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# Coexistence and intertidal zonation of chthamalid barnacles along central Chile: Interference competition or a lottery for space?

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# ARTICLE INFO

# ABSTRACT

Keywords: Barnacles Coexistence Competition Recruitment In systems with open populations, both local (e.g. hierarchical interference competition) and regional processes (e.g. recruitment limitation and source-sink dynamics) can be important in determining patterns of abundance and coexistence of species. In this study, we define patterns of local distribution and recruitment of two common intertidal chthamalid barnacles (Jehlius cirratus and Notochthamalus scabrosus) at 15 sites along the shore of central Chile. Surveys revealed patterns of adult distribution to be consistent across the study region; Jehlius was numerically dominant at the highest intertidal levels and Notochthamalus was more abundant at lower shore levels. Despite slight spatial segregation, our results show that there is ample overlap in the distribution of these species, with inter-specific mixing over scales of few centimeters, occurring over 60-80% of the entire barnacle zone. Recruitment rates of the two species were highly correlated among sites (separated by kms), suggesting similar determinants of onshore larval transport between these species. Additionally, we found evidence that Notochthamalus was recruitment limited while Jehlius experienced higher post-settlement mortality. Densities of established individuals were generally positively correlated at scales of just 25 cm<sup>2</sup> and largely uncorrelated over scales of 2500 cm<sup>2</sup> across sites and tidal levels, indicating that asymmetric inter-specific competition is unlikely to affect adult populations. After monitoring individuals under various crowding conditions (single individuals, surrounded by conspecifics, and surrounded by heterospecifics) and at different tide elevations for more than a year, we found no evidence of negative intra- or inter-specific effects on individual growth rates. We conclude that lottery-type interactions and species-specific post-settlement mortality rather than an inter-specific competitive hierarchy likely determine patterns of coexistence of Jehlius and Notochthamalus in central Chile. © 2010 Published by Elsevier B.V.

# 1. Introduction

Discerning under what set of conditions species coexist in nature remains a central goal of ecological sciences, as it relates to many theoretical and applied issues in ecology and conservation biology (Tilman and Pacala, 1993; Chesson, 2000a; Amarasekare, 2003; Navarrete, 2007). After a strong emphasis on the roles of local species interactions and environmental conditions as determinants of patterns of distribution and coexistence, there is a recent and growing appreciation for the potential interplay between local and regional processes in spatially-structured communities in general (Amarasekare, 2003, 2004; Leibold et al., 2004; Holyoak et al., 2005) and within marine systems in particular (Menge, 2000a; Steele and Forrester, 2002; Pfister, 2006; Sale et al., 2006; White, 2007; Navarrete et al., 2008; Poloczanska et al., 2008; Wieters et al., 2008). In rocky shore communities, the outcome of competition for space is usually exemplified as the deterministic consequence of competitive hierarchies that leads to monopolization of the limited resource by a single, competitively dominant species (e.g. Menge, 1976; Paine, 1984). Coexistence is then mediated by physical disturbances, physiological tolerances, and vulnerability to consumers, which prevent complete monopolization of space or establish sharp zonation patterns across environmental gradients through niche partitioning. In contrast to competitive hierarchies, species could be similar in competitive abilities and once settled on the rock they could hold the space against other species. In this case, a pre-emptive "lottery" type of interaction characterizes the system, where adults appropriate resources by "chance" arrival and the relative proportions of adults are directly reflective of the pool of arriving propagules (Sale, 1977, 1978). Stable coexistence through time can be a function of temporal or spatial storage effects (Warner and Chesson, 1985; Chesson, 2000b; Miller and Chesson, 2009) and regional source-sink or "mass effects" (Leibold et al., 2004), where species dominance varies as adult habitat conditions or propagule supply favors one species over another. This type of competitive coexistence has been documented in tropical territorial fish (Sale 1977, 1978), but it is not often considered in rocky shore systems.

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Coexisting barnacle populations are a ubiquitous feature along shores, worldwide (Luckens, 1975; O'Riordan et al., 2004; Chan 2006; Navarrete et al., 2008) and have often served as empirical and model systems for examining competitive coexistence (Connell 1961a,b; Dayton, 1971; Denley and Underwood, 1979, Roughgarden et al., 1985; Hyder et al., 2001). At the local scale, strong, asymmetric competition for space has long been established as an important component of barnacle inter-specific interactions (Connell, 1961a; Luckens, 1975; Wethey, 1983). Dominant species can overgrow and undercut neighboring barnacles (Newman and Stanley, 1981) or preemptively occupy space through early settlement or high settlement density (Dungan, 1985; Chan and Williams, 2004), effectively restricting the range of sub-dominant species. Local, tide elevation dependent patterns of adult barnacles may also be mediated by physiological stress (Wethey, 1984; 2002; Menge, 2000b; Sousa et al., 2000), predation (Connell, 1961b; Carroll, 1996), or bulldozing by grazing gastropods (Dayton, 1971; Gosselin and Qian, 1996).

Barnacle populations can be remarkably open over comparatively large spatial scales (Roughgarden et al., 1988), with reproductive potential (Leslie et al., 2005) and rates of recruitment (Jenkins et al., 2000; Navarrete et al., 2002; Menge et al., 2004; O'Riordan et al., 2004) varying dramatically throughout species' ranges. Empirical work has identified a number of adult barnacle populations that are structured by larval supply processes, which determine patterns of abundance between regions, among sites, or across environmental gradients (Miyamoto et al., 1999; Hills and Thomason, 2003; Grosberg, 1982; Raimondi, 1991). Moreover, studies have also found barnacle distributions to be the result of the interactive effects of competition and recruitment (Connell, 1961a; Carroll, 1996; Menge, 2000b; Zabin, 2009).

Along the central-northern coast of Chile, the higher elevations of rocky intertidal communities are dominated by two chthamalid barnacles, Jehlius cirratus and Notochthamalus scabrosus (Guiler, 1959; Castilla, 1981). In addition to a broad overlap in their geographical distributions (1000 s of km, Castilla, 1981; Fernández et al., 2000), these morphologically similar species overlap extensively across intertidal elevations, with Jehlius numerically dominating slightly higher on the shore and Notochthamalus slightly lower (Castilla, 1981; Paine, 1981). Regionally, recruitment of Jehlius and Notochthamalus is highly correlated in both space and time (Lagos et al., 2007; Navarrete et al. 2005), though total recruitment rates can vary dramatically along the coastal shelf (Navarrete et al., 2002, 2008). Although these and other barnacles along the Chilean coast were described by Charles Darwin over 175 years ago (Castilla, 2009), to date, we know little about the processes that regulate the coexistence of Jehlius and Notochthamalus. Given their similarity in size and general morphology, most intertidal studies have simply pooled them together into a chthamalid barnacle functional group. As a result much is unknown about variability in intertidal distribution across sites and environmental gradients. Based on field observations in central Chile, Paine (1981) suggested that Jehlius is competitively dominant over Notochthamalus, displacing heterospecifics by overgrowth and crowding. In contrast, manipulative experiments near Puerto Montt, southern Chile, suggest an opposite hierarchy, where Jehlius suffers high mortality where Notochthamalus is abundant (Lopez and Gonzalez, 2003). In contrast, our observations in central Chile suggest that there is no competitive dominance of one species over the other, suggesting that local coexistence between these two species might conform to a lottery-type of system.

Here we quantify regional and local patterns of distribution, abundance and recruitment of *Jehlius* and *Notochthamalus* at several sites along the central coast of Chile. We determine how variable these patterns of coexistence and distribution are across sites and attempt to identify whether they could be better explained by recruitment limitation, hierarchical interference competition for space, or a lottery-type of interaction.

# 2. Materials and methods

### 2.1. Study sites and species

All experiments and surveys were conducted at 15 sites spanning 6° of latitude along the rocky shores of the central coast of Chile (see Supplementary material, Fig. 1). Sites are characterized as high wave exposure with variable, upwelling-driven sea surface temperatures, semidiurnal tide cycle and similar tidal ranges of ca. 1.8 m across the study region (Navarrete et al., 2005; Finke et al., 2007). In this section of the coast the distributions of Jehlius and Notochthamalus overlap extensively in the high intertidal, from the "splash zone" to lower elevations where mussels or macroalgae species dominate (Fig. 1a, and see Results). Both species have planktotrophic larvae that spend between 20 and 30 days in the water to develop to competent cypris stage (Venegas et al., 2000) and all larval stages can be found in surface waters a few kilometers offshore (Vargas et al., 2003, 2006), suggesting comparatively large dispersal potential in these species (see also Wares et al., 2009). Although sites below 32° S experience strong top-down forcing from predators (Navarrete et al., 2005), the 'chthamalid zone' occupies the highest intertidal elevations and is above the range of most common and effective intertidal predators, and are thus usually considered to have little effect on the post-settlement mortality of Jehlius and Notochthamalus at this tidal level (Lopez and Gonzalez, 2003). Toward the mid and low intertidal zones, several consumers (crabs, sea stars, whelks, and chitons) consume barnacle spat or adults and create bare rock spaces of varying sizes within the barnacle beds (Navarrete and Castilla, 1990; Navarrete and Castilla, 2003; Aguilera and Navarrete, 2007). There is no evidence of selective predation (between the two chthamalids) by any of these predators.

### 2.2. Local patterns of distribution

In the austral summers (Dec–Feb) of 2007, 2008 and 2009, we examined local patterns of intertidal distribution of *Jehlius* and *Notochthamalus* at 6 to 15 sites across the region. Ten  $50 \times 50$  cm quadrats were haphazardly placed in each of the high, mid, and low shore levels (see Fig. 1a). Within each quadrat, species-specific barnacle density and percent cover were quantified in  $105 \times 5$  cm sub-quadrats. Only 6 sites were surveyed in 2007 at all 3 tidal levels, which showed very low barnacle cover in the low zone (see Results). In 2008 we increased the number of sites to 12, but sampled only the high and mid intertidal zones to be able to finish surveys within a single month. In 2009 we added 3 additional sites.

In the summer of 2009, we also conducted 3 vertical contiguous transects per site across tidal levels to better distinguish patterns and transitions in species dominance across the chthamalid zone at 14 sites in the study region. Beginning in the splash zone, at the upper limit of barnacle occurrence,  $10 \times 10$  cm quadrats were photographed (using an Olympus 1030 W digital camera) at 30 cm intervals through the vertical extent of the chthamalid occurrence (see Fig. 1). Transects were of variable length, depending mostly on inclination of the substrate and slight differences in wave exposure, and terminated with the intertidal platform or where barnacles recede into mussel or algal dominance. From photographs, the number of individuals of *Jehlius* and *Notochthamalus* were counted. Species are distinguished by their distinctive opercular plate patterns.

# 2.3. Barnacle recruitment

To characterize recruitment patterns of *Jehlius* and *Notochthamalus*, we took advantage of an on-going monitoring program established in 1997 that includes the 15 sites considered in this study (Navarrete et al., 2002, 2008). Once monthly, 5  $10 \times 10$  cm settlement collectors, consisting of plexiglass plates covered with a standard rugosity (Safety Walk, 3 M), were deployed and retrieved from the upper shore, at



**Fig. 1.** a) Generalized depiction of intertidal chthamalid barnacle zonation patterns on the central coast of Chile. The upper shore is further subdivided into high, mid, and low barnacle zones (HBZ, MBZ, and LBZ, respectively) to illustrate patterns of coexistence between *Jehlius* and *Notochthamalus*. b) Mean percent coverage ( $\pm$ SE) of *Jehlius* and *Notochthamalus* at high, mid, and low shore levels, average across survey years (2007–2009). Sites that were excluded from surveys are noted by EX.

approximately the middle of the chthamalid zone (MBZ, Fig. 1). In the laboratory, juvenile barnacles, newly metamorphosed spat, and cyprid larvae were identified to species level under a dissecting microscope. Since the time plates were exposed in the field varied somewhat depending on tidal cycles and sea conditions, recruitment was expressed as the number of individuals per day of exposure per collector (see Lagos et al., 2008; Navarrete et al., 2008). Only spring-summer months (Sept–Feb) were considered in calculations as settlement the rest of the year is nearly null (Lagos et al., 2005; Navarrete et al. 2008).

### 2.4. Intra- and inter-specific effects on growth rates

To examine the potential effects of intra- and inter-specific crowding on individual growth rates, in April 2008 we installed 10  $10 \times 10$  cm plots in each of the 3 chthamalid sub-zones along the upper shore of one site (Pichilemu): the high barnacle zone, where Jehlius numerically dominates; the mid barnacle zone, where Jehlius and Notochthamalus are well mixed; and the low barnacle zone, where Notochthamalus numerically dominates (see Fig. 1a and Results). Plots were marked with two stainless-steel screws anchored directly in the upper left and bottom right corners and photographed with a digital camera (Olympus 1030 W) approximately every 3 months, with the final photos taken in June 2009. For this study, we selected from the photographs 10 individuals of each Jehlius and Notochthamalus in each of the 3 sub-zones which were found under the following conditions: 1) individual barnacles existing singly, not sharing walls with any neighboring barnacles; 2) individuals that were in aggregated groups, surrounded by conspecific individuals only; 3) individuals that were in aggregated groups, surrounded by heterospecifics. Total barnacle cover in these plots varied between 14 and 78%. Target individuals were relocated over time with the aid of the marking screws, which also served as scale reference, and their maximum opercular carino-rostral length and opercular width were measured. With these measurements we estimated the opercular area simply multiplying opercular length × width (Lopez and Gonzalez, 2003). ImageJ Image Analysis (Abramoff et al., 2004) was used to score and analyze photos.

### 2.5. Data analyses

We compared density of individuals between species (Jehlius and Notochthamalus, fixed factor), among tidal levels (high and mid, fixed factor) and among sites (12 sites, random factor) with a three-way ANOVA, using the most complete dataset on adult densities collected in the field in 2008. To determine whether there were differences between species in the way individuals use space, we calculated the relationship between density and cover of individuals in the  $10 \times 10$  cm quadrats for each species and tidal level (high and mid zone) at each site and quadrat. To this end, we used ordinary least square regressions between density and cover. We then compared the slopes of these regressions between species (Notochthamalus, Jehlius, fixed), tidal level (high and mid, fixed factor) and sites (random) using a 3-way ANOVA. To examine whether there is evidence of negative relationships (e.g. interference competition and segregated settlement) at the scale of quadrats  $(50 \times 50 \text{ cm})$  and at the scale of sub-samples  $(5 \times 5 \text{ cm})$  we calculated Pearson correlations between Jehlius and Notochthamalus densities for each site and quadrat, respectively.

### Table 1

Results of a mixed model ANOVA of the mean density of *Jehlius* and *Notochthamalus* using 3 factors: Site (random), Zone (fixed), and Species (fixed). Mean are expressed on a per-quadrat level, averaged across all sub-samples.

Source	DF	MS	F	р
Site	11	822.517	19.06	<.0001
Zone	1	839.714	3.92	0.0733
Species	1	1516.504	3.13	0.1044
Species × zone	11	214.259	4.45	<.0001
Site × species	11	484.013	11.19	<.0001
Zone×species	1	3279.298	9.32	0.0110
Site × zone × species	11	351.824	8.13	<.0001
Error	432	43.259		

To characterize the vertical extent of overlap between the chthamalid barnacle species with respect to tidal elevation and its variability across sites, we calculated the proportion of barnacle species expressed as the ratio of *Jehlius* to total barnacle density  $(J/(J + N)_{\text{adults}} = \text{density of$ *Jehlius*/ total barnacle density) in each quadrat along the vertical photographic transects. Moreover, because transect length and inclination differed within and among sites, relative tidal elevations were calculated for each quadrat dividing its position on the transect (in cm) starting from the highest point, by the total transect length. In this manner vertical distribution patterns were not confounded with differences in overall barnacle density among sites and vertical changes were expressed relative to the extension of the barnacle zone.



**Fig. 2.** a) Patterns of space occupation expressed as the change in percent cover by the density of individuals for *Jehlius* (closed circles) and *Notochthamalus* (open circles). Species-specific regression coefficients are indicated by subscripts J (*Jehlius*) and N (*Notochthamalus*).

#### Table 2

Source	DF	MS	F	р
Species	1	2.566	3.71	0.1024
Zone	1	3.869	10.07	0.0193
Site	6	7.265	34.68	<.0001
Species × zone	1	4.761	3.65	0.1045
Species × site	6	0.692	3.30	0.0038
Zone×site	6	0.384	1.83	0.0929
Species × zone × site	6	1.303	6.22	<.0001
Error	252	0.210		

Using only the portions of the vertical transect where *Jehlius* and *Notochthamalus* co-occur within the  $10 \times 10$  cm quadrats  $(0 < J/(J + N)_{adults} < 1)$ , we calculated the extent of the transition zone or rate of change from *Jehlius* to *Notochthamalus* domination. To this end, we regressed the proportion of *Jehlius* against relative tidal elevation using ordinary least square linear regression for each transect. A sharp zonation pattern (narrow transition zone) was then reflected in steep slopes, while extensive mixing through the barnacle zone was reflected in shallow slopes. We then examined whether variation in the extent of the mixing zone (slopes of linear regressions) across sites was related to changes in barnacle recruitment rates, using linear regression on log-transformed data.

To examine species-specific trends in recruitment across the study region we simply plotted long-term (1997–2008) mean recruitment rates across all sites ordered geographically and examined the correlation in recruitment between species across sites using Pearson correlation on log-transformed data.

To evaluate the contribution of recruitment to the pattern of abundance in the upper shore (barnacle zone), i.e. whether there is evidence of recruitment limitation across the region, we compared average daily recruitment rates of the two species for the years 2006-2008 to the average density of adults the following year within MBZ level of the barnacle zone using linear regression on log-transformed data. This comparison was done across sites and not following individual cohorts (e.g. Connell, 1985; Menge, 2000a,b), and therefore the adult density in a given year represents the recruitment cohort of the prior year as well as carry over from earlier cohorts. Thus, we also examined the relationship using the previous two years of recruitment. Similarly, to determine whether the pattern of relative abundances of adults of the two species could be explained by the relative abundance of recruits, we used a linear regression between *I*/  $(I+N)_{\text{adults}}$  for years 2006–2008 against  $I/(I+N)_{\text{recruits}}$  for the year before and also examined the previous two years.

Individual growth rates (final area – initial area)/days were compared among species, tidal elevation, and the three "crowding" conditions (single, surrounded by conspecifics, and surrounded by heterospecifics) using a 3-way ANOVA, considering all factors fixed. Before analysis, individual growth curves were inspected for nonlinearity or seasonal trends. Growth rate increments were examined against initial opercular area and no evidence of size-dependent growth was found (see Results).

## 3. Results

### 3.1. Local patterns of distribution

The abundance of both *Jehlius* and *Notochthamalus* varied across tidal levels (Fig. 1b). In the upper shore, where overall cover of chthamalids was highest, *Jehlius* generally was more abundant than *Notochthamalus* across the region, except at one site (Temblador) at the northern end of the study region (Fig. 1b). In the mid shore level at most but not all sites, *Notochthamalus* cover was higher. In the low

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Fig. 3. Correlations between the densities of Jehlius and Notochthamalus at the upper (closed circles, US) and mid (open circles, MS) shore levels, by site.

shore, both species were rare, rarely reaching over 5% cover and at most sites Notochthamalus was more abundant than Jehlius. Changes in relative abundances of species across tidal levels and differences in numerical dominance at some sites were reflected in a significant interaction among these three factors in a 3-way ANOVA (Table 1). Overall, there were tight linear relationships ( $R^2 > 0.84$ ) between the number of individuals (density) and percent cover for both species (Fig. 2). Although the slopes of the relationships were similar between species when averaging across sites and tidal levels (Fig. 2, Table 2), suggesting overall similar patterns of per capita space occupation, there were significant differences in the slopes between tidal levels and sites, which also varied between species (Table 2, significant three-way interaction). We interpret this as an indication that local processes determine per capita space occupation (e.g. size structure, recruitment, or post-settlement mortality) and that these processes are not consistent across the region.

Correlations between the densities of *Jehlius* and *Notochthamalus* within the  $5 \times 5$  cm sub-quadrats were generally positive and centered around a correlation r = 0.23 on the upper shore and r = 0.34 in the mid shore, which differed significantly from the null expectation of no correlation (Supplementary material Fig. 2). Only 3 significantly negative correlations were observed out of the 527

correlations examined at the scale of the  $5 \times 5$  cm quadrats. At the scale of the  $50 \times 50$  cm quadrats (averaging all sub-samples within quadrats to provide estimates of density at the quadrat level), correlations were generally non-significant at all sites and zones (Fig. 3). Only 4 significantly positive relationships were identified at this scale, 2 in the upper (El Quisco, Pichilemu) and 2 in the mid shore (ECIM Norte, Guanaqueros), and no negative correlations were observed (Fig. 3). We interpret the lack of negative correlation between species-specific chthamalid density at both the  $5 \times 5$  cm and  $50 \times 50$  cm scales as an indication that the relative abundance of one species does not inhibit the other. The generally positive correlations at the smallest scale suggest that there are site and shore level specific conditions that benefit both species or contribute to inter-specific aggregated settlement.

Across shore levels and among sites, *Jehlius* and *Notochthamalus* were found to overlap extensively in their vertical distribution (Fig. 4). At all sites *Jehlius* dominated in the highest tidal elevations while at most sites *Notochthamalus* dominated in the lowest part of the barnacle zone. Although all sites exhibited these transitions in species dominance, the rate of transition from *Jehlius* to *Notochthamalus*, or the sharpness of zonation, varied considerably among sites (Fig. 7a). At a few of the sites, the transitions of species dominance



**Fig. 4.** Site-specific patterns of co-occurrence of *Jehlius* and *Notochthamalus* across relative tide elevation. Co-occurrence is expressed at the proportional densities of *Jehlius* to *Notochthamalus*  $(J:(J+N)_{\text{adults}} = \text{density Jehlius/total barnacle density})$ . Dotted reference line indicates where species would be in equal proportion  $(J:(J+N)_{\text{adults}} = 0.5)$ . See Materials and methods for details.

were likely affected by intertidal shores that are truncated abruptly (Montemar and Punta Talca) or are influenced by strong changes in inclination along the rock surface (Quintay), never reaching a zone of clear dominance by *Notochthamalus*. More striking than species

transitions, however, was that at the majority of sites, high levels of mixing occurred throughout most of the sampled area from about 60–80% of the entire chthamalid zone, indicating high levels of local spatial coexistence between *Jehlius* and *Notochthamalus*.



**Fig. 5.** Regional annual mean recruitment rates  $(\pm SE)$  of *Jehlius* and *Notochthamalus* from 1997 to 2008. Graphical insert depicts the correlation between recruitment rates of *Jehlius* and *Notochthamalus* across sites and years.

## 3.2. Regional patterns of recruitment

Mean daily recruitment rate varied across four orders of magnitude across sites, with generally higher recruitment rates in southern sites (Fig. 5, and see Navarrete et al. 2005, for details of these patterns). With the exception of one site (Temblador), recruitment rates of *Jehlius* exceeded those of *Notochthamalus* throughout the study region. Recruitment rates of *Jehlius* and *Notochthamalus* were also highly correlated across the study region (Fig. 5).

Across sites, the density of adult *Notochthamalus* was significantly and linearly associated with recruitment rates the year before for all three years examined (Fig. 6a). This positive relationship suggests that *Notochthamalus* may be recruitment limited across the study region. The density of adult *Jehlius*, however, was poorly explained by recruitment rates of the previous years for all years examined (Fig. 6a). Although the causes for such a pattern are difficult to establish with existing data, we interpret these results as indicative that larval supply is not limiting in this species and that postsettlement factors might be more important in determining local adult abundance. Analyses of the relationship between adult abundance and recruitment two years prior were all non-significant.

Removing density effects, the proportion of recruits  $(I:(I+N)_{recruits})$ was a good predictor of the proportion of adult barnacles in the upper shore  $(J:(J+N)_{adults})$  on two (2007 and 2009) out the 3 years examined (Fig. 6b), although the low number of sites in 2007 rendered the relationship non-significant (p = 0.0596). Of the two years with linear relationships, in 2007 the slope was close (slope = 0.89) to the expected slope of 1.0 (proportions of adults reflecting proportion of recruits). However, the slope from 2009 was significantly less than 1.0 (p = 0.0081), indicating that in 2007 relative adult abundances across sites followed changes in relative recruitment rates of the species, but in 2009 Jehlius experienced higher post-settlement mortality with increasing Notochthmalus recruitment. In 2008 adult proportions were not associated to the relative recruitment observed the previous year. Relationships with recruitment the previous 2 years were all nonsignificant. Moreover, in all years there was a slight trend to underestimate the proportion of adult Jehlius to total barnacle abundance, indicating a greater abundance of Notochthamalus in the adult population than would be predicted by the recruitment fraction (Fig. 6b). Combined with saturating recruitment densities, lower proportional density of Jehlius suggests that Jehlius may be experiencing higher post-settlement mortality than *Notochthamalus* on the upper shore, but this mortality appears to be unrelated to the proportion of *Notochthamalus*, at least in 2007 and 2009.

Across the expanse of the chthamalid zone, the rates of change of species dominance across tidal elevation (transition slopes) increased in magnitude with increasing mean total recruitment (Fig. 7b), indicating that as recruitment increases, the zonation from *Jehlius* to *Notochthamalus* dominance was sharper, with less mixing between the species.

# 3.3. Growth rates and effects of intra- and inter-specific crowding

Opercular growth was observed in all marked barnacles and there was no size-dependent growth rate in either of the species (Fig. 8). Examination of individual growth curves revealed linear trends with an absence of seasonal peaks. Moreover, mean growth rate did not vary between Jehlius and Notochthamalus, irrespective of tide elevation or crowding condition (Fig. 8, Table 3), i.e. intra- or interspecific crowding had no measurable effects on growth rates with respect to isolated individuals (Supplementary material Fig. 3). Moreover, growth rates were not correlated to the total cover of barnacles within the  $10 \times 10$  cm2 plots (linear fit  $R^2 = 0.02$ , p = 0.5558), suggesting that neither local crowding scenarios nor the proximal density of individuals have significant effects on growth. Survivorship of all barnacles (target and non-target individuals) was generally high, with mortality only noted at the level of the entire  $10 \times 10$  cm plot, in which the majority or all the barnacles present within the plot were removed, independent from experimental crowding treatments. The causes of this mortality, which occurred with greater frequency in the plots lower on the shore, are under investigation. Furthermore, we found no visual evidence of interference competition in terms of overgrowth or under cutting among marked individuals.

# 4. Discussion

Patterns of distribution of chthamalid barnacles were largely consistent across the study region in central Chile and generally followed previous descriptions of zonation between these species (Guiler, 1959; Castilla, 1981); *J. cirratus* was numerically dominant at the highest intertidal levels and *Notochthamalus* was relatively more abundant at lower shore levels (Figs. 1, 2, and 4). However, our results show that there is a very ample overlap in the distribution of these species, with mixing between individuals at small spatial scales occurring over 60–80% of the entire barnacle zone. Based on our results on per capita use of space, recruitment and adult abundances at multiple sites and years, and on growth rates under different scenarios of neighborhood competition, we conclude that a combination of subtle tidal segregation and a lottery-type of space occupation with no competitive hierarchy is the best working hypotheses to explain coexistence patterns of these species.

Close examination of recruitment patterns and the relationships with adult distributions shed light on several important features of coexistence between *Jehlius* and *Notochthamalus*. First, differences over several orders of magnitude were found in recruitment of the species among sites (Fig. 5). Moreover, although the relative proportion of recruits of the two species varied somewhat from site to site and from year to year (see below), recruitment of the two species was highly correlated across the region. We interpret this as an indication that both chthamalids are experiencing generally similar effects of transport processes over scales of kilometers. Although we do not have information on reproductive output for these sites, the high correlation in recruitment among sites suggests that a source-sink type of dynamics across sites (Iwasa and Roughgarden, 1986; Pulliam, 1988) is unlikely to play an important role in favoring coexistence between these species.



**Fig. 6.** a) Annual patterns of density of *Jehlius* (closed circles) and *Notochthamalus* (open circles) on the upper shore by the mean recruitment rate of the previous year. b) Annual proportion of adult barnacles  $(J:(J + N)_{adults} = density Jehlius/total barnacle density)$  on the upper shore by the proportion of recruits  $(J:(J + N)_{recruits} = density of Jehlius$  recruits/total recruit density) of the previous year. Dotted reference line indicates where  $J:(J + N)_{recruits}$  perfectly predicts  $J:(J + N)_{adults}$  (slope = 1.0).

Second, the relationship between recruitment rates and adult abundances suggested that *Notochthamalus* but not *Jehlius* might be recruitment limited. A linear relationship between density of recruits and subsequent adult density has historically been interpreted as evidence that the arrival rates of larvae from the plankton, or the subsequent mortality during the first days of benthic life, are limiting local population size (Connell, 1985; Carroll, 1996; Menge, 2000a,b). In our study, this relationship was evaluated across sites and with non-manipulative surveys (no clearings to follow single cohorts), thus our assessments of adult distributions are estimating the pooled outcome of site-specific influences, population input rate (recruitment), and turnover rates (postsettlement mortality). When turnover rate is low, populations become saturated more quickly, regardless of larval supply, and thus will not appear to be strongly recruitment limited. Our analyses of the relationships between the recruitment and adult fractions are liable to be confounded by the carryover of adult populations from previous years, but nevertheless, under these conditions we found significant relationships between recruitment and adult abundance only in *Notochthamalus*. In contrast, *Jehlius* recruits generally arrived at higher densities, but postsettlement mortality rather than recruitment seems to determine adult population abundance across sites. Although the possibility and consequences of species-specific recruitment, slightly offset by tide elevation, should be further explored, the observed patterns suggest that the upper limit and population abundance of *Notochthamalus* within the barnacle



**Fig. 7.** a) Regional species dominance transition rates  $(\pm SE)$  calculated by regressing the rate of change of the relative proportion of chthamalid species  $J:(J+N)_{adults}$  by relative tidal elevation, using only the portions of the transect where *Jehlius* and *Notochthamalus* co-occur  $(0 < J:(J+N)_{adults} < 1)$ . b) Linear regression of site-specific species dominance transition rates  $(J:(J+N)_{adults})$  relative tide elevation) by daily recruitment rates from 2008.

zone is self-limited by recruitment and not the result of competitive interactions with *Jehlius*. Recruitment limitation and not inter-specific competition has been shown to set the distribution limits in other coexisting barnacle species (Denley and Underwood, 1979; Grosberg, 1982; Miyamoto et al., 1999). It must be noted, however, that even under relatively low recruitment competition for space can still occur in the form of neighborhood competition if, for instance, settlement of the species are highly correlated over small spatial scales (Lloyd and White, 1980; Weiner, 1982). This is clearly the case in these chthamalid species (see below) and suggests that bare space might not be a good indicator of resource availability.

Third, although total recruitment rates varied substantially among sites, the relative proportion of adults was correlated to the relative proportion of recruits the previous year on two of the three years examined. The slope of this relationship was close to 1 in 2007, suggesting that relative abundances of adults were set by recruitment and not by post-recruitment processes. However, low number of sites on that year rendered the relationship non-significant. In 2009 the relationship between relative proportions of recruits and adults was significant, but the recruit fraction significantly (slope<1) overestimated the relative abundance of adult *Jehlius*. This could be an indication of asymmetrical, pre-emptive occupation of attachment substrate (Denley and Underwood, 1979; Schoener, 1982) or interference competition for space with *Notochthamalus* (Connell, 1961a,b; Wethey, 1983), or simply the result of strong species-specific densitydependent mortality in *Jehlius* (Jenkins et al., 2008). This particular analysis gives us some conflicting evidence as to the existence and importance of asymmetric competition in setting adult abundances in the mixed barnacle zone. The fact that in all years the final relative abundance of *Jehlius* was under-estimated from the recruitment and that the difference in the proportion of *Jehlius* as recruits versus adults was not related to *Notochthamalus* recruitment (Supplementary material Fig. 4) suggest that these patterns are better explained by stronger species-specific post-settlement morality of *Jehlius*.

In sharp contrast with Paine's (1981) observations that suggested dominance of Jehlius over Notochthamalus, we found weak evidence of competitive hierarchies or inter-specific interference competition for space between the chthamalids. Since Jehlius and Notochthamalus had nearly equal per capita use of space (from relationships of cover versus density), it is unlikely that "passive" pre-emption of space, when it occurs, could be asymmetric. We showed that increased recruitment rates of the species across sites led to sharper transitions from Jehlius to Notochthamalus dominance across the chthamalid zone. This pattern is further suggestive of recruitment segregation by tide elevation, and that symmetrical pre-emptive competition for space may play a more important role at higher recruitment densities. The absence of asymmetric interference competition was also suggested by the existence of positive, instead of negative correlations between densities of these species even within 25 cm<sup>2</sup> quadrats. Generally positive correlations at these small scales are probably the result of similar larval selectivity for settlement sites, a possibility that warrants further exploration (Jenkins, 2005). At slightly larger spatial scales of 2500 cm<sup>2</sup>, densities appeared uncorrelated, which is probably the results of random and unbiased variation in sources of mortality over these scales.

Perhaps the most compelling evidence in favor of weak and symmetrical competitive interactions between the chthamalids within the upper shore are the results of growth rates under different neighborhood conditions. These results show that, at least in terms of growth rates, Jehlius and Notochthamalus are competitively equivalent and are not affected by crowding. As reported for other chthamalids, Jehlius and Notochthamalus, exhibited relatively slow, linear growth rates (Barnes, 1956) and as reported by Lopez and Gonzalez (2003), the opercular area was a size-independent measure of growth. Notably, even the smallest individuals, identified in the early post-settlement phase, grew at the same rate as larger individuals, regardless of crowding condition or of overall plot level cover of barnacles (a correlate of overall density). It is important to note, however, that these observations were conducted at a single site, Pichilemu; large intertidal platform, characterized by moderate-low recruitment and a moderate cross-shore transition rate between Jehlius and Notochthamalus. Moreover, considering the slow growth rates of both species, it is possible that competitive interactions are occurring, but the time scope of our observations was not sufficient to observe its manifestation on barnacle growth. Future studies should investigate variability in competitive interactions among sites and, in particular, the potential effects on barnacle survival, which we were not able to fully address in this study.

Coexistence between *Jehlius* and *Notochthamalus* may also be favored by small-scale niche partitioning. Despite extensive mixing of species through the chthamalid zone, slight segregation by tidal height was apparent, creating "local refugia" for each species. It is unknown what creates and maintains this slight segregation. Further scrutiny of settlement patterns may reveal slight differences in tide elevationspecific settlement or post-settlement mortality (Jenkins, 2005). In any case, these findings are consistent with other work on co-occurring



Fig. 8. Mean specific growth rates of *Jehlius* and *Notochthamalus* (expressed as the change in growth by initial size) growing in different crowding conditions: no competition (closed circles), intra-specific competition (open circles), and inter-specific competition (inverted triangles). Results are shown for each high, mid, and low barnacle zones (HBZ, MBZ, and LBZ, respectively).

barnacles where adult distributions depend on species-specific responses to shore level and site effects such as desiccation stress and wave exposure (Carroll, 1996; Menge 2000b; Delany et al., 2003). These

# Table 3

Results of an ANOVA of the mean growth rates of *Jehlius* and *Notochthamalus* using 3 fixed factors: species, barnacle zone (within the upper shore), and crowding condition (CC).

Source	DF	MS	F	р
Species	1	0.826	0.10	0.7555
Zone	2	21.933	2.58	0.0786
CC	2	4.197	0.50	0.6108
Species × zone	2	17.207	2.03	0.1350
Species × CC	2	0.313	0.04	0.9638
Zone×CC	4	9.695	1.14	0.3386
Species × CC × zone	4	8.597	1.01	0.4024
Error	162	8.487		

factors should be investigated through replicated transplant experiments across tidal elevations.

In summary, we believe that coexistence and mixing between these chthamalid species are the result of: a) slight tidal segregation, probably maintained by small tidal differences in recruitment rates which might or might not relate to competition past, b) overall weak competition for space at many, perhaps most sites due to recruitment limitation of *Notochthamalus* within the mixed barnacle zone, and c) absence of interference for space and equal competitive abilities of the two species, which allows them to hold the space once settled even at sites of high recruitment rates and limited rock surface. Thus, this two-species system appears to have similar elements of a lottery-type of competitive coexistence as proposed for territorial reef fish (Sale 1977). The slight sorting of species across tidal elevations might be sufficient to prevent that a species recruiting in greater density could monopolize space and exclude heterospecifics, but variation in competitive ability across sites should be further investigated. It is clear that detailed experiments are

badly needed to evaluate these propositions if we are to improve our understanding of distribution and coexistence of the species that fascinated a young Charles Darwin more than 150 year ago.

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# Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2010.04.033.

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