Lottery Coexistence on Rocky Shores: Weak Niche Differentiation or Equal Competitors Engaged in Neutral Dynamics?

Jennifer L. Shinen* and Sergio A. Navarrete

Estación Costera de Investigaciones Marinas, Las Cruces, and Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

abstract: Reconciling how niche and neutral processes may be important in species coexistence has revealed two important weaknesses in our collective understanding of species diversity: few empirical studies have determined whether species are truly coexisting, and fewer still have properly evaluated whether coexistence is achieved through niche differentiation or ecological equivalence. Here, we ask whether two common barnacles, *Jehlius cirratus* and *Notochthamalus scabrosus*, coexist locally and whether the slight but persistent differences in their distribution provide sufficient fitness trade-offs to overcome differences in competition. Both species recovered after experimental reduction; that is, they coexist, with no indication of hierarchical exclusion. No fitness inequalities affected species performance or interference effects on vital rates at any shore level, indicating no trade-offs in intra-interspecific effects across the ecological gradient. Additionally, no relationship was found between per capita population growth rates of either species with its own relative abundance; that is, neither species has a demographic advantage when rare. Instead, a lottery for space during settlement largely determines species' distributions, evidenced by the positive correlation across sites and tidal elevations between the relative abundances of adults and the recruits of the prior season. We conclude that *Jehlius* and *Notochthamalus* coexist neutrally, or nearly so, but discuss whether small, nonsignificant, and probably ephemeral fitness differences, which are inconsistent across the tidal gradient, could provide enough niche differentiation to promote coexistence.

Keywords: coexistence, niche vs. neutral, competition, lottery recruitment, barnacles, rocky intertidal.

Introduction

Understanding coexistence, that is, when two or more species persist together indefinitely, continues to be a central focus of theoretical and empirical ecological research (Tilman and Pacala 1993; Chesson 2000; Amarasekare 2003).

* Corresponding author; e-mail: jlshinen@bio.puc.cl.

When species share a common resource, coexistence is possible if external sources of mortality (e.g., predation, disturbance) keep the population of the competitively dominant species from excluding others (Connell 1978; Chase et al. 2002), or if each species experience a demographic advantage when rare; that is, as the frequency of a given species increases in a habitat, it must limit itself more than it limits other species (Chesson 2000; Adler et al. 2010). Although these "stabilizing" niche-based mechanisms of coexistence preoccupied ecologists for decades, in their recent review, Siepielski and McPeek (2010) challenged the empirical evidence establishing or assuming species "coexistence." They argue that only a handful of studies that inferred coexistence performed the critical analyses necessary to demonstrate that each species is able to recover from periods of rarity (the "invasibility" criterion; Chesson 2000). Without satisfying this criterion, conclusions drawn from the vast majority of published studies illustrating competitive-driven resource partitioning (sensu MacArthur 1968; Schoener 1974) between "co-occurring" members of a community may actually be examples of one species deterministically, albeit slowly, driving one or more of the others to extinction rather than truly coexisting (Siepieslki and McPeek 2010).

This distinction between coexistence through demographic balancing mechanisms and simple co-occurrence has become particularly important in light of the alternative explanation, which posits that coexistence between species that share resources can be achieved not through the differences that generate fitness trade-offs but through functional equality (Sale 1977; Hubbell 1997, 2001). Under this neutral explanation, species are equivalent in terms of their competitive ability, demographic rates, and dispersal potential and are therefore unable to exclude individuals of other species once they arrive in a local habitat (Hubbell 1997, 2001; Bell 2001). Rather than being self-

limiting populations, species are limited by the cumulative abundance of all species in the metacommunity and species persistence is subject to drift and local extinctions. No stabilizing forces are required to achieve indefinite persistence and they may be said to be truly coexisting (Chesson 2000; Gravel et al. 2006; Leibold and McPeek 2006; Siepielski et al. 2010). Real species differ, however. The important question is whether such differences are sufficient promote stable coexistence or if only minor differences underlie a protracted exclusion of an inferior competitor. With increasing species similarity, the smaller the fitness trade-off or advantage required to achieve stable coexistence or drive a competitor inexorably toward extinction (Adler et al. 2007). Here, we examine whether two co-occurring barnacle species, shown to compete for space on rocky intertidal shores, can coexist in this system owing to fitness trade-offs, are coinciding over a prolonged progression of an extinction of the inferior competitor, or represent a case of neutral coexistence in which their relative abundances fluctuate according to spatiotemporal fluctuations in physically driven recruitment. Although several studies have found features of neutral dynamics in the structure of natural assemblages (Munday 2004; Wootton 2005; Kelly et al. 2008; Caro et al. 2010; Siepielski et al. 2010; Delong and Vasseur 2012), the majority of these studies were conducted over relatively short time periods or small spatial scales (e.g., Munday 2004; Wootton 2005; Delong and Vasseur 2012) or have examined regional patterns in large assemblages of species without testing for the invasibility criterion or explicitly considering any stabilizing mechanisms that could promote coexistence (e.g., Dornelas et al. 2006; Kelly et al. 2008; Caro et al. 2010). Here we experimentally evaluate the invasibility criterion and test whether preemptive or interference competition for space generates demographically stabilizing trade-offs between species across the tidal gradient and among sites of varying environmental and recruitment conditions.

Rocky intertidal systems are well known for canonical examples of competitive hierarchies for space leading to spatial or niche segregation (Connell 1961; Dayton 1971; Menge 1976; Paine 1984). Co-occurring barnacle species, in particular, are a common feature along shores (Luckens 1975; O'Riordan et al. 2004; Jenkins 2005; Chan 2006; Navarrete et al. 2008) and have often served as model systems for examining competitive coexistence (Connell 1961; Dayton 1971; Denley and Underwood 1979; Roughgarden et al. 1985; Berlow and Navarrete 1997; Hyder et al. 2001). Owing to their biphasic life histories and the large dispersal potential of planktonic larval stages, new individuals arriving at any local site can be largely independent of local reproduction ("open populations" sensu Roughgarden et al. 1985). To complete development, larvae must find an appropriate rocky surface to settle on,

metamorphose, and grow to adult reproductive size. Barnacles therefore can compete at the time of settlement through preempting the space from other individuals, a process commonly observed also in territorial reef fish and that is completely neutral to species identity (e.g., Sale 1977; Munday 2004). Soon after settlement, however, species differences may become apparent as variability in survival or reproduction can generate competitive hierarchies (Iwasa and Roughgarden 1986; Berkeley et al. 2010). Once established in the adult habitat, barnacles then interact through direct interference with each other by overgrowing, crushing, smothering, and undercutting neighbors (Connell 1961; Dayton 1971; Berlow and Navarrete 1997) or through exploitative competition for food when feeding from the plankton (Bertness et al. 1998). Our study is centered along the coast of Chile where two similarly sized chthamalid barnacles, *Jehlius cirratus* and *Notochthamalus scabrosus*, occur in overlapping distributions in the high intertidal zone of wave-exposed rocky shores (Shinen and Navarrete 2010). Although these two species have been described together as early as Darwin's voyage along the coast of Chile more than 180 years ago (Castilla 2009), the interaction between *Jehlius* and *Notochthamalus* is not well understood. The species exhibit some differences in their vertical zonation, typical of many co-occurring barnacle species (e.g., Connell 1961; Dayton 1971; Berlow and Navarrete 1997), with *Jehlius* only slightly offset to the higher intertidal zone than the distribution of *Notochthamalus* (Castilla 1981; Paine 1981; Shinen and Navarrete 2010). However, unlike most other co-occurring barnacles, they share much (>75%) of their vertical range, and adults are highly correlated in space at even very small (25 cm²) spatial scales (Shinen and Navarrete 2010). At many sites, these two species often cover nearly 100% of the available space, and therefore, competition for space is expected to be intense. However, accounts of competition between *Jehlius* and *Notochthamalus* are contradictory. Based on field observations from central Chile, Paine (1981) concluded that *Jehlius* is competitively dominant over *Notochthamalus*, the former displacing the latter to lower levels on the shore by overgrowth and crowding. In contrast, results from manipulative experiments conducted near Puerto Montt, southern Chile, suggest an opposite hierarchy, where *Jehlius* suffers high mortality where *Notochthamalus* is abundant (López and González 2003). More recently, observational evidence from several sites in central Chile suggest that *Jehlius* and *Notochthamalus* may be competitively equivalent and that the relative abundance of adult barnacles may be determined by the relative abundance of recruits (Shinen and Navarrete 2010). Recruitment rates of *Jehlius* and *Notochthamalus* are also highly correlated in both space and time (Lagos et al. 2007; Shinen and Navarrete 2010), although total recruitment rates vary dra-

matically along the coast (Navarrete et al. 2002, 2008) and are correlated with the extent of interspecies mixing (Shinen and Navarrete 2010).

While slight differences in distribution have traditionally been considered sufficient evidence of coexistence through resource partitioning and associated fitness trade-offs (Siepielski and McPeek 2010), we aimed to test these notions experimentally at multiple sites. We evaluate (1) whether the two barnacle species do compete for space under natural conditions at all or most sites, (2) whether the invasibility criterion for species coexistence is satisfied at all sites, (3) whether there is interference or exploitative interspecific competition for space among established individuals, (4) the existence of any trade-offs in fitness or competitive ability across the ecological gradient (tidal elevation) set by settlement or interference, and (5) the role of recruitment fluctuations on local and among site barnacle abundance.

Material and Methods

Study System

For a robust test of these hypotheses and to capture both local and among site heterogeneity that may be important in determining patterns of barnacle abundance, we experimentally manipulated the total and relative abundances of adult barnacles at three elevations along the vertical shore gradient at four sites separated by tens to hundreds of kilometers at rocky shores along central Chile (fig. 1*a*). All four sites are characterized by high wave exposure, semidiurnal tidal cycle, and a tidal range of ca. 1.8 m (Navarrete et al. 2005; Finke et al. 2007). The experimental sites at Temblador, Guanaqueros, Estación Costera de Investigaciones Marinas at Las Cruces (ECIM), and Matanzas were specifically chosen because they also represent a wide range of barnacle recruitment rates typical of the region (Navarrete et al. 2002; Shinen and Navarrete 2010). Both species have planktotrophic larvae that spend between 20–30 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 moderate to large dispersal potential in these species. Once settled, metamorphosis takes place within 1–3 days (Tapia and Navarrete 2010), and individuals can be readily identified to the species level under a dissecting microscope. Identification in the field is possible after 4–6 weeks, when individuals are easily distinguished by distinctive opercular patterns (fig. 1*b*). Within the "barnacle zone," the highest tidal level corresponds to the subzone where *Jehlius* numerically dominates, with low representation (<10%) of *Notochthamalus*; the mid tidal level corresponds to the

subzone where *Jehlius* and *Notochthamalus* are well mixed; and the lower tidal level corresponded to the subzone where *Notochthamalus* numerically dominates, with low representation (<20%) by *Jehlius* (see Shinen and Navarrete 2010 for further details of zonation patterns). While barnacles are readily preyed on 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 experiments were conducted (Castilla 1981).

Competition Experiment

Since chthamalid barnacle individuals cannot be successfully removed and transplanted to the rock surface, to examine the effects of intra- and interspecific crowding on barnacle growth, survival, and the potential for species to recover from low density (invasibility criterion; Chesson 2000), we manipulated density and cover of adult barnacles by selective removal of established individuals. In November–December 2008 we installed a series of 10 × 10-cm plots, distributed among three (high, mid, and low) vertical subdivisions of the upper shore or barnacle zone, targeting areas of higher *Jehlius* abundance, equal species abundance (greatest interspecies mixing), and higher *Notochthamalus* abundance, respectively (fig. 1). Only high and mid barnacle zones plots were established at Guanaqueros due to an abrupt drop in the rock platform, leaving insufficient space for replicate plots in the low barnacle zone.

All manipulations of barnacle abundances were standardized across sites and subzones by the available bare space in experimental plots. Previous work in this system has demonstrated that the remaining barnacle cover correlates closely with total barnacle density at small spatial scales (Shinen and Navarrete 2010). At the onset of the experiments (November 2008), the abundance of barnacles in the plots was manipulated to establish a range of total adult barnacle cover (species pooled) between 0% and 80%. In the high barnacle zone, *Jehlius* was numerically dominant ($n = 20$ plots per site), and the cover of *Notochthamalus* individuals within these plots was manipulated so their cover did not exceed 15%. Similarly, in the low barnacle zone plots ($n = 12–20$ per site), *Notochthamalus* was established as numerically dominant, and cover of *Jehlius* did not exceed 15%, with the exception of Matanzas, where the smaller size of barnacles limited identification of species in the field, and the resultant *Jehlius* cover was higher (10%–40%). In the mid barnacle zone, three species-dominance treatments were established ($n = 10$ plots per treatment, per site): *Jehlius* dominance (*Notochthamalus* <15% of individuals in the plot), *Notochthamalus* dominance (*Jehlius* <15% of individuals), and
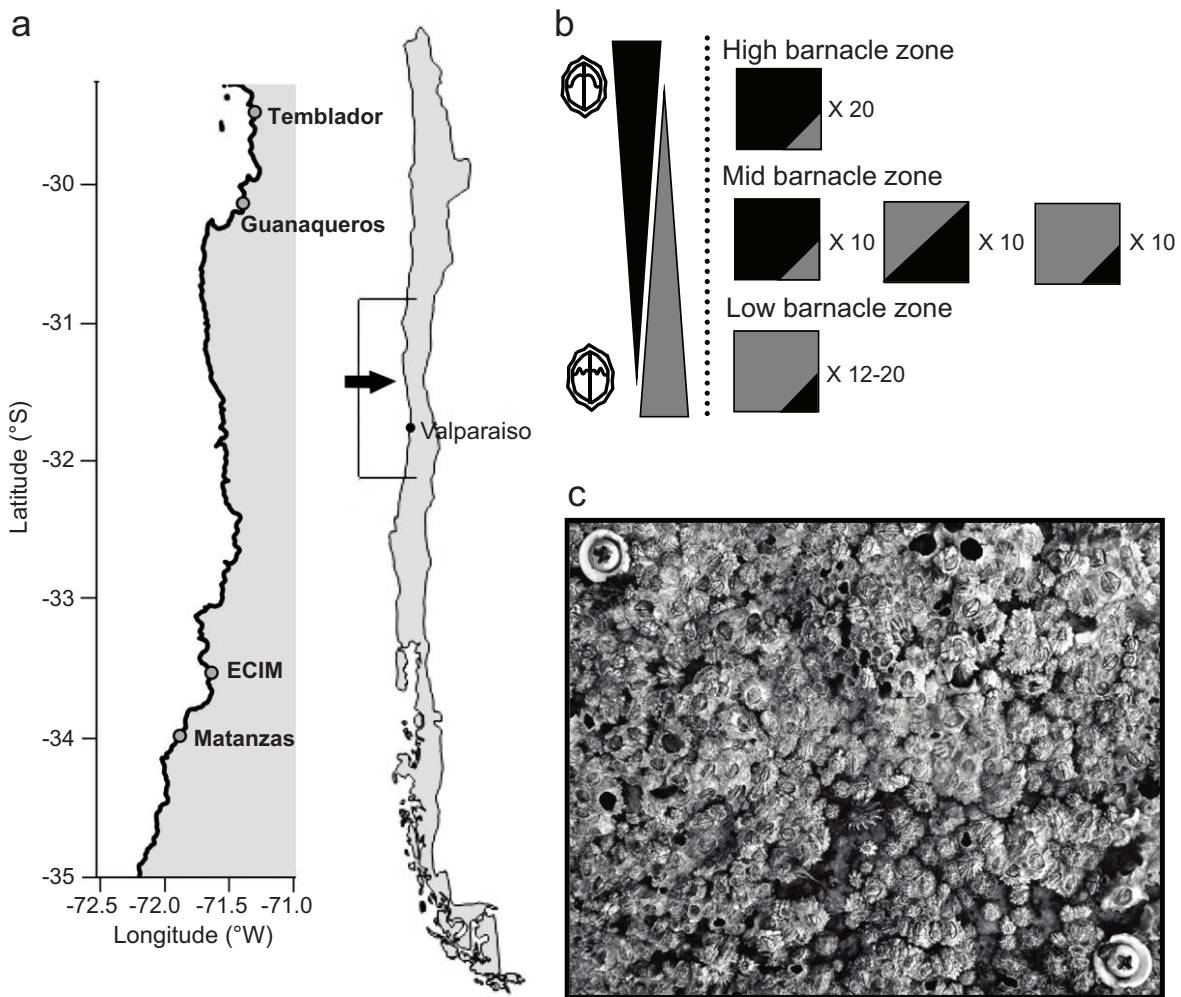
Figure 1: *a*, Map depicting study sites in central Chile. *b*, Generalized relative distributions of *Jehlius* (in black) and *Notochthamalus* (in gray) across tidal elevation along the upper shores of central in Chile and schematic of experimental design and replication at the four study sites. Initial manipulations established a range of total adult barnacle cover (species pooled) between 0% and 80% in all 10 × 10-cm² plots. In the high barnacle zone (*n* = 20 plots per site), *Jehlius* was numerically dominant and the cover of *Notochthamalus* did not exceed 15%. In the mid barnacle zone, three species dominance treatments were established (*n* = 10 plots per treatment, per site): *Jehlius* dominance (*Notochthamalus* <15% of individuals in the plot), equal dominance (roughly 50% individuals of each *Jehlius* and *Notochthamalus*), and *Notochthamalus* dominance (*Jehlius* <15% of individuals). In the low barnacle zone plots (*n* = 12–20 per site), *Notochthamalus* was numerically dominant and cover of *Jehlius* did not exceed 15%. Note depictions of the distinctive opercular patterns used to distinguish between species. See text for further details. *c*, Image of an experimental plot (from the mixed zone of Guanaqueros), where *Jehlius* and *Notochthamalus* are found in high density and relatively equal abundances.

equal dominance (roughly 50% individuals of each *Jehlius* and *Notochthamalus*). All plots were marked with two stainless steel screws in the upper left and bottom right corners and photographed approximately every 3 months with a digital camera (Olympus 1030W). Final photos were taken in July 2010. From the photos we estimated total barnacle cover and abundance of adult *Jehlius* and *Notochthamalus*. Barnacle "recruits" (individuals <0.75 mm carino-rostral length) were counted, pooled by species as they are too small to be identified in the photos.

To estimate per capita intra- and interspecific interference effects on growth and survival among established juveniles and adults, we followed between 150–200 individuals of each species at each site (distributed among the three barnacle subzones) under three different "crowding conditions": (1) "isolated individuals" with less than 25% of their shells in contact with neighboring barnacles of any species; (2) "conspecific crowding" individuals that were in aggregated groups, with a minimum of 50% and up to 100% of their shells in contact with other adult

individuals of the same species; and (3) "heterospecific crowding" individuals that were in aggregated groups with 50%–100% of their shells in contact with adults of the other species. The maximum opercular carino-rostral length, survival, and number of neighboring individuals were recorded roughly every 3 months. ImageJ image analysis (Abramoff et al. 2004) was used to score and analyze photos. All data gathered from photos and used in subsequent analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.95br2 (Shinen and Navarrete 2013).

Recruitment Rates

Recently settled barnacles were difficult to identify from photos, and therefore, recruitment was quantified in two different ways. First, we classified new barnacle individuals from photos that were large enough to be unequivocally assigned to species after reaching juvenile stage. Individuals below this size threshold were considered "recruits," both species pooled. This estimate of recruitment can be dependent on availability of free space and, therefore, on the total barnacle density within the plots (see below). Secondly, to get a recruitment estimate that better reflects variability in settlement from the plankton, we used 10 × 10-cm^2 Plexiglas plates covered with a standard rugosity surface (Safety Walk, 3M) that were replaced once monthly over the peak recruitment season of November 2009–April 2010. Five plates were deployed and retrieved from the high, mid, and low barnacle subzones at each site (Guanaqueros included) then taken to the laboratory where 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 average number of individuals per days of exposure per collector (see Navarrete et al. 2008). In all cases, the plates provided the same settlement surface that was free from the presence of adult barnacles. All data gathered from recruitment collectors and used in subsequent analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.95br2 (Shinen and Navarrete 2013).

A Framework for Competition for Space: Recruitment Lottery and Adult Interference

As mentioned previously, there are two general ways in which barnacle species can compete for space: (1) at the time of settlement, individuals can compete for free space that is not already taken by individuals of self or the other species; i.e., a lottery type of competition (Iwasa and Roughgarden 1986; Berkley et al. 2010). (2) After settle-

ment and as individuals grow in size, juveniles and adults can crush, undercut, or overgrow other individuals, killing them or stunting their growth (e.g., Connell 1961; Dayton 1971; Berlow and Navarrete 1997). A simple two-stage model can then provide a framework to tease apart these two forms of competition between *Jehlius* and *Notochthamalus*:

$$R_{i(t)} = S_i(K - N_i - N_j) - m_{si}S_i, \tag{1}$$

$$N_{i(t+1)} = N_{i(t)}(1 - a_{ii}N_i - a_{ij}N_j) + R_{i(t)} - m_iN_{i(t)}, \tag{2}$$

where the number of recruits of species i, R_i, observed at time t in a given experimental area is determined by the settlement of larvae from the plankton, $S_{i(t)}$, and the density independent mortality of those settlers, $m_{si}S_i$ that occurred until they are counted as new recruits in the plots. Settlement is assumed to depend on availability of free space ($K - \sum_{i=1}^{s} N_i$), that is, space that is not occupied by either the target species or its competitor j (Iwasa and Roughgarden 1986). Thus, if settlement rates are sufficiently high, species will compete for space. Since both species are of similar size, we assumed their use of space was directly proportional to the number of individuals. Competition for space in marine organisms has also been modeled using a Beverton-Holt recruitment function (Berkeley et al. 2010), but we prefer the above representation for sessile organisms because of the finite availability of space (e.g., Iwasa and Roughgarden 1986) and because competition does not only involve settlers. The number of adult individuals in the experimental plots, N_i at time $t + 1$ is then a function of the number of individuals found at time t, plus the individuals that successfully recruited to the population one time interval before. Reductions in population size occur because of density independent mortality of adult individuals in the plot, m_i, and because of intra- (a_{ii}) and interspecific interference (a_{ij}) for the limited space.

If adult individuals do not interfere with each other, that is, $a_{ii} = a_{ij} = 0$, then equation (2) reduces to

$$N_{i(t+1)} = (N_{i(t)} + R_{i(t)}) - m_iN_{i(t)}, \tag{3}$$

which can be rewritten as in Warner and Chesson (1985) as

$$N_{i(t+1)} = N_{i(t)}(1 + m_i) - R'_{i(t)}N_{i(t)}, \tag{4}$$

where $R'_{i(t)}$ is the per capita recruitment rate of species i. Note that if $a_{ii} = a_{ij} \neq 0$ throughout the tidal gradient where species occur, then interference between adults cannot provide a stabilizing source of coexistence (Adler et al. 2007), and interference can then be considered a stochastic, density-dependent mortality source (Chase and Myers 2011).

Competition for Space and Coexistence Where Barnacles Are Well Mixed

Since at most sites and tidal levels within the barnacle zone the space occupied by chthamalid barnacles can reach nearly 100% of the available surface over extensive areas, competition for space is expected (López and González 2003; Shinen and Navarrete 2010). Per capita recruitment rate should then decline as local population size increases. We therefore examine whether $R'_{(t)}$ (both species pooled) was negatively related to $(N_i + N_j)$ in the different barnacle zones and sites.

Before examining the mechanisms favoring coexistence between these barnacle species, we evaluated the basic criterion for coexistence between competing species: "each species must be able to increase when it is rare and the others are at their typical abundances" (Siepielski and McPeek 2010, p. 3153). To this end, in the well-mixed mid barnacle zone, we calculated the per capita population growth rate of each species as the "invader" after that it had been experimentally reduced to low abundance or even completely removed from the experimental plots while the other was left undisturbed as the "resident" species as $r_i^0 = \ln(N_{i(t+1)}/N_{i(t)})$, calculated over 544 days of monitoring. Values of r_i^0 were obtained for each experimental plot and then averaged within sites. Different plots were used for different invader-resident species treatments. Using a Student t-test, we tested whether values of r_i^0 were significantly greater than zero after experimental reduction, which is considered an indication of coexistence. In addition, we compared population growth rates between species (fixed factor) and among sites (random factor) using a two-way ANOVA.

Survival, Individual Growth, and Interference Competition

We evaluated whether estimates of the $a_{ij} \neq 0$, that is, whether direct interference among adults led to reduced survival or individual growth rates, as suggested from previous observations (Paine 1981; López and González 2003) and has been shown to occur among other barnacle species (Connell 1961; Navarrete 1996; Berlow and Navarrete 1997). Approximations to these local, interference components of competition were obtained from the individuals followed in the photographs under different neighborhood crowding conditions. First, an estimate of natural adult mortality for each species (m_i) was obtained from the slope of the linear regression between $\ln(N_t^c/N_0^c)$ over time, where N_0^c is the initial number of individuals identified as part of a cohort (c) at the beginning of the experiment and which were in isolation from all other con- or heterospecific individuals. Then, N_t^c is the number of those individuals in the cohort found alive in a given plot at

time t. Second, estimates of total mortality rate were obtained, in the same manner, for treatments where individuals were in contact with conspecifics or heterospecifics. In these cases, the slopes estimate total mortality under these crowding conditions, and we therefore subtracted the natural mortality rate obtained from isolated individuals (m_i) over the same period of time. These mortality rates, corrected by natural mortality, were then divided by the average number of individuals surrounding the target individual over the study period to obtain estimates of a_{ii} and a_{ij}; that is, we attributed the effect on survival equally to all conspecific or heterospecific individuals in contact with the target individuals. Individual growth rates were estimated for each sample interval as (final carino-rostral length − initial carino-rostral length)/days of focal individuals, in each subzone, site, and crowding condition. Per capita effects on individual growth were calculated by subtracting the growth rate observed when individuals were isolated from growth when surrounded by con- or heterospecifics and dividing by the average number of neighboring individuals. Note that when calculated in this manner, increased mortality due to crowding leads to significantly positive a_{ii} and a_{ij} values, while significantly negative crowding effects on individual growth lead to negative a_{ii} and a_{ij} values. To facilitate comparisons and to visually represent the direction of the effect, in all figures we present values of $-a_{ii}$ and $-a_{ij}$ for mortality. Error estimates for a_{ii} and a_{ij} were obtained through standard error propagation theory (Taylor 1997). We compared mortality rates (m_i) and individual growth rates measured in isolated individuals using three separate two-way ANOVAs with species and sites as fixed and random factor, respectively. Similarly, statistical significance of crowding treatment effects on total mortality rates (uncorrected by natural mortality) and growth rates (uncorrected by growth rate of isolated individuals) were compared using separate three-way ANOVAs for each barnacle zone, with barnacle species and crowding condition as fixed factors and site as a random factor. We preferred to conduct separate analyses for each tidal elevation to simplify interpretation of interactions and because the low level at Guanaqueros was missing (see above), preventing us from conducting one fully factorial design. Tests of hypotheses were conducted following Kuehl (1994) and the Satterthwaite correction was applied when necessary (Kuehl 1994). It should be born in mind that our manipulations cannot separate effects of physical interference for space from effects of interference when filter feeding.

Stabilizing Mechanisms of Coexistence: Niche Partitioning across the Tidal Gradient

As we stated earlier, although the two species overlap amply in their intertidal distributions, there is a persistent

pattern of segregation across all the central coast of Chile, where *Jehlius* is more abundant in the high intertidal zone than *Notochthamalus*, while *Notochthamalus* is more abundant than *Jehlius* lower on the shore (Shinen and Navarrete 2010). Typically, this kind of distribution pattern, together with evidence of direct interactions between species (Paine 1981; López and González 2003), is deemed sufficient as evidence of competition-driven resource partitioning (niche differentiation) and coexistence through competitive trade-offs at extremes of the environmental gradient. The important question here is whether the resulting intertidal distribution of the two species could generate sufficient fitness trade-offs in species' performance or competitive ability across the gradient to be considered a stabilizing mechanism of coexistence (sensu Chesson 2003; Adler et al. 2007; Siepielski and McPeek 2010).

We first evaluated whether interference among adults after recruitment to a local site could provide the basis for such differentiation. Provided that species can sustain positive population growth, per capita recruitment rates of both species are approximately similar across the intertidal gradient ($R' \approx R'ji$), and natural mortality rates are low, fitness trade-offs favoring coexistence can occur when the difference $a_{ii} - a_{ji}$ is significantly greater than zero at different ends of the intertidal gradient for the different species, i.e., when intraspecific effects of one species on itself are greater than interspecific effects it has on the other species over distinctive portions of the tidal gradient. We therefore examined whether the $a_{ii} - a_{ji}$ difference changed predictably across the tidal gradient with the slightly offset species distributions. We also evaluated trends in natural mortality rates, m_i, between the species. If natural mortalities are high enough and in opposite direction through the gradient, they can alter effective density and lead to effective competitive trade-offs, even under similar per capita effects.

The effectiveness of any mechanism of postrecruitment niche differentiation through differential adult performance across the intertidal gradient depends on other sources of density-dependent variation being similar across the gradient, notably the intensity and direction of competition for space at the time of settlement. To evaluate the potential for local fitness trade-offs considering both preemption and interference, we regressed the changes in the abundance of *Jehlius* and *Notochthamalus* per unit time, that is, per capita growth rates, $r_i = \ln(N_{i(t+1)}/N_{(t)})$, over their relative abundances in experimental plots ($N_i/[N_i + N_j]$) while holding total adult barnacle abundance approximately constant (140 ± 65 individuals per plot) and 40%–60% total barnacle cover for each barnacle subzone. A significantly negative relationship is indicative of stabilizing mechanisms of local coexistence as species become more self-limiting as they reach greater relative abundances, whereas a slope of zero would indicate species equality such that growth rates are independent of relative abundances (Adler et al. 2007). Before calculating population growth rates, we added one individual to all observations ($N_i + 1$) to prevent the estimates from becoming undefined when no individuals were observed at time t. This had virtually no effect on growth rate estimates (correlation between estimates based on N_i and $N_i + 1$: $r = 0.997$ and $r = 0.996$ for *Jehlius* and *Notochthamalus*, respectively) but allowed us to use a larger number of observations. Note that changes in barnacle abundance between time intervals occur through both recruitment of new individuals and mortality of existing individuals due to density-dependent and density-independent processes.

Recruitment Fluctuations, Storage Effect, and Relative Abundances

The two chthamalid barnacle species possess all the essential attributes for "storage effect" to play a significant role in species coexistence (see Warner and Chesson 1985); temporal fluctuations in recruitment of new individuals characterize both species (Navarrete et al. 2008; Tapia and Navarrete 2010), they possess an adult life stage that can survive several recruitment events and suffer comparatively low mortality (see "Results"), and they both have comparatively high per capita reproductive output that is fairly synchronous in the population. We should note that since mortality rates are low and not significantly different between the two species (see "Results"), we can disregard the relative nonlinearity of competition (Armstrong and McGee 1980; Kang and Chesson 2010) as an important coexistence mechanism (see Chesson 2003). Unfortunately, we could not separate new recruits to species level from the photographs until they were several weeks old and had, potentially, already experienced competition effects. Moreover, a much longer species-specific time series of recruitment and population size data would be required to provide a more formal evaluation of storage effects (e.g., Cáceres 1997). Nevertheless, a preliminarily assessment of the potential contribution of storage effects was conducted by looking at the temporal correlation in recruitment of the two species observed in the barnacle plates at the different sites and tidal levels. Since the plates were replaced each month, reducing adult population size to zero, variability in recruitment rates can be considered estimates of the "environmental" component of recruitment fluctuation in jargon of storage effect theory (Chesson 2003). Low covariance (correlation) between species suggests high potential for storage effect to be important (Chesson and Warner 1981).

Finally, to determine whether the relative abundance of adult barnacles is a direct reflection of the relative abundance of arriving recruits, as would be predicted by neutral
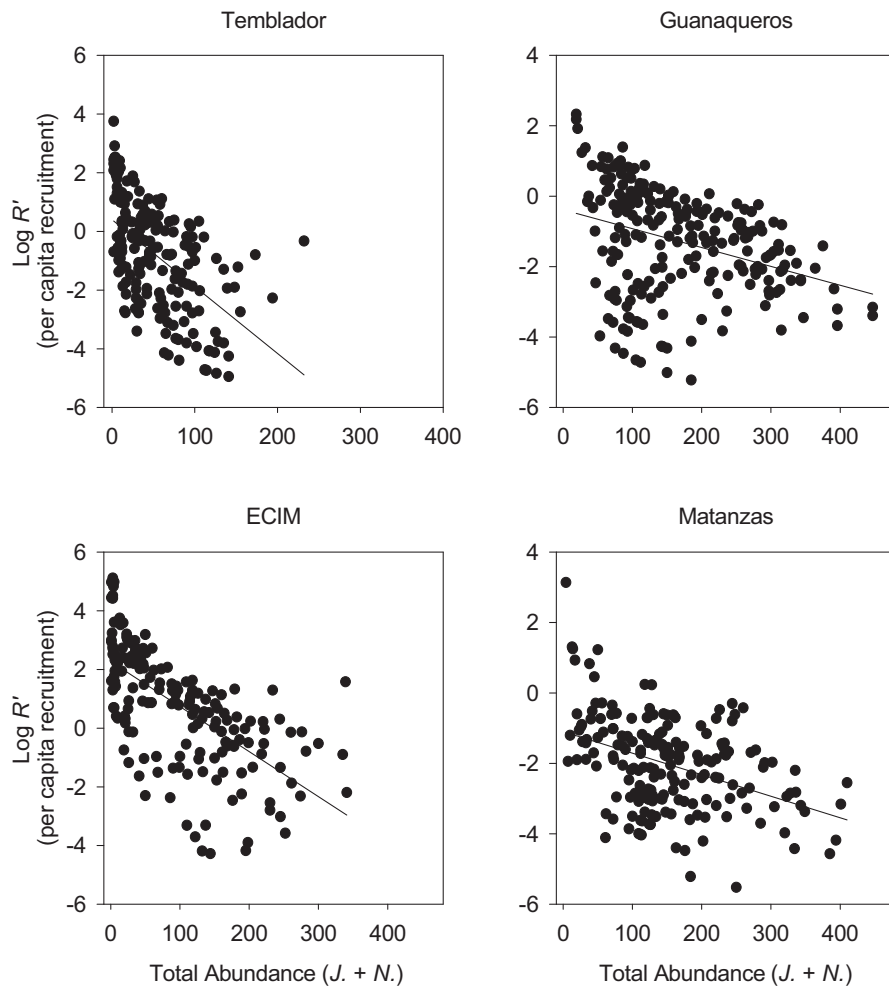
Figure 2: Per capita recruitment (log transformed) of *Jehlius* and *Notochthamalus* inside experimental plots within the mid zone, where species are well mixed, by the total adult barnacle abundance.

models (Hubbell 2001), we compared the relative proportion of adult barnacles inside experimental plots (expressed as the ratio of *Jehlius* to total barnacle density) from fall 2010 against the mean relative density of recruits over the 2009–2010 season using a Pearson correlation. This comparison was done across sites and not following individual cohorts (e.g., Connell 1985; Menge 2000), and therefore, the adult density is reflective of the recruitment cohort of the 2009–2010 season as well as any carry over from earlier cohorts of juveniles.

Results

Competition for Space and Coexistence in the Well-Mixed Barnacle Zone

The per capita recruitment rate (R') of new individuals was drastically reduced with increasing abundance (population

size) of established individuals in experimental plots in the well-mixed mid intertidal barnacle zone of all sites (fig. 2). Similar patterns were observed at the high and low barnacle zones (appendix, available online). As expected from stochasticity in settlement of sessile organisms (Siegel et al. 2008; Berkeley et al. 2010), a considerable spread characterized the relationship; that is, areas with comparatively low abundance of established individuals could still receive low per capita settlement of new individuals (fig. 2).

Experimentally reducing the density of *Jehlius* within experimental plots of the well-mixed mid barnacle zone, leaving *Notochthamalus* at natural density, led to significantly positive population growth rates of *Jehlius* at all sites (fig. 3). Similarly, removing *Notochthamalus* and leaving *Jehlius* at natural density within the same general area but different experimental plots led to significantly positive population growth rates of *Notochthamalus* (fig. 3). That
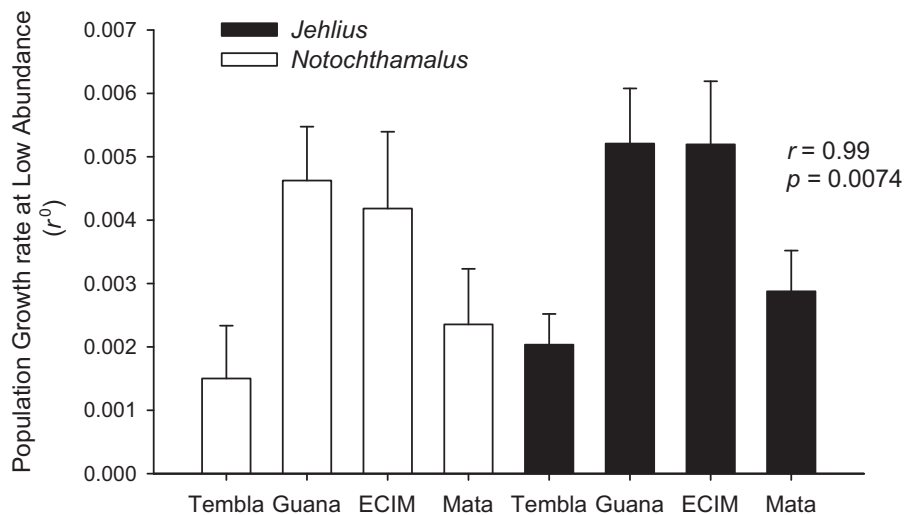
Figure 3: Population growth rate (r^0) of *Jehlius* and *Notochthamalus* after being manipulated to low abundance inside experimental plots within the mid zone. Tembla = Temblador, Guana = Guanaqueros, ECIM = Estación Costera de Investigaciones Marinas at Las Cruces, and Mata = Matanzas.

is, despite the existence of competition for space, both species can recover from low density when the other is at "equilibrium" (unaltered) abundance, and therefore, they coexist. Among site variation in the magnitude of population growth rates was remarkably similar between species ($r = 0.99$, $P = .0074$) and a two-way ANOVA with site and species as main fixed factors showed highly significant differences among sites ($F = 6.35$, df $= 3, 72$, $P = .0007$) but no statistical differences between species or interaction between these factors ($P > .05$). Note that in all cases individuals of the resident species also recruited to the cleared areas in experimental plot, but this increase in abundance had only a minor effect on the resident per capita population growth rate.

Survival, Individual Growth and Interference Competition

No consistent differences in per capita mortality rates of isolated individuals (m_i) were observed between the two barnacle species across sites at the three tidal levels (fig. 4a–4c; table 1, nonsignificant main effect of Species). Although slight variation in mortality between species was observed at some sites and tidal levels, this variability was not sufficient to render the species × site interaction significant, at any tidal level (table 1). Moreover, variation in per capita mortality from site to site was significantly correlated between the two species at the scale of the plots (fig. 4d). Significant differences among sites were only observed in the mid intertidal zone (table 1), with higher mortality rates at ECIM and Matanzas for both barnacle species (fig. 4b).

Individual growth rates of isolated individuals were remarkably similar between the two species at all sites and tidal levels (fig. 4e–4h; table 1) and were positively correlated at the scale of plots across all sites (fig. 4h). Significant differences in individual growth rates among sites, at high and low intertidal zones, were consistent between the two barnacle species (table 1, nonsignificant site × species interaction).

Remarkably, intraspecific as well as interspecific "interference" effects on per capita survival (crowding effects) were positive for both species; that is, conspecific and heterospecific individuals had a facilitative effect on individual survival of similar magnitude (fig. 5a–5g). The estimates of crowding effects were negative at only 4 of the 44 site × tidal level combinations for both species, but in those cases they were not significantly different from zero (fig. 5). At most other sites effects on individual survival were significantly positive. No significant correlation was found between intraspecific effects (uncorrected by natural mortality; fig. 5d), but a significant positive correlation was found between interspecific effects (uncorrected by natural mortality; fig. 5h) across all sites and tidal levels. ANOVA comparison of total mortality rates (uncorrected by natural mortality) under the different crowding treatments showed nonsignificant differences between species at all tidal levels and highly significant effect of crowding and among-site variation in the high and mid intertidal zones (table 2). In the mid intertidal zone, the effect of crowding varied significantly among sites, but it was consistent between the two species.

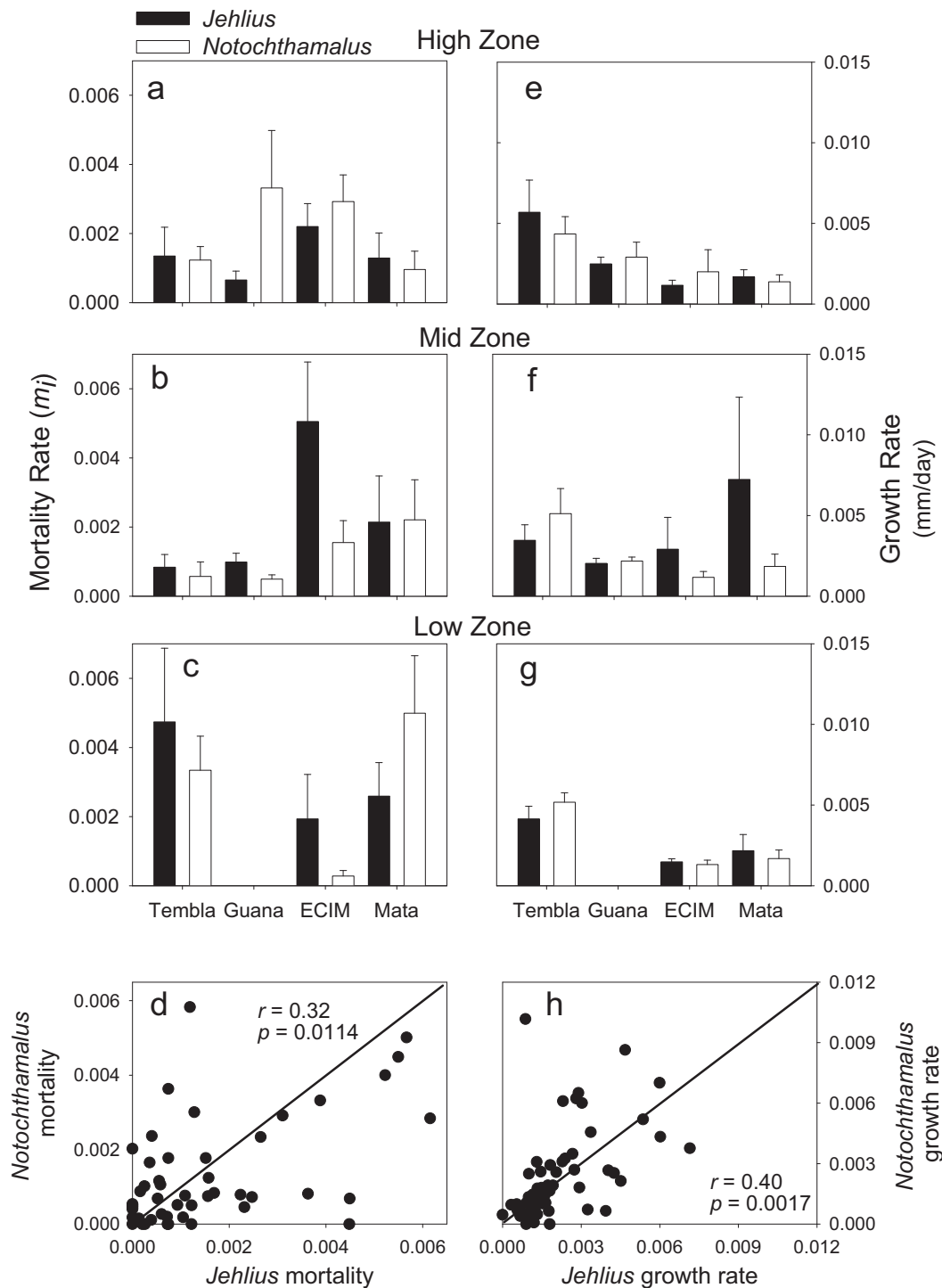In contrast to effects of crowding on survival, surround-

Figure 4: Mean (±1 SE) mortality rates (*a, b, c*) and growth rates (*e, f, g*) of isolated *Jehlius* and *Notochthamalus* inside experimental plots within the high, mid, and low barnacle zones and at each site. Panels *d* and *h* show results of correlation analyses of species mortality and growth rates, respectively, across all sites and tidal elevations. See figure 3 for location abbreviation definitions.

Table 1: Results of two-way ANOVAs comparing per capita mortality rates (m_i) and individual growth rates (mm^2/day) of isolated individuals in experimental plots between species (fixed factor) and among sites (random factor) for the three tidal zones

Source	Mortality				Individual growth			
	df	MS	F	P	df	MS	F	P
High zone:								
Species	1	6.92	.98	.3959	1	.11	.05	.8400
Site	3	5.89	1.09	.3645	3	24.92	4.51	**.0073**
Species × site	3	7.08	1.30	.2840	3	2.32	.42	.7396
Error	47	5.43			48	5.53		
Mid zone:								
Species	1	11.06	1.52	.3050	1	19.47	.87	.4202
Site	3	17.25	3.72	**.0198**	3	20.66	1.17	.3321
Species × site	3	7.26	1.57	.2143	3	22.42	1.27	.2966
Error	36	4.64			41	17.63		
Low zone:								
Species	1	.36	.03	.8882	1	.12	.07	.8223
Site	2	22.72	2.06	.1481	2	30.85	12.27	**.0002**
Species × site	2	14.11	1.28	.2955	2	1.77	.70	.5042
Error	26	11.04			25	2.51		

Notes: All four sites were used in the high and mid zones and 3 sites in the low zone. Boldface indicates significant effect at $\alpha = 0.05$. Mean squares (MS) are presented as MS × 10^6 to facilitate presentation.

ing neighbors had significantly negative effects on individual growth rates at all sites and tidal levels (fig. 6). The magnitude of both intra- and interspecific effects varied from site to site but with no consistent differences between species (fig. 6). Consequently, statistical comparisons of growth rates showed no differences between species at any tidal level and significant effects of crowding treatment (table 2). Crowding effects did vary across sites, but they were consistent between species. As with crowding effects on mortality, we found no significant correlation between intraspecific effects on growth rate (uncorrected by growth rates of isolated individuals; fig. 6d), but a significant positive correlation was found between interspecific effects (uncorrected by growth rates of isolated individuals; fig. 6h) across all sites and tidal levels.

Stabilizing Mechanisms of Coexistence: Niche Partitioning across the Tidal Gradient

As expected from the results presented above, the difference between the intraspecific effect of each species on itself (a_{ii}) and the interspecific effects it had on heterospecific (a_{ij}) survival or individual growth was not significantly different from 0 at any site or tidal level, with no trend to switch in direction across the tidal gradient (fig. 7). In some cases, either the negative intraspecific effect was slightly greater than the effect of interspecific facilitation/competition or

the interspecific facilitative/competition effect was greater than the intraspecific facilitative effect.

Per capita population growth rates (r_i) did not decrease with increasing relative abundance of either species in any of the intertidal zones (fig. 8), as would be expected when there are stabilizing mechanisms facilitating coexistence (Adler et al. 2007). Population growth rates were widely spread around zero, partly as a result of stochastic variation in recruitment from plot to plot and variation in established adult density but largely indicating that both species suppress themselves, as well as their competitors, equally.

Recruitment Variability

Monthly recruitment rates onto plate collectors from the 2009–2010 season varied greatly over time, but were tightly and positive correlated between species over time at all sites and tidal zones, except at the mid zone of ECIM (fig. 9a). At ECIM, positive temporal correlations were much weaker than at all other sites and almost completely uncorrelated in the mid shore. Averaging over time, recruitment of *Jehlius* measured on these plates was consistently and significantly higher than that of *Notochthamalus* (fig. 9b, 9c; table 3). Significantly higher rates for both species were observed at Temblador and generally higher rates at the mid and low subzones than the high subzone for both species across the region (fig. 9b, 9c; table 3; Tukey P < .05).
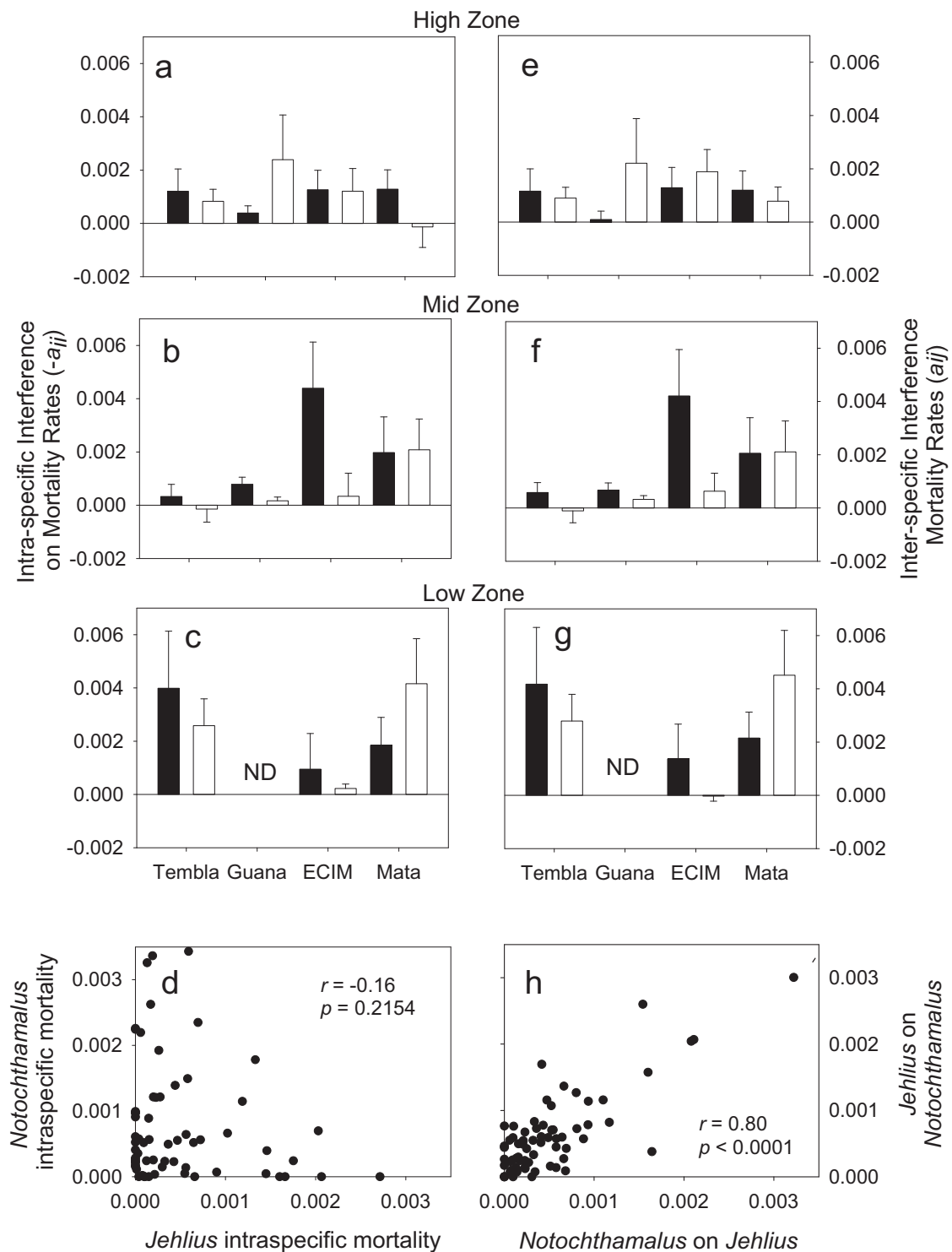
The relative abundance of recruits of both barnacle spe-

Figure 5: Mean (±1 SE) mortality rates of *Jehlius* and *Notochthamalus* individuals engaged in intraspecific interference (conspecific crowding; *a*, *b*, *c*) and interspecific interference (heterospecific crowding; *e*, *f*, *g*) inside experimental plots within the high, mid, and low barnacle zones and at each site. Panels *d* and *h* show results of correlation analyses of species intraspecific and interspecific mortality rates, respectively, across all sites and tidal elevations. See figure 3 for location abbreviation definitions.

Table 2: Results of three-way ANOVAs comparing per capita mortality rates (m_i) and individual growth rates (mm^2/day) in experimental plots between species (spp, fixed), crowding treatment (crwd, fixed), and among sites (random) for the three tidal zones

Source	Mortality				Individual growth			
	df	MS	F	P	df	MS	F	P
High zone:								
Species*	1	11.71	3.92	.1374	1	.12	.34	.5834
Crowding*	2	21.89	27.66	**.0004**	2	31.19	12.06	**.0068**
Site	3	9.16	4.34	**.0058**	3	16.62	8.16	**<.0001**
Spp × crwd*	2	1.06	.46	.6527	2	.29	.24	.7919
Spp × site	3	3.02	1.43	.2365	3	.58	.28	.8376
Crwd × site	6	.74	.35	.9088	6	5.55	2.73	**.0156**
Spp × crwd × site	6	2.32	1.10	.3654	6	1.13	.56	.7654
Error	141	2.11			139	2.04		
Mid zone:								
Species*	1	2.11	.97	.3939	1	.01	.01	.9399
Crowding*	2	23.01	5.26	**.0462**	2	80.18	8.34	**.0156**
Site	3	13.61	8.45	**<.0001**	3	18.01	1.77	.1571
Spp × crwd*	2	5.12	1.66	.2643	2	20.65	1.07	.3967
Spp × site	3	2.21	1.37	.2549	3	2.00	.20	.8988
Crwd × site	6	4.49	2.79	**.0141**	6	9.59	.94	.4690
Spp × crwd × site	6	3.16	1.96	.0765	6	19.63	1.92	.0817
Error	122	1.61			127	10.20		
Low zone:								
Species*	1	.89	.13	.7532	1	.26	.97	.4250
Crowding*	2	59.83	8.21	**.0379**	2	36.67	5.71	.0671
Site	2	10.99	2.97	.0570	2	22.23	25.60	**<.0001**
Spp × crwd*	2	.09	.02	.9786	2	.49	.54	.6184
Spp × site	2	6.90	1.86	.1616	2	.26	.30	.7380
Crwd × site	4	7.32	1.98	.1057	4	6.46	7.44	**<.0001**
Spp × crwd × site	4	4.15	1.12	.3530	4	.90	1.03	.3944
Error	82	3.70			81	.87		

Notes: All four sites were used in the high and mid zones and 3 sites in the low zone. Boldface indicates significant effect at $\alpha = 0.05$. Mean squares (MS) are presented as MS $\times 10^6$ to facilitate presentation.

* Values of F and P with Satterthwaite correction.

cies recruited onto collecting plates during spring–summer 2009–2010 was significantly and positively correlated to the relative proportion of adult *Jehlius* and *Notochthamalus* across sites in fall 2010 (fig. 10). However, many observations fell below the line of equivalency, indicating that at the lower subzones, *Jehlius* experienced higher postsettlement mortality than *Notochthamalus*.

Discussion

Our results demonstrate that *Jehlius* and *Notochthamalus* compete for space along rocky shores of central Chile and especially in the ample zone of overlap of their intertidal distributions. Both species are able to recover when rare and the other is at natural density; that is, the two species coexist with no indication that one is slowly being excluded by the other. However, despite the slight but consistently offset intertidal distribution between the species, which

might lead to suggest the existence of niche-based mechanisms of coexistence, we discovered no apparent fitness inequalities across the ecological (tidal emersion) gradient affecting individual growth, per capita survival, or per capita population growth rates. Instead, results from experimental manipulations indicate that intra- and interspecific interference effects of established individuals on per capita natural mortality, which were generally positive (facilitation), and that interference effects on individual growth rates, which were generally negative, are similar in magnitude and "equal" between *Jehlius* and *Notochthamalus*, with no evidence of any trend or trade-off in intra- and interspecific effects across the intertidal gradient. Per capita population growth rates of neither *Jehlius* or *Notochthamalus* exhibited the expected negative relationship with its own relative abundance, that is, no demographic advantage at low relative abundances or self-limiting at higher relative abundance. Moreover, natural mortality and in-
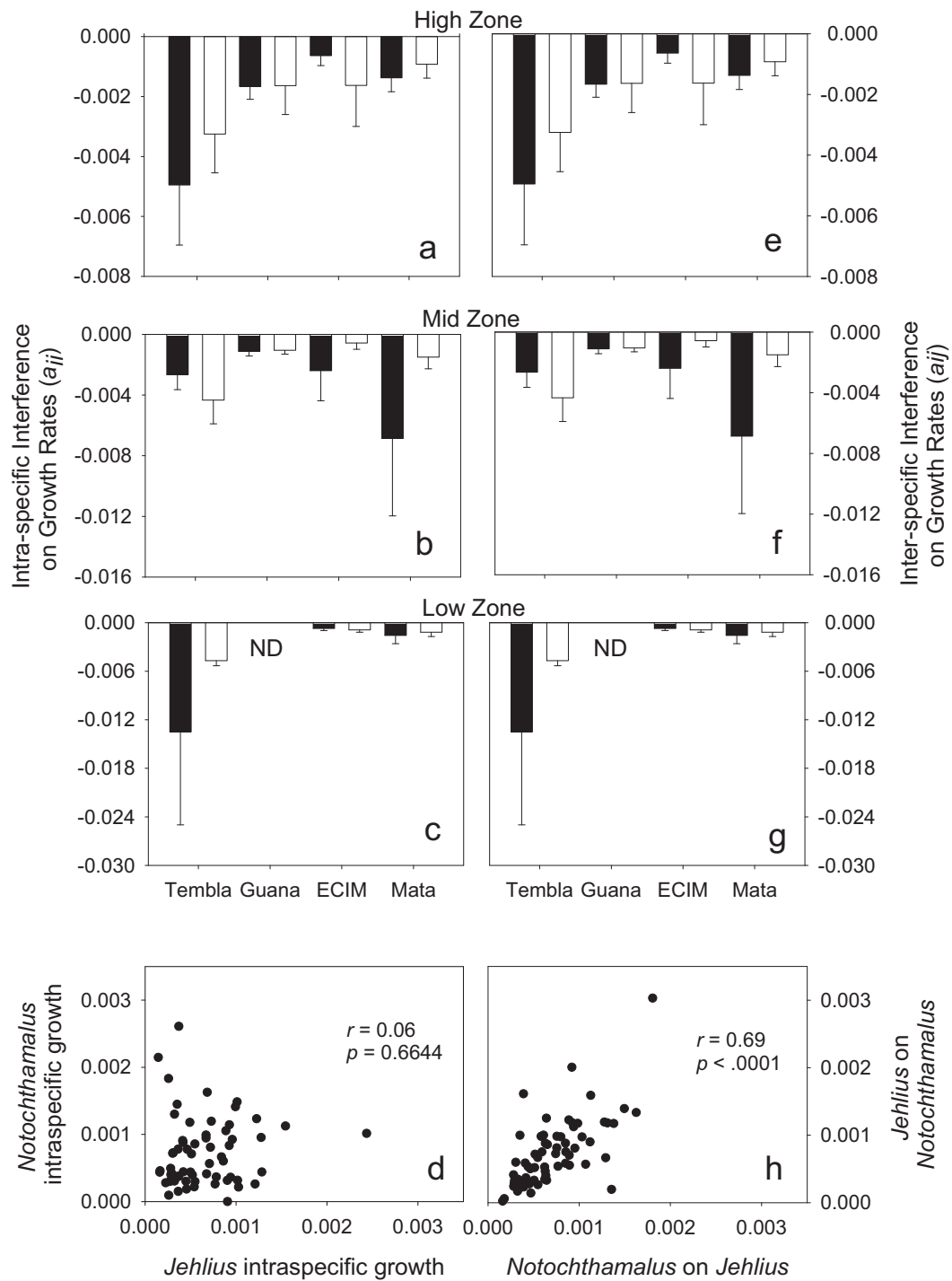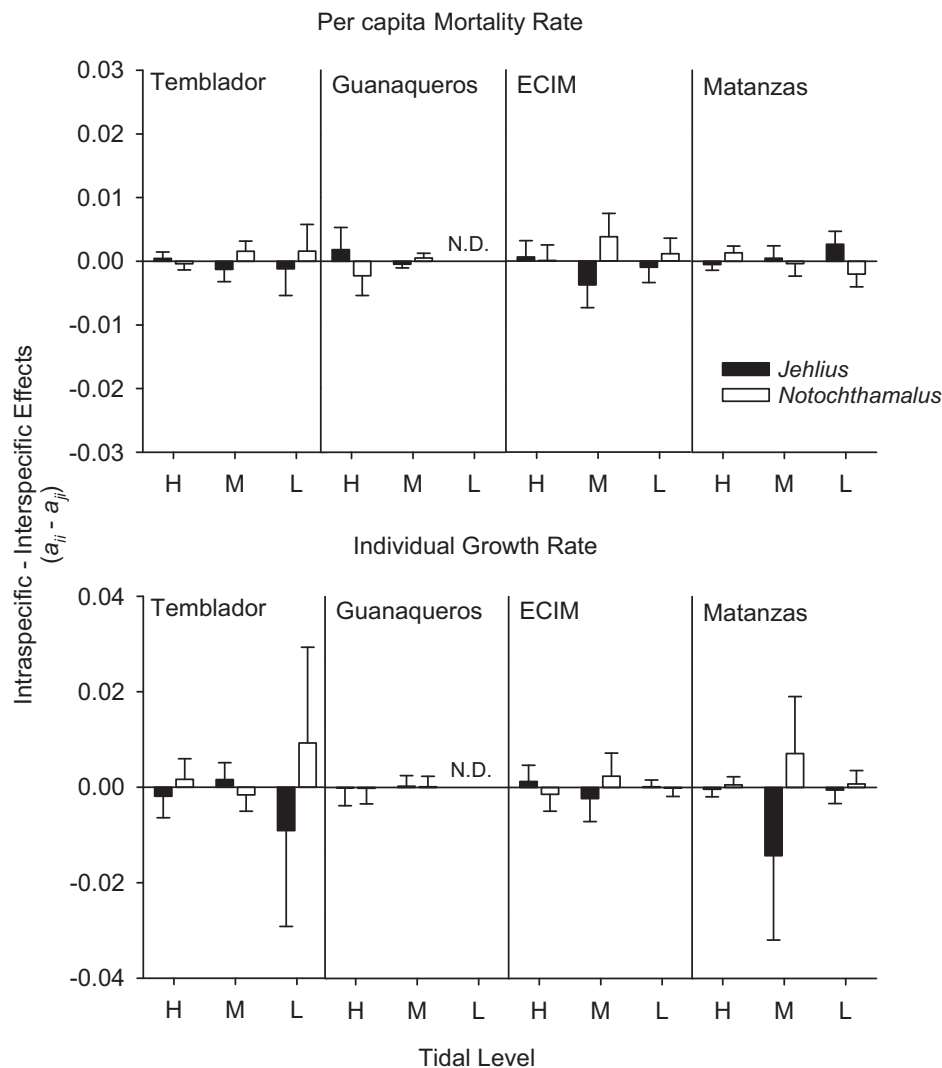
Figure 6: Mean (±1 SE) growth rates of *Jehlius* and *Notochthamalus* individuals engaged in intraspecific interference (conspecific crowding; *a, b, c*) and interspecific interference (heterospecific crowding; *e, f, g*) inside experimental plots within the high, mid, and low barnacle zones and at each site. Panels *d* and *h* show results of correlation analyses of species intraspecific and interspecific growth rates, respectively, across all sites and tidal elevations. See figure 3 for location abbreviation definitions.

Per capita Mortality Rate

Individual Growth Rate

Figure 7: Differences between the intra- and interspecific effects of neighborhood competition on per capita mortality and growth rates of adult *Jehlius* and *Notochthamalus* by site and by high (H), mid (M), and low (L) barnacle subzones.

dividual growth rates, as well as intra- and interspecific effects on themselves and on heterospecifics, were either noncorrelated or significantly positively correlated across the tidal gradient and across the four study sites. Although the role of storage effect on species coexistence could not be formally assessed, highly positive temporal correlations in recruitment, together with positive correlations in intraspecific effects, suggest its role in coexistence of these species might be limited. In summary, our results strongly suggest that these two species might very well constitute the best example thus far of a completely neutral coexistence, or at least nearly so, structured by physically driven temporal and among-site fluctuations in recruitment of new individuals. The positive correlation between relative

abundance of recruits and those of adults across tidal levels and sites support this model explanation. Yet since the similarities between the two species are so great, the stabilizing forces required to maintain coexistence through niche differentiation may also be immeasurably small (Adler et al. 2007). In the unlikely scenario that we missed a true superior competitor, the small nonsignificant and possibly ephemeral variability observed in species performance across sites, which was inconsistent across the tidal gradient, could possibly play a role stabilizing coexistence in the form of variable "species sorting" mechanism (Leibold et al. 2004), in which the inferior competitor gains a slight relative advantage at a site and acts as a temporary source of larvae for other sites. Distinguishing between
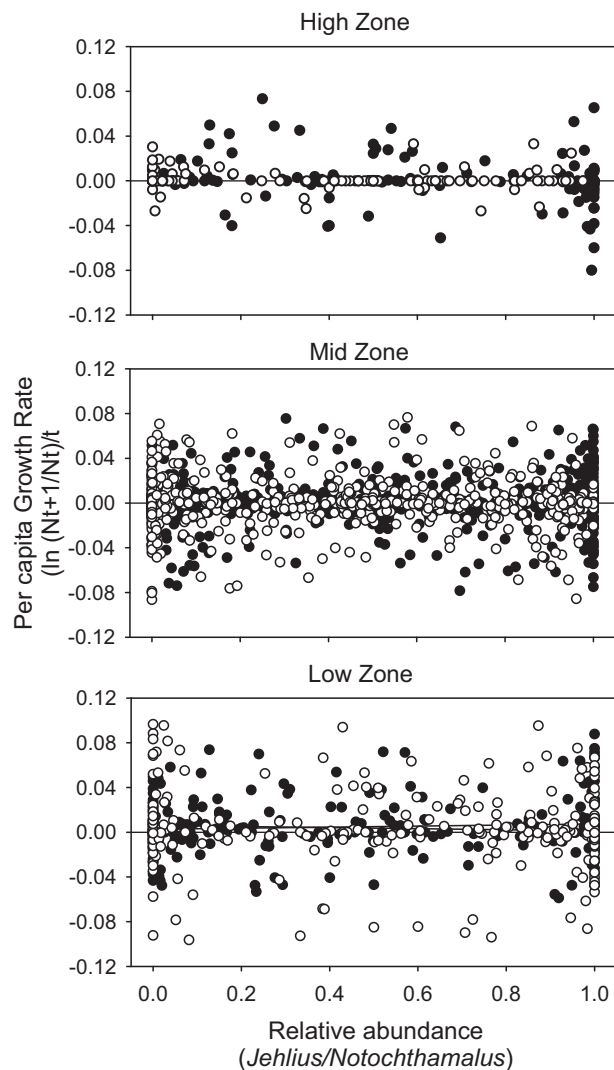
Figure 8: Per capita growth rates of *Jehlius* (black circles) and *Notochthamalus* (open circles) abundance per unit time by its relative abundance, for each barnacle subzone. Analyses were conducted using experimental plots where total barnacle cover at time interval $t - 1$ was at 40%–60% (ca. 140 ± 65 individuals per plot).

these two alternatives is a formidable challenge and illustrates the difficulties associated with testing neutral models in real ecological systems.

Surprisingly, given previous albeit conflicting reports of strong, asymmetrical competition structuring patterns of abundance of *Jehlius* and *Notochthamalus*, we found overwhelming evidence that symmetrical facilitation of survival and symmetrical interference on individual growth plays an important role in this system. Intra- and interspecific effects on individual survival were generally positive and of equal magnitude between species at all shores and tidal levels. The mechanisms for such positive effects on survival

are not clearly understood, but we suspect that they are related to amelioration of the typically stressful aerial conditions encountered in Chilean rocky shores (Finke et al. 2007). We speculate that surrounding individuals can ameliorate desiccation and temperature stress by increasing retention of extracorporal water, decreasing rock surface temperature, and/or increasing wind boundary layer, reducing wind velocities and desiccation. These possibilities should be further explored. Although facilitative effects of intraspecific aggregations and overcrowding or "hummocking" have been found for other barnacle species (Bertness et al. 1998; Leslie 2005) and especially under environmentally stressful conditions (Bertness 1989), equally facilitative effects of interspecific barnacle aggregations, such as those found between *Jehlius* and *Notochthamalus*, have not been reported elsewhere. Negative effects, as those previously reported by López and González (2003), are most likely related to a reduction in feeding when surrounded by con- or heterospecifics, as shown in other barnacle species (Bertness et al. 1998). This could result from exploitative competition, that is, individuals depleting plankton in the surrounding water column, or from direct interference among filter feeding apparatuses. Careful observations and manipulations of food availability in the laboratory seem to be the only way to separate these alternatives. Thus, living gregariously, both intra- and interspecifically, represents a trade-off between the benefit of increased survival and reduced growth rates. Rather than observing competitive hierarchy and displacement, as has been reported in the past for these species (Paine 1981; López and González 2003) and is the norm among many rocky shore organisms and for barnacles in particular (Connell 1961; Dayton 1971; Wethey 1983; Farrell 1991; Berlow and Navarrete 1997; but see Miyamoto et al. 1999 for exception), we found that contact with conspecifics and heterospecifics did not lead to overgrowth or undercutting nor did it contribute to the slightly segregated distribution of *Jehlius* and *Notochthamalus*.

The positive population growth rates observed for both species after being reduced to near zero abundance unequivocally show that, under most environmental conditions, recruitment overcomes all sources of postsettlement mortality. Because these species are functionally equivalent, the strength of intraspecific effects are equal to interspecific effects and invasion success of either species is a function of total barnacle density rather than the relative density of con- or heterospecifics. Even as space becomes limiting, recruitment is a "lottery" process and no matter how abundant a species might be in the area, it cannot prevent settlement and establishment of the other, as long as some amount of free space is available. Thus, local invasibility is guaranteed in the short term for both species as long as fecundity is greater than a critical threshold
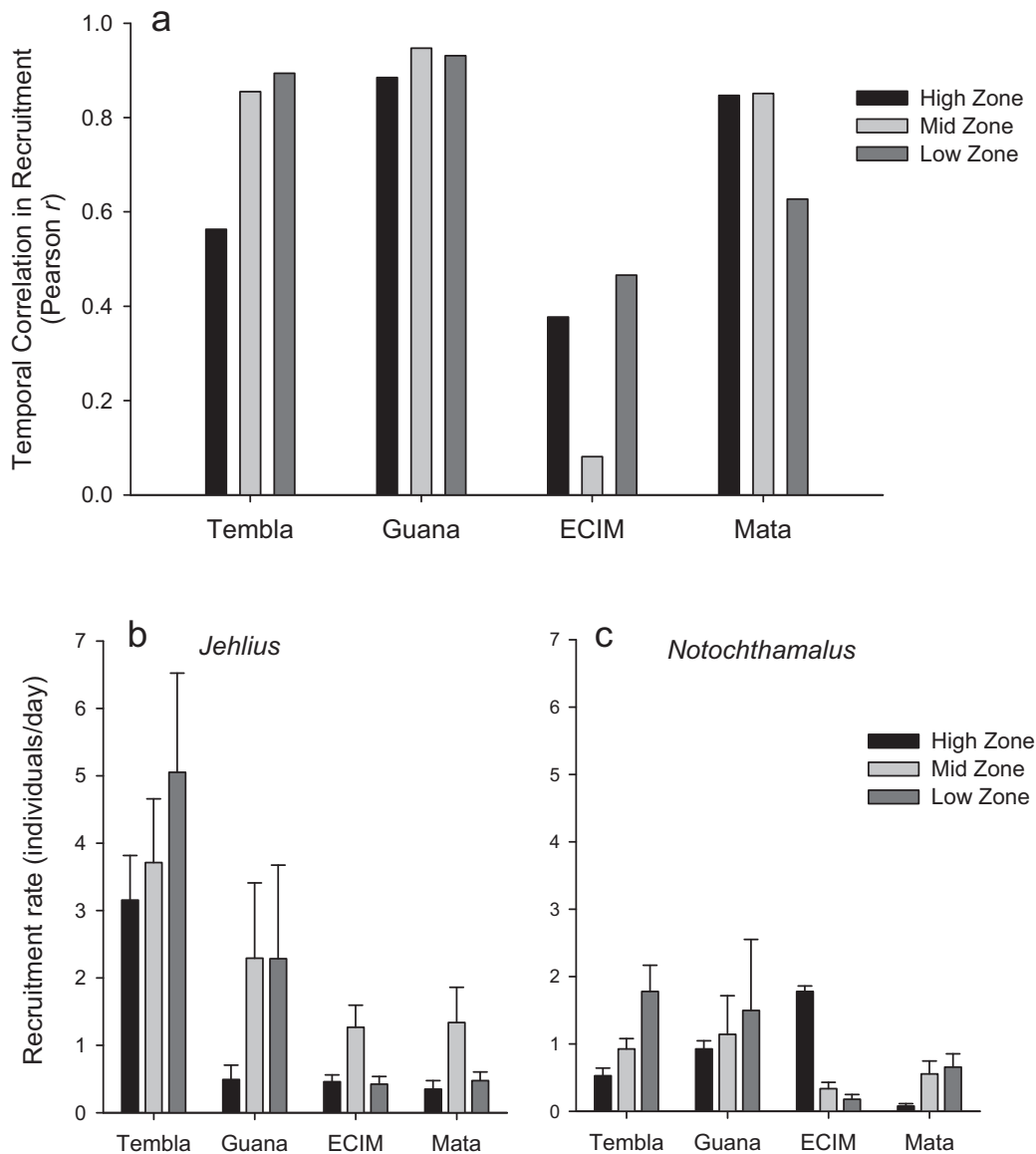
Figure 9: Temporal correlation between (*a*) and mean (± 1 SE) daily recruitment rates (*b*, *c*) of *Jehlius* and *Notochthamalus* at each site and subzone over the November 2009–April 2010 recruitment season. See figure 3 for location abbreviation definitions.

level. Separate experimental manipulations also demonstrated the absence of self-regulation in population growth rate as the relative abundance of a species increased within experimental areas at all shore levels. This means that per capita population growth rates, which are the net result of the arrival of new recruits from the plankton and mortality of established individuals, show no indication of the existence of "balancing" mechanisms of coexistence, as would be expected when fitness trade-offs play a role in species coexistence (Adler et al. 2007).

Temporally variable recruitment can be critical in fa-

voring coexistence through the mechanism of a storage effect (Chesson and Warner 1981) and has been shown to play an important role in coexistence of diverse organisms, such as fish, plants, and zooplankton (Warner and Chesson 1985; Cáceres 1997; Kelly and Bowler 2002). Both *Jehlius* and *Notochthamalus* possess all the essential attributes for such a storage effect to play a significant role in coexistence, but to formally test for such an effect, multiple years of per capita recruitment rates, reproductive output, and population abundance of each species are required, and we do not currently have such data. However, temporal

Table 3: Results of a three-way ANOVA comparing mean monthly recruitment rates between species (fixed factor), among sites (random factor), and among all three tidal zones (fixed factor)

Source	df	MS	F	P
Species	1	22.35	35.71	**<.0001**
Site	3	20.20	32.29	**<.0001**
Zone	2	6.30	10.07	**<.0001**
Species × site	3	.62	1.00	.3949
Species × zone	2	1.61	1.86	.1575
Site × zone	6	1.12	1.79	.0986
Species × site × zone	6	.10	.15	.9887
Error	448	.63		

Note: MS = mean squares. Boldface indicates significant effect at $\alpha = 0.05$.

fluctuations in recruitment of new individuals to empty plates, which can be considered a measure of the environmental component in recruitment fluctuations, were positively correlated between species at all sites, suggesting that species respond in similar ways to environmental fluctuations. Since we showed that the effects of established individuals are remarkably similar between species, it is unlikely that the adults have different specific effect on recruits. Therefore, the potential role of storage effect in this system may be rather limited, but longer-term recruitment and abundance data should be used to provide a more robust evaluation. Dispersal-based mechanisms of coexistence may also play a role in this and other spatially structured populations. Indeed, the nature of dispersal in a finite ocean and other advective environments provides at least four distinct mechanisms for persistence of an inferior competitor and/or invasion of an equal competitor to the system (Berkeley et al. 2010; Salomon et al. 2010; C. M. Aiken and S. A. Navarrete, forthcoming). Unfortunately, it is still unclear what kind of empirical tests, short of knowledge of the local and global dispersal kernels, can be used to test for these mechanisms.

Variability in recruitment of the two species among sites and subzones was a key factor determining patterns of abundance of *Jehlius* and *Notochthamalus*. As predicted by neutral models (Hubbell 2001), relative abundance of adults followed variability in the relative abundance of recruits, as shown by the significant correlation between the relative abundance of adults in fall 2010 with both local (among subzones within sites) and regional (among sites) recruitment patterns of the prior season. Thus, the lottery for space at the time of settlement leaves a strong and largely unmodified signal in the relative proportion of adult abundances. However, the proportion of species arriving as recruits in the lower shore levels corresponded to lower relative abundance of adult *Jehlius* than would

be expected by its higher relative abundance as arriving recruits. Given that adult mortality rates of the two species were similar across subzones (see "Results"), the likely explanation is that *Jehlius* may experience greater early postsettlement mortality than *Notochthamalus*. Early post-settlement mortality can be high on rocky shores and is known to be an important determinant of adult distribution patterns for a wide range of taxa (Gosselin and Quian 1996; Hunt and Scheibling 1997; Harms et al. 2000). Although it is possible that the differential mortality of settlers in the lower subzones may be due to selective bulldozing by limpets (Connell 1961) or consumption by predators, our own experiments and observations with a suite of intertidal predators (J. L. Shinen and S. A. Navarrete, unpublished manuscript), show no indication of selectivity or differential vulnerability between these barnacle species. Further research is needed to determine the source of the apparently higher early postsettlement mortality of *Jehlius* and whether such a difference plays any role as a niche-based mechanism. However, given the lack of consistent population growth of either species at low relative density, we would expect even an early, postsettlement-based stabilizing force to be a relatively weak one.

Our conclusion is therefore that the two species coexist owing to being similar or even "equal" in terms of competitive abilities, dispersal potential, and vital rates rather
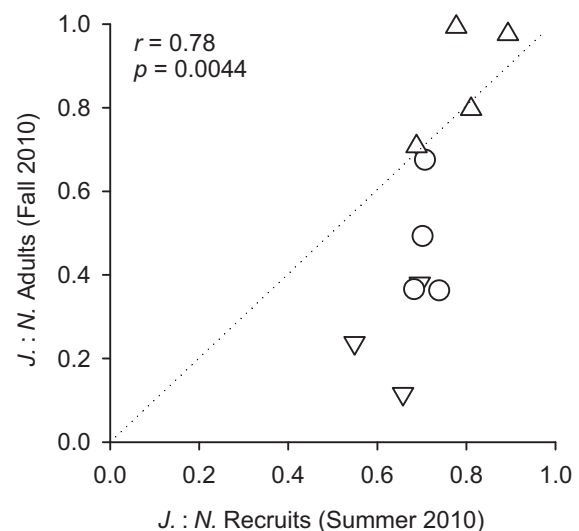

Figure 10: Pearson correlation between the relative proportion of recruits (expressed as the ratio of *Jehlius* to total barnacle density) from recruitment collectors during summer 2010 and the relative proportion of adult barnacles inside experimental plots in the following season (fall 2010). The dotted reference line indicates where recruits and adult barnacles would be at equal proportion. Circles indicate mean values from the mid subzone while up triangles and down triangles indicate high and low subzones, respectively.

than by differentiating along a niche axis. The slight offset in intertidal distribution across all sites is largely determined by a lottery for space during settlement, but the subtle differences in vertical distribution may help, to some extent, to buffer populations against the potential monopolization of the extensive mixed zone by one species as new individuals arrive from the plankton, as far as those individuals at the tidal extremes produce and export enough larvae. There is no indication, however, that the offset distribution has emerged as a result of competition (Newman and Stanley 1981; Paine 1981) and its real role in long-term coexistence has yet to be assessed. As species that compete for a limited resource become more similar, fitness trade-offs necessary to balance competition become increasingly smaller (Chesson 2000; Adler et al. 2007) and therefore much harder to quantify in the field. Therefore, we cannot completely reject the hypothesis that the observed small and nonsignificant among-site variability in vital rates (individual growth, natural mortality) and competitive ability are sufficient to provide fitness trade-offs that balance the system and prevent competitive exclusion. That is, most of the vital rates of these species are highly positively correlated, but they are not perfect, allowing for the possibility that either species might be able to exploit one or more of these small spatial decorrelations. However, if one or more stabilizing or niche mechanism is critical in determining patterns of barnacle abundance, negative correlations among species' performance should still be evident, yet this is not the case. Given that these two species exhibit similar patterns of abundance across thousands of miles of coastline, it is much more probable that *Jehlius* and *Notochthamalus* coexist owing to their similarities rather than their differences. Coexistence occurs because *Jehlius* and *Notochthamalus* suppress one another and their own populations equally rather than self-limit via any niche or stabilizing processes.

Our study joins a growing effort to unite the niche-based theory of coexistence with neutral theory (Chesson 2000; Liebold and McPeek 2006; Adler 2007; Siepielski et al. 2010). Neutral theory is in fact not mutually exclusive with classic niche theory, rather it is complementary and defines the special case where species' fitnesses are equal, or nearly so, and the stabilizing forces required for their coexistence may be immeasurably small (Chesson 2000). Until now, this special case of coexistence has been theorized (Adler et al. 2007), but no empirical examples have been provided. Here we present a case that might function in this manner. We would expect species such as these that are coexisting "nearly neutrally" to also be sensitive to stochastic events that drastically influence settlement and eventual recruitment into the adult population. Although theoretical advances of neutral theory have been published at a rapid pace in the last decade, appropriate empirical tests of model predictions have lagged behind (Siepielski and McPeek 2010). This work highlights the value of examining both local interactions among species and their regional or at least among-site variability. They also highlight the importance of questioning segregation in the use of resources between competitors as evidence of niche-based coexistence. Future efforts should include investigation into larger suites of species across diverse systems to determine how prevalent both niche and neutral mechanisms of coexistence are in natural communities as well as further inclusion of species similarity and facilitation in promoting long-term coexistence.

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