

Jenifer E. Dugan · Eduardo Jaramillo ·
David M. Hubbard · Heraldo Contreras ·
Cristian Duarte

Competitive interactions in macroinfaunal animals of exposed sandy beaches

Received: 2 December 2002 / Accepted: 27 February 2004 / Published online: 6 April 2004
© Springer-Verlag 2004

Abstract The influence of biotic interactions in structuring macroinfaunal communities of exposed sandy beaches, an unstable habitat characterized by strong physical forces, is generally considered negligible. We investigated the hypothesis that competitive interactions during burrowing could potentially affect the intertidal distribution and abundance of macroinfaunal animals of sandy beaches using two species of invertebrates, a hippid crab, *Emerita analoga*, and a bivalve, *Mesodesma donacium*, common along the coast of Chile. Spatial overlap in the intertidal distributions of these species was dynamic, varying with abundance, location, time of year and tide. Highest density zones of each species were often distinctly separated at low tide and spatial overlap in their distributions decreased significantly with increasing density, suggesting density dependence of the interactions. Negative relationships between densities of the two species at the smallest spatial scale examined also suggested active interactions among individuals. Over a tidal cycle, peak densities of the two species overlapped suggesting that interactions could occur frequently. Burrowing performance of *E. analoga* varied between size classes in three experimental densities of clams (5, 10 and 15 clams 0.008 m⁻²) and in controls with no clams. Burrowing times of large crabs were significantly longer (~twofold) in all densities of clams than in controls, while those of small crabs did not differ significantly among treatments and controls. Large crabs also displaced clams from the sand while burrowing

suggesting that two mechanisms of direct interference can occur, both of which could increase exposure of individuals involved to active swash and transport across or along the beach with potentially negative consequences. Our results suggest that competitive interactions capable of affecting zonation and population and community biology on a number of scales can occur among burrowing macroinfauna on exposed sandy beaches. Those interactions could be more ecologically significant than previously appreciated and may contribute to patterns observed in community structure and zonation on sandy beaches. Our results illustrate the potential importance of negative biological interactions in a physically stressful environment.

Keywords Interference competition · Intertidal zonation · Burrowing

Introduction

Understanding the relative importance of competitive interactions in structuring natural communities has challenged ecologists, particularly when investigating communities in extreme, harsh or fluctuating environments, where population growth and densities may be low and non-equilibrium conditions may prevail. Stressful and variable environmental conditions were long thought to primarily affect organisms through direct effects on population growth of individual species rather than through effects on biotic interactions (e.g., Menge 1979; den Boer 1986). It has also been argued that harsh conditions may potentially promote coexistence by reducing the intensity and importance of competitive interactions (e.g., Wiens 1977; Menge and Sutherland 1987). Recent ecological studies of rocky shores and salt marshes have suggested that harsh conditions may, in fact, promote some positive interspecific biological interactions (e.g., Bertness and Leonard 1997; Bertness et al. 1999; Menge 2000). In contrast, Chesson and Huntly (1997) argue that environmental harshness can cause a population

J. E. Dugan (✉)
Marine Science Institute, University of California,
Santa Barbara, CA 93106-6150, USA
e-mail: j_dugan@lifesci.ucsb.edu
Fax: +1-805-8938062

E. Jaramillo · H. Contreras · C. Duarte
Instituto de Zoología, Universidad Austral de Chile,
Valdivia, Chile

D. M. Hubbard
Museum of Systematics and Ecology, Department of Ecology,
Evolution and Marine Biology, University of California,
Santa Barbara, CA 93106, USA

to be less tolerant of competition and accelerate competitive exclusion, even at relatively low levels of interaction.

For intertidal marine communities on relatively stable substrates, such as rock and mud, competition for space can be quite important to zonation patterns and community structure (e.g., Connell 1961; Dayton 1971; Menge and Sutherland 1976; Peterson 1977; Underwood and Denley 1984; Wilson 1991). However, for exposed sandy beaches, considered by many to be the most physically stressful and unstable intertidal habitat, the influence of biotic interactions has generally been regarded as negligible. In contrast, physical processes, such as the action of waves and tides on unconsolidated sediments and the intertidal swash climate, have been considered the major factors influencing community structure of the macroinfauna (e.g., McLachlan 1990, 2001; Brown and McLachlan 1990; McArdle and McLachlan 1991, 1992). Ocean waves generally break at a distance from shore. Therefore, wave energy reaches the intertidal zone of a beach as swash. Intertidal swash climate (swash frequency, velocity and upwash distance) varies predictably with beach type (McArdle and McLachlan 1992). The swash exclusion hypothesis articulated by McLachlan et al. (1993, 1995) proposes that the intertidal swash climate may exert the greatest and most direct influence on community structure on exposed sandy beaches and may explain observed patterns of decreasing richness, biomass and abundance of macrofaunal communities along a physical gradient from relatively benign dissipative to harsher reflective beaches. In addition, human activities have recently been shown to alter community and population structure and dynamics on exposed sandy beaches, including artificial sand nourishment or replenishment (Peterson et al. 2000) and the removal of stranded macrophytes by grooming (Dugan et al. 2000b, 2003).

The density and abundance of macroinfauna can be relatively high on exposed sandy beaches, up to 10,000 individuals (ind.) m^{-2} of surface area and exceeding 80,000 ind. $linear\ m^{-1}$ of shoreline (Dugan et al. 2000b, 2003; Jaramillo et al. 2001). On beaches where the macroinfauna are abundant and densely aggregated in the active intertidal zone, the potential for intertidal distributions to be influenced by biotic interactions could be great. Despite this potential, very little convincing evidence exists to support a role of biological interactions, including predation and interspecific and intraspecific competition, in the structure, dynamics or zonation of macroinfaunal communities of exposed sandy beaches (e.g., McLachlan and Jaramillo 1995). The most compelling evidence of competition among the macroinfauna of exposed sandy beaches provided to date was reported by Croker and Hatfield (1980), who demonstrated potentially important interspecific interactions among amphipods using long-term studies of zonation and laboratory experiments. Other information supporting a possible role of biotic interactions in community structure on sandy beaches is primarily indirect and unsupported by experimental studies, therefore requiring cautious inter-

pretation (e.g., Defeo and De Alava 1995; Defeo et al. 1997).

The macroinfaunal animals of exposed sandy beaches are mobile and often exhibit regular tidal migration and swash riding behaviors (Trueman 1971; McLachlan et al. 1979; Ansell 1983; Eilers 1995a, 1995b; Brown 2001; Jaramillo et al. 2001). Those behaviors enable invertebrates to spend more time in the active intertidal swash, a zone which provides better feeding opportunities for suspension feeders and scavengers, while serving as a refuge from vertebrate predators, both avian from above and piscine from below. Those behaviors combined with the dynamics of the swash zone also make investigations of biotic interactions among the macroinfauna of exposed sandy beaches challenging (Peterson 1991; McLachlan 1998).

A key adaptation for many sandy beach species is the ability to burrow rapidly in unconsolidated sand (McLachlan et al. 1996; Nel et al. 1999; Dugan et al. 2000a; Lastra et al. 2002). Burrowing species, such as hippid crabs and mesodesmatid and donacid bivalves, often dominate the macroinfaunal community across a range of beach morphodynamic types (e.g., Jaramillo and McLachlan 1993; Dugan et al. 2000b, 2003). One important prediction of the swash exclusion hypothesis defined earlier is that burrowing ability may determine which species of macroinfauna can successfully inhabit the intertidal zone and characteristic swash climate of a particular beach (McLachlan et al. 1993, 1995). Burrowing ability varies considerably among the major macroinfaunal taxa and species inhabiting beaches, such as molluscs (Alexander et al. 1993; McLachlan et al. 1996), polychaetes, and crustaceans (Nel et al. 1999; Dugan et al. 2000a), and may thus be a factor in determining the distribution of species and community structure among beaches of different types. For example, bivalves burrow slowly and very few taxa inhabit a wide range of beach morphodynamic types (McLachlan et al. 1996). In contrast, hippid crabs burrow extremely rapidly and inhabit nearly all beach types (Dugan et al. 2000a; Jaramillo et al. 2001; Lastra et al. 2002). The burrowing performance of individual species can be affected by a variety of factors, including body size (Alexander et al. 1993; McLachlan et al. 1996; Dugan et al. 2000a; Jaramillo et al. 2000; Nel et al. 2001), sediment grain size (Alexander et al. 1993; Nel et al. 1999, 2001; Dugan et al. 2000a), and water temperature (McLachlan and Young 1982; Donn and Els 1990). The influence of biotic interactions, such as competition for space, on burrowing performance and behavior has not been widely examined in the macroinfaunal animals of sandy beaches (McLachlan 1998).

We hypothesized that competition for space could potentially modify or alter the physical influence of intertidal swash climate on the distribution of species of macroinfauna on sandy beaches through burrowing interactions. Specifically, direct interactions, such as interference or displacement, during burrowing could decrease burrowing performance and/or the ability to

maintain position in the active intertidal zone. Decreased burrowing performance or displacement would expose fauna to more swashes and higher potential transport from an optimal zone or area. This could be manifested by variation in the intertidal distribution of the competing species. To investigate that hypothesis, we:

1. Compared the distribution and zonation of two abundant suspension-feeding and tidal migrant species of infaunal animals inhabiting exposed sandy beaches of the Chilean coast, a hippid crab, *Emerita analoga* (Stimpson), and a bivalve, *Mesodesma donacium* (Lamarck) across different beaches, in different times of year and over the daily tidal cycle.
2. Experimentally examined the effects of clam density on burrowing performance in the crab and that of crab burrowing on the displacement of clams.

Materials and methods

Two intertidal species of suspension-feeding animals were chosen for study, the hippid crab, *E. analoga* and the bivalve, *M. donacium*. The hippid crab occurs on exposed sandy beaches of all types on the coasts of North and South America. This crab can burrow rapidly in fine to coarse sands, has excellent orientation and swimming abilities, and inhabits the full range of beach types from fully reflective to dissipative morphodynamic states (Dugan et al. 2000a; Jaramillo et al. 2001). This hippid crab is an active tidal migrant and intertidal zonation patterns in this species can vary seasonally, across the tidal cycle, and among beaches (Cubit 1969; Fusaro 1980; Artacho 2001). Juveniles of *E. analoga* and other hippid crabs generally occupy a notably higher intertidal level than adult crabs (Fusaro 1980; Haley 1982). Adult crabs can occur as deep as the shallow subtidal zone during higher tides, periods of beach erosion and on some beach types (Jaramillo et al. 2000).

The clam, *M. donacium*, occurs on exposed sandy beaches of high intermediate to dissipative types along the Pacific coast of South America (5–43°S latitude) (McLachlan et al. 1996). Juvenile clams and individuals up to a size of ~50 mm in shell length are found primarily in the intertidal zone above the lowest swash (Jaramillo et al. 1994; McLachlan and Jaramillo 1995). Larger adult clams (up to 100 mm shell length) occur primarily in the subtidal surf zone (Jaramillo et al. 1994; McLachlan and Jaramillo 1995) and are harvested throughout Chile (McLachlan et al. 1996).

We used three sources of data, both descriptive and experimental, to examine our hypotheses:

1. Data on the intertidal zonation and population abundance of *E. analoga* and *M. donacium* from the four beaches along the Chilean coast where the two species co-occurred [Rodillo (26° 59'S, 70°48'W), Tongoy (30°16'S, 71°30'W), Carelmapu (41°38' S, 73°42'W) and Mar Brava (41°55'S, 73°59'W)] were collected between 1996 and 1998 during quantitative surveys of intertidal macroinfaunal communities. In those surveys, cores (0.03 m², 30 cm deep) were collected with plastic cylinders at ten to 15 levels distributed at uniform distances along three to four shore-normal transects (separated by 1 m) that extended from above the spring high tide drift line (DL) to the bottom of the intertidal zone. The uppermost core sample was located above the high tide DL, the second on the DL and the last at the lowest tide level (LT) equivalent to the lower limit of the swash zone. The sediment from each core was sieved through a 1-mm mesh and the organisms collected were stored in 5% formalin until sorting. The number of animals from each core was quantified in the laboratory. These data were used to describe the distribution and abundance of both species across the intertidal zone.

2. Data on tidal variability in intertidal zonation and population abundance of *E. analoga* and *M. donacium* at Mar Brava beach in south central Chile were collected during March 1999. Core samples were collected at five to six vertical levels of the beach across 10 h of the tide cycle on three shore-normal transects. The transects were separated by 15 horizontal m of beach to avoid disturbance to the animals on the adjacent transects. Starting with the morning low tide, samples were collected every 2 h from 0900 to 1900 hours at the following levels: one below the lowest swash zone (below the LT), two to three in the active swash zone, one in the uppermost level of this zone [effluent line (EL) or the highest zone of sand that was fully saturated by water], and one in the damp sand zone above the EL. The distance between levels sampled on each set of three transects depended upon the zone widths and varied among the sampling times. Ten 10-cm-diameter cores (0.0078 m²) were collected haphazardly along a line parallel to the shore at each sampling level and time and then pooled to make up each sample. Each sample was sieved through a 1-mm mesh, retaining the animals. The organisms collected in each sample were counted to estimate abundance for each sampling level of the transect.
3. Data from field experiments conducted in February 2002 were used to examine the burrowing behavior of two size classes of *E. analoga* in relation to different densities of *M. donacium*. Ambient densities of *E. analoga* and *M. donacium* were first estimated from haphazard collection of 100 core samples (0.008 m² to a depth of 0.3 m) from the intertidal zone of highest *M. donacium* density at Mar Brava during low tide in February 2002. The density of clams ranged from 0 to 9 core⁻¹ and the mean density was 2 ind. core⁻¹ (0.008 m²) or 250 ind. m⁻². The density of crabs was much lower ranging from 0 to 3 crabs core⁻¹ and averaging 0.3 crabs core⁻¹ or 38 ind. m⁻². The experimental treatments consisted of three densities of *M. donacium* (5, 10 and 15 clams 0.011 m⁻²) with shell lengths of 28–50 mm and a control with no clams. Two of the experimental densities (five and ten clams, 442 and 884 ind. m⁻², respectively) were within the natural densities observed at Mar Brava and the third (15 clams, 1,326 clams m⁻²) just exceeded the highest natural density observed at Mar Brava in that week. Each treatment and the control had 21 replicates. The 21 experimental chambers were 1-l plastic containers (12 cm in diameter) with 60 mm sand and 65 mm of water column. Fresh sand collected from the swash zone of Mar Brava (mean grain size=0.180 mm) was sieved to remove all macroinfauna and used in experimental containers. Water temperatures in the experimental containers were maintained at ambient surf zone levels (13.0–13.5°C). To prepare each treatment, freshly collected clams were randomly selected and haphazardly placed in the sediments in a natural position (i.e., foot down) at the densities above. Freshly collected crabs were wrapped in wet fine-mesh fabric in a well-shaded plastic colander and flushed every 10–15 min with clean recently collected seawater to maintain condition. We measured burrowing behavior of two size classes of crabs: males of 11–17 mm carapace length (CL) and ovigerous females of 25–32 mm CL. Each crab was observed individually and released after one burrowing trial. Freshly collected individuals of crabs and clams in undamaged condition were used in each replicate of all treatments and controls.

Two components of burrowing behavior of individual *E. analoga* (pre-burrowing and burrowing times) were measured in the experimental (three densities of clams) and control treatments (no clams). Using a stopwatch, the pre-burrowing time of each individual crab was timed from the initiation of swimming at release until beginning of burrowing (abdomen in contact with the sediments, uropod activity). This component was used to investigate whether the presence of clams causes migrating crabs to continue swimming in search of a suitable location to burrow. Burrowing time for each crab was measured with a stopwatch from the initiation of burrowing to the disappearance of the crab under the sediment surface. Each experimental crab was measured to the nearest 0.1 mm CL. The numbers and sizes of clams displaced from

the substrate by individual *E. analoga* during each burrowing trial were recorded.

Estimated mean densities (ind. m⁻²) and SEs of *E. analoga* and *M. donacium* at each sampling level were used to plot the distribution of the two species across the intertidal zone at all the sites and sampling dates. Spatial variation in abundance of each species across the intertidal zone was examined using one-way ANOVA for each sampling site and date. Variation in abundance between species at each site and date and among sampling sites and dates was examined using one-way ANOVA. To investigate negative interactions in the community samples on a smaller spatial scale, the log density of *E. analoga* as a function of the log density of *M. donacium* in each core where one of these species occurred was fitted to a hyperbolic function [$y(x) = A - a \exp(x - c)$, where A = value of curve in y -axis and the x -intercept = $\ln(A/a) + c$] for each sampling site and date. Spearman's rank correlation was also used to examine correlations between the log-transformed abundance of clams and crabs in individual cores where at least one of the species occurred in the community samples (Sokal and Rohlf 1995). To investigate the possible effect of density on spatial distribution patterns of the two species, relationships between differences in the mean densities of the two species at each sampling level and the mean density of *M. donacium* at that level were examined for the four sample sites and for the four sample dates using ordinary least squares (OLS) regression analysis. Mean densities (ind. m⁻²) of *E. analoga* and *M. donacium* were used to construct kite diagrams of the distribution of the two species across the intertidal zone over the tidal cycle at Mar Brava beach. Variation in the abundance of each species with tidal level and sampling time was examined using two-way ANOVA on $\log(n+1)$ -transformed data. Data on pre-burrowing and burrowing times were analyzed with one-way ANOVA and the a posteriori test Tukey's honest-significant-difference (HSD) (Sokal and Rohlf 1995). Statistical analyses were performed on SYSTAT 9.0.

Results

To illustrate the dynamic nature of intertidal zonation and the potential results of interference competition for space in *E. analoga* and *M. donacium* across beaches, the densities of these species for ten to fifteen intertidal sampling levels at four beaches spanning 15° of latitude along the Chilean coast during spring or summer are shown in Fig. 1a–d. The overall mean intertidal abundance of *E. analoga* and of *M. donacium* varied significantly among the four beaches (one-way ANOVA, $F_{3,10}=60.34$ for crab and $F_{3,10}=28.33$ for clam, $P < 0.001$) as did the relative abundance of the two species. Mean abundance of *E. analoga* ranged from 85 to 4,127 ind. m⁻² and that of *M. donacium* ranged from 147 to 3,860 ind. m⁻² among beaches.

At the northernmost beach, Rodillo, the overall mean intertidal abundance of *E. analoga* (1,053 ind. m⁻²) was significantly higher than that of *M. donacium* (147 ind. m⁻²) (one-way ANOVA, $F_{1,4}=31.40$, $P=0.005$). The intertidal densities of *E. analoga* and *M. donacium* each varied significantly with sampling level (one-way ANOVA, $F_{9,20}=32.46$ for crab and $F_{9,20}=4.81$ for clam, $P < 0.005$) and little overlap was evident in the spatial distribution of the two species (Fig. 1a). The clam, *M. donacium*, was distributed from above the EL to the LT with peak densities high on the beach, above the EL. The highest sampling level where *E. analoga* occurred was below the EL and peak densities occurred low on the

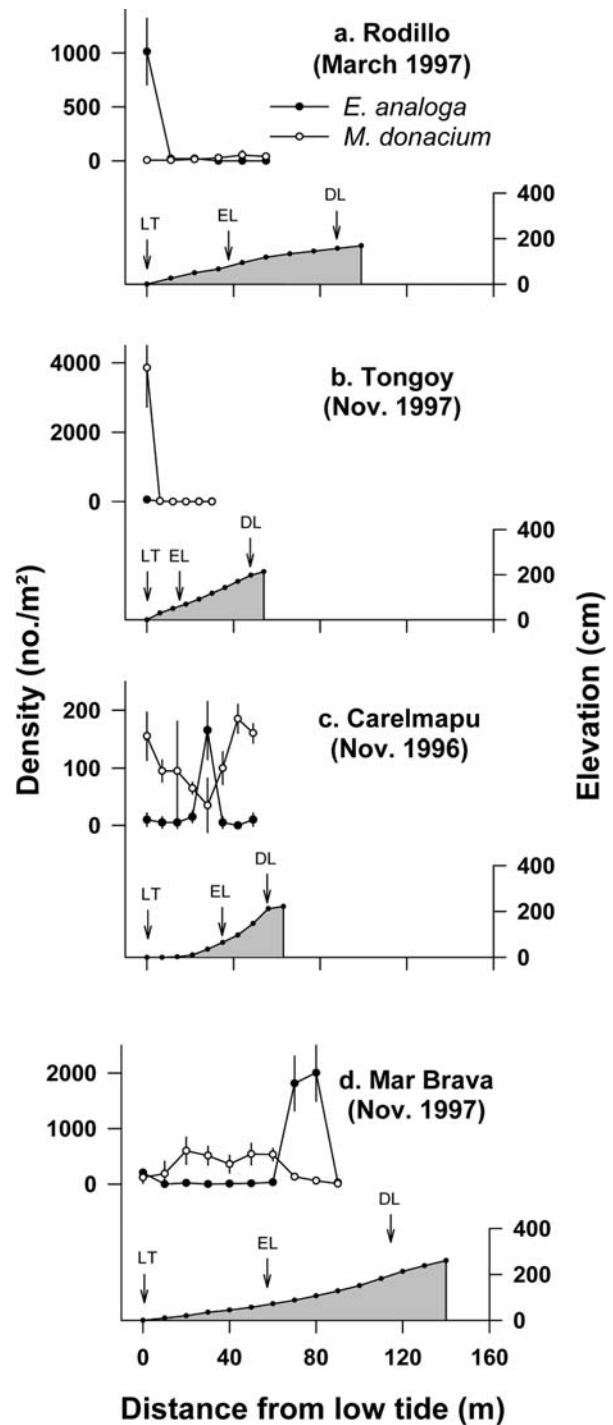


Fig. 1 Intertidal distributions as mean densities and SEs of *Mesodesma donacium* (○) and *Emerita analoga* (●) during low tide at four beaches, **a** Rodillo, **b** Tongoy, **c** Caremapu, and **d** Mar Brava, of the Chilean coast on the dates indicated. The beach face profile for each beach on the sampling date is shown in the lower section of the plot and pertinent landmarks are labeled. DL Drift line, EL effluent line, LT lowest tide level, Nov. November

beach in the vicinity of the LT. In contrast at Tongoy, the mean intertidal abundance of *M. donacium* (3,880 ind. m⁻²) was significantly higher than that of *E. analoga* (85 ind. m⁻²) (one-way ANOVA, $F_{1,4}=44.40$, $P=0.001$). Again, the

intertidal densities of *E. analoga* and *M. donacium* varied significantly with sampling level (one-way ANOVA, $F_{9,30}=10.25$ for crab, $F_{9,30}=46.45$ for clam, $P < 0.001$). However, the sampling levels with peak densities were reversed between the species, with peak densities of *M. donacium* evident in the low intertidal (at the LT) at this beach (Fig. 1b).

At the southern beaches of Carelmapu and Mar Brava, the degree of overlap in the spatial distributions of the two species was greater than at the two northern beaches (Fig. 1c, d). At Carelmapu, the overall mean intertidal abundance of *M. donacium* (890 ind. m⁻²) was significantly higher than that of *E. analoga* (215 ind. m⁻²) (one-way ANOVA, $F_{1,6}=171.40$, $P < 0.001$) and the intertidal densities of *E. analoga* and *M. donacium* varied significantly with sampling level (one-way ANOVA, $F_{9,30}=32.42$ for crab and $F_{9,30}=12.65$ for clam, $P < 0.001$) (Fig. 1c). Although both species were distributed continuously from just below the DL to the low intertidal (LT), two peaks in density were evident for *M. donacium* and one for *E. analoga*. The highest density of *E. analoga* occurred in the mid-intertidal and corresponded with the lowest density of *M. donacium* in the zone of overlap at this beach. Yet another pattern was evident at Mar Brava where the mean abundance of both species was high, 4,127 and 3,053 ind. m⁻² for *E. analoga* and *M. donacium*, respectively. The mean overall intertidal abundance did not differ significantly between species at this beach (one-way ANOVA, $F_{1,4}=3.80$, $P = 0.123$) on this date, but intertidal densities of *E. analoga* and *M. donacium* varied significantly with sampling level (one-way ANOVA, $F_{14,30}=39.41$ for crab and $F_{14,30}=11.12$ for clam, $P < 0.001$) (Fig. 1d). Both species were present in saturated sand of the mid to low intertidal zone from ~10 m above the EL to the LT. Peak densities of *E. analoga* occurred high on the beach (above the EL), while peak densities of *M. donacium* occurred lower in the intertidal (between the EL and the LT). Densities of *M. donacium* were low in the zone of high *E. analoga* density. Similarly, very low densities of *E. analoga* were present across the zone of higher *M. donacium* density. A small increase in the density of *E. analoga* in the lowest intertidal corresponded to decreasing density of *M. donacium*.

A significant effect of density on the degree of overlap in the spatial distributions of the two species was apparent for the combined results from the four beaches. Differences between the mean densities of the two species at each sampling level increased significantly as the mean density of *M. donacium* increased (OLS regression, $y=1.06x - 213.48$, $r=0.83$, $n=26$, $P < 0.001$).

The separation of the two species in the intertidal zone was also evident on a much smaller spatial scale, that of individual core samples (Fig. 2a–d), suggesting active interactions between individuals of the two species. When data from individual core samples (0.05 m²) in which at least one of the species was present were examined for each of the four beaches, the density of *E. analoga* was negatively correlated with that of *M. donacium* at three of the four beaches where they co-occurred (Rodillo,

Carelmapu and Mar Brava, Spearman's rank correlation, $r=-0.66$, $r=-0.50$, and $r=-0.47$ respectively, $P < 0.05$) (Fig. 2a, c, d). The strength of that negative correlation did not increase with density on the scale of individual cores. A non-significant positive correlation occurred at Tongoy (Spearman's rank correlation, $r=0.57$, $P=0.07$) (Fig. 2b), where densities of *E. analoga* were very low (<100 ind. m⁻²). A more informative description of the actual relationship between the densities of *E. analoga* and *M. donacium* was provided by the hyperbolic fits to these results shown in Fig. 2a, c, d, indicating that although the two species can be found in similar densities on this small spatial scale, when the density of one species is high, that of the other species is generally low. The curvilinear fit yielded a higher correlation coefficient for the data from all beaches, except Tongoy, than the simple rank correlation.

The spatial distribution and abundance of both species also varied seasonally as illustrated by the results from four sampling dates from a single beach, Mar Brava, during 1997–1998 (Fig. 3a–d). The overall mean intertidal abundance of *E. analoga* and of *M. donacium* varied significantly among the 4 months (one-way ANOVA, $F_{3,8}=39.95$ for crab and $F_{3,8}=326.61$ for clam, $P < 0.001$) with highest abundance for both species in November 1997 and lowest in December 1998. The mean abundance of *E. analoga* declined from 4,127 to 450 ind. m⁻² and that of *M. donacium* from 3,053 to 63 ind. m⁻² over 14 months, representing declines in abundance of 89% and 98%, respectively. In November, the distribution and abundance of the two species was as described for Fig. 1 (Fig. 3a). In all subsequent months (March, July and December), the overall mean intertidal abundance of *E. analoga* (843, 457, and 450 ind. m⁻², respectively) was significantly greater than that of *M. donacium* (337, 77, and 63 ind. m⁻², respectively) (one-way ANOVA, $F_{1,4}=13.66$ for March, $F_{1,4}=49.99$ for July, and $F_{1,4}=85.71$ for December, $P < 0.02$). The intertidal densities of *E. analoga* and *M. donacium* each varied significantly with sampling level on every sampling date (March, July and December, one-way ANOVA, $F_{9,20}=8.57$, 22.23 and 9.28, respectively for crab, and $F_{9,20}=34.73$, 11.48 and 2.44, respectively for clam, $P < 0.05$) (Fig. 3b–d). In March, the distributions of crabs and clams overlapped primarily in the mid-intertidal zone with little overlap in the lower intertidal zone (Fig. 3b). Highest densities of *M. donacium* occurred in the mid-intertidal zone (at the EL). Two peaks in density of *E. analoga* were evident, the zone of highest density occurred in the lower intertidal and corresponded with the lowest densities of *M. donacium* on that date. A secondary zone of increased density of *E. analoga* higher on the beach coincided with the decrease in density of *M. donacium* below the EL. In July, the overall distributions of the two species overlapped broadly but the peaks in their densities were distinctly separated in the intertidal zone with peak density of *E. analoga* in the low intertidal and that of *M. donacium* much higher on the beach (Fig. 3c). By contrast in December, when the abundance of both species was lowest, peak densities of *E. analoga* and

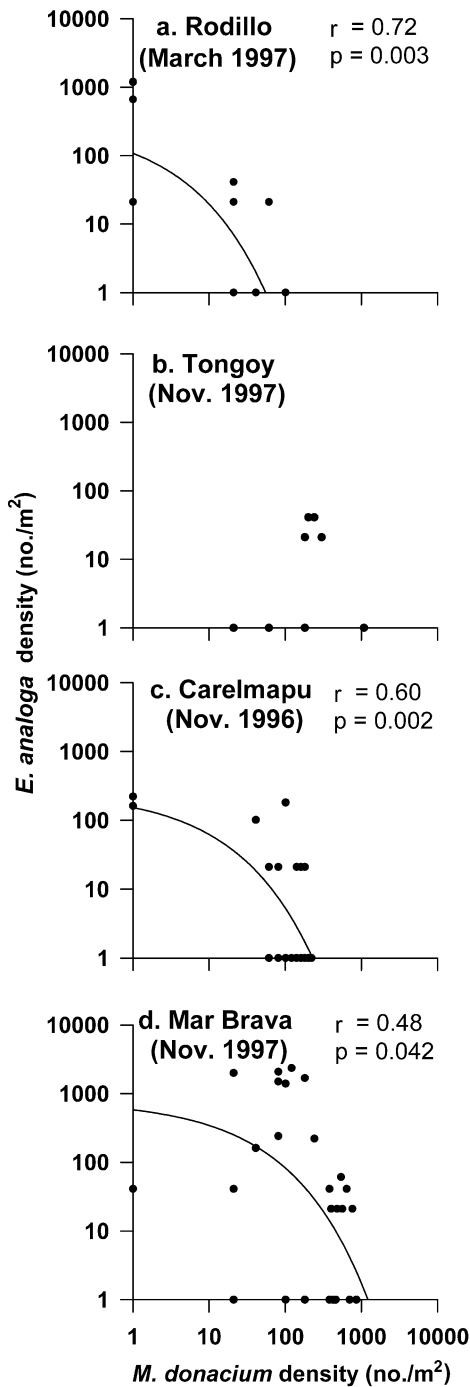


Fig. 2 Scatter plots of densities of *E. analoga* and *M. donacium* in individual cores and values of r and P for the curvilinear fit for data shown in Fig. 1 from the four beaches, **a** Rodillo, **b** Tongoy, **c** Carelmapu, and **d** Mar Brava, and sampling dates

M. donacium overlapped in the lower intertidal zone (Fig. 3d).

As found in the comparison of distributions of *E. analoga* and *M. donacium* among beaches, a significant effect of density on the amount of overlap in the spatial distributions of the two species was apparent for the combined results from the four sampling dates. Differences in mean density between the two species at each

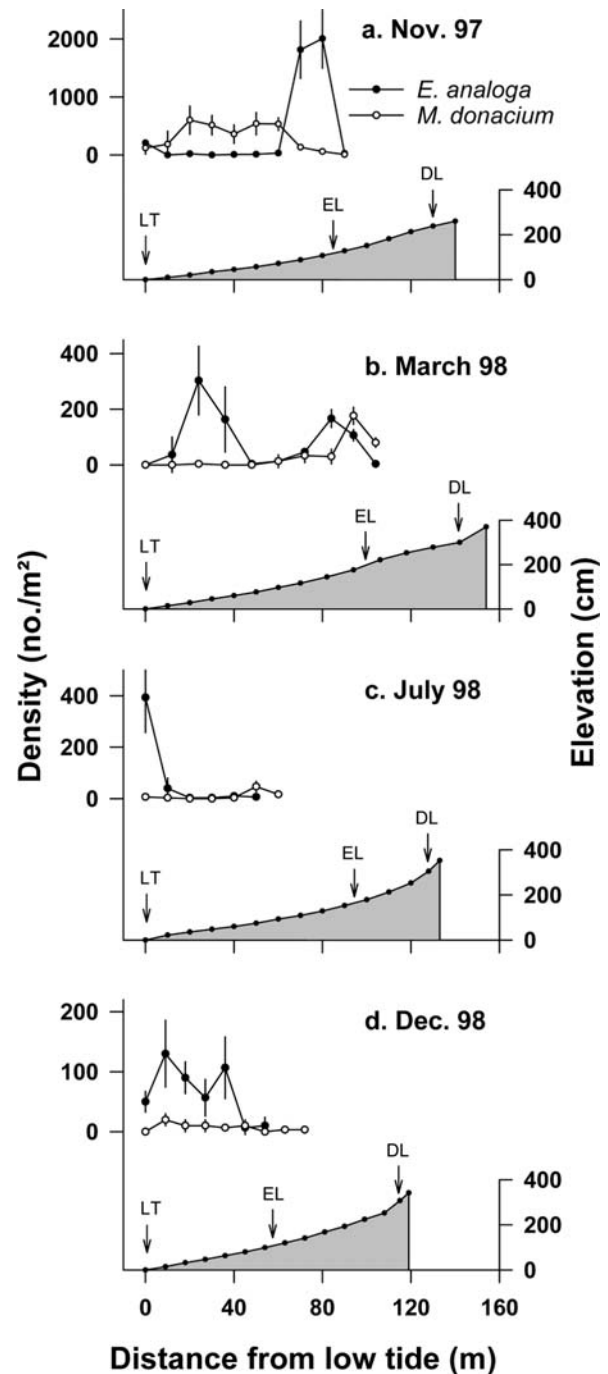


Fig. 3 Intertidal distributions as mean densities and SEs of *M. donacium* (○) and *E. analoga* (●) and beach profiles (as described in Fig. 1) during low tide on four sampling dates, **a** Nov. 1997, **b** March 1998, **c** July 1998, and **d** December (Dec.) 1998 at Mar Brava. Data from Nov. 1997 also appear in Fig. 1. For other abbreviations, see Fig. 1

sampling level increased significantly as the mean density of *M. donacium* increased (OLS regression, $y = 1.12x - 180.16$, $r = 0.42$, $n = 33$, $P = 0.014$).

On the smallest spatial scale investigated, individual core samples (0.05 m²) in which at least one of the species was present, the separation of the two species in the intertidal zone was again apparent (Fig. 4a–d), suggesting

active interactions were taking place. The density of *E. analoga* was negatively correlated with that of *M. donacium* for two of the four sample dates at Mar Brava (November, July, Spearman's rank correlation, $r = -0.47$, $r = -0.51$, respectively, $P < 0.05$, Fig. 4a, c) and negative but marginally non-significant correlations were found in March and December (Spearman's rank correlation, $r = -0.41$, $P = 0.06$ and $r = -0.40$, $P = 0.08$, respectively) (Fig. 4b, d). As seen in the among-beaches comparisons, the strength of those negative correlations did not increase with density on the scale of individual cores. For these comparisons, a hyperbolic fit was used to better describe the actual shape of the relationship at this spatial scale and yielded a higher correlation coefficient for two of the four sampling dates (Fig. 4a–d). Again, this result suggests that although the two species can be found in similar densities on this smaller spatial scale, when the density of one species is high, that of the other species is generally low.

To illustrate the distributional dynamics and infer the potential for interactions between these two species over a single day, the distributions of *M. donacium* and *E. analoga* over a spring tide cycle at Mar Brava are shown in Fig. 5. The overall intertidal abundance of *E. analoga* (304 ind. m^{-2}) was significantly higher than that of *M. donacium* (60 ind. m^{-2}) on this date (one-way ANOVA, $F_{1,10} = 37.50$, $P < 0.001$). The distribution of both species varied over the tidal cycle as the animals responded to the changing tide through migration and other behaviors (e.g., burrowing more deeply). For both species, density varied significantly with tidal level but not with sampling time and there was a significant interaction between tidal level and sampling time associated with migration during the tide cycle [two-way ANOVA on $\log(n+1)$ -transformed data: *E. analoga*, $F_{5,72} = 10.43$ for level, $P < 0.001$, $F_{5,72} = 1.35$ for time, $P = 0.25$, $F_{25,72} = 3.84$ for interaction, $P < 0.001$; *M. donacium*, $F_{5,72} = 2.82$ for level, $P < 0.05$, $F_{5,72} = 1.67$, $P = 0.15$ for time, $F_{25,72} = 1.82$ for interaction, $P < 0.05$]. During the morning low tide (0900 hours), the distribution of *E. analoga* overlapped that of *M. donacium* but extended much lower in the intertidal and peaked well below the lowest *M. donacium* individual found. As the tide filled and during high tide, *E. analoga* migrated up in the beach such that peak densities completely overlapped that of the clam. Peak densities of both species coincided spatially on the rising tide samples (1100 and 1300 hours) (Fig. 5). At high tide and as the tide dropped (1500 and 1700 hours), *E. analoga* moved down the beach and the peak densities of the crab again occurred below that of the clam. During the evening low tide (1900 hours), the distribution of the two species appeared to overlap entirely across much of the intertidal zone again; however, densities of both were very low at this sampling time making overlap difficult to evaluate.

In burrowing trials, the pre-burrowing times of *E. analoga* did not vary significantly with size class in controls (one-way ANOVA, $F_{1,40} = 0.253$, $P = 0.618$) (Fig. 6a, b). Pre-burrowing times of *E. analoga* were not affected by clam density and treatments did not differ

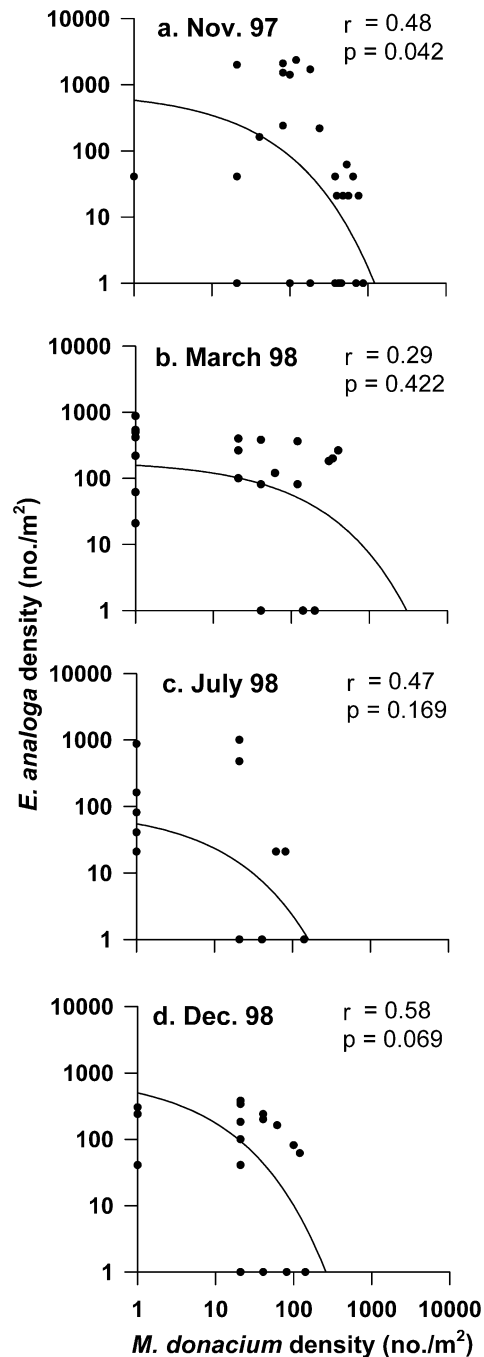


Fig. 4 Scatter plots of densities of *E. analoga* and *M. donacium* in individual cores and values of r and P for the curvilinear fit for data shown in Fig. 3 from the four sampling dates, **a** Nov. 1997, **b** March 1998, **c** July 1998, and **d** Dec. 1998 at Mar Brava. Data from Nov. 1997 also appear in Fig. 2

significantly from controls for either size class (Fig. 6a, b); however, power was relatively low for these tests.

Burrowing times of *E. analoga* varied significantly with size class, with small crabs (11–17 mm) burrowing in shorter times (~4 times faster) than large crabs (25–32 mm) in controls (one-way ANOVA, $F_{1,40} = 14.84$, $P < 0.001$) (Fig. 6c, d). No effect of clam density was detected for burrowing times of small crabs and the

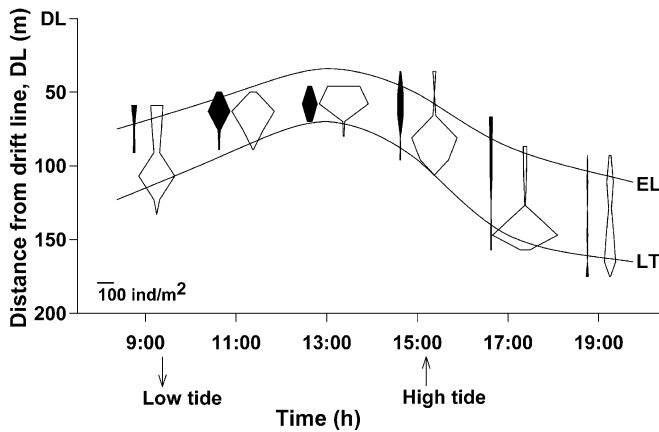
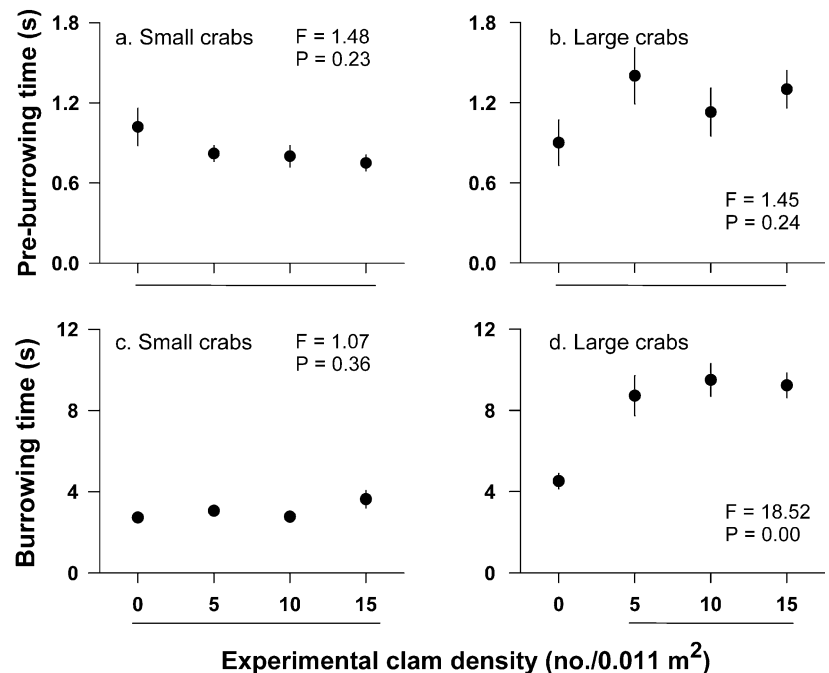


Fig. 5 Changes in the intertidal distribution of *M. donacium* (solid symbols) and *E. analoga* (open symbols) relative to the changing position of the EL and the LT through a complete tidal cycle at Mar Brava beach in March 1999. For each sampling time on the x-axis, the widths of kite diagrams represent the mean population abundance m^{-2} (scale bar provided in the lower left) at each of the five to six sampling levels for three transects. The heights of the kite diagrams along the y-axis show the intertidal levels where the species were distributed as a function of meters below the uppermost intertidal zone, the DL. Positions of the EL and the LT across the tidal cycle as a function of meters below the drift line are shown as curved lines. Ind Individual; for other abbreviations, see Fig. 1

treatments did not differ significantly from controls; however, power was relatively low for this test (Fig. 6c). For large crabs, burrowing times were significantly longer, averaging 2 times greater, in all clam density treatments than in control treatments and there were no significant differences in burrowing times among the three clam density treatments tested (Tukey HSD) (Fig. 6d).

In 19% of the trials in experimental treatments, large crabs displaced one to three clams from the sand as they

Fig. 6 Mean values (± 1 SE) of pre-burrowing time of **a** small [11–17 mm carapace length (CL)] and **b** large crabs (25–32 mm CL), and burrowing time of **c** small (11–17 mm CL) and **d** large crabs (25–32 mm CL) for *E. analoga* in three experimental densities of *M. donacium* and a control with no clams ($n=21$ for each density). Values of $F_{3,80}$ and P are given for one-way ANOVA and horizontal lines below the x-axis on each plot link means that did not differ significantly (Tukey's honest-significant-difference a posteriori test)



burrowed (Fig. 7). Small crabs never displaced clams while burrowing. Displacement of clams by large crabs was observed in all experimental densities. The percentage of trials in which displacement of at least one clam was observed increased with increasing clam density [5% (one trial), 14% (three trials) and 38% (eight trials), respectively for the five, ten, and 15 clam treatments]. As clam density increased across the experimental treatments, the average number of clams displaced per crab also increased significantly ($r = 0.990$, $P < 0.01$) from an average of 0.10 clam trial⁻¹ in the five clam treatment, to 0.48 clam trial⁻¹ in the 15 clam treatment (Fig. 7). When displacement occurred, most displaced clams were ejected entirely from the sediments and left lying on the sediment surface with the foot and siphons withdrawn. In a few cases, the affected clam was displaced only upward and not ejected from the sediments, resulting in the exposure of the majority of the shell length to the water column with $< 1/4$ of the shell length remaining in the sediments.

Discussion

We hypothesized that biotic interactions, specifically interference competition for space during burrowing, could modify the physical influence of intertidal swash and affect the distribution of the mobile animals of exposed sandy beaches. Our results from burrowing experiments and the shape and strength of the negative associations found on the smallest spatial scale we examined imply that interference during burrowing occurs frequently and is a likely mechanism of interspecific competition in this habitat. Interference during burrowing could potentially affect the exposure to and the ability of animals to respond to the swash climate of a beach and to

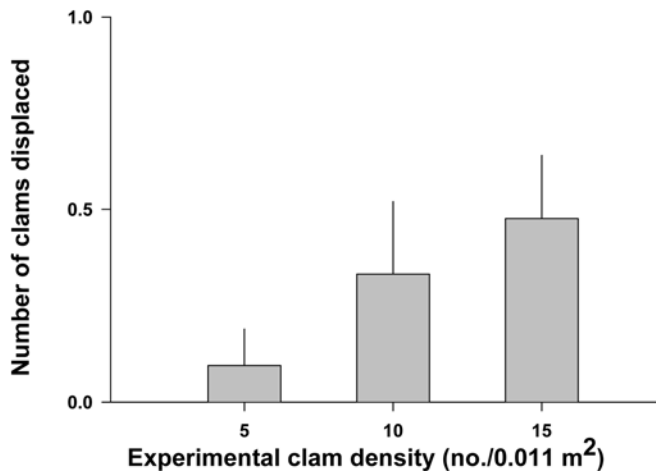


Fig. 7 Mean values (+1 SE) of the number of clams displaced by burrowing of large crabs (25–32 mm CL) for *E. analoga* in three experimental densities of *M. donacium* ($n=21$ for each density)

occupy optimal zones for feeding and avoiding predation. The displacement of clams by large crabs and the increase in burrowing times for large crabs in the presence of clams shown in our study would expose individuals involved in those interactions to additional action by active swash and a number of potentially negative consequences. Exposure to swash action could result in differential transport of competing individuals across or along the beach and increase the incidence of stranding at higher tidal levels, exposure to turbulence in the low intertidal, and exposure to either avian or fish predators. For suspension feeders, such as *E. analoga* and *M. donacium*, increased transport by swash would also reduce feeding time and residence time in optimal intertidal zones. By exposing animals to more swashes, interference competition during burrowing could affect the zonation and distribution and ultimately the survival of competing individuals. Interference interactions during burrowing thus could provide a viable explanation for the observed patterns of reduced overlap in intertidal distributions at times and beaches of high clam density and may contribute to the variation in overall abundance of these species observed among times and beaches.

Physical and biological processes affecting intertidal zonation may interact in substantially different ways and on different time scales among habitat types (Peterson 1991; Wilson 1991). Although some similarities exist between the zonation of intertidal macroinfauna of exposed sandy beaches and that of rocky shores (e.g., McLachlan and Jaramillo 1995), zonation on beaches is considerably more dynamic, as shown here for distributions of hippid crabs and clams and reported in other studies (e.g., Ansell et al. 1972; Jaramillo et al. 1993, 1996; Brazeiro and Defeo 1996), and is subject to distinctly different controlling mechanisms.

Competition for space contributes to the creation and maintenance of recognizable zones or strata of sessile and sedentary organisms in intertidal rocky shore (e.g., Connell 1961; Menge and Sutherland 1976; Lubchenco

1980; Underwood and Denley 1984) and mudflat (e.g., Peterson 1977) communities. As presented in our study, interference competition for space may also contribute to the zonation dynamics of mobile burrowing animals on sandy beaches, particularly at higher densities. Contrasts in the stability of different intertidal habitats and the mobility of the organisms results in substantial and important differences in the manifestation of competitive interactions. For example, on exposed sandy beaches, all species are mobile and many migrate regularly with the tides, using a number of intertidal levels in each tide cycle as shown in our results. Hence, competitive interactions and interference could potentially occur during every tidal cycle as species migrate across the intertidal zone with any resulting negative effects on feeding, position in the swash, or abundance accruing rapidly over time.

Our results from surveys and experiments suggest that significant and density-dependent competitive interactions can occur frequently between two abundant species of macroinfaunal animals and that those interspecific interactions could affect zonation, spatial distribution and population biology on a number of spatial and temporal scales. Competitive interactions have not generally been investigated directly or reported from experimental studies for sandy beach macroinfauna in part because of the difficulty of conducting standard enclosure/exclosure experiments in this dynamic habitat (Peterson 1991). Interactions during burrowing have been investigated in only one other published study of beach macrofauna (McLachlan 1998). In that study of two sympatric clam species (*Donax* spp.) on South African beaches, McLachlan (1998) suggested that important intra- and interspecific interactions during burrowing occurred only at exceptionally high densities (400–600 ind. m⁻²), equal to or exceeding natural densities of the larger species, *D. serra*, and that the smaller species, *D. sordidus*, had relatively little effect on the burrowing time of conspecifics or congeners. Croker and Hatfield (1980), who found horizontal and vertical spatial partitioning in three sympatric species of haustoriid amphipods, along with differential survival in coexistence experiments in the laboratory, provide the only other report containing direct evidence of the potential effects of competitive interactions among sandy beach macroinfauna.

The possible importance of negative interactions among hippid crabs and clams is supported by the distributional results presented here and by implications noted from other studies. Leber (1982) suggested that late summer stranding of *Donax variabilis* on a beach in North Carolina, concurrent with the movement of a congener, *D. parvula*, into subtidal zones, may have been a response to vast numbers of mole crabs, *Emerita talpoida* and clams (*Donax* spp.) migrating together in the swash zone at that time. Interactions between *Emerita* and *Donax* congeners were also invoked by Sastre (1985) as an explanation of the aggregated pattern of dispersion observed for *D. denticulatus* in Puerto Rico. Other observations on distributions of hippid crabs and bivalves support this idea. For example, high densities of *E. analoga* and two

bivalves, *D. gouldii* and *Tivela stultorum*, do not generally occur sympatrically on beaches in southern California (Dugan et al. 2000a, 2000b). The observations of Osorio et al. (1967) seem to point in the same direction: juveniles of *M. donacium* occurred in high abundance in the low intertidal, while population abundance of *E. analoga* was greatest in a higher intertidal zone on a beach in central Chile (ca. 33°S). Temporal changes in the relative dominance of hippid crabs and bivalves on a beach may also be related to biotic interactions. Arntz et al. (1987) cite Penchaszadeh (1971) to illustrate that during a period of dominance of *E. analoga*, *M. donacium* was absent on a Peruvian beach. Based on the observation that dense beds of *M. donacium* dominated the same beach in a later period, Arntz et al. (1987) suggested that dense populations of clams may competitively exclude the hippid crab.

Interference competition for space, such as that observed in our study between sympatric hippid crabs and bivalves, may be more widespread and important to patterns of zonation on exposed sandy beaches than previously recognized. Across-shore differences in distribution and abundance of those taxa reported from sandy beaches elsewhere, including *Emerita portoricensis* and *Donax denticulatus* in Jamaica (Wade 1967), *E. rathbunae* and *D. panamensis* in Panama (Dexter 1972), *E. holthuisi* and *D. incarnatus* in South West India (Ansell et al. 1972), *E. austroafricana* and *D. madascariensis* in South Africa (Dye et al. 1981) and *E. analoga* and *D. peruvianus* in Peru (Bocanegra et al. 1985) may well be a result of competitive interactions, specifically interference during burrowing.

Our results provide new evidence of the potential intensity and effects of negative biological interactions possible among the macroinfaunal animals of exposed sandy beaches. Competitive interactions, such as those that we observed, could potentially affect not only the intertidal distributions and zonation of macroinfauna but also community structure, as negative effects accrue over time. On exposed sandy beaches, interference competition for space could increase exposure to physical processes, such as swash and wave action, and act in concert with the strong physical forces characteristic of this environment to exclude inferior competitors from optimal zones or from communities. Our results from macroinfaunal animals of exposed sandy beaches also provide a marine example illustrating the potential importance of negative biotic interactions in environments characterized by strong physical forces and harsh and fluctuating conditions.

Acknowledgements We thank E. Daforo, M. H. Avellanal and S. Cifuentes for assistance in the field, and S. Silva and M. González for sample analyses. We are very grateful to S. Diehl, C. H. Peterson and two anonymous reviewers for their insightful and constructive comments on this manuscript. Financial support for this study and manuscript preparation was provided by CONICYT-CHILE (Proyecto FONDECYT nos. 7000423 and 1000423) and Proyecto MECESUP AUS 01-11 (Chile), Xunta de Galicia (Spain) and the National Science Foundation Long-Term Ecological Research Program (USA).

References

- Alexander RR, Stanton RJ Jr, Dodd JR (1993) Influence of sediment grain size on the burrowing of bivalves—correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios* 8:289–303
- Ansell AD (1983) Biology of the genus *Donax*. In: McLachlan A, Erasmus T (eds) *Sandy beaches as ecosystems*. Junk, the Hague, pp 607–635
- Ansell AD, Sivadas P, Narayanan B, Sankaranarayanan VN, Trevallion A (1972) The ecology of two sandy beaches in south west India. I. Seasonal changes in physical and chemical factors, and in the macrofauna. *Mar Biol* 17:38–62
- Arntz WE, Brey T, Tarazona J, Robles A (1987) Changes in the structure of a shallow sandy-beach community in Peru during an El Niño event. *S Afr J Mar Sci* 5:645–658
- Artacho P (2001) Distribución espacial y estructura poblacional de *Emerita analoga* (Stimpson, 1857) (Crustacea, Anomura, Hippidae) en diferentes tipos morfodinámicos de playas arenosas del litoral chileno. Tesis Biología Marina, Universidad Austral de Chile, Valdivia
- Bertness MD, Leonard, GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989
- Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726
- Bocanegra C, Carbajal W, Oliva J, Ancieta H (1985) Estructura de la comunidad de macroinvertebrados bentónicos en las playas arenosas de Trujillo. *Cong Nac Biol Pesq Truj (Perú)* 1:213–218
- Boer PJ den (1986) The present status of the competitive exclusion principle. *Trends Ecol Evol* 1:25–28
- Brazeiro A, Defeo O (1996) Macroinfauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments? *Estuar Coast Shelf Sci* 42:523–536
- Brown AC (2001) Surfing in the sandy-beach whelk, *Bullia digitalis* (Dillwyn). *Afr Zool* 36:121–127
- Brown A, McLachlan A (1990) *Ecology of sandy shores*. Elsevier, Amsterdam
- Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* 50:519–553
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle, *Chthamalus stellatus*. *Ecology* 42:133–146
- Crocker RA, Hatfield EB (1980) Space partitioning and interactions in an inter-tidal sand-burrowing amphipod guild. *Mar Biol* 61:79–88
- Cubit J (1969) Behavior and physical factors causing migration and aggregation of the sand crab, *Emerita analoga* (Stimpson). *Ecology* 50:118–123
- Dayton PK (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41:351–389
- Defeo O, De Alava A (1995) Effects of human activities on long term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Mar Ecol Prog Ser* 123:73–82
- Defeo O, Brazeiro A, De Alava A, Riestra G (1997) Is sandy beach macrofauna only physically controlled? Role of substrate and competition in isopods. *Estuar Coast Shelf Sci* 45:453–462
- Dexter DM (1972) Comparison of the community structures in a Pacific and an Atlantic Panamanian sandy beach. *Bull Mar Sci* 22:449–462
- Donn TE Jr, Els SF (1990) Burrowing times of *Donax serra* from the south and west coasts of South Africa. *Veliger* 33:355–358

- Dugan JE, Hubbard DM, Lastra M (2000a) Burrowing abilities and swash behavior of three crabs, *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall and *Lepidopa californica* Efford (Anomura, Hippidae), of exposed sandy beaches. *J Exp Mar Biol Ecol* 255:229–245
- Dugan JE, Hubbard DM, Engle JM, Martin DL, Richards DM, Davis GE, Lafferty KD, Ambrose RF (2000b) Macroinfauna communities of exposed sandy beaches on the Southern California mainland and Channel Islands. Fifth California Islands Symposium. OCS study, MMS 99-0038, pp 339–346
- Dugan JE, Hubbard DM, McCrary M, Pierson M (2003) The response of macroinfauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuar Coast Shelf Sci* 58S:133–148
- Dye AH, McLachlan A, Wooldridge T (1981) The ecology of sandy beaches in Natal. *S Afr J Zool* 16:200–209
- Ellers O (1995a) Behavioral control of the swash-riding in the calm *Donax variabilis*. *Biol Bull* 189:120–127
- Ellers O (1995b) Discrimination among wave-generated sounds by a swash-riding clam. *Biol Bull* 189:128–137
- Fusaro C (1980) Diel distribution differences in the sand crab, *Emerita analoga* (Stimpson) (Decapoda, Hippidae). *Crustaceana* 39:287–300
- Haley SR (1982) Zonation by size of the Pacific mole crab, *Hippa pacifica* Dana (Crustacea: Anomura: Hippidae) *J Exp Mar Biol Ecol* 58:221–231
- Jaramillo E, McLachlan A (1993) Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. *Estuar Coast Shelf Sci* 37:615–624
- Jaramillo E, McLachlan A, Coetzee P (1993) Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. *Mar Ecol Prog Ser* 101:105–118
- Jaramillo E, Pino M, Filón L, González M (1994) Longshore distribution of *Mesodesma donacium* (Bivalvia: Mesodesmatidae) on a sandy beach of the south of Chile. *Veliger* 37:192–200
- Jaramillo E, Stead R, Quijón P, Contreras H, González M (1996) Temporal variability of the sand beach macroinfauna in south-central Chile. *Rev Chil Hist Nat* 69:641–653
- Jaramillo E, Dugan J, Contreras H (2000) Abundance, tidal movement, population structure and burrowing rate of *Emerita analoga* (Stimpson 1857) (Anomura, Hippidae) at a dissipative and a reflective beach in south central Chile. *Mar Ecol* 21:113–127
- Jaramillo E, Contreras H, Duarte C, Quijón P (2001) Relationships between community structure of the intertidal macroinfauna and sandy beach characteristics along the Chilean coast. *Mar Ecol* 22:323–342
- Lastra M, Dugan JE, Hubbard DM (2002) Burrowing and swash behavior of the Pacific mole crab, *Hippa pacifica* (Anomura, Hippidae) on tropical sandy beaches. *J Crustacean Biol* 22:53–58
- Leber KM (1982) Bivalves (Tellinacea:Donacidae) on a North Carolina beach: contrasting population size structures and tidal migrations. *Mar Ecol Prog Ser* 7:297–301
- Lubchenco JM (1980) Algal zonation in the New England rocky community: an experimental analysis. *Ecology* 61:333–344
- McArdle S, McLachlan A (1991) Dynamics of the swash zone and effluent line on sandy beaches. *Mar Ecol Prog Ser* 76:91–99
- McArdle S, McLachlan A (1992) Sand beach ecology: swash features relevant to the macrofauna. *J Coast Res* 8:398–407
- McLachlan A (1990) Dissipative beaches and macroinfauna communities on exposed intertidal sands. *J Coast Res* 6:57–71
- McLachlan A (1998) Interactions between two species of *Donax* on a high energy beach: an experimental approach. *J Mollusc Stud* 64:492–495
- McLachlan A (2001) Coastal beach ecosystems. In: *Encyclopedia of biodiversity*, Vol 1. Academic Press, London pp 741–751
- McLachlan A, Jaramillo E (1995) Zonation on sandy beaches. *Oceanogr Mar Biol Annu Rev* 33:305–335
- McLachlan A, Young N (1982) Effects of low temperature on the burrowing rates of four sandy beach molluscs. *J Exp Mar Biol Ecol* 65:275–284
- McLachlan A, Woodridge T, Van der Horst G (1979) Tidal movements of the macrofauna on an exposed sandy beach in South Africa. *J Zool* 188:433–442
- McLachlan A, Jaramillo E, Donn TE, Wessels F (1993) Sandy beach macroinfauna communities and their control by the physical environment: a geographical comparison. *J Coast Res* 15:27–38
- McLachlan A, Jaramillo E, Defeo O, Dugan J, De Ruyck A, Coetzee P (1995) Adaptations of bivalves to different beach types. *J Exp Mar Biol Ecol* 187:147–160
- McLachlan A, Dugan J, Defeo O, Ansell A, Hubbard D, Jaramillo E, Penchaszadeh P (1996) Beach clam fisheries. *Oceanogr Mar Biol Annu Rev* 34:163–232
- Menge BA (1979) Coexistence between the seastars *Asterias vulgaris* and *A. forbesi* in a heterogeneous environment: a non-equilibrium explanation. *Oecologia* 41:245–272
- Menge BA (2000) Testing the relative importance of positive and negative effects on community structure. *Trends Ecol Evol* 15:46–47
- Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition and spatial heterogeneity. *Am Nat* 110:351–369
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Nel R, McLachlan A, Winter D (1999) The effect of sand particle size on the burrowing ability of the beach mysid *Gastrosaccus psammodytes* Tattersall. *Estuar Coast Shelf Sci* 48:599–604
- Nel R, McLachlan A, Winter DPE (2001) The effect of grain size on the burrowing of two *Donax* species. *J Exp Mar Biol Ecol* 265 (2):219–238
- Osorio C, Bahamonde N, López MT (1967) El limanche (*Emerita analoga* Stimpson) en Chile. *Bol Mus Hist Nat* 29:61–116
- Penchaszadeh PE (1971) Observaciones cuantitativas preliminares en playas arenosas de la costa central del Peru con especial referencia a los poblaciones de muy-muy (*Emerita analoga*) (Crustacea Anomura Hippidae), vol 6. UNESCO, Montevideo
- Peterson CH (1977) Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Mar Biol* 43:343–359
- Peterson CH (1991) Intertidal zonation of marine invertebrates in sand and mud. *Am Sci* 79:236–249
- Peterson CH, Hickerson DHM, Johnson GG (2000) Short-term consequences of nourishment and bulldozing on the dominant large invertebrates of a sandy beach. *J Coast Res* 16:368–378
- Sastre MP (1985) Aggregated patterns of dispersion in *Donax denticulatus*. *Bull Mar Sci* 17:149–174
- Sokal R, Rohlf F (1995) *Biometry: the principles and practice of statistics in biological research*. Freeman, New York
- Trueman ER (1971) The control of burrowing and the migratory behaviour of *Donax denticulatus* (Bivalvia: Tellinacea) *J Zool* 165:453–469
- Underwood AJ, Denley EJ (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong DR, Simberloff D, Thistle AB (eds) *Ecological communities: conceptual issues and evidence*. Princeton University Press, Princeton, N.J., pp 151–180
- Wade BA (1967) Studies on the biology of the West Indian beach clam, *Donax denticulatus* Linné. 1. Ecology. *Bull Mar Sci* 17:149–174
- Wiens JA (1977) On competition and variable environments. *Am Sci* 65:590–597
- Wilson HW (1991) Competition and predation in marine soft-sediment communities. *Annu Rev Ecol Syst* 21:221–241