



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



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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 mediating 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.

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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 Emler, 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 Emler, 2007; Bertness, 1989; Gedan et al., 2011; Harley and Helmuth, 2003; Southward, 1958; Wetthey, 1983, 1984a), however much of this work focused on either a single life history stage (i.e. Harley and Helmuth, 2003; Wetthey, 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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Semibalanus balanoides survivorship, but only at warmer sites. Varying temperatures can also change the outcome of interspecific competition. In his 1983 study, Wetthey 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 Católica 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 rostrorcarinal 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

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