dr Katie O’Shaughnessy, Maria Teresa Guerra, Agapery Pattinasarany
470 Induara England, Stacey Gilbert, Clara Long, Laura Millet and Jane Akerman for technical
471 assistance. The project was funded by a University of Plymouth Graduate studentship award
472 to AA

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- 652

Appendix

Daily mean temperature (\pm SE) recorded during periods of the winter (01/01 to 28/02), spring (24/05 to 20/06), summer (27/06 to 9/08) and autumn (01/10 to 30/11), excluding gaps in the data, on north and south facing gullies, on the mid-intertidal of four locations of the SW Peninsula of England – Bantham and SMS (South Milton Sands) on the south coast, and Croyde and Bude, on the north coast. North- and south-facing temperature were recorded on the same gully. Due to gaps in the data set, mean for some seasons/aspect was not possible to do and the empty cells were greyed. Significant difference in temperature ($P < 0.05$) between aspect is in bold.

		Winter		Spring		Summer		Autumn		All seasons	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing
South coast	Bantham	7.6 \pm 0.30	8.2 \pm 0.30	15.9 \pm 0.16	16.0 \pm 0.20	17.0 \pm 0.18	18.0 \pm 0.26	11.6 \pm 0.27	12.6 \pm 0.36	12.2 \pm 0.30	13.0 \pm 0.31
		$F_{1,117} = 2.06, P = 0.154$		$F_{1,54} = 0.02, P = 0.886$		$F_{1,86} = 8.92, P = 0.004$		$F_{1,120} = 4.78, P = 0.031$		$F_{1,382} = 2.73, P = 0.099$	
South coast	SMS	6.9 \pm 0.33	8.8 \pm 0.22	16.8 \pm 0.23	17.0 \pm 0.28	16.6 \pm 0.03	17.8 \pm 0.21	11.9 \pm 0.35	13.2 \pm 0.33	12.2 \pm 0.32	13.5 \pm 0.30
		$F_{1,114} = 20.62, P < 0.001$		$F_{1,54} = 0.28, P = 0.602$		$F_{1,86} = 30.59, P < 0.001$		$F_{1,120} = 6.72, P = 0.011$		$F_{1,380} = 8.33, P = 0.004$	
North coast	Bude		8.0 \pm 0.20	15.2 \pm 0.10	15.3 \pm 0.16	17.0 \pm 0.11	17.6 \pm 0.15	13.0 \pm 0.26	13.1 \pm 0.18	15.0 \pm 0.07	15.1 \pm 0.02
				$F_{1,54} = 0.55, P = 0.460$		$F_{1,86} = 9.09, P = 0.003$		$F_{1,100} = 0.48, P = 0.490$		$F_{1,244} = 0.13, P = 0.720$	
North coast	Croyde	7.4 \pm 0.15	7.8 \pm 0.19	15.6 \pm 0.11	16.7 \pm 0.23			12.0 \pm 0.21	13.0 \pm 0.29	10.9 \pm 0.28	11.7 \pm 0.32
		$F_{1,111} = 2.30, P = 0.132$		$F_{1,54} = 20.77, P < 0.001$				$F_{1,121} = 8.19, P = 0.005$		$F_{1,289} = 2.92, P = 0.089$	
All sites		7.3 \pm 0.16	8.2 \pm 0.14	16.0 \pm 0.09	16.4 \pm 0.12	16.9 \pm 0.08	17.8 \pm 0.12	11.9 \pm 0.14	12.9 \pm 0.15	12.6 \pm 0.16	13.5 \pm 0.15
		$F_{1,345} = 18.87, P < 0.001$		$F_{1,278} = 5.17, P = 0.024$		$F_{1,262} = 40.89, P = 0.000$		$F_{1,448} = 22.18, P < 0.001$		$F_{1,1339} = 12.75, P < 0.001$	

