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Both like it hot? Influence of temperature on two co-occurring intertidal barnacles in central Chile

Emily A. Lamb [a,b], Heather M. Leslie [b], Jennifer L. Shinen [a,*]

[a] Estación Costera de Investigaciones Marinas, Pontificia Universidad Católica de Chile, Casilla 114-D, Alameda 340, Santiago, Chile
[b] Dept. of Ecology and Evolutionary Biology & Center for Environmental Studies, Brown University, Box 1943, Providence, RI 02912, United States

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ABSTRACT

Jehlius cirratus and *Notochthamalus scabrosus*, two chthamalid barnacles common to the upper rocky intertidal coast of Chile, often overlap extensively in their vertical distribution, with *Jehlius* extending slightly higher on the shore. Previous studies examining competition between *Jehlius* and *Notochthamalus* have come to differing conclusions regarding the nature and direction of their relationship within a hierarchy for space, but together suggest that temperature may play an important part in meditating their competitive interactions. Here, we address the role of temperature during emersion on *Jehlius* and *Notochthamalus* via species-specific responses in abundance, growth and reproduction to varying thermal conditions during tidal emersion. Results from a shading experiment conducted at two high intertidal elevations indicated that both species responded similarly to reduced temperatures in terms of abundance and space occupation. Growth rates differed between species, however, suggesting that *Notochthamalus* may be more limited by higher temperature than *Jehlius*, but growth rates of both species were similar under the warmest (high zone, unshaded) and coolest (mid zone, shaded) treatments. Although we found a greater proportion of *Notochthamalus* individuals brooding eggs in unshaded control areas (where sample size allowed analysis) and greater numbers of *Jehlius* individuals brooding under shades, no differences in reproductive output (egg mass) were found among brooding individuals between shading treatments and tidal elevation for either species. Overall, we found no evidence of temperature mediated tradeoffs in performance between adult *Jehlius* and *Notochthamalus*. Instead, our results indicate a lack of a strong competitive hierarchy between *Jehlius* and *Notochthamalus* and suggest that temperatures experienced during emersion may reinforce vertical patterns of adult abundance established during settlement.

1. Introduction

Temperature is frequently a key determinant in marine community structure (Harley, 2008) and is inversely related to the upper limit of many sessile organisms, particularly in intertidal systems (Mathieson et al., 1998). However, its role in the rocky intertidal is often complex, affecting not only species' physiology but also their distributions (e.g. Crisp et al., 1981; Helmuth and Hofmann, 2001; Southward, 1958), survival (Gedan et al., 2011) and potentially their interactions with other species (Broitman et al., 2009). Interspecific interactions across larger geographic ranges can also change depending on the combination of physical characteristics of a site (Hawkins et al., 2009; Sousa et al., 2000). Additionally, non-parallel or decoupled species' responses to changing temperatures may change the frequency or intensity of species interactions, which in turn may have dramatic effects on abundance and distribution of species. For example, Morelissen and Harley (2007) found that experimentally altered temperatures affected producers in a distinct manner from consumers across their ranges of co-occurrence. The overall effects of global temperature change or projected long-term temperature increases will depend not only on species' responses to environmental characteristics throughout their various life history stages, but also how communities as a whole respond.

Intertidal barnacles, in particular, could be especially sensitive to temperature increases as they may already be living at the limit of their thermal stress tolerance (Berger and Emlet, 2007; Bertness, 1989; Southward and Crisp, 1954). Indeed, barnacle distributions on rocky shores and the role of physical stress in setting those patterns have received considerable attention (e.g., Berger and Emlet, 2007; Bertness, 1989; Gedan et al., 2011; Harley and Helmuth, 2003; Southward, 1958; Wethey, 1983, 1984a), however much of this work focused on either a single life history stage (i.e. Harley and Helmuth, 2003; Wethey, 1983 1984a) or a single species in an established competitive setting (i.e. Bertness et al., 1991; Gedan et al., 2011; Leslie, 2005; but see Dayton, 1971; Menge, 2000 for exceptions). Just as in the rocky intertidal community more broadly, temperature often plays complex and varied roles in the determination of population distributions, vital rates, and intraspecific interactions of barnacles. For instance, Bertness (1999) found that greater adult densities enhanced individual

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* Corresponding author. Tel.: +56 352431670.
E-mail address: jlshinen@bio.puc.cl (J.L. Shinen).

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Semibalanus balanoides survivorship, but only at warmer sites. Varying temperatures can also change the outcome of interspecific competition. In his 1983 study, Wethey found that at cooler sites the competitively dominant barnacle was able to exclude the competitively inferior species, present at warmer sites, from the entire barnacle zone.

In central Chile, two barnacle species co-occur extensively on the upper-most portion of wave-exposed rocky shores, *Jehlius cirratus* and *Notochthamalus scabrosus* (hereafter *Jehlius* and *Notochthamalus*). The vertical distributions of *Jehlius* and *Notochthamalus* overlap extensively (Shinen and Navarrete, 2010), but *Jehlius* is present in greater abundance in the highest portion of the barnacle zone whereas, *Notochthamalus* occurs in greater abundance in the lower portion of the barnacle zone. Intriguingly, previous studies addressing the competitive mechanisms maintaining the patterns of zonation between these two barnacles, each conducted at single locales of varying latitude along the coast of central Chile, arrived at conflicting conclusions. At warmer, centrally located sites, Paine (1981) found not only that mixed-species patches tended towards *Jehlius* dominance over time, but also that *Jehlius* overgrew adjacent *Notochthamalus* individuals 100% of the time. At a cooler southerly site, López and González (2003) found that the presence of *Notochthamalus* increased the mortality rate of *Jehlius* and suggested that *Notochthamalus* was competitively inhibiting *Jehlius*. More recently at a latitudinally intermediate locale, Shinen and Navarrete (2010) followed adult individuals of both species at several tidal elevations and found that growth and mortality rates were similarly affected by inter- and intraspecific crowding, suggestive of competitive equivalence. Although none of these studies specifically addressed nor controlled for physical characteristics, together, they suggest that environmental conditions that often vary widely among sites separated by 100s to 1000s of kilometers, such as temperature, may mediate interspecific interactions between *Jehlius* and *Notochthamalus*. Additionally, each of the prior studies focused on either a single species (López and González, 2003) or a single life stage (Paine, 1981; Shinen and Navarrete, 2010) thereby potentially limiting their ability to fully understand the effects of temperature on these two species. Understanding the influence of thermal regimes at multiple life stages is essential to fully understand the complex ways species interactions are mediated by physical conditions (Helmuth et al., 2006; Wernberg et al., 2010).

Here we investigate how varying aerial temperature during exposure at low tide may mediate the growth, space occupation, and reproductive potential of *Jehlius* and *Notochthamalus* in central Chile (33° 31′ S; 71° 37′ W). This experiment first quantifies the thermal differences between the high barnacle zone and the mid barnacle zone (described in Section 2.1). Then, through experiments where we reduced emersion temperatures by shading barnacles in situ, we evaluated how changes in temperature affect the vital rates of *Jehlius* and *Notochthamalus*. Finally, we consider the role of temperature across a competitive gradient as well as throughout several life history stages of both *Jehlius* and *Notochthamalus*, providing new insight into the dynamic coexistence of these two ecologically important species.

2. Methods

2.1. Study system

The study was conducted on the central Chilean coast within *Estación Costera de Investigaciones Marinas* (ECIM), a no-take marine protected reserve associated with *Pontificia Universidad Catolica de Santiago*. It is an upwelling driven, wave-exposed site with a semidiurnal tidal cycle and a tidal range of ca. 1.8 m (Finke et al., 2007; Navarrete et al., 2005). The site is also characterized by high recruitment rates of both *Jehlius* and *Notochthamalus* (Shinen and Navarrete, 2010) that peak for both species twice a year in early spring and in late summer, with very low recruitment in between (Navarrete et al., 2008). *Jehlius* and *Notochthamalus* are small chthamalid barnacle species. Adults achieve similar maximum sizes of 15–20 mm rostrocarinal length and remain under 15 mm of height (Venegas et al., 2000).

Jehlius and *Notochthamalus* dominate the highest tidal elevation while mytilid mussels and macro-algae dominate the lower tide heights. While barnacles are readily preyed upon by a suite of predators in the mid and low intertidal zones (Castilla and Paine, 1987; Navarrete and Manzur, 2008), few benthic predators prey on them in the higher tidal elevations where this study was conducted (Castilla, 1981). For the purpose of this study the highest intertidal zone, or “barnacle zone,” was subdivided into two zones: high and mid. What we classified as the high barnacle zone is dominated by *Jehlius* and stretches from the upper limit of barnacles at the edge of the “splash zone” to what we classify as the mid barnacle zone, where *Notochthamalus* occurs in equal abundance with *Jehlius* (see Shinen and Navarrete, 2010, for zonation details).

2.2. Experimental manipulation of thermal conditions

To investigate the effect of emersion temperature on the growth, cover and reproductive output of *Jehlius* and *Notochthamalus*, we shaded ten 10 × 10 cm plots in each of the high and mid barnacle zones. Shading was accomplished with plastic mesh and shade-cloth installed 5 cm above the rock surface of the plots, creating “rooftops” with all sides open facilitating water flow. All experimentally shaded areas had similar total barnacle cover (~50%) at the start of the experiment. Ten control areas (unshaded 10 × 10 cm plots) of similar total barnacle cover were selected in each barnacle zone from an ongoing study of the same species (Shinen and Navarrete, in press). Since we could not create roof controls without causing unintentional shading (Harley and Lopez, 2003; Hayworth and Quinn, 1990), additional treatment controls were not included. However, given the constant wave action characteristic of our study site (Finke et al., 2007) and the extended height of our roofs, we feel that any potential artifacts affecting water flow and food supply were minor. In order to avoid confounding effects of shading on settlement processes or affecting settlement directly, roofs were installed in the late summer after the final peak of barnacle settlement. Photographs were taken approximately bi-monthly of all plots from February to August 2010 with a Pentax Optio W30 digital camera. This sampling schedule allowed us to follow the fate of established adult barnacles and the spring/summer cohort of new recruits exposed to high aerial temperatures at the end of the austral summer season up until the peak reproductive season of the following early spring.

In order to characterize thermal conditions in each zone and the efficacy of the experimental shading treatment, we monitored rock temperatures over the course of the study. Two approaches were used. A temperature logger (Onset Tidbit loggers) was installed directly to the unshaded rock surface in both the high and mid barnacle zones, each of which recorded ambient temperature at ten minute intervals over the course of the study, providing a profile of the thermal conditions at each intertidal elevation. To quantify the effectiveness of our shading treatments, infrared temperature readings (KINTRIX IRT0401 Infrared Thermometer) of rock surfaces underneath shaded plots and of the unshaded control plots every 1–2 months during afternoon low tides on both sunny and cloudy days. A minimum of three infrared temperature readings were made of each plot and in all cases readings were taken approximately 3 cm above the plot at an angle of 90° to the rock surface.

2.3. Analysis of reproduction

Samples for reproductive analysis were taken in August 2010 and stored in 70% alcohol until January 2011 when they were processed following a standard protocol (M. Fernandez, *pers com*). Because chthamalid barnacles do not have a basal plate, individuals attached directly to the rock were chiseled out of shaded plots and stored in alcohol until dissection. Only individuals that remained intact after removal from the rock were used for analysis to ensure that no part of the gonad was missing. Control (unshaded) samples were taken in the same manner as shaded plots but from areas adjacent to, not within, the control plots so as not to disrupt the ongoing study. Individuals were dissected to quantify the proportion of adult barnacles brooding egg masses of each species across the treatments. The soft body and egg masses of each reproductive individual were dried and weighed to calculate reproductive output, calculated as the ratio of the egg mass weight to the weight of the soft body parts of an individual.

2.4. Data analysis

Photographs of plots were analyzed using ImageJ (National Institutes of Health, USA, 2009). Abundance and percent cover of adult individuals of both species, which are readily identified by their distinctive opercular plates in the photographs, were obtained from each plot. Recruits, which were classified as individuals too small to be identified to the species level (rostro-carinal length < 1.0 mm), were also counted within the plots as both *Jehlius* and *Notochthamalus*, pooled. Recruits were not included in estimates of space occupation. Photographs of control and manipulated plots were taken on separate days, so we standardized changes in abundance and percent cover by time (days elapsed). Estimates of species-specific growth rates were obtained by subtracting the initial from the final opercular rostro-carinal length of ca. 50 adult individuals of each species, per zone and shading treatment (selected randomly from the final set of photos) and standardized by total days elapsed. Rostro-carinal growth rates have been shown to be a density independent measure of growth (López and González, 2003; Shinen and Navarrete, 2010).

2.5. Statistical analysis

All analyses were conducted with JMP 7.0 (SAS Instit. 2007). Infrared rock temperatures were compared in shaded and unshaded areas using a one-way fixed factor ANOVA. We used two-way fixed factor ANOVAs to assess how barnacle growth rates varied as a function of barnacle zone and the experimental shading treatment for each species. Total changes in cover of adult barnacles were log transformed in order to meet the requirements of ANOVA and then analyzed in the same manner as growth data. Similar two-way fixed factor ANOVAs were also used to assess total change in adult barnacle abundances. To assess any changes in the numerical dominance of species within plots, we used one-way fixed factor ANOVAs to compare initial and final proportions of barnacle abundance (J:N = number of *Jehlius*/total barnacle abundance) under the different shading treatments and in both barnacle zones. Changes in recruit abundance based on barnacle zone and shading treatment were compared using a two-way fixed factor ANOVA. A two-way fixed factor ANOVA was used to compare reproductive output of *Jehlius* by barnacle zone and shading treatment. Due to the low sample size of reproductive *Notochthamalus* individuals in the high zone, single factor ANOVA was used to compare how the reproductive output of individuals varied by shading treatment in the mid barnacle zone only. Reproductive output data was log transformed to meet the requirements of ANOVA. Tukey HSD tests were used to conduct post hoc multiple comparisons among the treatment groups ($p < 0.05$).

3. Results

3.1. Temperature observations

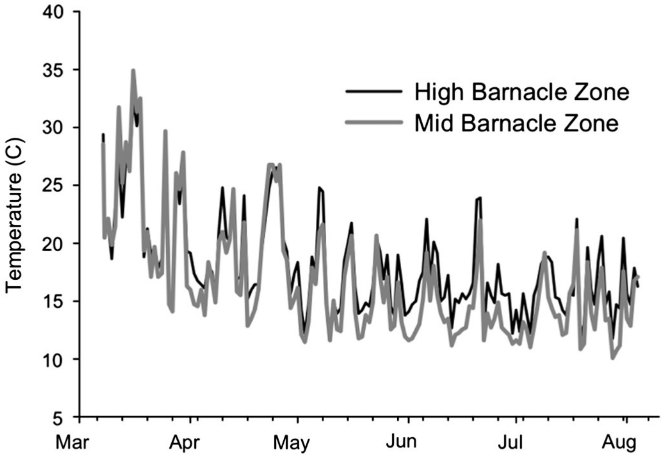

Fig. 1. Daily maximum temperatures recorded in the high (black) and mid (gray) zones.

Temperature monitoring from March to August 2010 revealed that on average, high barnacle zone daily maximum rock temperatures were 1.4 °C (±SD 0.12; note that the error range for Onset Tidbit loggers is ±0.4 °C) warmer than the mid zone temperatures (Fig. 1). Mean temperatures outside of shaded plots, measured with infrared temperature sensors, were 1.6 °C (±SD 0.27) warmer ($F_{1,94} = 4.21$, $p = 0.043$) than temperatures inside shaded plots on sunny days in both barnacle zones. On cloudy days there was no significant difference in temperatures within and outside of the shaded plots ($F_{1,116} = 1.28$, $p = 0.26$).

3.2. Tidal elevation and shading effects on barnacle abundance and cover

Tidal elevation affected final abundance of both species, with little to only slight decreases in the high barnacle zone and increases in abundance in the mid barnacle zone ($F_{1,38} = 5.18$, $p = 0.029$ for *Jehlius*, $F_{1,38} = 77.45$, $p < 0.0001$ for *Notochthamalus*, Table 1). For *Jehlius*, changes in abundance were highly variable both inside and outside the shaded areas (Fig. 2a), thus we ultimately found no shading effects on changes in adult abundance in either intertidal zone (Table 1). Nevertheless, certain trends were observed. In the high barnacle zone, *Jehlius* abundance tended to increase when shaded, whereas in unshaded controls *Jehlius* abundance tended to decrease. Changes in *Notochthamalus* abundance in the high zone were essentially zero in the high zone. A Tukey HSD test ($p < 0.05$) indicated that the total change in abundance in the mid barnacle zone unshaded areas was significantly less than the shaded treatments in the same zone, but greater than the total change in both high barnacle zone treatments.

Changes in percent cover were generally consistent with the changes in barnacle abundance despite high variability among plots (Fig. 2). Neither significant effects of shading nor interactions among main effects were detected for either species (Table 1). In the mid zone, where both species responded similarly, cover increased over the course of the experiment. In the high barnacle zone however, *Notochthamalus* experienced little to slightly positive changes in cover whereas *Jehlius* tended towards a decrease in cover.

The relative proportions of the *Jehlius* and *Notochthamalus* did not change over the course of the study in the high barnacle zone, regardless of shading treatment ($F_{1,18} = 1.12$, $p = 0.3051$ for controls; $F_{1,19} = 0.46$, $p = 0.5068$ for shaded plots; Fig. 3). In the mid barnacle zone, however, control plots showed a decrease in the relative proportion of *Jehlius* ($F_{1,19} = 5.51$, $p = 0.03060$), while shaded plots remained unchanged ($F_{1,16} = 0.09$, $p = 0.7745$).

Recruit abundance decreased under both shaded and unshaded conditions and in both zones (Fig. 4), reflecting a combination of mortality of recruits over the course of the experiment and growth of small individuals into identifiable adult size classes. While the experimental shading treatment did not affect changes in recruit abundance ($F_{1,35} = 0.473$, $p = 0.49$), plots in the mid barnacle zone experienced larger decreases in recruit abundance ($F_{1,35} = 6.44$, $p = 0.015$) than those in the high barnacle zone (Table 2).

Table 1
Results from 2 way fixed factor ANOVAs showing changes in total adult abundance and percent cover for *Jehlius* and *Notochthamalus* between March and August 2010. Bold text indicates p values less than 0.05.

Response	Species	Source	df	MS	F	p
Abundance	*Jehlius*	Zone	1	3.722	5.183	**0.029**
		Shading	1	0.407	0.5668	0.456
		Zone × shading	1	4.707	6.556	0.0149
		Error	35	0.7181		
	Notochthamalus	Zone	1	1.711	77.45	<**.0001**
		Shading	1	0.8563	38.75	<**.0001**
		Zone × shading	1	0.8611	38.96	<**.0001**
		Error	35	0.7734		
Percent cover	*Jehlius*	Zone	1	0.0001166	5.317	**0.0272**
		Shading	1	0.00000049	0.0225	0.881
		Zone × shading	1	0.00001037	0.4728	0.496
		Error		0.000022		
	Notochthamalus	Zone	1	0.00001075		**0.0013**
		Shading	1	0.00000030		0.563
		Zone × shading	1	0.00000030		0.562
		Error	35	0.00003038		

3.3. Shading effects on growth

Overall, growth rates of both *Jehlius* and *Notochthamalus* reflected similar responses to tidal elevation and shading treatment (Fig. 5). Among adult *Jehlius* individuals, growth rates varied significantly with the experimental shading treatment ($F_{1,181} = 8.56$, $p = 0.0039$, Table 3). For *Notochthamalus*, higher growth rates were observed in both the high barnacle zone ($F_{1,71} = 7.59$, $p = 0.0075$) and in shaded plots ($F_{1,71} = 18.7$, $p < 0.0001$). Moreover, a Tukey HSD test ($p < 0.05$) showed the growth rates of *Notochthamalus* in the high zone shaded plots to be higher than all of the other shading × zone treatments. Although measures of growth rates of each species are not independent and cannot be statistically compared, we observed that individual *Notochthamalus* generally grew twice as fast as *Jehlius* in the

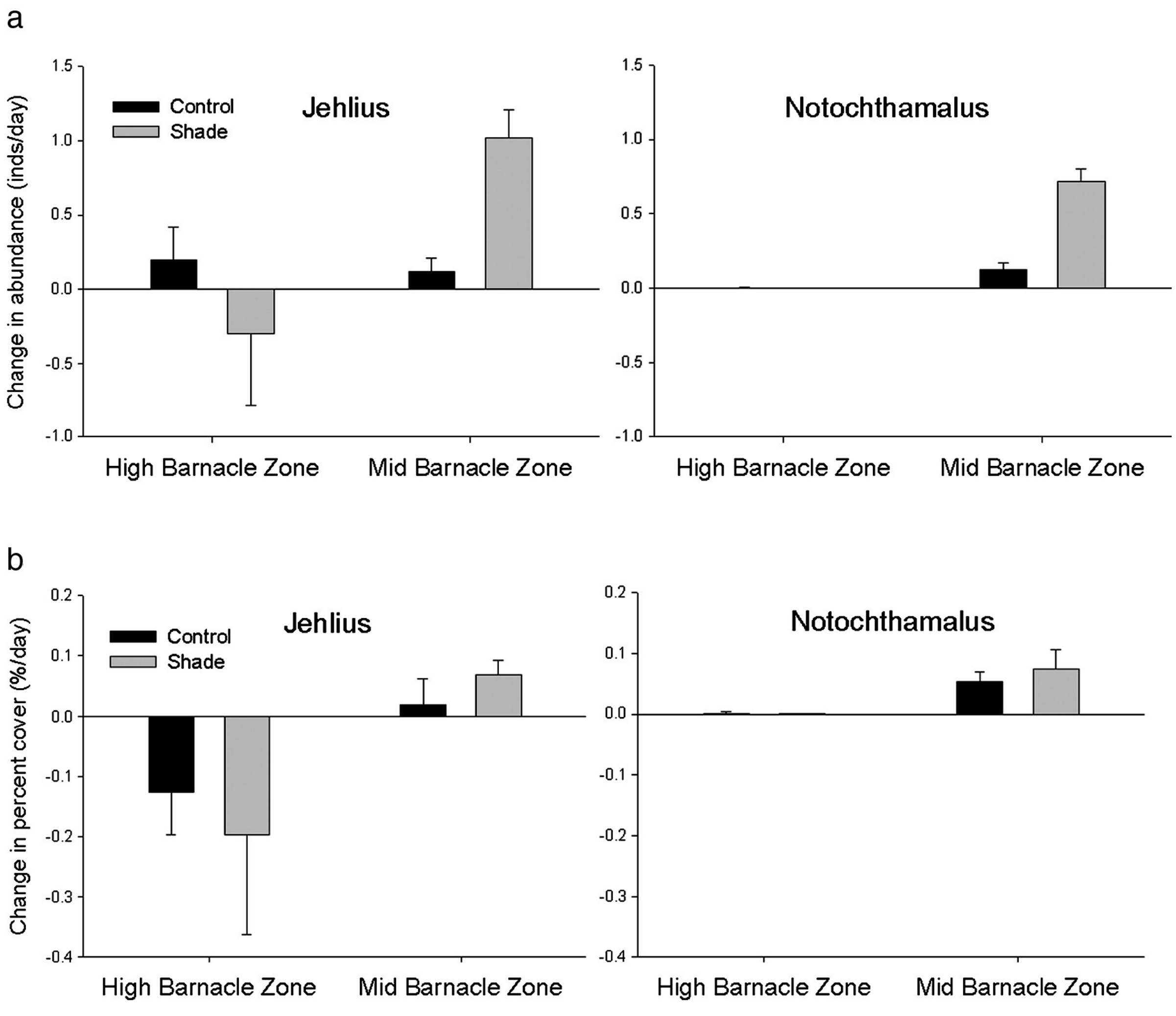

Fig. 2. Mean change in (a) abundance (+SE) and (b) percent cover (+SE) of *Jehlius* and *Notochthamalus* in both barnacle zones over the course of the study.

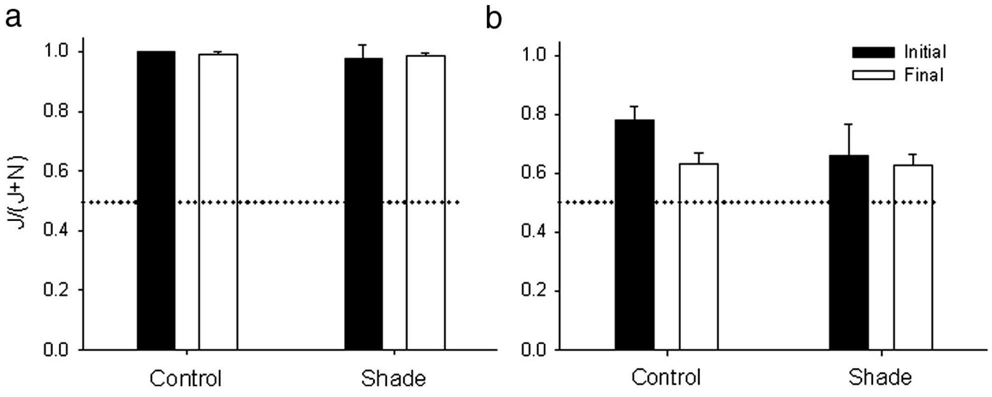

Fig. 3. Mean proportion of *Jehlius* individuals (J) to total individuals (J + N) in the high (a) and mid (b) barnacle zones and the beginning and end of the study.

high zone shaded plots, whereas within the unshaded plots both species grew at similar rates. In the mid barnacle zone, adult *Jehlius* growth rates in the unshaded control plots were higher than mid barnacle zone control *Notochthamalus* growth rates (Fig. 5).

3.4. Shading effects on reproduction

Removal of rock chips for reproductive samples was highly destructive, and as a result we were not able to obtain equal sample sizes of both species. Overall, we sampled more *Jehlius* than *Notochthamalus* at both tidal elevations, however, a greater number of *Notochthamalus* individuals were found brooding eggs. Very few *Notochthamalus* individuals were present in the high barnacle zone and fewer still were successfully removed for reproduction analysis. Although we've presented the results of both species from the high barnacle zone for reference, we have limited our analyses and interpretation of *Notochthamalus* to the mid barnacle zone, where we obtained a large enough sample size. Among the *Jehlius* individuals sampled, a greater proportion of unshaded individuals were reproductive than shaded individuals — in both the mid and high barnacle zones (Fig. 6). In contrast, we found a greater proportion of brooding *Notochthamalus* individuals in shaded than unshaded areas in the mid barnacle zone. Despite differences in the proportion of individuals brooding in the mid barnacle zone, there were no significant differences in reproductive output (egg mass/total body mass) among brooding *Notochthamalus* individuals based on experimental shading treatment ($F_{1,20} = 0.801$, $p = 0.38$). *Jehlius* individuals similarly did not show differences in reproductive output based on experimental shading treatment ($F_{1,6} = 3.18$, $p = 0.12$) or barnacle zone ($F_{1,6} = 0.666$, $p = 0.44$).

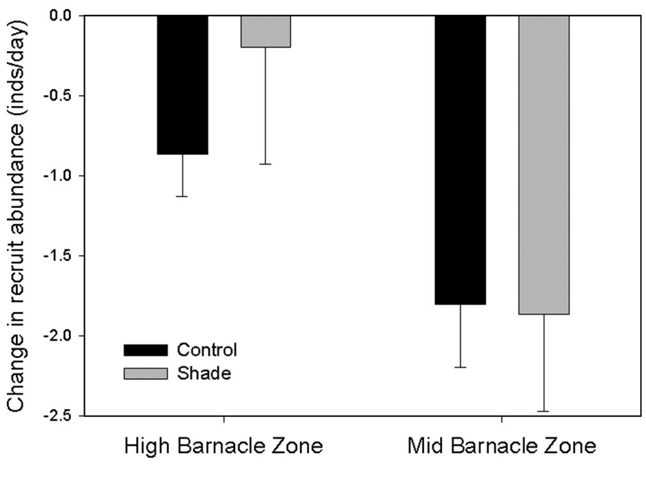

Fig. 4. Mean change in abundance of recruits (+SE) in the high and mid barnacle zones over the course of the study.

4. Discussion

Overall, our results suggest that warmer emersion temperature affects adult abundance and cover similarly for both species and may not be an important determinant of the slightly off-set distribution pattern of *Notochthamalus* and *Jehlius*, at least over the short term. At an individual level however, warmer temperatures during tidal emersion periods may be an important factor influencing growth and reproduction, which over time, may have important consequences for space occupation. Among plots, mean *Notochthamalus* growth rates were always higher in shaded conditions than in unshaded conditions, regardless of barnacle zone, suggesting that this species' growth is limited by temperature at both tidal elevations. Growth of *Jehlius* however, was only limited by temperature at the highest elevation, evidenced by higher growth rates under shaded conditions in only the high barnacle zone whereas in the mid barnacle zone *Jehlius* growth rates were equivalent inside and outside of shaded plots. The variable effect of shading on the growth rates of the two species implies that *Jehlius* and *Notochthamalus* have different physiological responses to emersion temperature, and perhaps emersion time, phenomena found frequently among intertidal organisms (Somero, 2002). These results are consistent with past work demonstrating *Jehlius* to be very tolerant of warm temperatures and to have a high capacity for aerial respiration, which helps it thrive in the high barnacle zone (Castro et al., 2001).

Recruit abundance decreased in shaded and unshaded plots and in both zones, with greater reduction in recruit abundance in the mid barnacle zone. Because we followed the fate of an entire cohort of recruits (*Jehlius* + *Notochthamalus* species, pooled) rather than the fate of individual recruits, changes in recruit abundance represent both recruit mortality and the growth of both species into adult size classes. Once any surviving individuals were large enough to be identified to the species level, they were included in species-specific estimates of adult abundance and cover. Thus changes in adult cover reflect both the change in number of adults and the average size of the remaining individuals. Therefore when we consider changes in abundance of adults

Table 2
Results from a 2 way fixed factor ANOVA showing changes in recruit abundance between March and August 2010. Bold text indicates p values less than 0.05.

Source	df	MS	F	p
Zone	1	15.69	6.448	**0.0157**
Shading	1	1.150	0.4739	0.4957
Zone × shading	1	1.051	0.4322	0.5152
Error	35	2.433		

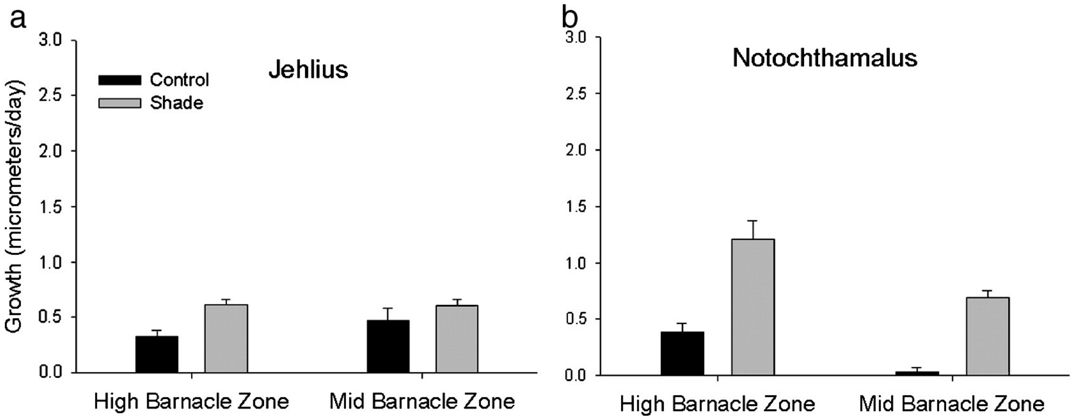

Fig. 5. Mean growth rates (+SE) of (a) *Jehlius* and (b) *Notochthamalus* in shaded and control plots in both the high and mid barnacle zones.

and of recruits together with any concomitant change in adult cover, we can be reasonably confident about the relative contribution of recruits from the start of the experiment to the final adult abundance. The decrease in recruit abundance the high barnacle zone, where there was little to slight negative change in adult abundance and cover of both species, is likely due to greater rates of early, post-settlement mortality rather than large numbers of recruits graduating into recognizable adults. Conversely, in the mid barnacle zone, where adult abundances increased without concomitant increases in cover, an important fraction of the reduction in recruit abundance is attributable to greater early post-settlement survivorship and growth into the smallest adult size classes. We found no effects of shading on changes in recruit abundance within barnacle zones, suggesting that emersion time may be more important for recruit survival and growth than emersion temperature.

Consistent with other investigations of barnacle reproduction, which have found that physical stress negatively influences reproductive potential (Barnes and Barnes, 1956; Hines, 1978; Leslie, 2005), we found a higher proportion of reproductive *Notochthamalus* under the experimental shading treatments in the mid barnacle zone. In contrast, the proportion of brooding *Jehlius* individuals was higher outside of shaded plots in both zones. Since temperature can also affect the timing of reproduction events (Kearney et al., 2009), an alternate explanation for the trend seen in the proportion of individuals brooding is that the shading treatment altered the timing of reproduction, not fecundity itself (e.g. Leslie et al., 2005). More extensive sampling in space and time is needed to evaluate these hypotheses. Furthermore, although reproductive output can be a good indicator of individual performance under varying thermal or competitive conditions (Leslie, 2005; Petes et al., 2008b; Wethey, 1984b), it is unclear whether higher output across a temperature gradient directly influences adult distributions in decoupled life cycles characteristic of intertidal barnacles (Morgan, 2001).

The evidence gathered in our study is consistent with a lack of strong competitive hierarchy between *Jehlius* and *Notochthamalus*, but suggests that emersion temperatures may enforce patterns of adult abundance established via a recruitment lottery for space (Shinen and Navarrete, 2010). In the high barnacle zone, the relative proportions of species remained largely unchanged, suggesting that reducing temperatures during emersion has little effect on competition or interactions between adults. Furthermore, growth rates of *Notochthamalus* in this zone appeared to be at least equal to if not greater than *Jehlius*, indicating that this species is limited by its recruitment into the high zone rather than adult interspecific interactions – temperature mediated or otherwise – with *Jehlius*. The slight decrease in relative abundance of *Jehlius* in the mid zone control plots may be indicative of a competitive advantage of *Notochthamalus* over *Jehlius*, consistent with negative impacts of *Notochthamalus* on *Jehlius* survival observed in cooler, southerly locations in Chile (López and González, 2003), but if temperature mediated this hierarchy, we would expect these effects to intensify under shaded treatments, yet this did not occur. Neither did we see any evidence of the intense competitive dominance of *Jehlius* over *Notochthamalus* described by Paine (1981). Although it has been demonstrated that competitive interactions of intertidal species may be driven by changing intensity of interspecific and intraspecific interactions along thermal gradients (Connell, 1961, 1972; Southward and Crisp, 1954; e.g. Bertness, 1999; Broitman et al., 2009; Crain, 2008; Harley, 2011; Petes et al., 2008a; Pincebourde et al., 2008), we found no evidence of consistent temperature mediated tradeoffs in performance or competitive ability between adult *Jehlius* and *Notochthamalus*. Instead, our results are consistent with a slightly offset pattern of species zonation being determined by species specific settlement patterns into each of the barnacle subzones (Shinen and Navarrete, in press) and that emersion time rather than temperature strongly influences the growth and survival of recruits.

Table 3
Results from 2 way fixed factor ANOVAs of adult growth rates for *Jehlius* and *Notochthamalus* observed from March to August 2010. Bold text indicates p values less than 0.05.

Species	Source	df	MS	F	p
Jehlius	Zone	1	0.1177	0.7769	0.3793
	Shading	1	1.298	8.567	**0.0039**
	Species × zone	1	0.1683	1.111	0.2934
	Error	178	0.1515		
Notochthamalus	Zone	1	1.234	7.597	**0.0075**
	Shading	1	3.052	18.79	<**.0001**
	Zone × shading	1	0.02093	0.1289	0.7207
	Error	68	0.1623		

It is important to note that the differences in temperature we recorded between intertidal elevations and shading treatments are small (~1.5 °C); but that differences were consistent throughout the course of our study. This is likely due to the consistent effect of wave splash and run-up typical of the study area cooling the rock surface and reducing the differences in thermal conditions among experimental plots. However, even a small-scale variation in temperature can have drastic metabolic and ecological effects, particularly on organisms with limited thermoregulatory capacity, such as barnacles (Gedan et al., 2011; Lathlean et al., 2013; Somero, 2002). With respect to barnacle recruits in particular, small differences in temperature have been shown to affect early growth and survival after settlement (Lathlean et al., 2013). Indeed, as noted above, individual growth rates and reproductive output of *Jehlius* and *Notochthamalus* were influenced by these small temperature differences even though this influence was not translated into differential adult abundance or percent cover.

Another important consideration is that our study was conducted over a relatively short timescale and at a single site, capturing only a portion of the growth and reproductive cycle of these barnacles. Study

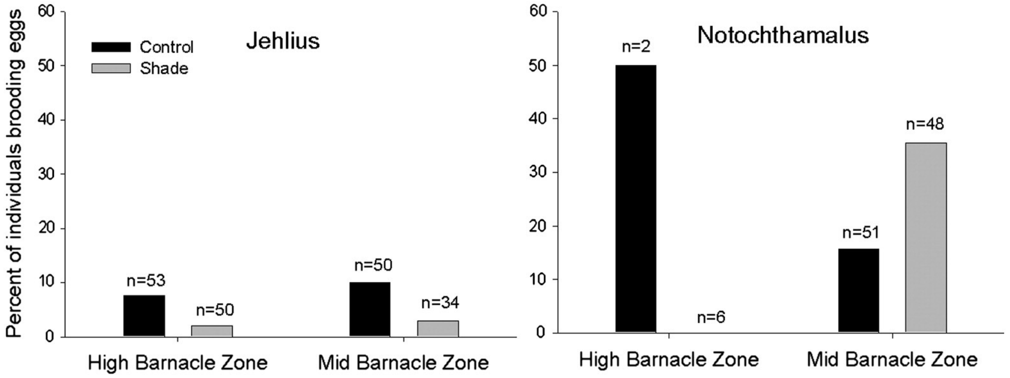

Fig. 6. Percent of *Jehlius* and *Notochthamalus* individuals found reproductive in the high and mid barnacle zones.

of early post-settlement survival under various emersion scenarios is required to determine if adult distribution patterns are indeed driven by species-specific settlement processes and then maintained by the slightly different adult capabilities described above. Also our study was conducted over the cooler fall and winter months, where our shades only altered thermal conditions by 1.6 °C. Our estimates of the effects of emersion temperature on *Jehlius* and *Notochthamalus* are therefore conservative and differences in species' responses may be accentuated during warmer summer months Finally, shades cannot account for any potential impact of solar radiation which may also have important consequences for intertidal barnacles (Gosselin and Jones, 2010).

While experiments such as ours employing artificial shades or conducted over relatively limited time scales have their limitations, our findings represent a necessary first step towards addressing the potential influence of temperature on the disputed nature of coexistence between two archetypal barnacle species. Understanding the complex ways environmental factors influence *Jehlius* and *Notochthamalus* throughout their life cycles is essential to understanding the potential impacts of changing physical regimes on the central Chilean coast and other rocky intertidal ecosystems. Given the depth of existing knowledge, the relative tractability of conducting intertidal experiments, and the considerable esthetic and economic value of coastal habitats, rocky shores continue to offer a sentinel system for understanding the multifaceted effects of climate variability on the structure and functioning of coastal marine ecosystems.

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