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Performance of a warm-water limpet species towards its poleward range edge compared to a colder-water congener

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ABSTRACT: The demography and individual performance of species at their range edges provide important insight into how climate warming is impacting species distributions. The boreal limpet *Patella vulgata* and the Lusitanian limpet *P. depressa* have overlapping geographic ranges and local distributions in Britain. We measured individual performance at the 2 leading edges of *P. depressa* distribution (North Wales and South/South-east England) and in non-range edge populations in South-west England. Individuals of *P. depressa* towards both leading edges were expected to have reduced growth rates and higher mortality rates when compared with non-range edge populations. Conversely, *P. vulgata* was expected to have equivalent performance across regions, coinciding with the centre of its range. Tagged individuals did not show between-species differences in growth and mortality over a 12 mo period. Nonetheless, individual growth rates and population mortality rates of both *Patella* species were higher towards the range edge of *P. depressa* in South/South-east England, when compared with populations at its poleward edge and those in South-west England. Further analysis showed that growth and mortality rates were higher in denser populations for both *P. depressa* and *P. vulgata*, with equivalent site-specific performance patterns for both species in all regions. Thus, performance patterns of *P. depressa* reflected local factors in the same way as *P. vulgata*, overriding patterns of declining performance expected towards species borders. Comparisons between key congeneric species and their unexpected patterns of performance across their ranges provide insights into processes setting species boundaries and thereby their responses to climate change.

KEY WORDS: Climate change · Range edges · Leading edge · Intertidal ecology · *Patella* spp.

1. INTRODUCTION

There has been a resurgence of interest in biogeography prompted by recent rapid global warming that has driven shifts in ranges of species on land (Parmesan & Yohe 2003), in freshwaters (Parmesan 2006) and in the oceans (Poloczanska et al. 2016). In the marine environment, wide-ranging evidence shows that plankton (Beaugrand et al. 2002), fish (Perry et al. 2005) and benthic invertebrates are all responding to climate change (Helmuth et al. 2006a). Intertidal invertebrates, which are common and easy

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to access, have been a particular focus of attention to elucidate the mechanistic basis by which geographic distributions of species are shifting as environments change (see Gilman 2006, Herbert et al. 2009, Moore et al. 2011 for details). Individuals are performing better than previously at their poleward range edges, showing faster growth rates (Herbert et al. 2009) and greater reproductive output, including extended breeding seasons (Moore et al. 2011) and hence greater and more consistent larval recruitment to populations (Poloczanska et al. 2008). The result is increased abundance in leading-edge populations (Southward et al. 2005, Mieszkowska et al. 2007), which has driven poleward range expansions in many (Mieszkowska et al. 2006) but not every species (Herbert et al. 2009) in all places (Hawkins et al. 2009, 2019).

Demographic attributes of populations, determined by the performance of individuals, play a major role in establishing species ranges (Guo et al. 2005), being to a large extent ultimately influenced by latitudinal patterns in temperature (Pironon et al. 2017). Performance of individuals and populations of a species may, however, be affected by mesoscale processes, such as upwelling (Lima et al. 2006), timing of tides (Helmuth et al. 2002) and mosaics of local environmental conditions (Helmuth et al. 2006b, Seabra et al. 2016), which may not conform to the expected latitudinal gradient (Seabra et al. 2015, Lima et al. 2016). Thus, the abundance and structure of populations within the geographic range of a species reflect the interacting influences of limiting physical factors and dispersal as well as intrinsic density-dependent processes (Brown et al. 1996). Peripheral populations generally tend to be spatially more fragmented (Sexton et al. 2009), with lower abundance of individuals as well as lower intra-population genetic diversity (Pironon et al. 2017) when compared with non-range-edge populations. Hence, the study of range-edge populations can enable the forecast (Sexton et al. 2009) and prediction of future population trajectories (Poloczanska et al. 2008) in the context of rapid climate change.

Ranges, and their limits, are highly species-specific and determined by multiple factors (Hawkins et al. 2009, 2019). For instance, larval recruitment is influenced by variable transport regimes (Keith et al. 2011) and tidal fronts (Herbert et al. 2009), but also varies depending on specific life-history traits (e.g. fecundity, direct or larval development, pelagic larval duration; Byers & Pringle 2006). Such variation in recruitment of new individuals to local populations influences local processes such as density-dependent competition and mortality (e.g. Jenkins et al. 2008, Pironon et al. 2017). Range-edge populations tend to have limited or variable recruitment (Lewis et al. 1982, Kendall & Lewis 1986); therefore, intraspecific competition may be less intense (Guo et al. 2005), leading to faster growth of individuals than in core populations (Lewis et al. 1982). Hence, population dynamics at species boundaries may be more variable due to the complex interaction between stressful environmental conditions, increasing climate variability at local and regional levels and species traits (Helmuth et al. 2006a,b).

On intertidal rocky shores of the northeastern Atlantic, *Patella depressa*, a warm-water, low-latitude species, and *P. vulgata,* a cold-water, higher-latitude species, are the most common limpet species at mid-shore levels (Orton et al. 1956, Orton & Southward 1961, Moore et al. 2007). They differ in their geographical ranges and local optimal habitats but coexist from Portugal (Boaventura et al. 2002a, Silva et al. 2003) to the British Isles (Fig. 1a,b; Southward et al. 1995 reviews earlier work). In Britain, *P. depressa* has 2 separate leading edges (Fig. 1c), in North Wales (N Wales; Crisp & Knight-Jones 1954) and in South and South-east England (S/SE England; Crisp & Southward 1958), characterised by different patterns of abundance and distribution (Oróstica 2018). These include different responses to decadal fluctuations during warm and cold periods (1950s–1980s, see Kendall et al. 2004) before more recent rapid warming since the late 1980s (Southward et al. 1995). As temperatures have risen in recent decades (see Mieszkowska et al. 2014, their Fig. 2), phenological comparisons (Moore et al. 2011) suggest that increases in the abundance of *P. depressa* in non-range-edge populations (i.e. South-west England [SW England]; see Hawkins et al. 2008, their Fig. 4) may be driven by an advance in gonadal development, leading to a longer reproductive season with multiple broods compared to observations from the 1940s (Orton & Southward 1961). Conversely, its congener *P. vulgata* has shown a reduction in the proportion of advanced gonad stages and has failed to breed in some years (cf. Orton et al. 1956, with Moore et al. 2011), possibly leading to reduced abundance on certain shores in Britain (Moore et al. 2011). Therefore, changes in the abundance of both *Patella* species could be explained by different phenological responses to climate variability driving total reproductive output and hence recruitment success (Hawkins et al. 2008, Moore et al. 2011, Borges et al. 2015).

Individual growth and population mortality rates may serve as important indicators of performance

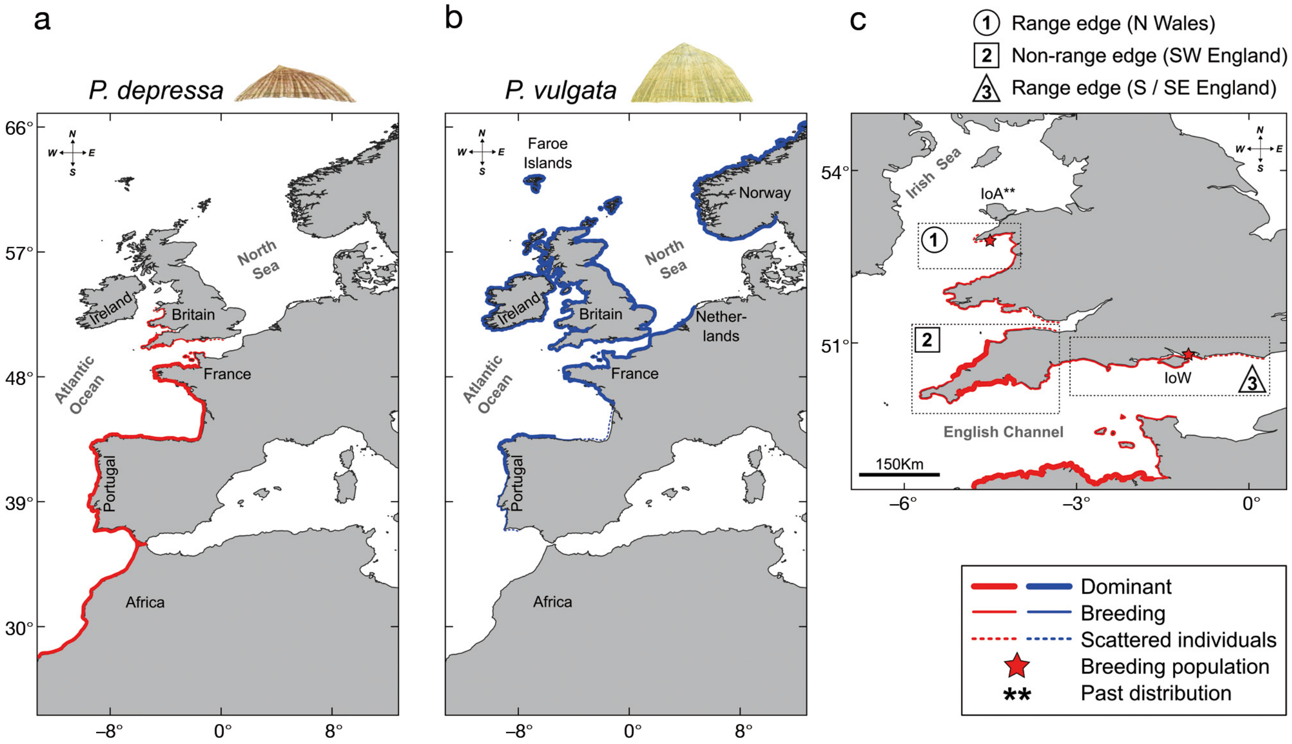

Fig. 1. Geographic range of (a) *Patella depressa* (red line; from N Wales to S/SE England to Senegal [not shown on map], Africa) and (b) *P. vulgata* (blue line; southern limit in the Algarve, Portugal; northwards around all coasts of the British Isles, including Ireland; from France to northern Norway and the Arctic Circle [not shown on map]; and the Faroe Islands but not Iceland [not shown on map] in the northeastern Atlantic). (c) Regions selected to measure growth and mortality rates of both limpet species at the 2 leading edges of the range of *P. depressa*, (1) northern (N Wales) and (3) eastern (S/SE England), and in non-range-edge populations in (2) SW England. Abundance of both species (in a and b) and details of distribution and abundance of *P. depressa* in Britain are shown in (c), based on Crisp & Knight-Jones (1954), Crisp & Southward (1958), Southward et al. (1995), Kendall et al. (2004), Borges et al. (2015) and S. J. Hawkins unpubl. data. Thicker lines (red and blue) indicate where the species is dominant in its optimal local habitat (i.e. >50% of total limpets). Finer lines (red and blue) indicate potential breeding populations in its optimal local habitat (i.e. 1–50% of total limpets, Frequent to Common, see ACFOR scale adapted from Crisp & Southward 1958 for details). Dashed lines (red and blue) represent scattered individuals at range edges even in optimal local habitat (Occasional to Rare, see ACFOR scale adapted from Crisp & Southward 1958 for details). In (c), the 2 red stars indicate last breeding populations of *P. depressa* towards both range edges in Britain (S. J. Hawkins & M. H. Oróstica pers. obs.). IoA: Isle of Anglesey (for past distribution, see Crisp & Knight-Jones [1954] for details); IoW: Isle of Wight

towards and at the range limits of a species (Clarke et al. 2004, Gilman 2006, Herbert et al. 2009). As unsuitable thermal conditions would curtail species performance at their range edges (Brown et al. 1996), populations of *P. depressa* towards the 2 range limits (i.e. N Wales and S/SE England, Fig. 1c) are expected to have reduced individual growth as well as higher mortality rates, when compared with non-range-edge populations in SW England, where *P. depressa* has consistently constituted more than 50% of the limpet population on barnacle-dominated mid-shore levels of more-exposed shores since the 1950s (Fig. 1c; Southward et al. 1995, Kendall et al. 2004, Hawkins et al. 2008). The alternative hypothesis is that local conditions and/or density-dependent processes override expected patterns when comparing performance traits of non-range-edge with range-edge populations. In contrast, *P. vulgata* is expected to have equivalent growth and mortality rates between these 3 regions (Brown et al. 1996), as it may be considered to be at the centre of its range in the British Isles (Southward et al. 1995, Lima et al. 2016).

In this study, performance was determined by measuring individual growth (using von Bertalanffy growth parameters, see Clarke et al. 2004) and population mortality rates (instantaneous rate of total mortality, see King 2007) by using tagged limpets from non-range-edge populations of *P. depressa* (i.e. SW England) and those towards the 2 leading edges of *P. depressa*. These rates were compared to co-occurring and potentially competing (Boaventura et al. 2002b) populations of *P. vulgata*, all of which can be considered as central (Fig. 1b; Southward et al. 1995). We explored whether local conditions including recruitment-driven density-dependent processes may lead to non-conformity of the expected performance patterns at range edges (Brown et al. 1996); thus, the relationships between growth and mortality of both *Patella* species against total density of limpets were also explored. We also addressed the question of whether site conditions influenced both species in the same way by determining the level of correlation between the site-specific performance (i.e. growth and mortality rates) of *P. depressa* and that of *P. vulgata*.

2. MATERIALS AND METHODS

2.1. Study area

Britain and Ireland straddle a biogeographic boundary zone for southern-Lusitanian species expanding northwards since the last Ice Age and now reaching poleward limits around S/SE England, N Wales, Northern Ireland and Scotland (reviewed in Hiscock et al. 2004, see also Southward et al. 1995, Hawkins et al. 2019). Cold-water boreal species overlap with the Lusitanian species in this region, creating a natural laboratory where comparisons among species with differing biogeographical affinities can be made (Crisp & Southward 1958, Southward et al. 2005, Hawkins et al. 2008).

The British Isles display sharp climatic gradients along its coasts (Robinson et al. 2017). The widest range of temperatures can be found along the eastern English Channel, which can experience continentally influenced extremely cold winters and hot summers (Robinson et al. 2017), reflected in both summer and winter temperatures (Lewis 1964). This region coincides with the poleward limits for several warm-water species (Crisp & Southward 1958). The ~500 km from west to east along the English Channel is analogous to a poleward gradient (Herbert et al. 2009). Both air and sea temperatures are also influenced by the eastward inflow of Gulf Stream waters through the English Channel (Lewis 1964), which produces a marked ocean temperature gradient from the western half towards the eastern half (Crisp & Southward 1958, Hoch & Garreau 1998). In contrast, the shores of N Wales (i.e. the northerly limit of *Patella depressa*) and SW England show a more maritime weather pattern (Robinson et al. 2017), owing to the exposure to moist air masses from the tropical sector of the Atlantic Ocean (Lewis 1964). Consequently, maximum air and sea summer temperatures fall progressively with increasing latitude (Lewis 1964), but at the winter minimum, the west coast is generally warmer than northern and eastern shores of Britain for both air and sea (Robinson et al. 2017).

2.2. Species focus

Patella species are an accessible and tractable marine species (Lewis & Bowman 1975). Their sessile nature and homing behaviour mean that observations of individual growth and mortality in the field are relatively straightforward (Jenkins & Hartnoll 2001). In northern latitudes, the geographical ranges of *P. vulgata* and *P. depressa* overlap with 2 different leading edges of *P. depressa* in N Wales and S/SE England (Fig. 1c; Kendall et al. 2004). The last northerly and easterly breeding populations of *P. depressa* occur at Abersoch in N Wales and Southsea in S/SE England, respectively (Fig. 1c; S. J. Hawkins & M. H. Oróstica pers. obs.). In contrast, its congener, *P. vulgata*, is distributed from southern Portugal (Fig. 1b; Ribeiro et al. 2009, Lima et al. 2016) to northern Norway (Southward et al. 1995). In SW England (Fig. 1c), *P. depressa* makes up over 50% of the total limpet population (Fig. 1c; see also Hawkins et al. 2008, their Fig. 4), with patches on the shore where up to 100% can be found (S. J. Hawkins unpubl. data); such proportions of *P. depres*sa can be found in populations further south in France, Spain or Portugal (Fig. 1a; Borges et al. 2015).

2.3. Leading- and non-range-edge locations with thermal regimes

Locations were selected reflecting past and current *P. depressa* abundance patterns towards the 2 range edges in Britain (Fig. 1c; see Kendall et al. 2004 for details). Thus, locations with at least 20% of *P. depressa* in relation to the total number of individuals of all other *Patella* species (e.g. *P. vulgata* and *P. ulyssiponensis*) were selected (Oróstica 2018). A total of 6 locations were selected during mid-2015 (Fig. 2a) and were grouped in 3 regions defined by the 2 leading range edges (i.e. N Wales and S/SE England) and by non-range-edge populations (i.e. SW England) of *P. depressa*. Locations towards the 2 range edges of *P. depressa* were Criccieth and Shell Island in N Wales plus Portland Bill and Swanage in S/SE England (Fig. 2a).

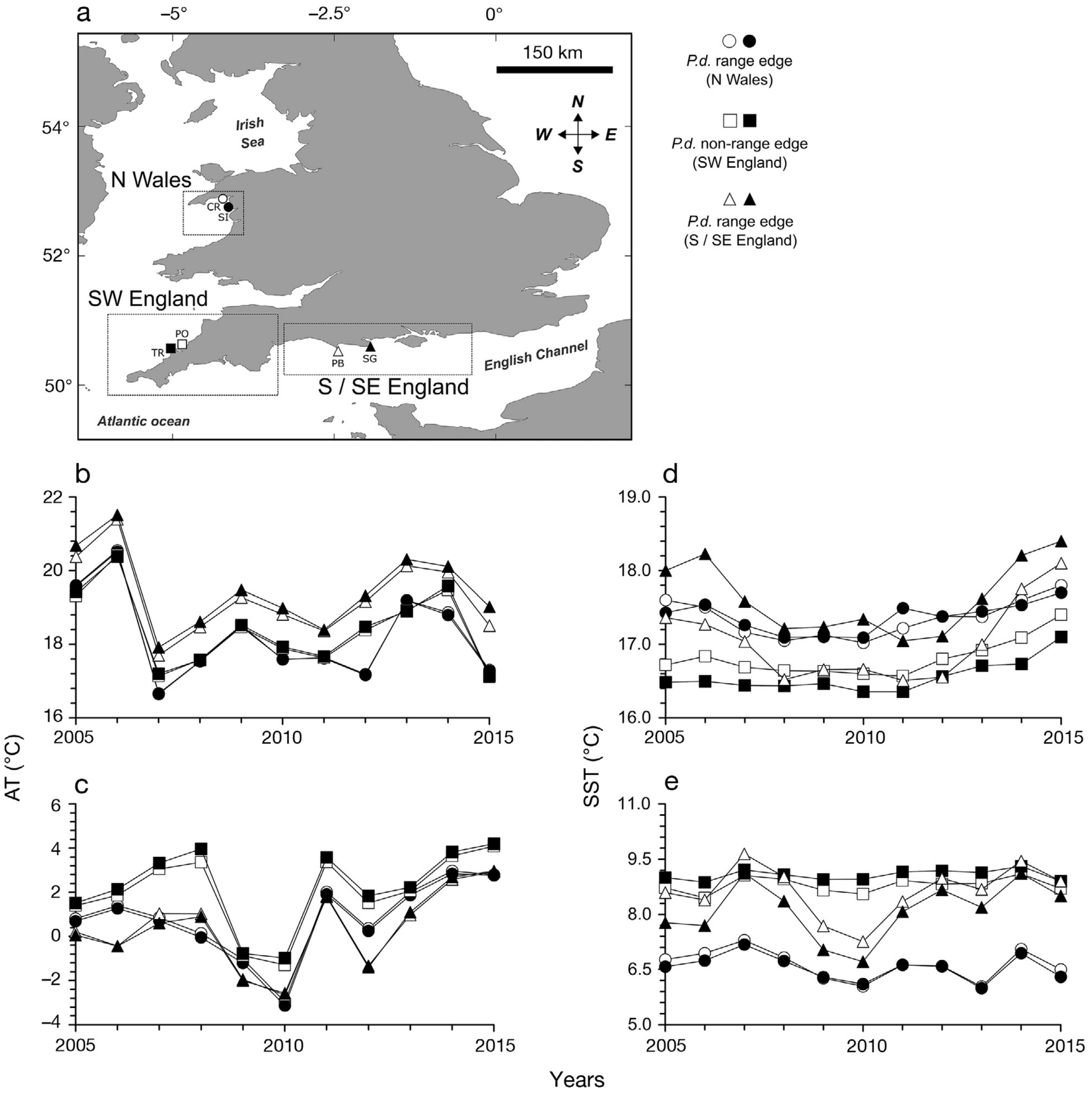

Fig. 2. (a) Locations selected (n = 6) to measure growth and mortality rates of both limpet species and average of summer maxima (July–September) and winter minima (December–February) of daily (b,c) air temperature (AT) and (d,e) sea surface temperature (SST) from 2005 to 2015. The 3 regions are defined by 2 range edges of *Patella depressa* (*P.d.*), North Wales (○ Criccieth [CR]; ● Shell Island [SI]) and South/South-east England (△ Portland Bill [PB]; ▲ Swanage [SG]), and by non-range-edge populations in South-west England (□ Polzeath [PO]; ■ Trevone [TR])

The 2 leading edges show different patterns of temperature, with warmer summer and colder winter air temperatures (ATs; 2005–2015) at locations in S/SE England when compared to N Wales (Fig. 2b,c). However, both range limits of *P. depressa* tend to have similar values of maximum sea surface temperatures (SSTs; 2005–2015), but with Portland Bill being more similar to SW England during some years (Fig. 2d). In contrast, the SST during wintertime is much cooler at the range edge in N Wales than locations at the range edge in S/SE England (Fig. 2e).

Locations selected representing non-range-edge populations of *P. depressa* were Polzeath and Trevone in SW England (Fig. 2a). These locations exhibited milder winter ATs than both range edges (2005–2015, Fig. 2c), while in the summer, temperatures were similar to N Wales but lower than S/SE England (Fig. 2b). Maximum SST in SW England was lower than both range edges in summer (2005–2015, Fig. 2d), but winter minima were generally higher (Fig. 2e). This difference of winter minima was particularly apparent in the colder winters between 2009 and 2011. Thus, SW England had more even temperatures following its exposure to moist air masses from the Atlantic Ocean (Lewis 1964) when compared with both range edges of *P. depress*a.

SST was obtained from the Atlantic European North West Shelf Ocean–ODYSSEA Sea Surface Temperature Analysis provided by the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/) and based on a re-analysis of satellite data from both infrared and microwave radiometers, with a spatial resolution of 0.02° latitude and 0.02° longitude and a daily temporal resolution. AT was taken from the Environmental Information Platform of the Centre for Ecology & Hydrology (https://www.ceh.ac.uk/), based on an atmospheric evaporative demand model, which is determined by meteorological variables with a spatial resolution of 1 km^2 and a daily temporal resolution (see Robinson et al. 2017 for details).

2.4. Tagged limpets

To estimate growth and mortality rates of both *Patella* species, between 85 and 280 individuals of both limpet species across the range of sizes present were selected at each location. The area of study extended over a horizontal distance of ~5 m from approximately mean high water neap to mean tide level, where both limpet species overlap and *P. depressa* reaches maximum abundance on open rock on both semi-exposed and exposed shores (Orton et al. 1956, Orton & Southward 1961, Moore et al. 2007).

Individual-marking methods have been widely used in limpet species to examine growth and mortality rates (see Jenkins & Hartnoll 2001, Clarke et al. 2004 for details). Shells were initially gently scraped, cleaned and dried close to the apex. After that, glue was placed to fix a small (5 × 5 mm) waterproof numerical label (Brady®, TMM-0-49-PK model, https://www.bradyid.com). Double labels were used to account for tag loss. Additionally, 2 different colours of nail varnish were applied to identify each *Patella* species. All limpets tagged were located on open seaward-facing rock with 0 to 60° slope but avoiding crevices, rock pools and canopy-forming algae, as *P. depressa* does not usually occur under fucoid clumps, unlike *P. vulgata* (Moore et al. 2007).

The maximum initial shell length (L_0) of each individual was recorded at a single point in time during June–July 2015 (t_0). After that, measurements were taken 3 times over a 1 yr period until late May 2016, for measurable limpet growth to take place (e.g. Jenkins & Hartnoll 2001). Thus, changes in limpet shell length record individual growth over 3 periods: (1) from t_0 to September 2015 (t_1), which corresponds to the summer months; (2) from t_1 to December 2015 (t_2), which reflects autumn months; and (3) from t_2 to late May 2016 (t_3), over the winter/early spring months.

When a previously labelled limpet was not found, a thorough search was performed over a period of ~20 to 30 min. After that, if that tagged limpet was not found, that limpet was considered dead and replaced by another one with the same length. Nail varnish on the shell lasts between 3 and 4 mo (M. H. Oróstica pers. obs.), therefore individuals that had both labels missing were easily re-identified following the colour on their shells and their position on a small-scale map showing individual limpets, which was drawn for each study location.

Additionally, the abundance of both limpet species was estimated at each location at the end of the study using ten 0.5 × 0.5 m quadrats located ~1 m apart along a transect parallel to the coastline.

2.5. Von Bertalanffy growth parameters: Forced Gulland-Holt plot approach

To compare growth performance between both *Patella* species from populations in different regions, we estimated the von Bertalanffy growth parameters, namely the theoretical maximum length (L_∞) and growth coefficient (K) (see King 2007). The von Bertalanffy growth function is defined by the equation:

$$L_t = L_\infty\,[1 - \mathrm{e}^{-K\,(t - t_0)}] \tag{1}$$

where L_t is the length at time t, L_∞ is the theoretical maximum length that the species would reach, the K parameter is a growth coefficient estimating how fast the individual approaches its L_∞, and t_0 is the theoretical age at zero length which often has a small negative value (King 2007). Forced Gulland-Holt plots were used to estimate both L_∞ and K, because this approach allows the use of length data collected over a specific time through a mark–recapture method (see King 2007 for details). Nevertheless, it is not possible to calculate t_0 using this method (King 2007). To this end, forced Gulland-Holt plots show the linear relationship between individual growth rates (y-axis) against individual mean length (x-axis), which is the average between 2 individual lengths measured at 2 different times, e.g. initial length (L_{initial}) and final length (L_{final}). Growth rates correspond to the difference between L_{final} and L_{initial}, divided by change in time, i.e. $L_{\text{final}} - L_{\text{initial}} / t_{\text{final}} - t_{\text{initial}}$ (King 2007). In this relationship, the intercept on the x-axis (i.e. where the growth rate is zero) is an estimate of L_∞ and can be calculated as the negative of the y-axis intercept, divided by the slope, i.e. $L_\infty = a / -b$ (King 2007). R^2 was calculated for each relationship to estimate how much individual growth rates can be explained by the mean individual size of limpets for each region and species (i.e. the forced Gulland-Holt approach). To calculate K, forced Gulland-Holt plots fix a value of L_∞ on the x-axis, which is defined by the formula K = mean growth rate / L_∞ – mean length (King 2007).

Estimations of both L_∞ and K were based on individuals that survived the whole sampling period from June–July 2015 (t_0) to late May 2016 (t_3). Estimates of L_∞ and K were pooled by region and calculated for each species following the previous regional growth comparisons made by Clarke et al. (2004) for patellids across different latitudes. Furthermore, as in fishes and invertebrates, whose growth process can be described by the von Bertalanffy growth curve, comparisons were also made through the overall growth performance index, i.e. $Ø' = \log K + 2\log L_\infty$ (see Clarke et al. 2004 for details). According to Pauly (1979), $Ø'$ describes the growth rate at the point of inflection of the von Bertalanffy growth curve (i.e. maximum growth rate). The TropFishR package was used to build forced Gulland-Holt plots and estimate growth parameters from tagging data in the CRAN R project environment (R Core Team 2019, v3.5.3; Mildenberger et al. 2017).

The loss of limpets in a target population through death can be estimated as the instantaneous rate of total mortality (i.e. mortality rate [Z]) over a time interval (King 2007). This parameter takes values greater than 1 and is defined by the equation:

$$Z = \ln(N_{t+1}) - \ln(N_t) \qquad (2)$$

where N_{t+1} is the number of individuals at t_{final}, and N_t is the number of individuals at t_{initial} (King 2007).

2.6. Statistical analysis

To determine whether growth and mortality rates differed between both *Patella* species and regions, we used a generalized linear mixed model (GLMM) for each response variable. Variables were analysed using Gaussian family errors (identity link function) for growth rates and beta family errors (logit link function) for mortality rates (Cribari-Neto & Zeileis 2010).

In terms of growth rates, temporal non-independence was included in the analysis (i.e. repeated measures; Bolker et al. 2009). The repeated measures analysis refers to multiple measurements made on the same experimental unit (i.e. each tagged limpet) observed either over time or space and was added as a random factor to the analysis of growth measurements of the same individual (Bolker et al. 2009). Unlike forced Gulland-Holt plots, which use mean size as an independent variable, the initial length (L_0) of each individual at each sampling period (t_1, t_2 and t_3) was considered as a co-variable as well as a random factor in this analysis. Further, there were also 3 fixed factors: (1) region, with 3 levels: N Wales, SW England and S/SE England; (2) sampling period, with 3 levels: summer (from t_0 to t_1), autumn (from t_1 to t_2) and winter/early spring (from t_2 to t_3); and (3) species, with 2 levels: *P. depressa* and *P. vulgata*. Additionally, location was a nested random factor within region. Since limpet growth curves show an asymptotic shape during their life span (Ekaratne & Crisp 1984), the analysis was made only on individuals below 30 mm in length, including those replaced because of mortality. Thus, this approach captured variables that are influencing actively growing individuals.

For the instantaneous rate of total mortality, the analysis performed considered the following fixed factors: (1) region (3 levels: N Wales, SW England and S/SE England) and (2) species (2 levels: *P. depressa* and *P. vulgata*). Further, location was a nested random factor within region.

We used diagnostic plots (i.e. histogram of residuals and residuals vs. linear predictor) to evaluate both model fitness and statistical assumptions of residuals (Zuur et al. 2010). For each variable response (growth and mortality rates), when interaction terms were significant ($\alpha = 0.05$), Tukey's post hoc tests were carried out for pairwise comparisons (Bolker et al. 2009).

All statistical analyses were made in the CRAN R project environment (R Core Team 2019, v3.5.3). We used the glmmTMB package (i.e. GLMMs using Template Model Builder) to fit both growth and mortality rate data sets. Tukey's post hoc tests were carried out using the emmeans package (estimated marginal means [least-squares means]).

2.7. Density-dependent effects on performance traits of *Patella* species

We estimated the effect of density-dependent processes calculating mean total limpet density (i.e. no. of *P. vulgata* plus no. of *P. depressa*) for each location (quadrat number = 10) and determining the relationship with mean growth and mortality rates of each *Patella* species. In addition, we assessed the interspecific and intraspecific relationships between the mean growth and mortality rates of both limpet species using linear regressions and the R^2 for each relationship.

3. RESULTS

3.1. Tagged individuals and background abundance

The number of limpets tagged between June–July 2015 and late May 2016 at each location varied from 85 to 181 individuals for *Patella depressa* and from 130 to 280 for *P. vulgata* (see Table 1 for details of individuals relocated plus percentage of lost tags during each sampling period).

The size range of limpets selected to measure growth and mortality rates across all regions (June–July 2015) was between 5.8 and 43.1 mm in length for *P. depressa* (n = 858) and between 5.0 and 53.1 mm for *P. vulgata* (n = 1042; Fig. 3). Frequency histograms showed that most of the individuals tagged were between 10 and 30 mm in length at all locations (Fig. 3). Larger sizes were more common for both species at the 2 range edges of N Wales and S/SE England of *P. depressa* (Fig. 3a,c), when compared with non-range-edge populations in SW England (Fig. 3b), except for *P. depressa* at Trevone on slightly more sheltered, gently sloping ledges (Fig. 3b).

The limpet abundance survey indicated a higher density of *P. depressa* at the leading edge in S/SE England when compared with non-range-edge pop-

Table 1. Initial number (IN) of limpets labelled between June and July 2015 and individuals recaptured (IR) of both *Patella* species at 3 different sampling periods over 12 mo. There are 3 regions, defined by 2 range edges of *P. depressa* (*P.d.*), North Wales (CR: Criccieth; SI: Shell Island) and South/South-east England (PB: Portland Bill, SG: Swanage), and by non-range edge populations in South-west England (PO: Polzeath; TR: Trevone). Labels lost (%) is also indicated. (–) no data

Location	Sampling period	Time	*P. depressa*			*P. vulgata*		
			IN	IR	Labels lost (%)	IN	IR	Labels lost (%)
P.d. range edge, N Wales								
CR	Jun–Jul 2015	t_0	162	–	–	164	–	–
	Sep–Oct 2015	t_1	162	134	10	164	130	13
	Dec 2015–Feb 2016	t_2	162	124	17	164	123	8
	Apr–May 2016	t_3	162	118	10	164	128	14
SI	Jun–Jul 2015	t_0	85	–	–	280	–	–
	Sep–Oct 2015	t_1	85	77	5	280	262	8
	Dec 2015–Feb 2016	t_2	85	75	12	280	206	13
	Apr–May 2016	t_3	85	67	9	280	238	14
P.d. non-range edge, SW England								
PO	Jun–Jul 2015	t_0	181	–	–	152	–	–
	Sep–Oct 2015	t_1	181	160	9	152	114	11
	Dec 2015–Feb 2016	t_2	181	156	10	152	125	16
	Apr–May 2016	t_3	181	147	9	152	107	14
TR	Jun–Jul 2015	t_0	138	–	–	130	–	–
	Sep–Oct 2015	t_1	138	97	12	130	76	16
	Dec 2015–Feb 2016	t_2	138	107	11	130	89	11
	Apr–May 2016	t_3	138	111	16	130	95	8
P.d. range edge, S/SE England								
SG	Jun–Jul 2015	t_0	141	–	–	147	–	–
	Sep–Oct 2015	t_1	141	74	16	147	71	16
	Dec 2015–Feb 2016	t_2	141	90	17	147	84	17
	Apr–May 2016	t_3	141	79	15	147	92	15
PB	Jun–Jul 2015	t_0	151	–	–	169	–	–
	Sep–Oct 2015	t_1	151	98	9	169	109	15
	Dec 2015–Feb 2016	t_2	151	76	11	169	76	13
	Apr–May 2016	t_3	151	75	13	169	84	11

ulations in SW England and range-edge populations in N Wales (Fig. 4a; Kruskal-Wallis test, $\chi^2 = 37.70$, df = 2, $p < 0.05$). Differences were found between both range edges (N Wales vs. S/SE England; pairwise comparisons test, $p < 0.05$; Fig. 4a) and between populations in N Wales and SW England (pairwise comparisons test, $p < 0.05$; Fig. 4a). However, both non-range-edge populations in SW England and range-edge populations in S/SE England showed similar patterns of density of *P. depressa* (pairwise comparisons test, $p > 0.05$; Fig. 4a). The density of *P. vulgata* was also higher at the range edge of *P. depressa* in S/SE England (Fig. 4b; Kruskal-Wallis test, $\chi^2 = 28.68$, df = 2, $p < 0.05$), but comparisons showed differences between all regions (pairwise comparisons test, $p < 0.05$; Fig. 4b).

3.2. Growth rates of *Patella* species in Britain

Individuals that survived from June–July 2015 (t_0) to the end of the sampling period (~late May 2016; t_3) exhibited a significant negative relationship between growth rate and mean length (Fig. 5), conforming to the von Bertalanffy growth model. For *P. depressa* populations, the highest R^2 was found at the range edge in S/SE England (Fig. 5c), when compared with populations at the range edge in N Wales (Fig. 5a) and non-range-edge populations in SW England (Fig. 5b). For *P. vulgata* populations, R^2 values were similar across the 3 regions (i.e. R^2 = 0.20–0.26; Fig. 5a,b,c).

Von Bertalanffy parameters (K and L_∞) as well as the Ø′ value of both *Patella* species are shown in Table 2. *P. vulgata* reached larger L_∞ than *P. depressa* at both range edges (Table 2). The highest K and Ø′ values were found at the range edge of *P. depressa* in S/SE England for both *P. depressa* and *P. vulgata* (Table 2). Thus, limpet growth measured as K and Ø′ differed between the 2 separate boundaries of *P. depressa* in Britain. In addition, K and Ø′ values of *P. vulgata*, which can be considered at the centre of its distribution, showed equivalent values to *P. depressa* at all study regions (Table 2).

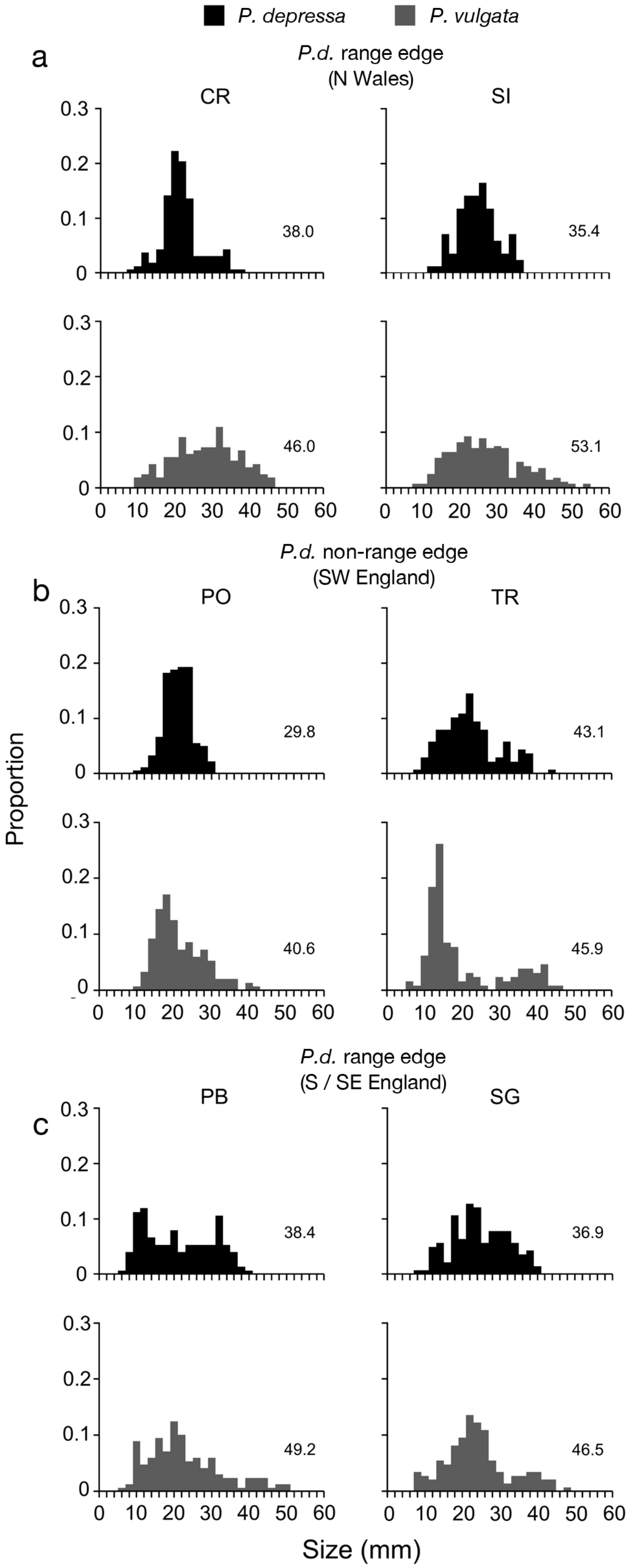

Fig. 3. Frequency (proportion) of individual initial sizes (maximum length, separated by 2 mm) selected to measure growth and mortality rates of both limpet species, *Patella depressa* (*P.d.*) and *P. vulgata* in (a) N Wales, (b) SW England and (c) S/SE England. The 3 regions and locations are defined in Table 1. Each plot (right bottom) indicates maximum size of individuals selected at each location

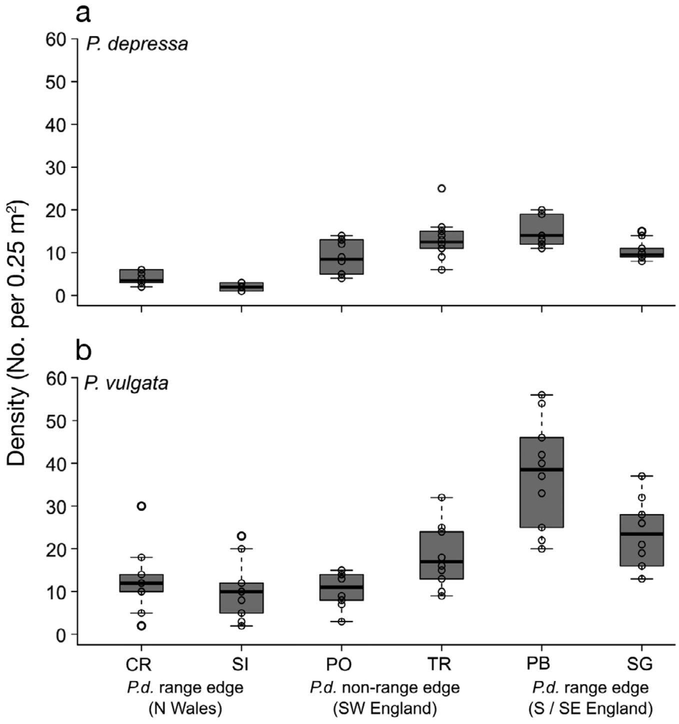

Fig. 4. Density of (a) *Patella depressa* (*P.d.*) and (b) *P. vulgata* (n = 10 quadrats of 0.5 × 0.5 m^2) at each location (n = 6) selected to measure growth and mortality rates. The 3 regions and locations are defined in Fig. 2

In terms of growth rates (Fig. 6), the GLMM analysis showed a significant interaction between species, region and sampling period (Table 3). Post hoc analysis of this 3-way interaction showed that higher limpet growth rates were recorded in populations at the range edge of *P. depressa* in S/SE England when compared with non-range-edge populations in SW England and range-edge populations in N Wales (Fig. 6; Tukey's post hoc test, $p < 0.05$; see also Fig. A1 in the Appendix); there was no clear difference in limpet growth rates between populations in N Wales and SW England (Fig. 6a,b; Tukey's post hoc test, $p > 0.05$). In addition, at the range edge of *P. depressa* in S/SE England (Fig. 6c), individuals of *P. depressa* showed significantly higher growth rates than *P. vulgata*, particularly over both summer and autumn but not over late winter and early spring (Fig. 6c; Tukey's post hoc test, $p < 0.05$; see also Fig. A1).

3.3. Mortality rates of *Patella* species in Britain

No differences in mortality rates were found between *Patella* species (Table 4). However, mortality rates of limpet species differed significantly between regions (Fig. 7; Tukey's post hoc test, $p < 0.05$). Mortality was significantly higher at the range edge of *P. depressa* in S/SE England, when compared with the range edge in N Wales and non-range-edge populations in SW England (Fig. 7a,b,c, Table 4). There were no differences in limpet mortality between the range edge in N Wales and populations in SW England (Fig. 7a,b; Tukey's post hoc test, $p > 0.05$). Thus, mortality rates of both limpet species were higher in the faster-growing populations at the range edge of *P. depressa* in S/SE England (Fig. 7c), at locations such as Portland Bill and Swanage.

3.4. Density-dependent effects on performance traits of *Patella* species

Examination of local density-dependent effects on growth and mortality rates of *Patella* species showed that mean growth and mortality rates of both *Patella* species were positively related with the mean of total limpet density at each location (Fig. 8a,b; $p < 0.05$). Higher growth (Fig. 8a) and faster mortality rates (Fig. 8b) occur at the range edge of *P. depressa* in S/SE England, particularly in locations such as Portland Bill and Swanage (Fig. 8a,b), with higher mean abundances of both *Patella* species across the 3 regions.

Additionally, interspecific (Fig. 9a,b) and intraspecific (Fig. 9c) relationships in growth and mortality rates across sites indicated a clear positive relationship between the growth rate of *P. vulgata* and *P. depressa* at each site; where *P. depressa* performed well, *P. vulgata* also did well (Fig. 9a; $p < 0.05$). Similarly, mortality rates of the 2 species were closely related at each site across regions (Fig. 9b; $p < 0.05$). Furthermore, there also was a positive relationship between growth and mortality rates for both species, with faster-growing limpet populations also dying quicker (Fig. 9c; $p < 0.05$), indicating that both *P. depressa* and *P. vulgata* have equivalent regional and site-specific performance patterns across the 2 range edges as well as in non-range edge populations of *P. depressa* in SW England (Fig. 9a,b,c).

4. DISCUSSION

Our results showed an interesting regional differentiation in the performance of both focal species of patellid limpet. The theoretical expectation of lower growth and higher mortality rates at the leading

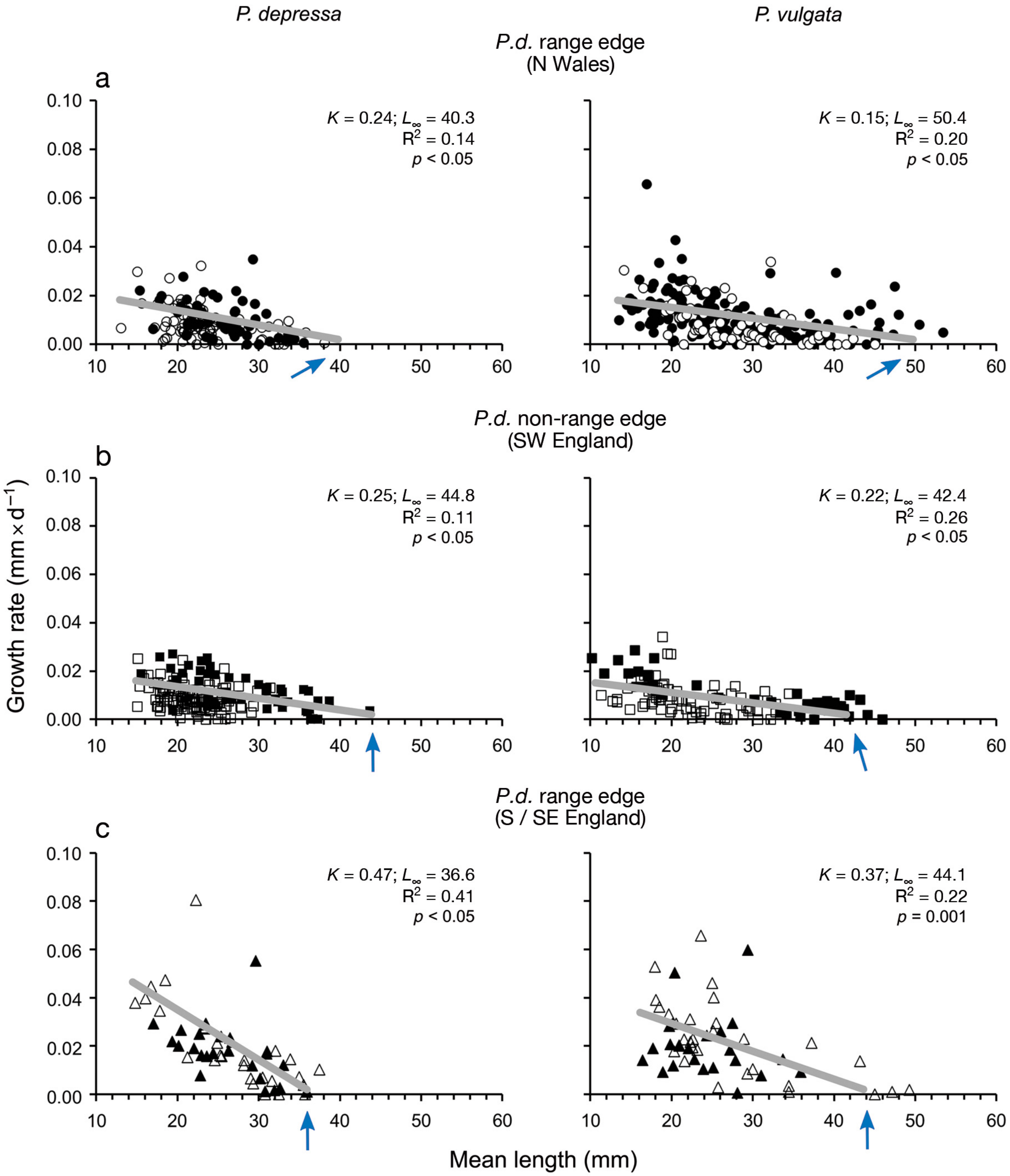

Fig. 5. Forced Gulland-Holt plots for individuals of both *Patella depressa* (*P.d.*) and *P. vulgata* that survived from June–July 2015 (t_0) to late May 2016 (t_3). The 3 regions are defined by two range edges of *P. depressa*, (a) N Wales (○ CR; ● SI) and (c) S/SE England (△ PB; ▲ SG), and by (b) non-range-edge populations in SW England (□ PO ; ■ TR). Dots indicate individual growth rates against the individual mean length without replacement of limpet because of individual mortality. The growth coefficient (K) and theoretical maximum length (L_∞; blue arrows) parameters estimated by forced Gulland-Holt plots are indicated for each region and each *Patella* species. R^2 is also indicated. Locations defined in Fig. 2

edges of *Patella depressa* was not supported. The 2 leading edges showed remarkably different patterns. *P. depressa* grew faster, but also showed higher mortality rates at the range-edge in S/SE England, when compared with range-edge populations in N Wales and with non-range-edge populations in SW England. Thus, the performance traits of the poleward-advancing species (Hawkins et al. 2008), *P. depressa*,

Table 2. Comparison of L_∞ and K parameters estimated by forced Gulland-Holt plots for both *Patella* species at each region from June–July 2015 (t_0) to late May 2016 (t_3). The 3 regions are defined by 2 range edges of *P. depressa* (*P.d.*), N Wales and S/SE England, and by non-range-edge populations in SW England. L_∞ and K were calculated without individual replacement because of limpet mortality (see Fig. 5). L_∞ is the theoretical maximum length that a species can reach; K is a measure of the rate at which maximum size can be reached. Growth performance index (Ø′) is also indicated, i.e. $Ø' = \log K + 2\log L_\infty$ (see Clarke et al. 2004)

Region	*P. depressa*				*P. vulgata*			
	No. of ind.	L_∞ (mm)	K (yr^{-1})	Ø′	No. of ind.	L_∞ (mm)	K (yr^{-1})	Ø′
P.d. range edge, N Wales	145	40.3	0.24	5.76	268	50.4	0.15	5.86
P.d. non-range edge, SW England	166	44.8	0.25	5.77	115	42.4	0.22	5.79
P.d. range edge, S/SE England	53	36.6	0.47	6.51	52	44.1	0.37	6.60

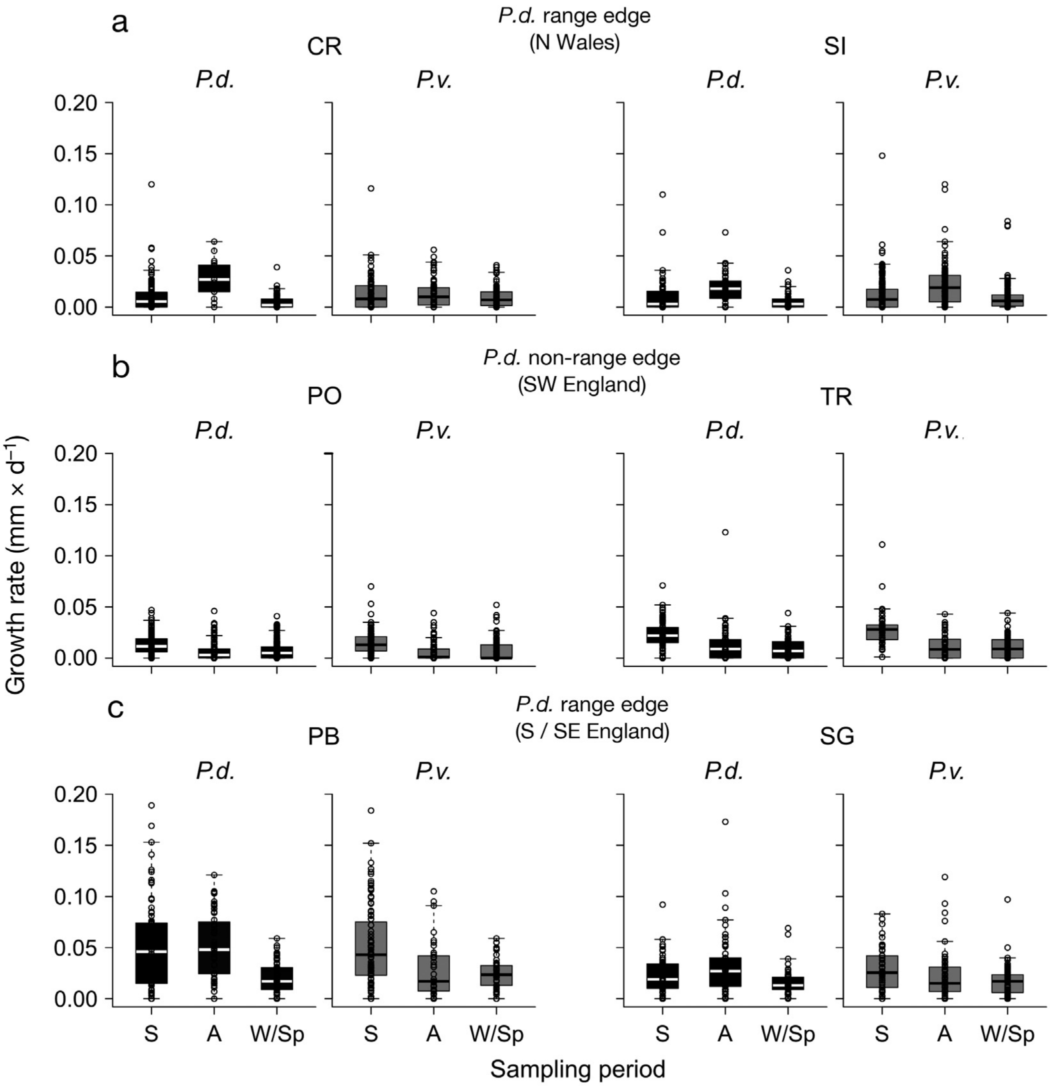

Fig. 6. Growth rates for *Patella depressa* (*P.d.*) and *P. vulgata* (*P.v.*) measured from June–July 2015 (t_0) to late May 2016 (t_3). The 3 regions and locations are defined in Table 1. Sampling period indicates growth rates estimated during summer (S; t_0 to t_1), autumn (A; t_1 to t_2) and winter/early spring (W/Sp; t_2 to t_3). Lines extending from the boxes (whiskers) indicate minimum and maximum values excluding outliers, which are above the whiskers. Horizonal white (*P.d.*) and black lines (*P.v.*) indicate the median values of each group. From those lines, the first and third quartiles on boxes (lower and upper quartiles, respectively) are the median of the lower and upper half of the data-set, respectively. Dots indicate individual growth rates for individuals <30 mm in length including those replaced because of mortality

Table 3. Summary of GLMM performed with fixed and random effects on both limpet growth rates measured from June–July 2015 to late May 2016 at 3 different sampling periods over 12 mo. Fixed effects: region (N Wales, SW England and S/SE England), sampling period (t_1, t_2 and t_3) and species (*Patella depressa* and *P. vulgata*). Random effects: ID tagged (i.e. individual tag), initial length (i.e. L_0) and location nested within region (N Wales [Criccieth and Shell Island], SW England [Polzeath and Trevone] and S/SE England [Portland Bill and Swanage]). **Bold:** $p < 0.05$

Fixed effect	Estimate	SE	*Z*-value	p
Intercept	0.014	0.003	4.243	**<0.05**
Species	0.001	0.002	0.316	0.752
Region	0.024	0.005	5.194	**<0.05**
Species × region	0.002	0.002	1.123	0.261
Species × sampling period	−0.007	0.002	−1.307	**<0.05**
Species × region × sampling period	−0.005	0.004	−3.350	**<0.05**
Random effect	**Variance**	**SE**		
ID tagged	0.0004	0.007		
Initial length	0.0001	0.012		
Location (region)	0.0002	0.004		
Residuals	0.0002	0.015		

Table 4. Summary of GLMM performed with fixed and random effects on the instantaneous rate of total mortality of both limpet populations measured over 12 mo (June–July 2015 to late May 2016). Fixed effects: region (N Wales, SW England and S/SE England) and species (*Patella depressa* and *P. vulgata*). Random effects: location nested in region, i.e. N Wales (Criccieth and Shell Island), SW England (Polzeath and Trevone) and S/SE England (Portland Bill and Swanage). **Bold:** $p < 0.05$

Fixed effect	Estimate	SE	*Z*-value	p
Intercept	0.208	0.043	4.855	**<0.05**
Species	0.010	0.055	0.181	0.856
Region	0.373	0.061	6.152	**<0.05**
Species × region	0.118	0.078	1.517	0.129
Random effect	**Variance**	**SE**		
Location (region)	0.0001	0.025		
Residuals	0.0090	0.096		

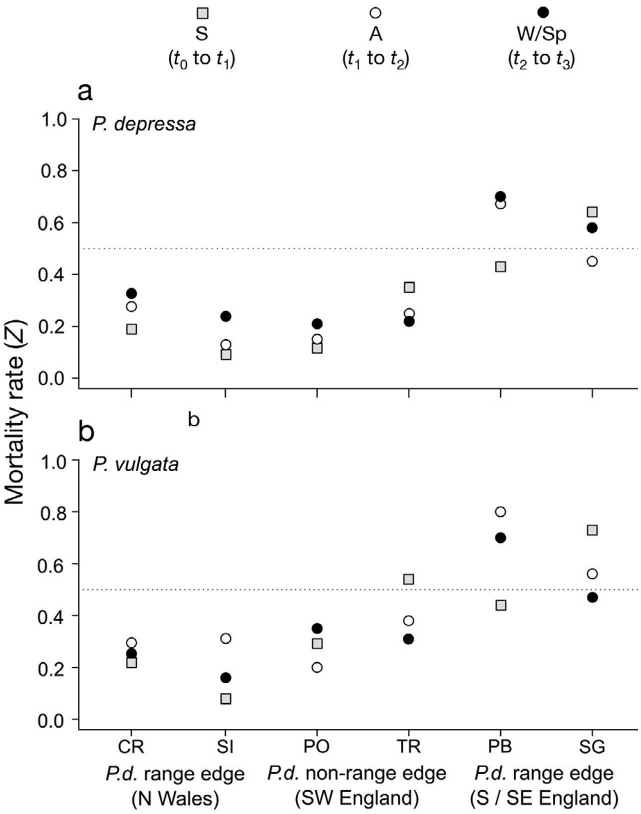

Fig. 7. Instantaneous rate of total mortality of (a) *Patella depressa* (*P.d.*) and (b) *P. vulgata* calculated for each measuring period (n = 3) from June–July 2015 to late May 2016. S: summer; A: autumn; W/Sp: winter/early spring. The 3 regions and locations are defined in Table 1. Dotted-grey horizontal line indicates a mortality rate of 0.5 on each plot, indicating 50% of mortality on limpet populations

differed between the 2 separate leading edges of its distribution. Moreover, there was no clear consistent separation in performance between non-range-edge populations in SW England and those at the range edge in N Wales. In addition, perhaps surprisingly, *P. vulgata*, which may be considered in the centre of its range across all regions in the British Isles (Lima et al. 2016), performed similarly to *P. depressa*. This result shows the primacy of local contextual factors (e.g. chlorophyll supply, Jenkins et al. 2001; mortality from physical stresses, Lima et al. 2016; and predation risk, Silva et al. 2008), together with seasonal differences across regions (Lewis 1964, Hiscock et al. 2004), which could override species performance patterns across non-range-edge populations and marginal populations (Hawkins et al. 2019).

4.1. Regional patterns of temperatures and their effects on growth and mortality of patellids

Seawater temperature is the ultimate factor driving geographic distributions of marine organisms, including intertidal species (Hutchins 1947), through its regulation of metabolism (Bozinovic & Pörtner 2015). Favourable temperatures close to the optimum for species will lead to more activity (Bozinovic & Pörtner 2015), greater growth and reproductive out-

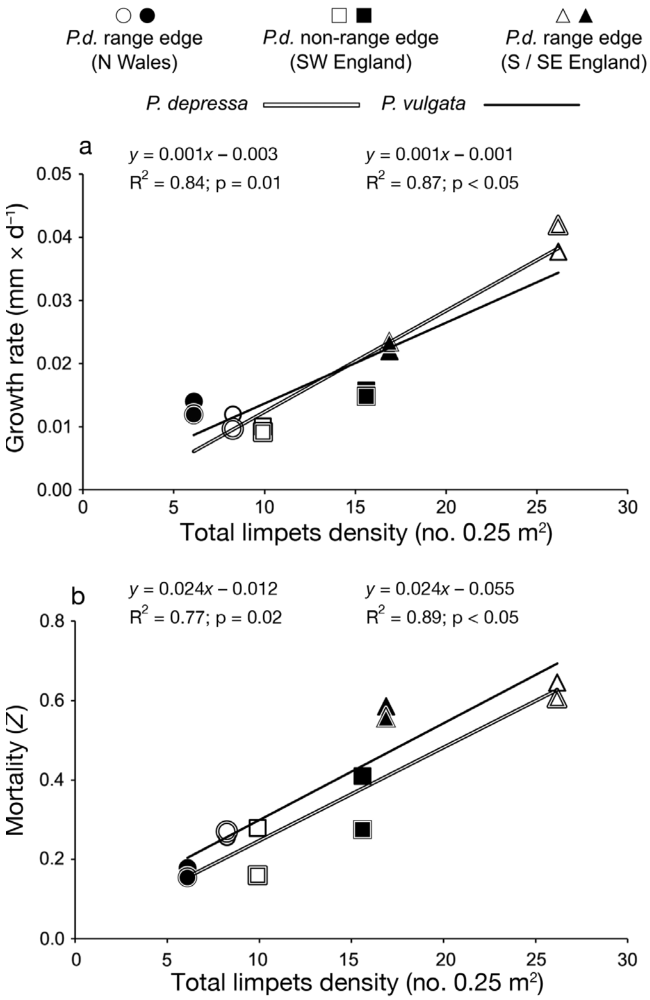

Fig. 8. Relationship between the mean total limpet density at each location (n = 10 quadrats) against (a) the average growth rates of both *Patella depressa* (*P.d.*; double black outline on symbols) and *P. vulgata* (single outline on symbols) and (b) mean of the instantaneous rate of total mortality of both *P. depressa* (double black outline on symbols) and *P. vulgata* (single outline on symbols). Growth and mortality rates were measured from June–July 2015 to late May 2016 over 3 different times. Limpet density was evaluated at the end of the sampling period (late May 2016). The 3 regions and locations are defined in Fig. 2. ○ CR; ● SI; △ PB; ▲ SG; □ PO; ■ TR. R^2 is indicated

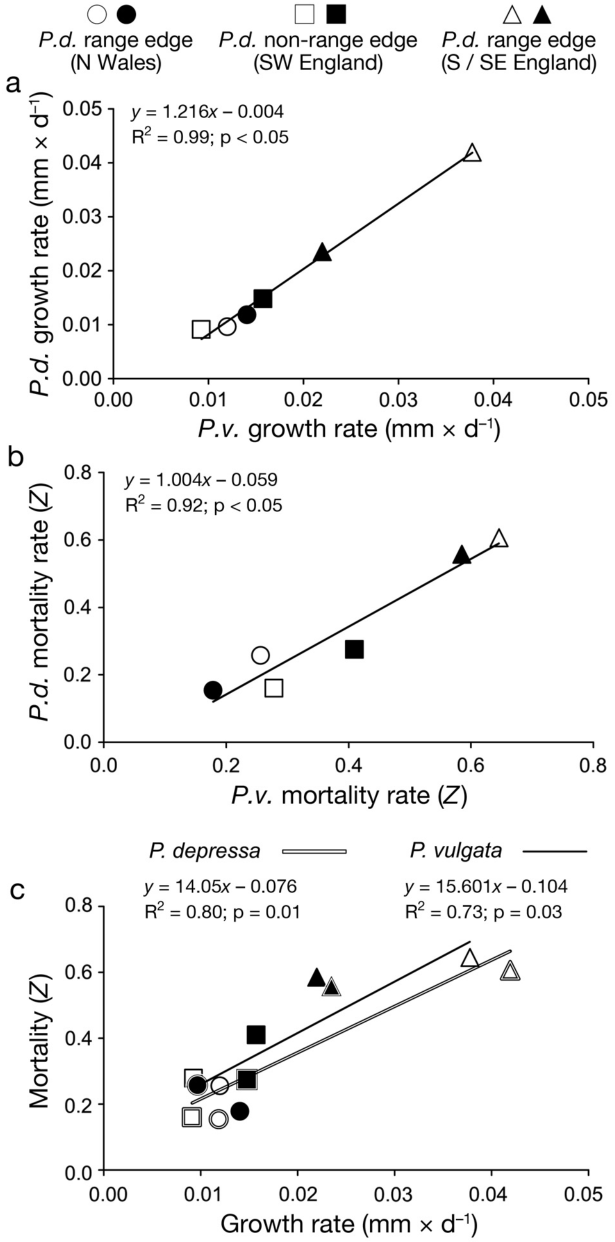

Fig. 9. Relationship between (a) the average growth rates of *Patella depressa* (*P.d.*) and *P. vulgata* (*P.v.*), (b) the mean of instantaneous rate of total mortality of both limpet species (*P.d.* and *P.v.*) and (c) the average growth rates against the mean of instantaneous rate of total mortality of *P.d.* (double black outline on symbols) and *P.v.* (single black outline on symbols). Both variables were measured from June–July 2015 to late May 2016 over 3 different times. The 3 regions and locations are defined in Fig. 2. ○ CR; ● SI; △ PB; ▲ SG; □ PO; ■ TR. R^2 is indicated

put, and ultimately, greater recruitment (Moore et al. 2011). AT is more likely to act as a proximate factor when the tide is out (Helmuth et al. 2006b), leading to sub-lethal stress and even mortality due to extreme heat (Lima et al. 2016) or extreme cold (Lewis & Bowman 1975). Examination of regional patterns of air and seawater temperature across our study area and patterns of seasonal variation provide some insight into the drivers behind growth and mortality rates. For instance, we observed different patterns of both air and sea temperatures between the 2 leading edges of *P. depressa* (Fig. 2). As a warm-water species (Hawkins et al. 2008), milder winter sea temperatures have been shown to extend the reproductive season in *P. depressa* (Orton & Southward 1961, Moore et al. 2011) as well as stimulate individual growth and reduce mortality in limpets (e.g. for *P. vulgata*; Lewis & Bowman 1975, Bowman & Lewis 1986). In contrast, cold AT during winters can stunt normal growth and produce irreversible shell damage, which could lead ultimately to death (Lewis & Bowman 1975). Thus, higher growth rates recorded in limpet populations at the range edge of *P. depressa* in S/SE England may be a consequence of milder winter SSTs when compared with N Wales (Fig. 2e). In contrast, extreme low winter ATs in S/SE England, driven by continental weather systems (Lewis 1964, Hiscock et al. 2004), may be a direct cause of higher mortality rates (Fig. 2c). In addition, it is also worth noting that the region experienced 2 extreme climate events in 2015, with exceptionally cold ocean temperatures in the first half followed by the warmest summer sea temperatures on record in the last 65 yr (Duchez et al. 2016). The differential exposure of our study regions to the extreme climatic background (Lewis 1964, Hiscock et al. 2004, Robinson et al. 2017) may have contributed to blur the expected spatial pattern of individual performance (Pironon et al. 2017).

4.2. Density-dependent effects at species range limits

A combination of ultimate and proximate factors determines species distributions (Hawkins et al. 2019), which can set idiosyncratic species-specific geographic limits (Keith et al. 2011) and spatial patterns of performance (Gilman 2006). Our results showed a complex performance pattern across non-range-edge and marginal limpet populations. We found that, rather than having predictable patterns between range-edge and non-range-edge populations, performance was closely related with density. However, rather than density negatively affecting growth rate, individuals in denser populations grew faster. As expected, mortality increased with density. The same patterns were true for both *P. depressa* and *P. vulgata*. Essentially, both growth and mortality rates were positively correlated with limpet density across all locations. Thus, a higher density of limpets irrespective of species (i.e. locations with good conditions for breeding and recruitment) led to faster-growing but quicker-dying individuals.

Range-edge populations are typically characterised by low densities, which can lead to better individual performance as a consequence of release from intense competition for resources (Guo et al. 2005). For instance, Lewis et al. (1982) and Kendall & Lewis (1986) speculated that higher growth rates in *Steromphala umbilicalis* (formerly *Gibbula umbilicalis*) at the most northern locations in its range may be a consequence of lower intraspecific competition. In our study, higher growth rates of *P. depressa* and *P. vulgata* were found at locations with the highest limpet densities (i.e. S/SE England) despite both intraspecific and interspecific competition having been demonstrated in experimental enclosures for both limpet species (Boaventura et al. 2002a,b). These shores may have higher productivity than northern ones (Notman et al. 2016) with denser microbial film which features in the diet of both species (Hill & Hawkins 1991) or even stranded detritus on which *P. vulgata* will feed (Notman et al. 2016). Furthermore, gut contents of *P. vulgata* have shown many pelagic diatoms (Hill & Hawkins 1991), which may be trapped in limpet mucus laid on the rocks and then consumed on subsequent foraging excursions (Davies et al. 1992). Thus, food supply may be linked to offshore productivity (e.g. Hoch & Garreau 1998), with positive density-dependent growth occurring up until carrying capacity is reached. High mortality rates at the sites in S/SE England may ensure that this carrying capacity is not reached and hence resources are not limiting. These observations emphasise the importance of local to mesoscale features (e.g. Lima et al. 2006) as in populations of *P. depressa* in Portugal (see Silva et al. 2003). Between-site differences in temperature extremes (e.g. Seabra et al. 2016) as well as food supply (Jenkins et al. 2001) could override species performance patterns across non-range edges and marginal populations of limpet species (Helmuth et al. 2006a) and patterns one might expect as a consequence of density (Guo et al. 2005).

4.3. Growth patterns in patellid limpets

Neither *P. depressa* nor *P. vulgata* showed a reduction in growth rates from southern to northern populations, as Clarke et al. (2004) has described for other cold-water patellacean species of the genera *Nacella*, *Scutellastra*, *Cymbula* and *Acmaea*. Both measures of growth in both species (i.e. *K* values and Ø') were higher towards the range edge of *P. depressa* in S/SE England, and they reached almost the same growth performance in populations between SW England (~50°) and N Wales (~53°). Values of growth parameters (*K* and Ø') we found were lower when compared with other patellacean species

(Clarke et al. 2004), although it should be noted when making such comparisons that temporal and spatial scales used varied.

4.4. Conclusions

Our study has documented individual growth and population mortality rates in poleward co-occurrence zones between *P. vulgata* and *P. depressa.* A potential explanation for the heterogeneity we document comes from the spatio-temporal structure of both AT and SST (Lewis 1964, Hiscock et al. 2004, Robinson et al. 2017), potential density-dependent effects (Guo et al. 2005, Jenkins et al. 2008) in both limpet species and other location-specific environmental factors (Seabra et al. 2015, 2016, Lima et al. 2016) such as food supply (Jenkins et al. 2001) and predation pressure (Silva et al. 2008), which may override patterns of performance expected based purely on latitude. Moreover, very similar patterns were seen in both species at each individual locality, indicating primacy of local factors irrespective of species and their biogeographic affinities. Our work shows that to better understand and predict range expansions of marine organisms, comparative measures of individual and population performance at range-edge and non-range-edge locations can be valuable. Evidence to support lower species performance at range edges is limited (i.e. Sagarin et al. 2006, Dallas et al. 2017). This is especially the case in marine systems where mesoscale and local factors can lead to variation in both individual performance and recruitment, which can drive density-dependent population processes (e.g. Jenkins et al. 2008) including surprising instances of positive density dependence as we found here.

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Appendix.

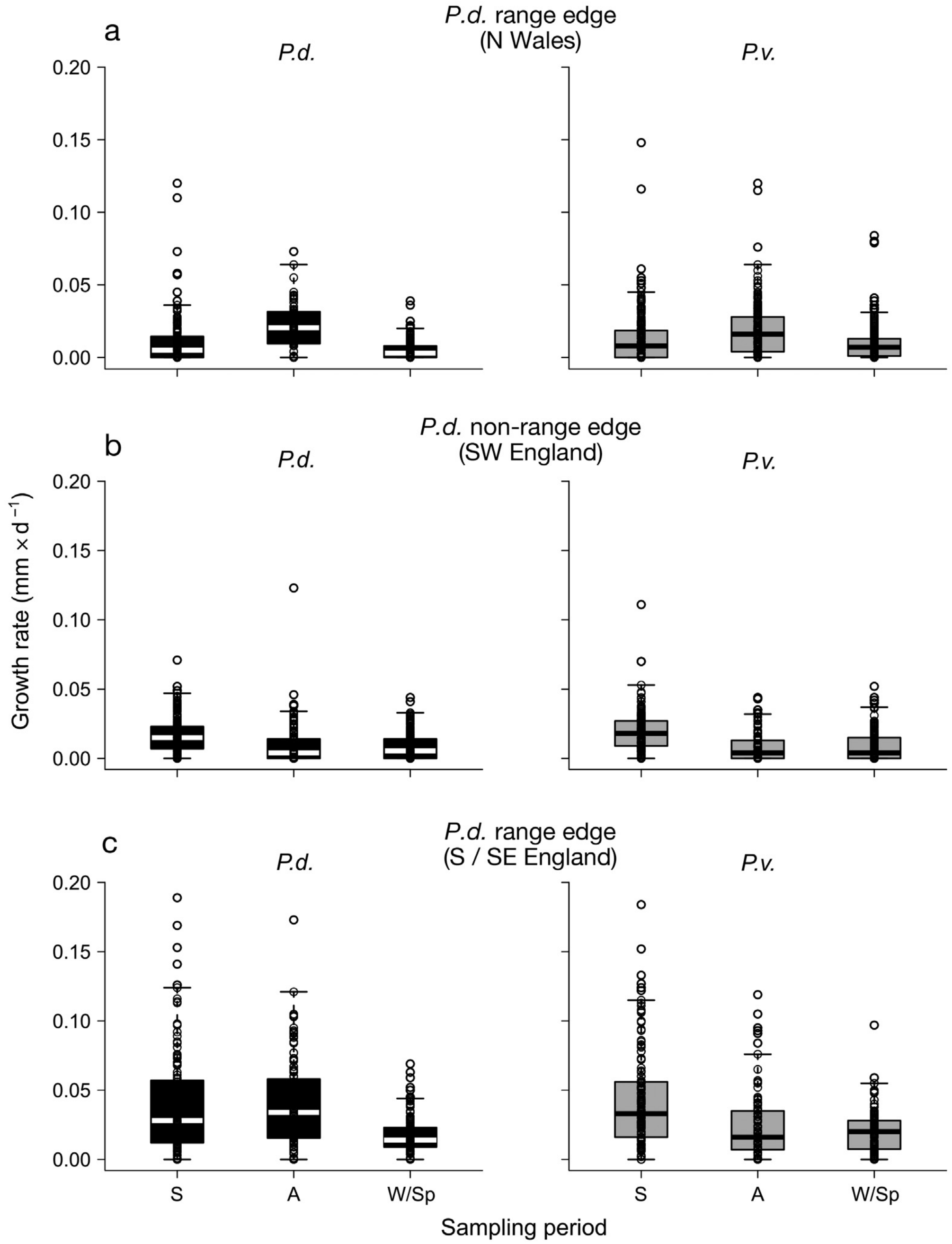

Fig. A1. Growth rates for *Patella depressa* (*P.d.*) and *P. vulgata* (*P.v.*) measured from June–July 2015 (t_0) to late May 2016 (t_3). There are 3 regions, defined by 2 range edges of *P.d.*, (a) North Wales and (c) South and South-east England, and by (b) non-range edge populations in South-west England. Sampling period indicates growth rates estimated during summer (S; t_0–t_1), autumn (A; t_1–t_2) and winter/early spring (W/Sp; t_2–t_3). Dots indicate individual growth rates for individuals less than 30 mm in length including those replaced because of mortality

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