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ORIGINAL ARTICLE

Early life-history processes and their implications for the invasion of the barnacle *Balanus glandula*

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ABSTRACT
As invasions become increasingly prevalent, it is important to understand how spread may be moderated by environmental conditions. This study considered the effect of location and changing substratum temperature on the early life-history processes of the alien barnacle *Balanus glandula* and its native comparator, *Chthamalus dentatus*, along the South African coast. Using settlement plates of different colours, temperature was manipulated to assess settlement, mortality, recruitment and growth of the two species. These variables were tracked over 10 weeks using repeat photography. Unexpectedly, there was no evidence of an effect of temperature on early life-history processes of either species. Settlement by the two barnacles was spatially segregated, with *B. glandula* occurring only on the West Coast where it is the dominant intertidal barnacle, while *C. dentatus* settled only on the South Coast, which has only recently been invaded by the alien. Despite this, it was notable that the relative settlement of *B. glandula* on rock was higher than that of *C. dentatus*. However, the lack of mortality of the native resulted in comparable levels of recruitment among the species. Nonetheless, the propensity of *B. glandula* to settle sporadically, coupled with fast growth, suggests that the invader may still possess the ability to become dominant along the newly invaded South Coast. This study highlights that measurements of early life-history parameters may not adequately predict the future range and impacts of alien species unless interpreted within the broader context of the nature of the recipient region and species-specific traits of the invader.

Introduction

Biological interactions such as competition and predation are well recognized as important structuring forces within intertidal communities (Dayton 1971; Gurevitch et al. 1992). Nonetheless, these biological interactions can be moderated by abiotic factors like wave exposure (Branch et al. 2010a), sand inundation (Littler et al. 1983) and temperature (Poloczanska et al. 2008). In light of warming trends in ocean temperatures in many regions (Bijma et al. 2013), the physiological and population-level implications of altered temperature regimes have received much attention (Harley et al. 2006). However, realized responses of species to changing temperatures are also dependent on the indirect effects that such changes have on the physiology, distribution, abundance and behaviour of other species with which they interact (Johnson et al. 2011; Wernberg et al. 2011).

Interspecific interactions are not restricted to those between native species and with rising rates of invasions (Ruiz et al. 2000), interactions among native and alien taxa are becoming increasingly common. As temperatures change and invasive species distributions shift, invasive species are placed in contact with new biota, resulting in novel interactions (Byers 2002; Shinen & Morgan 2009). As many invasive species are generalists and able to tolerate a broad range of environmental conditions (Sorte et al. 2010; Cockrell & Sorte 2013), there is a concern that changes in climate may favour alien species, placing further pressure on native biota (Byers 2002). As a result of these synergisms between changing temperature regimes and invasions, it has been suggested that the reorganization of biological communities is likely in the coming years (Walther et al. 2009), with greater homogeneity between and within biological systems (Doney et al. 2012; Sadchathswaran et al. 2015).

The acorn barnacle, *Balanus glandula* Darwin, 1854, is native to the Pacific coast of North America, but has invaded the cool temperate coasts of Japan

(Kado 2003), Argentina (Elías & Vallarino 2001) and South Africa (Laird & Griffiths 2008). On South African shores, this species is one of three dominant invaders that occur along the open coast (Sadchatheeswaran et al. 2015). Having been present since at least 1992 (Laird & Griffiths 2008), *B. glandula* is now the most abundant barnacle along the cool West Coast and has recently spread past the biogeographic break of Cape Point to the warmer South Coast (Robinson et al. 2015). This range extension has resulted in the barnacle moving into a region currently supporting well-established populations of native barnacles. One such barnacle is the toothed barnacle, *Chthamalus dentatus* Krauss, 1848. This species historically occurred along the whole South African coastline (Branch et al. 2010b) but, while initial surveys for *B. glandula* detected *C. dentatus* along the West Coast, albeit in low densities (Laird & Griffiths 2008), subsequent surveys have failed to record it (Pope 2015). It has been suggested that the dominance of *B. glandula* and concurrent reduction of *C. dentatus* is due to competition between the two species (Simon-Blecher et al. 2008). This therefore raises questions about the nature of potential competition between these barnacles, how such interactions might be altered under the warmer conditions of the South Coast, and how a continued trend of increasing air temperature in this region (Kruger & Shongwe 2004) may affect this interaction.

Within this context, this study aimed to elucidate the effects of location and varying substratum temperature on the settlement, mortality, recruitment and growth of *B. glandula* and *C. dentatus*. This will (1) provide insight into potential outcomes of the spread of *B. glandula* into the warmer South Coast waters and (2) provide a better understanding of how early life-history processes of these species may be altered by increases in substratum temperature that are expected to be associated with increasing air temperature.

Materials and methods

Sites where *Balanus glandula* and *Chthamalus dentatus* co-occurred could not be found, as *B. glandula* is the dominant barnacle along the West Coast and appears to have excluded *C. dentatus* within this range (Laird & Griffiths 2008). In contrast, the invasion of the South Coast by this alien is very recent (Robinson et al. 2015), with only very low densities of *B. glandula* occurring at sites where *C. dentatus* is also absent. As upwelling is known to influence barnacle recruitment (Pfaff et al. 2011), two West Coast sites within the Cape Columbine upwelling cell (i.e. Paternoster and Sandy Point) and two South Coast sites clustered within the Cape Hangklip upwelling cell (i.e. Rooiels and Cape Hangklip) were chosen (Figure 1). All sites experienced moderate wave action.

Following Lathlean & Minchinton (2012), at each site four treatments were used to manipulate rock temperature. Black, grey, white and clear granulated non-slip HW Aquac tape was secured onto clear PVC plates of 0.5 mm thickness using clear marine glue. As not all coloured tape was available with the same surface texture, clear tape was overlaid on all colours to standardize texture. This is important, as barnacles are sensitive to texture when settling (Savoya & Schwindt 2010). While black, grey and white plates were experimental treatments, clear plates acted as treatment controls (they were similar in colour to natural rock once overlaid), and natural rock quadrats acted as experimental controls. Six 10×10 cm plates of each treatment were randomly drilled into flat rock surfaces within the mid-shore zone. Plates were placed parallel with the underlying rock, but not against it so as to prevent conduction of heat from the rock surface to the plate. Additionally, six 10×10 cm natural rock quadrats were delineated at each site. All plates and quadrats faced north-west and were placed on surfaces orientated between 145° and 180°.

To validate differences in temperature among treatments (i.e. between black, grey, white and clear plates and bare rock), a digital infrared (IR) thermometer (Omega OS561) was used. To enable all measurements to be taken at the same time under the same conditions, rocks with a surface area of at least 0.0625 cm^2 and a depth of 10 cm were collected from each site. Prior to taking thermal readings, plates and rock
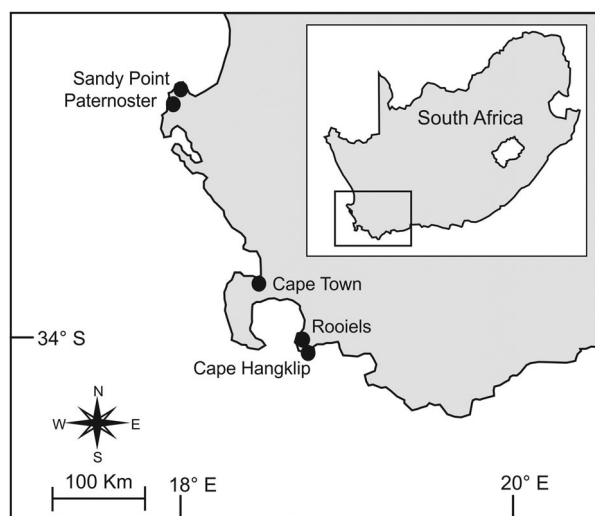

Figure 1. Location of sampling sites along the South African coast.

quadrats were orientated at 90° to the sun and allowed to warm for one hour. To minimize the effect of reflectance on readings, plates were shaded and all readings were taken 50 cm away from each plate at a 55° angle. The thermal resolution of the IR thermometer was 0.1°C and by recalibrating between measurements accuracy was ± 1°C. Emissivity (ε) (i.e. the measure of an object's ability to emit infrared energy) was set at 0.95, as rocky substrata and invertebrates in the intertidal zone often vary between 0.95 and 1.0 (Denny & Harley 2006). Readings were taken on two different days: the first was clear and sunny with a mean ambient air temperature of 27.1°C during the time of sampling, while the second day was cloudy with a mean ambient air temperature of 21.2°C. Five replicate readings were taken from three plates for each of the five treatments between 11h00 and 13h00 on each day. As no significant differences between readings from the triplicate plates/rock quadrats were detected for any of the treatments (ANOVA, $P > 0.05$ in all cases), readings were pooled to provide a total sample size of 15 readings per treatment. Temperatures of the treatment plates and rock quadrats were compared among treatments under warm and cool conditions using ANOVAs and Tukey HSD tests.

Photographs were taken of all plates at each sampling site every two weeks at low tide for 10 weeks from August to October 2013. These photographs were used to document the settlement, mortality, recruitment and growth of each species. Individual barnacles that settled on plates were numbered based on their positions and tracked through time. Settlement was documented by counting newly settled barnacles every two weeks. Mortality was considered as the loss of barnacles that had previously been present, and was quantified both as the density and percentage of barnacles lost during the experiment. Recruitment was defined as the number of live barnacles remaining at week 10. As the two barnacle species did not co-settle, data were analysed separately. Cape Hangklip was unavoidably excluded from all analyses due to extremely low settlement (i.e. only nine barnacles settled on experimental plates in total). For all analyses of settlement, mortality and recruitment West Coast sites were pooled (no effect of site, $P > 0.05$ in all cases), resulting in a sample size of $n = 12$ plates for *B. glandula*. For *C. dentatus*, the sample size was $n = 6$ plates due to the exclusion of Cape Hangklip. Settlement, mortality and recruitment per m^2 were compared among treatments using Kruskal–Wallis tests and Conover's test for multiple comparisons. To provide a measure of mortality that is comparable across treatments regardless of settlement, the percentage reduction in the number of barnacles due to mortality was also compared using Kruskal–Wallis tests and Conover's test for multiple comparisons.

Growth was assessed for individual barnacles that settled by week 2 and subsequently survived until week 6, as after this time mortality reduced the number of individuals meeting the above prerequisites to below the levels required for sound statistical analysis. The basal area (mm^2) of barnacles was measured from photographs using ImageJ software and was taken as a measure of total growth over the six-week period. To preclude effects of density-dependent impacts on growth, only individuals not touching other barnacles were included in this analysis. Basal area was compared among treatments using a Kruskal–Wallis test and Conover's test for multiple comparisons. All statistical analyses were conducted in R (v.3.0.1).

Results

Regardless of weather conditions, a significant effect of treatment on the temperature of experimental plates was evident (ANOVA, $P < 0.05$ in both cases) with black plates being hotter than grey, which in turn were hotter than white plates (Tukey HSD, $P < 0.05$ in all cases) (Figure 2). Under warm conditions, rock temperature was higher than that of clear plates at Rooiels (Tukey HSD, $P < 0.05$). Under cool conditions, no differences were found between rock and clear plates for any sites ($P > 0.05$).

The absence of *Chthamalus dentatus* from West Coast sites was confirmed as only *Balanus glandula* settled at Paternoster and Sandy Point. Here, settlement of the invader demonstrated a significant effect of treatment (Kruskal–Wallis, $\chi^2 = 10.83$, df = 4, $P = 0.029$). This was driven primarily by higher settlement on grey plates and lower settlement on rock ($P < 0.01$; Figure 3a), but with no differences found among the various temperature treatments. Settlement by *C. dentatus* displayed a similar pattern with an effect of treatment (Kruskal–Wallis, $\chi^2 = 14.23$, df = 4, $P = 0.007$) driven by low settlement on rock compared with all plates ($P < 0.01$; Figure 3b). Mortality of *B. glandula*, when quantified as the number of individuals lost per m^2, mirrored the pattern observed for settlement of this species (Figure 3c). Again, a significant effect of treatment was observed (Kruskal–Wallis, $\chi^2 = 13.97$, df = 4, $P = 0.007$) that reflected higher mortality on grey plates and lower mortality on rock (Figure 3c; $P < 0.01$), but with no differences found among the temperature treatments. When considering the percentage reduction in the number of
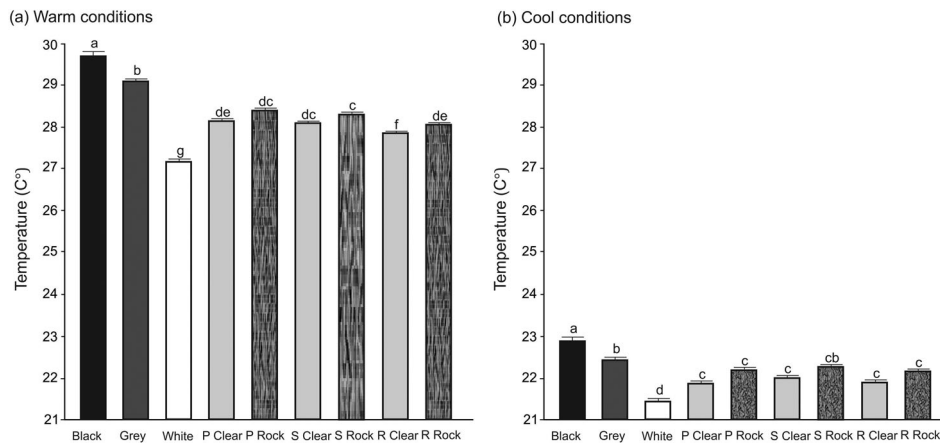
Figure 2. Mean temperature (°C; + SE) of treatment plates under (a) warm (air temperature 27.1°C) and (b) cool (air temperature 21.2°C) conditions. P = Paternoster, S = Sandy Point and R = Rooiels. Shared letters indicate no statistical difference ($P > 0.05$).

barnacles in each treatment, a difference was again found ($\chi^2 = 12.39$, df = 4, $P = 0.04$). However, when considering this mortality measure the highest loss was observed on rock (44%) and not on grey plates (29%). Notably pair-wise comparisons revealed no differences among treatments ($P > 0.05$). In contrast, mortality of *C. dentatus* was not affected by treatment regardless of the mortality measure used (Kruskal–Wallis, $P > 0.05$ in both cases; Figure 3d). It is important to note that this comparison among species excludes mortality on rock, because while mortality ranged between 46 and 94% on temperature treatments, no *C. dentatus* barnacles died on rock. As high levels of settlement by *B. glandula* on grey plates were matched by high levels of mortality, no effect of treatment was evident when considering recruitment after 10 weeks (Kruskal–Wallis, $\chi^2 = 5.75$, df = 34, $P = 0.219$; Figure 3e). Recruitment of *C. dentatus*, however, demonstrated variable and non-systematic effect of treatment (Kruskal–Wallis, $\chi^2 = 11.61$, df = 4, $P = 0.020$; Figure 3f), with lowest recruitment being recorded on rock.

Due to the differential settlement across the treatments and between the two species, the sample sizes used to assess growth were unavoidably variable. While growth of both species was found to vary among treatments (Kruskal–Wallis, $P < 0.005$ in both cases; Figure 4), there was a stark difference in variability between the invader and the native. Growth of *B. glandula* was most variable. Highest growth was recorded on grey plates and on rock, although high variability resulted in no statistical difference in the growth of individuals in these treatments and those on white plates (Figure 4a). A different pattern was observed for *C. dentatus*. The significant difference in growth among treatments for this species was driven

by higher growth on rock in comparison to all treatment plates (Figure 4b).

Discussion

As a result of sustained human movement and climate change, invasive species distributions are expected to shift and expand into new habitats, facilitating contact with previously unencountered native species (Hellman et al. 2008; Doney et al. 2012). While climate-driven temperature changes will act at the level of the individual by increasing physiological stress, impacts will also manifest at the population level due to effects on recruitment, mortality and growth rates (Findlay et al. 2010; Sorte et al. 2010; Lamb et al. 2014). In turn, these changes are likely to alter biotic interactions between invasive and native species (Helmuth et al. 2006; Shinen & Morgan 2009). It has been suggested that competition between the dominant invasive barnacle, *Balanus glandula*, and the native barnacle, *Chthamalus dentatus*, has caused an almost total loss of the indigenous barnacle along the West Coast of South Africa (Simon-Blecher et al. 2008). Within the context of rising temperatures and the recent spread of the invasive barnacle to the warmer South Coast where *C. dentatus* still occurs, this study aimed to investigate the effects of changing substratum temperature on the early life-history processes of these two species. We unexpectedly found no evidence of an effect of temperature on the early life-history processes of these two barnacles, suggesting that at least at the temperatures induced by our experimental plates, neither species was thermally constrained.

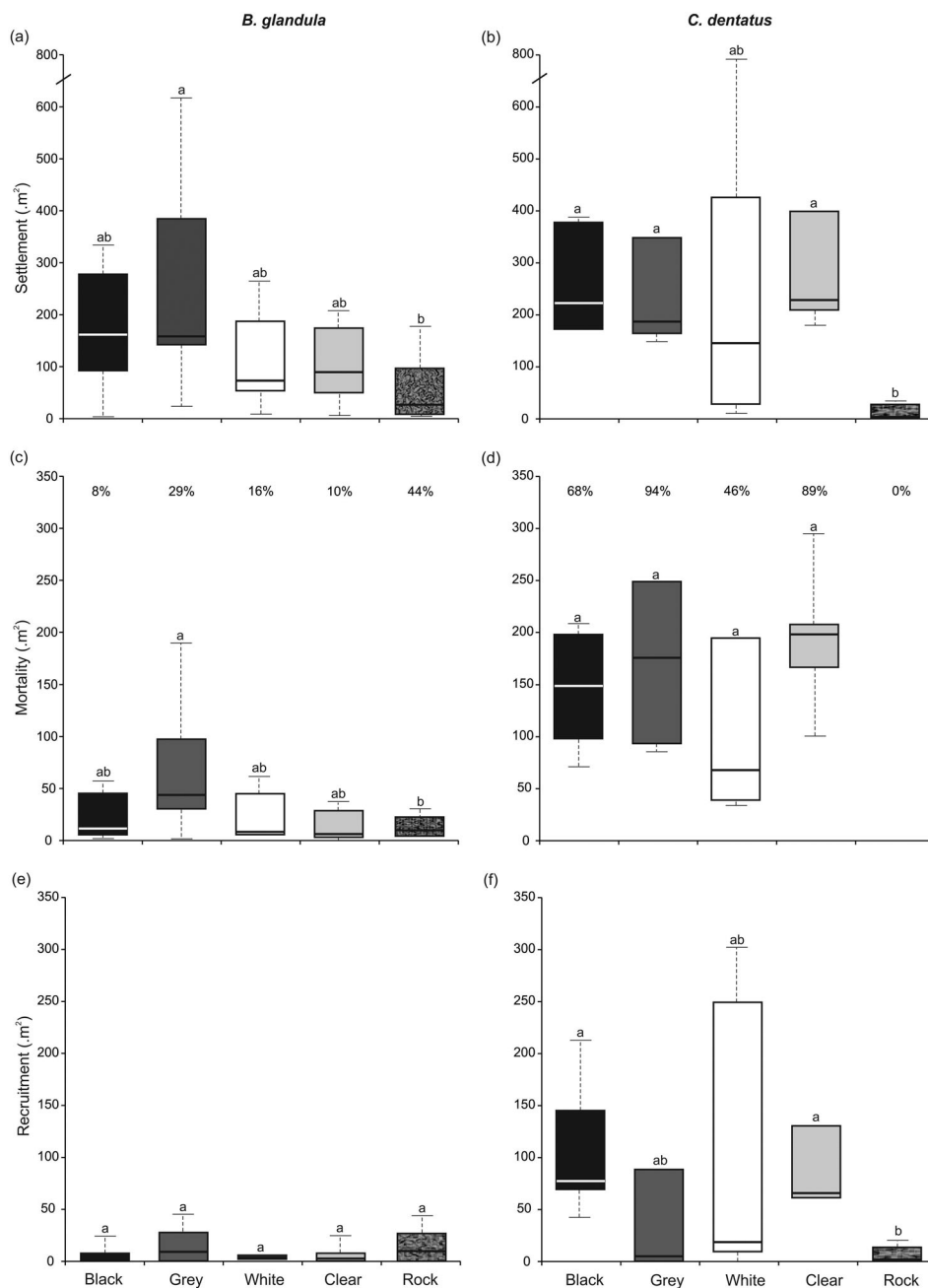While substratum temperature has been shown to influence the early life-history stages of various

Figure 3. Median (interquartile range, min and max) settlement (a,b), mortality (c,d) and recruitment (e,f) of *Balanus glandula* and *Chthamalus dentatus* recorded over 10 weeks. Shared letters indicate no statistical difference (*P* > 0.05). Percentages represent the per cent reduction in the median number of barnacles due to mortality.

intertidal organisms, including barnacles (Herbert & Hawkins 2006; Shanks 2009; Menge et al. 2010), no effect of temperature was recorded in the present study. Despite the treatment plates of different colours being found to differ in temperature during low tide conditions, the lack of a significant effect on either barnacle species could reflect one of two extremes. Either the temperatures of the settlement plates did not near the thermal limits of either species regardless of the colour (i.e. both barnacles

may have wide thermal tolerances), or the temperatures experienced on plates were so stressful that almost all barnacles were severely affected regardless of the treatment. While it is notable that the differences among temperature treatments in the present study are of a similar magnitude as those recorded by a study that detected an effect of temperature on the early life-history characteristics of the barnacle *Tesseropora rosea* Krauss, 1848 (Lathlean & Minchinton 2012), in the latter study temperatures sometimes exceeded
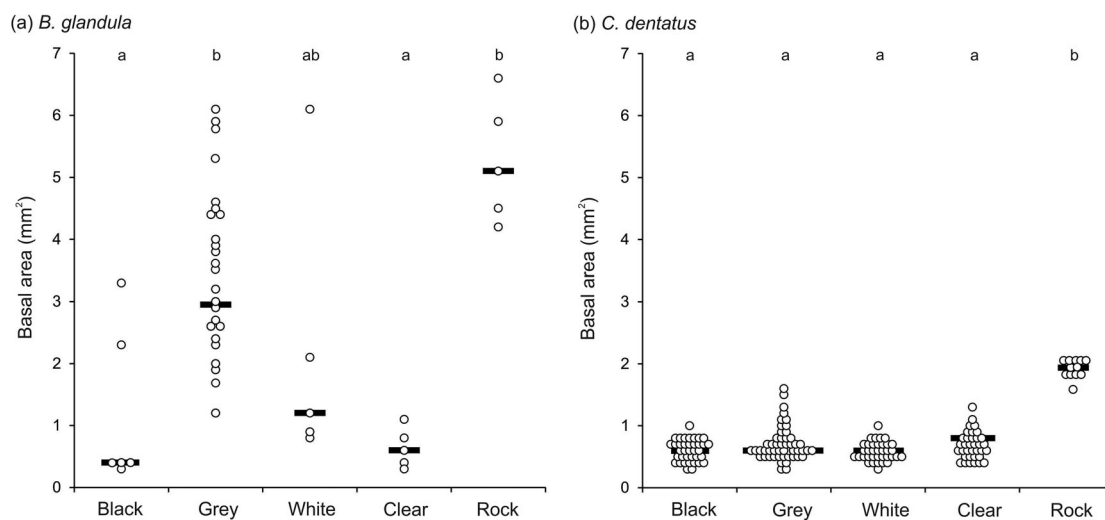
(a) *B. glandula*

(b) *C. dentatus*

Figure 4. Median (line) and raw measures (dots) of basal area (mm^2) of (a) *Balanus glandula* and (b) *Chthamalus dentatus* after six weeks.

30°C, with maximum temperatures on grey and black plates exceeding 32°C. This is in contrast to the work presented here, during which it is unlikely that treatments reached such high temperatures as the study took place in the spring of a year when air temperatures above 22°C were rare. This suggests that the temperatures induced may not have acutely, thermally challenged the barnacles, despite chronically exposing them to different temperatures. The lack of such acute temperature peaks may have dampened the differences among treatments and may ultimately explain why no evidence of an effect of substratum temperature was detected with respect to the early life-history processes of *C. dentatus* and *B. glandula*.

The elevated settlement of barnacles we observed on plates compared with natural rock, especially for *C. dentatus*, is a trend observed in previous studies (Menge et al. 2010; Lathlean & Minchinton 2012). It has been suggested that this could be representative of the increased surface texture of settlement plates compared with natural substrata (Menge et al. 2010) or differential biofilm communities that develop on different surfaces (Faimali et al. 2004). The fact that mortality (regardless of the measure used) and recruitment did not differ between treatment plates and rock for *B. glandula*, but notable differences were observed for *C. dentatus*, is interesting. Most noteworthy was the fact that *C. dentatus* experienced no mortality on rock despite high mortality on experimental plates, this despite predatory whelks being observed on both substrata. While the reasons for these differences are not clear, these findings highlight the potential for inter-specific differences in responses in early life-history processes, even in morphologically similar species.

While the fact that the two species under consideration did not settle at the same locations precludes direct statistical comparisons, insights can be gained from considering the trends displayed by each barnacle on rock. Although *B. glandula* had comparatively higher settlement on rock than *C. dentatus*, mortality removed almost half of these barnacles, with subsequent low levels of recruitment into the population. In contrast, *C. dentatus* experienced lower settlement but no mortality on rock, resulting in comparable levels of recruitment among the two species. While these results may appear to suggest that these species could co-exist in equal abundances along the newly invaded South Coast, three factors may moderate this outcome. Firstly, differential growth may be influential. The growth recorded in this study indicates that *B. glandula* reached roughly double the size of *C. dentatus* in the first six weeks post-settlement. Although these results do not reflect growth of the species when co-occurring, it is likely that *B. glandula* has even faster growth on the South Coast as it is under these conditions that the alien has its highest algal uptake rates (Pope et al. 2016). Thus, the present results suggest that *B. glandula* could well convert these elevated feeding levels into increased growth on the South Coast, offering it a competitive advantage over native barnacles. Secondly, barnacle recruitment is notoriously variable (Bonicelli et al. 2014; Rognstad et al. 2014). In fact, recruitment by *B. glandula* has been found to vary between 2 and 785 individuals per m^2 at a single site over a three-year period (Tamara Robinson, personal observations, 2013–2015). In contrast, *C. dentatus* recruitment varied between 0 and 72 individuals per m^2 over the

same period (Tamara Robinson, personal observations, 2013–2015). This suggests that in times of high recruitment, *B. glandula* may gain dominance of the primary substrate, pre-emptively outcompeting *C. dentatus*. This mechanism of competitive dominance has been reported for this barnacle in its Japanese invaded range (Kado 2003), as well as for other invaders that occupy primary rock space (Steffani & Branch 2003). Finally, phenotypic plasticity can vary within species even at scales of hundreds to thousands of kilometres (Sorte et al. 2011), a process often noted in relation to invasive species (Engel et al. 2011). As such, should *B. glandula* spread along the South Coast, individuals could display variability in thermal responses that may provide the species with a competitive advantage over native barnacles.

While further research is needed to confirm these findings, it appears that *B. glandula* may in fact possess the ability to become dominant along the newly invaded South Coast. This study highlights the fact that measurements of early life-history parameters alone may not adequately predict the future distribution and impacts of alien species. Answers to such complex questions are likely to come through the coupling of robust field experiments and sound laboratory investigations.

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