

Abundance, Tidal Movement, Population Structure and Burrowing Rate of *Emerita analoga* (Anomura, Hippidae) at a Dissipative and a Reflective Sandy Beach in South Central Chile

Eduardo Jaramillo^{1*}, Jenifer Dugan² & Heraldo Contreras¹

¹ Instituto de Zoología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

² Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106, USA.

With 5 figures and 4 tables

Key words: Sandy beaches, swash, *Emerita analoga*, south central Chile.

Abstract. To evaluate the effects of beach morphodynamics upon the abundance, tidal movement, population structure and burrowing rate of the crab *Emerita analoga* (Stimpson) (Anomura, Hippidae) we sampled two beaches in south central Chile (*ca.* 42° S), Mar Brava and Ahui with dissipative and reflective characteristics, respectively. The swash zone at the dissipative beach was 5–6 times wider than that of the reflective beach. At the dissipative beach, upwash speeds were higher and the number of effluent line crossings were lower by more than an order of magnitude. To examine the tidal movement of *E. analoga*, we collected crabs from 5 to 6 tidal levels of each beach every 2 h across 12 h of the tidal cycle. The intertidal distribution of crabs differed between beaches; *i. e.*, at the dissipative beach they were primarily located at the swash zone, while at the reflective beach they were mostly located at the low tide level and shallow subtidal. The change in position of crabs was pronounced across the tidal cycle at the dissipative beach (Mar Brava), with most of the animals remaining in the active swash zone. Body size data were used to construct size frequency distributions for each population. Crabs from the dissipative beach reached larger sizes than those at the reflective beach. Sediments were coarser at the latter versus the former beach. Crabs burrowed at similar rates in the sand from both beaches, a result which supports the idea that *E. analoga* is a “sediment generalist” capable of burrowing successfully in a wide range of sediment types. This characteristic is likely a key to the broad success of this species on the full range of beach morphodynamic types along the coasts of South and North America.

* Author to whom correspondence should be addressed. E-mail: ejaramil@valdivia.uca.uach.cl

Problem

Exposed sandy beaches are widespread dynamic coastal habitats which may be physically defined by sediment type and wave features (Brown & McLachlan, 1990). Sandy beaches have often been characterized in relation to single physical factors such as sand particle size, beach face slope, wave exposure and tidal range (*e.g.*, Eleftheriou & McIntyre, 1976; McLachlan, 1980; Dexter, 1992). However, researchers such as Wright *et al.* (1979, 1985), Short (1983, 1996) and Short & Wright (1983), among others, adopted a more holistic view of oceanic exposed sandy habitats and classified beaches across a spectrum of morphodynamic types, from reflective to dissipative. Reflective beaches are characterized by a virtual absence of surf zone, coarse sand, small waves and steep profiles. At the other end of the spectrum, dissipative beaches have a wide surf zone (*i. e.*, waves dissipate most of their energy before reaching the beach face), fine sands, large waves and flat profiles. Intermediate beaches lie between both extremes, with bar – trough systems, rip currents and variable conditions (Short, 1983, 1996; Short & Wright, 1983). The swash climate of exposed sandy beaches varies with the morphodynamic states. For example, reflective beaches have swashes with short periods, dissipative ones with longer periods, and intermediate beaches show intermediate swash periods (McArdle & McLachlan, 1992).

Some of the macroinfaunal species inhabiting the swash zone of exposed sandy beaches show a characteristic migratory tidal rhythm. These movements have been studied in anomuran decapods of the genera *Emerita* and *Hippa* (Cubit, 1969; Fusaro, 1980; Shepherd *et al.*, 1988), in bivalves of the genus *Donax* (Tiffany, 1972; McLachlan & Hesp, 1984; Donn *et al.*, 1986) and in the gastropod genus *Bullia* (Dye & McGwynne, 1980; Brown, 1982; McGwynne & McLachlan, 1985). Shepherd *et al.* (1988), for example, showed that the distribution of juvenile *Hippa australis* in a sandy beach of Australia maintains a close relationship with the boundaries of the swash zone. The molluscs *Donax sordidus* and *Bullia rhodostoma*, exhibit no intrinsic migratory behaviour: movements result from changes in the physical conditions of the beach, such as tide levels and variability of the swash line (McLachlan *et al.*, 1979). McGwynne & McLachlan (1985) suggested that the migratory movements of *Bullia rhodostoma*, *Bullia digitalis* and *Bullia pura* are directly related with the tidal cycle.

The hippid decapod crab *Emerita analoga* (Stimpson, 1857) is a typical tidal migrant of the swash zone in sandy beaches along the Pacific coast of America. Its geographical distribution extends from Alaska (*ca.* 58° N) to the extreme south coast of Chile (55° S), being interrupted in tropical regions and those with water temperatures above 20 °C (Efford, 1969; Nuñez *et al.*, 1974). A number of factors have been related to the migratory behaviour of this species. Cubit (1969) suggested a role of thixotropic changes in the substrate during the tidal cycles. Dillery & Knapp (1970) stressed long-shore currents, while Fusaro (1980) related the distribution of *E. analoga* to the level of tides.

The coast of south central Chile (*ca.* 39–42° S) has a variety of morphodynamic types of beaches inhabited by a rich and abundant macrofauna, often dominated by *E. analoga*. Abundance and biomass of the total macroinfauna along these beaches increase from reflective to intermediate and dissipative types (Jaramillo & McLachlan, 1993; Jaramillo *et al.*, 1993). McArdle & McLachlan (1991, 1992) suggested that dynamics of the surf – swash zone may be the most important factor structuring the in-

tertidal sandy beach macroinfauna. We hypothesize that different swash climates also affect the biology and behaviour of *E. analoga*. To test this hypothesis, we compared the population structure, tidal movement and burrowing rate of this species on two sandy beaches with reflective and dissipative characteristics in south central Chile.

Material and Methods

1. Study area

The two study sites were located on the coast near Ancud (ca. 42° S), Isla de Chiloé, south central Chile. The sites chosen were the beaches of Mar Brava (41° 54' S, 73° 59' W) and Ahui (41° 49' S, 73° 51' W) with dissipative and reflective features, respectively. While Mar Brava is fully exposed to the breaking waves of the Pacific Ocean, Ahui is located in a sheltered bay (Fig. 1). These beaches are affected by a semidiurnal tidal cycle with a tide range close to 1.2 m.

2. Beach and swash characteristics

To characterize the morphodynamic beach state, wave height and wave period were estimated at each beach during low tides on 16–17 March, 1999. Wave height ($n = 15$) was estimated by measuring the height of breaking waves with graduated poles against the horizon and adding that to the height difference between the location of the observer and the lowest point where the backwash met the next incoming swash bore. The wave period (measured with a stop watch) was the time interval between breakers. Sediment samples were collected from the lowest swash level with a plastic cylinder (3 cm in diameter) buried to an approximate depth of 3 cm. Grain size was analyzed using a settling tube (Emery, 1938), and mean grain size was calculated according to the moments computational method (Seward-Thompson & Hails, 1973). From estimated mean wave height, wave period and sand fall velocity, Dean's dimensionless parameter [Ω] (Short & Wright,

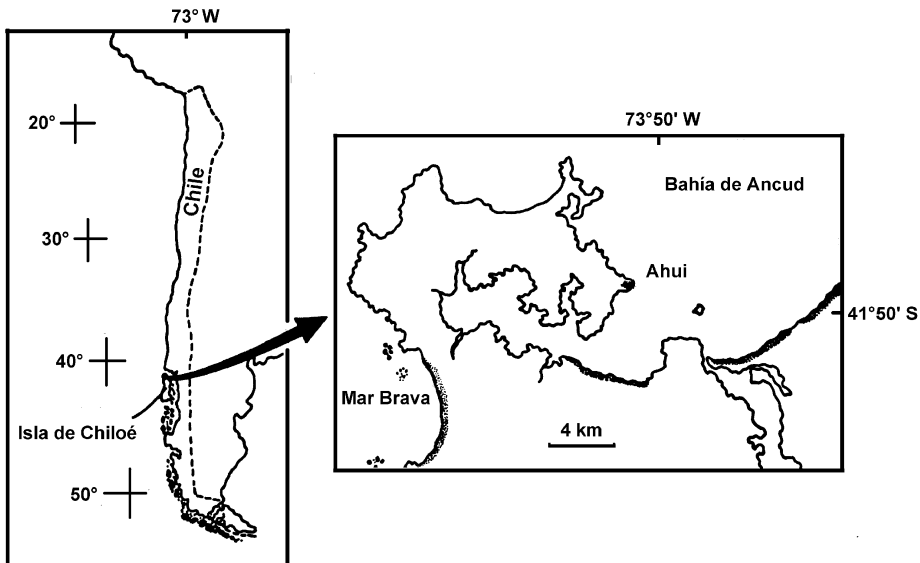


Fig. 1. Location of the beaches studied on the coast of Isla de Chiloé, south central Chile.

1983) was calculated for each beach: $\Omega = \text{wave height [cm]} / \text{sand fall velocity [cm} \cdot \text{s}^{-1}] \times \text{wave period [s]}$. Sand fall velocity values were obtained from mean particle size and following Gibbs *et al.* (1971). The morphology (*i. e.*, beach face slope) of each beach was determined by Emery's profiling technique (Emery, 1961).

The characteristics of the swash climate were measured continuously for 10 min every other 2 h during the crab sampling period of 12 h at each beach. Thus, space travelled and time of incoming swashes were measured during that 20 min period. Afterward, swash speed was estimated with that data. We noted the times any swash crossed the effluent line (intersection of groundwater table and beach face) during the 20 min period. We also took periodic measurements of the width of the swash zone (distance between the lower and upper limit of swash).

3. Tidal movement of *E. analoga*

To examine the tidal movement of *E. analoga* at both beaches, we collected crabs from 5 to 6 tidal levels of the beach across 12 h of the tide cycle on three transects (18–19 March, 1999). Transects were at least 15 m apart in order to avoid disturbance of the crabs in the adjacent transects. Sampling commenced on the morning low tide and new samples were collected every 2 h from 09:00 to 19:00. Samples were collected at the following tidal levels: one below the low swash line, two or three in the swash zone, one in the uppermost level of this zone (effluent line), and one in the retention zone above the effluent line. The distance between samples on each transect varied between sampling times and the sampled beaches. That interval depended upon the total width of the zone from the effluent line to the low swash, which varied with both time and beach type. We also noted the distance from the drift line to the top of the visible aggregation of *E. analoga* at each sampling time. Samples were collected with a 10 cm diameter corer and sieved through a 1 mm mesh. Ten cores were collected at each tidal level and pooled to make up each sample (0.08 m²). The number of crabs in each sample were counted and measured to the nearest 0.1 mm CL (carapace length) with vernier calipers. The sex and reproductive condition of each crab were recorded.

4. Population structure of *E. analoga*

Body size data were used to construct a size frequency distribution for each population. Analyses of population characteristics included female size at maturity (the smallest size at which 50 % of the crabs were ovigerous), largest ovigerous crab (95th percentile size), smallest ovigerous crab (5th percentile size), and largest male crab (95th percentile size) (*sensu* Dugan *et al.*, 1991, 1994).

5. Burrowing rate of *E. analoga*

We collected variously sized *E. analoga* and sediments from the intertidal of the two study sites during 18–19 March 1999. Burrowing rates of crabs from each beach were measured in sand from Mar Brava and Ahui. Injured, recently molted and late premolt crabs were not used in the burrowing trials. Burrowing trials were conducted in sediments from both sites immediately following the collection of the animals at each beach.

Burrowing rates were measured in the field in two 3.5 l tubs (28 cm in diameter) with 50 mm sand and 20 mm water column, one containing sediments from Mar Brava and the other sediments from Ahui. If necessary, the tubs were adjusted to create a level sediment surface. Sand and water temperatures during the burrowing trials ranged from 13.5–14.5 °C. The burrowing times of individual crabs were timed from the initiation of burrowing (abdomen in contact with the sediments, uropod activity) to the disappearance of the crab under the sediment surface. Crabs were removed from the sand immediately after burrowing and the sediments were reconsolidated by tapping the sides of the tub gently. We measured the carapace length (CL) to the nearest 0.1 mm. Mass was calculated from length-mass regressions for the *E. analoga* population at each beach. We calculated regressions for burrowing rates [s] with dry mass [g] for each population in each sediment type. The burrowing rates of the two populations were compared with ANCOVA.

Sediment samples were collected from the experimental tubs and analyzed as explained earlier for beach characterization. We also measured the shear strength of the sediments used in those tubs using a Pilcon hand vane tester (English Drilling Equipment Co. Ltd. England). The instrument comprises a torque head with a

direct reading scale which is turned by hand. A non-return pointer indicates the reading. The vane (33 mm diameter) which is screwed into the rear of the torque head was pushed 5 cm into the sediment (the same extension of the vane). The readings in $\text{kg f}\cdot\text{cm}^{-2}$ were converted to $\text{N}\cdot\text{cm}^{-2}$.

Results

1. Beach and swash characteristics

The physical characteristics of the beaches sampled at Mar Brava and Ahui are shown in Table 1. The intertidal of Mar Brava was wider and flatter than that of Ahui (about six and five times, respectively). Mean grain size of sediments of the swash zone at Mar Brava was finer than that at Ahui. Waves had higher heights and longer periods at Mar Brava. Dean's values indicate that Mar Brava has dissipative characteristics ($\Omega > 6$), whereas Ahui can be categorized as a reflective beach ($\Omega = 1.3$) (cf. Short & Wright, 1983).

Table 1. Physical characteristics of the beaches and sediments studied at the coast of Ancud, Isla de Chiloé. Standard deviations in parentheses.

	beach length [m]	maximum width of intertidal [m]	slope	mean grain size [μm]		wave height [cm]	wave period [s]	Ω
				top swash	low swash			
Mar Brava	4000	160	1/47	178 (1.6)	177 (0.7)	287 (8)	17.1 (5.1)	8.5
Ahui	200	28	1/10	280 (2.0)	326 (9.5)	13 (4)	2.4 (0.6)	1.3

The swash characteristics at both beaches are shown in Fig. 2. The swash zone at Mar Brava was about 5–6 times wider than that of Ahui; in the former beach this zone comprised up to 48 % of the total intertidal width. The swash zone at Mar Brava was wider during the morning low tide and after the afternoon high tide. The width of that zone at Ahui was somewhat wider during the high tide period, when it measured about 60 % of the total intertidal width (Fig. 2). During most of the sampling period, upwash speed was faster at Mar Brava, while the number of effluent line crossings per 10 min was higher in Ahui, especially during flooding (up to 38 and 45 crossings at 11:00 and 13:00) (Fig. 2).

2. Abundance of *E. analoga*

The mean population abundances (individuals per running meter of beach) of *E. analoga* during each sampling period at both beaches are shown in Fig. 3. Population abundances were up to 6.6 times higher at the dissipative beach of Mar Brava.

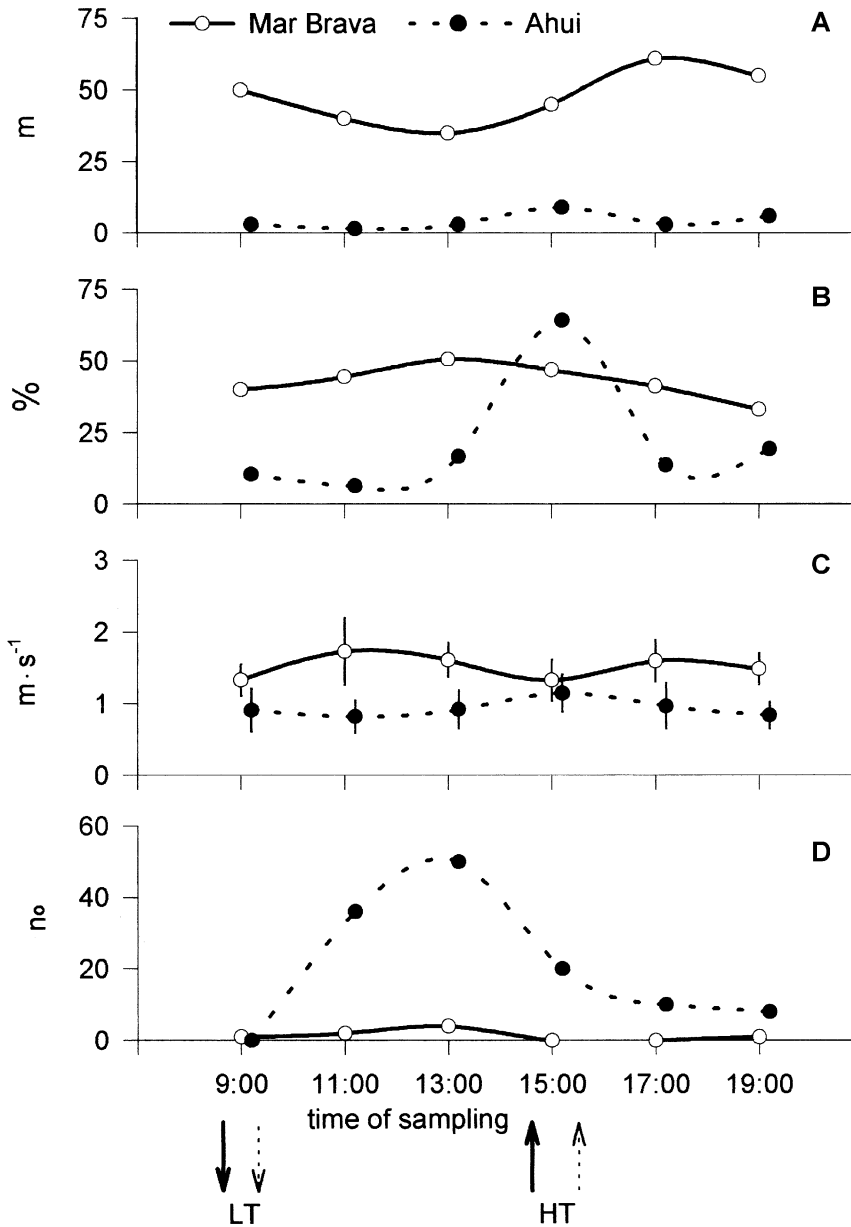


Fig. 2. Swash zone characteristics over the tidal cycle at the beaches of Mar Brava (open symbols) and Ahui (closed symbols). A. width of the swash zone; B. width of the swash zone (as a percentage) in relation to the total intertidal width (distance from drift line to the low tide level or lowest swash level); C. mean upwash speed ± 1 SD; D. number of swash crossings above the effluent line in a 10 min period. Approximate times of observed low tides (LT) and high tides (HT) are indicated by solid-lined arrows for Mar Brava and dashed-lined arrows for Ahui.

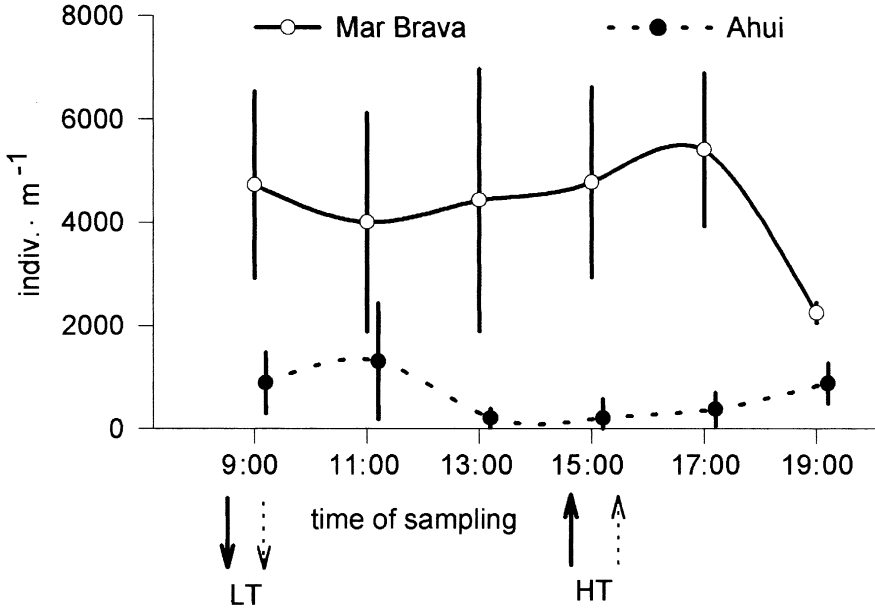


Fig. 3. Mean abundance of *Emerita analoga* at Mar Brava and Ahui. Approximate times of observed low tides (LT) and high tides (HT) are indicated by solid-lined arrows for Mar Brava and dashed-lined arrows for Ahui.

3. Tidal movement of *E. analoga*

The distribution of *E. analoga* at both beaches is shown in Fig. 4. At Mar Brava, the crabs remained in the area between the effluent line and the low tide level through the sampling period. In contrast, at Ahui, the crabs primarily occurred below the low tide level (*ca.* 1.2 m deep). The amplitude of change in the position of population modes of crabs was greater at Mar Brava than at Ahui; *i. e.*, that position moved a maximum of 107 m over the tidal cycle at Mar Brava and 16 m at Ahui. The range in the intertidal width (from 0 to lowest level of swash, Fig. 4) was 95 m at Mar Brava and 17 m at Ahui. Thus, crabs moved a greater percentage of the total width range at the dissipative beach (113 %) than at the reflective beach (94 %).

Emerita analoga abundance varied significantly with sampling level at both beaches (Table 2). At Ahui, there was significant variability in crab number through time (*i. e.*, abundance changed over the sampling period). At both sites, there was a significant interaction between the distribution of crabs among the sampling levels and sampling time (Table 2).

The tidal position of *E. analoga* aggregations varied between the beaches across the sampling period. At Mar Brava, aggregation was visible throughout the sampling period and the top of the aggregation coincided with highest crab abundance in each sampling time. At Mar Brava, highest abundance occurred in the lower half of the active swash zone during the morning low tide, moved to the upper half of that zone during the high tide and returned to the lower half of the swash zone as the tide dropped to the

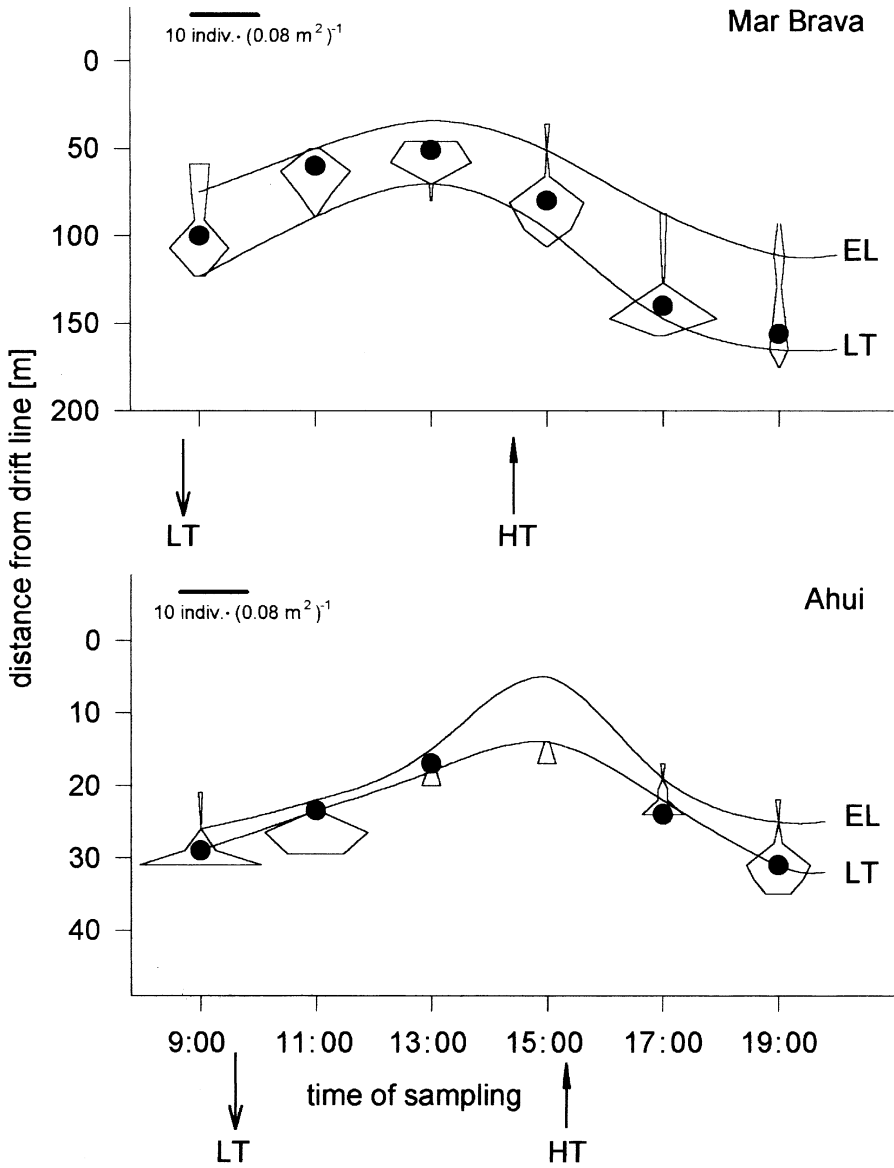


Fig. 4. Tidal movement of *Emerita analoga* relative to the position of the effluent line (EL) and low tide (LT) at Mar Brava and Ahui. The mean abundance [10 indiv. · (0.08 m²)⁻¹] of *E. analoga* for each sampling station is represented by the width of the kite at each sampling time. Black dots in each kite indicate the location of the top of visible aggregation of *E. analoga*. No aggregation was visible at 15:00 at Ahui. Approximate times of observed low tides (LT) and high tides (HT) are indicated by arrows for Mar Brava and Ahui, respectively.

evening low tide (Fig. 4). In Ahui, highest abundance occurred below the low tide level at all tides (Fig. 4).

Table 2. Summary of a two-way ANOVA to analyze the tidal movements of *E. analoga* at Mar Brava and Ahui. SS: sum of squares; MS: mean of squares.

		df	SS	MS	F	P
Mar Brava	sample time	5	118.49	23.70	0.527	0.7548
	sample station	5	2035.83	407.17	9.062	0.0001
	time × station	25	2275.16	91.01	2.025	0.011
	error	70	3145.33	44.93		
Ahui	sample time	5	501.66	100.33	1.678	0.1537
	sample station	4	1632.30	408.07	6.826	0.0001
	time × station	20	1808.51	90.43	1.513	0.1106
	error	60	3586.67	59.78		

4. Population structure of *E. analoga*

Polymodal population structures occurred in both populations, consisting primarily of a distinct mode of smaller male crabs and a mode of larger female crabs, most of which were ovigerous (Fig. 5). Those modes were separated by a noticeable gap in the size distribution at both beaches. Very few young of the year crabs occurred. The crabs inhabiting the dissipative beach, Mar Brava, reached larger sizes than those at the reflective beach, Ahui. For male crabs, the size of the 95th percentile was 13.8 and 11.6 mm at Mar Brava and Ahui, respectively. For female crabs, the 5th percentile size of ovigerous crabs was 19.0 and 16.6 mm, respectively. The 95th percentile size of ovigerous crabs was 29.2 and 21.9 mm, respectively. Finally, the size at maturity of female crabs was 22.0 mm at Mar Brava and 18.5 mm at Ahui.

5. Burrowing rate of *E. analoga*

Mean grain size of sediments used in burrowing trials differed significantly ($t = -0.61$, $P < 0.001$; results of t-test) between the two beaches, with finer sediments (top swash) at Mar Brava (mean ± 1 SD = $178 \mu\text{m} \pm 1.6$) and coarser at Ahui (mean ± 1 SD = $280 \mu\text{m} \pm 2.0$). The mean shear strength of the trial sediments also differed significantly ($t = -0.67$, $P < 0.001$; results of t-test), with more compact sediments at Mar Brava (mean ± 1 SD = $0.353 \text{ N}\cdot\text{cm}^{-2} \pm 0.07$) versus Ahui (mean ± 1 SD = $0.186 \text{ N}\cdot\text{cm}^{-2} \pm 0.01$).

Burrowing rate increased significantly with body weight of crabs in the original sediments at both beaches (Table 3). Regressions of burrowing time and crab size did not differ significantly between beaches in the original sediments (see results of ANCOVA, Table 3). Thus, crabs of similar size burrowed at similar rates at both beaches.

Burrowing rates increased significantly with body weight in all other sediments tested (*e. g.*, crabs from Mar Brava in sediments from Ahui and *vice versa*) (Table 4).

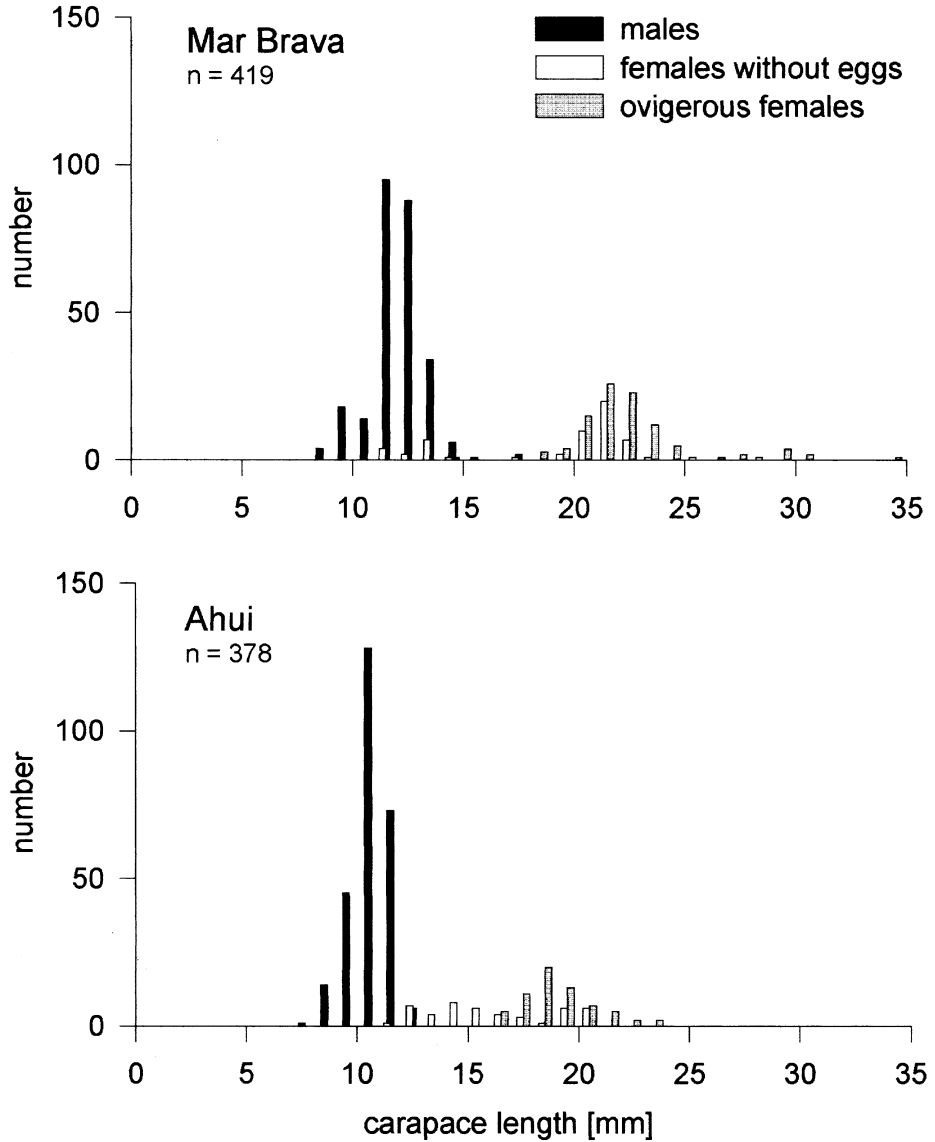


Fig. 5. Size frequency distributions of crabs collected at Mar Brava and Ahui.

Table 3. Summary of regression equations and ANCOVA between burrowing rates versus body weight of crabs collected at Mar Brava and Ahui. Values of r are significant at the 0.01 probability level.

	regression equation	r	n	ANCOVA F	df	P
<i>E. analoga</i> of Mar Brava	$y = 0.550 + 1.581 x$	0.77	30	slopes = 0.006	1, 54	0.940
<i>E. analoga</i> of Ahui	$y = 0.729 + 1.629 x$	0.66	28	adjusted means = 0.750	1, 55	0.392

Table 4. Summary of regression equations and ANCOVA between burrowing rates versus body weight of crabs tested at their original sediments and at the sands of the other beach. Values of r are significant at the 0.01 probability level.

	regression equation	r	n	ANCOVA F	df	P
<i>E. analoga</i> of Mar Brava						
at the original sands	$y = 0.550 + 1.581 x$	0.77	30	slopes = 1.048	1, 56	0.310
at the sands of Ahui	$y = 0.444 + 1.880 x$	0.93	30	adjusted means = 0.324	1, 57	0.571
<i>E. analoga</i> of Ahui						
at the original sands	$y = 0.729 + 1.629 x$	0.66	28	slopes = 1.118	1, 54	0.295
at the sands of Mar Brava	$y = 0.887 + 2.359 x$	0.62	30	adjusted means = 6.633	1, 55	0.013

Regressions of burrowing rate and size did not differ significantly between the sediments of crab origin and those of the other beach for crabs from Mar Brava (see results of ANCOVA, Table 4). When burrowing rates of Ahui crabs were compared in Ahui versus Mar Brava sands, there was a significant difference in adjusted means and the crabs burrowed significantly faster in their original beach sediments (see results of ANCOVA, Table 4).

Discussion

McArdle & McLachlan (1991, 1992) have shown that different morphodynamic beach types have noticeably different swash climates: dissipative beaches have faster upwash times, longer swash periods and lower number of effluent line crossings than intermediate and reflective beaches. We chose our study sites to represent those two different beach types in order to increase the possibility of detecting differences in the population biology and behavior of *E. analoga*. Beach morphodynamics and swash climate characteristics differed significantly between the two study sites. The dissipative beach of Mar Brava had a flatter intertidal, a wider swash zone, faster upwashes and lower frequency of swashes crossing above the effluent line than did the reflective beach of Ahui. However, despite the fully reflective wave and swash climate, the mean grain size of sands at Ahui were finer than those typically found on other reflective beaches of southern Chile (cf. Pino & Jaramillo, 1992; Jaramillo & McLachlan, 1993) or elsewhere (e.g., McLachlan, 1985; Defeo *et al.*, 1992).

Abundances of *E. analoga* per linear meter of beach were higher at the dissipative beach of Mar Brava. This is similar to the trend found by Jaramillo & McLachlan (1993), who compared the macroinfauna of ten beaches representing the range from reflective to dissipative conditions along the coast of Valdivia (about 250 km north of Isla de Chiloé). However, those trends are quite different from recent results (E. Jaramillo, unpubl. data), which show higher abundances on intermediate beaches of central Chile (ca. 32° S). Dugan & Hubbard (1996) also found a higher abundance and biomass of *E. analoga* on beaches of reflective to low intermediate morphodynamic states in southern California.

Population structure and life history traits of *E. analoga* also differed between the dissipative and reflective beach. The absence of a surf zone in Ahui probably results in lower phytoplankton abundances and food availability to suspension feeders, such as *E. analoga*, than on the dissipative beach of Mar Brava. Lower food availability may result in reduced growth rates and smaller body sizes at the reflective beach. This idea is supported by the field study of Dugan *et al.* (1994), which found that for sandy beaches of California, life history characteristics of *E. analoga* were positively correlated with surf zone chlorophyll *a*; this implies that body size increases with food resources. In related work which supports that finding, molt increments of *E. analoga* were positively correlated with surf zone chlorophyll *a* concentrations (Dugan, 1990). Also, as beach sediments become finer and better sorted and beach face slopes become flatter, as is typical of dissipative beaches, the size of smallest and largest ovigerous crabs and the size of the largest male crab increase in this species (Dugan *et al.*, 1994). This agrees with the prediction of the swash control hypothesis (McLachlan *et al.*, 1993) in the sense that smallest size would be selected as an advantage for animals living in the turbulent swash zone of reflective beaches as opposed to dissipative beaches.

The across-shore zonation of *E. analoga* differed between dissipative and reflective beach. At the dissipative site, Mar Brava, crabs were primarily located at the swash zone, while at the reflective beach, Ahui, they were mostly located at the low tide level and shallow subtidal (*ca.* 1.2 m deep). Changes in position across the swash zone and shallow subtidal suggest that tidal movements of *E. analoga* differed between the two beach morphodynamic types. Our results also suggest that these tidal movements also vary along the shore, particularly in reflective and intermediate beaches where features such as cusp horns and bays develop clearly. As shown by McLachlan & Hesp (1984) in a reflective beach of western Australia, swash climates differed between cusp and bay horns. For example, cusp horns had maximum upwash velocities, while cusp bays had maximum backwash velocities. These features were observed at Mar Brava and Ahui. McLachlan & Hesp (1984) reported higher concentrations of suspension feeding bivalves (*Donacilla angusta* and *Donax fava*) in the bays of those beaches, suggesting a dependence on swash to move across the shore.

Tidal changes in across-shore zonation of *E. analoga* as observed in our study may be related to changes in sediment compactness and thixotropic conditions as tides move up and down (*cf.* Cubit, 1969). The results of Fusaro (1980), however, suggest that other factors cause tidal movements, since abundance of *E. analoga* aggregations in a sandy beach of California varied between day and night.

Temporal variability in tidal migration of *E. analoga* is probably higher than that shown in the present study. Our sampling was conducted during spring tides when swash characteristics probably differed from those occurring during neap tides. Thus, tidal migration of *E. analoga* may well follow a gradual, semilunar and downward movement from spring to neap tides as has been reported for other sand beach organisms such as *Tylos punctatus* in South Africa (Kensley, 1974). In addition, during the night, tidal movement may be more extreme than we observed in this study, as suggested by the results for an intermediate sandy beach of southern Chile (E. Jaramillo, unpubl. data).

Fusaro (1980) and McLachlan & Hesp (1984) reported that this hippid crab moves up and down the swash zone to maintain a suitable water depth for feeding; *i.e.*, *E. analoga* moves to occupy positions coinciding with that depth as tides change through the day. This may also be an adaptation to avoid predators such as fishes and birds (*cf.* Carlisle

et al., 1960; MacGinitie, 1938). In this way, crabs would maintain position at a water depth not easily accessible to fishes and birds. Fishes such as *Cilus montii* and *Eleginopus maclovinus* and shorebirds such as *Numenius phaeopus* and *Calidris alba* are usually seen probing in the swash levels occupied by *E. analoga* along the coast of southern Chile. Pequeño (1979) reported a high frequency of this crab in stomach contents of *E. maclovinus* at Mehuín, about 250 km north of Isla de Chiloé. We also observed one individual of *Larus pipixcan* catching *E. analoga* from the shallow subtidal during the falling tide at Ahui.

Crabs burrowed at similar rates in sediments from both beaches. These results support the idea that *E. analoga* is a sediment generalist (Alexander *et al.*, 1993) and is able to burrow successfully in a wide range of sediment types. The field studies of Jaramillo *et al.* (1993) and Dugan & Hubbard (1996) and the experiments of Jaramillo (1987) confirm that this species has quite a broad range as far as sand grain sizes is concerned.

Summary

Differences in abundances, population structure and tidal migration of *Emerita analoga* between beach morphodynamic types and swash climates were observed. While the across-shore distribution of this species was wider at the dissipative beach of Mar Brava, crabs were confined to the low tide level and shallow subtidal at the reflective beach of Ahui. These results agree with the predictions of the swash control hypothesis proposed by McLachlan *et al.* (1993), which states that swash characteristics towards the dissipative end of beach types (*e.g.* longer swash periods) are more beneficial to suspension-feeder invertebrates such as *E. analoga*. Thus, although this study sampled only two of a broad range of beach types along the coast of southern Chile, we envision a range of tidal behaviour along a range of beach morphodynamic types and swash climates. That, and the broad range of grain sizes occupied by *E. analoga*, is likely the key to the broad success of this species along the sandy shores of South and North America.

Acknowledgements

We appreciate the collaboration of María Avellanal, Cristian Duarte and Andrés Sepúlveda (Instituto de Zoología, Universidad Austral de Chile) during field work. We thank David Hubbard (Marine Science Institute, University of California, Santa Barbara, USA), who provided helpful comments on the manuscript. We also thank two anonymous reviewers for comments. Financial support to carry out this study came from Project FONDAPE, Oceanografía & Biología Marina (Programa Mayor n° 3) of CONICYT (Chile).

References

- Alexander, R. R., R. J. Stanton, Jr. & J. R. Dodd, 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.
- Brown, A. C., 1982: The biology of sandy beach whelks of the genus *Bullia* (Nassariidae). *Oceanogr. Mar. Biol. Annu. Rev.*, **20**: 309–361.
- Brown, A. C. & A. McLachlan, 1990: *Ecology of Sandy Shores*. Elsevier Science Publishers, Amsterdam; 328 pp.

- Carlisle, J. G., J. Schott & N. J. Abramson, 1960: The barred surfperch (*Amphistichus argenteus* Agassiz) in Southern California. Calif. Fish. Bull., **109**: 1–79.
- Cubit, J., 1969: Behavior and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). Ecology, **50**: 118–123.
- Defeo, O., E. Jaramillo & A. Lyonnet, 1992: Community structure and zonation of the macroinfauna on the atlantic coast of Uruguay. J. Coastal Res., **8**: 830–839.
- Dexter, D. M., 1992: Sandy beach community structure: the role of exposure and latitude. J. Biogeogr., **19**: 59–66.
- Dillery, D. G. & L. V. Knapp, 1970: Longshore movements of the sand crab *Emerita analoga* (Decapoda; Hippidae). Crustaceana, **18**: 233–240.
- Donn, T. E., Jr., D. J. Clarke, A. McLachlan & P. Du Toit, 1986: Distribution and abundance of *Donax serra* Röding (Bivalvia, Donacidae) as related to beach morphology. I. Semilunar migrations. J. Exp. Mar. Biol. Ecol., **102**: 121–131.
- Dugan, J. E., 1990: Geographic and temporal variation in the life history, growth, and reproductive biology of the sand crab, *Emerita analoga* (Stimpson). Ph.D. dissertation. University of California, Santa Barbara, CA, USA; 329 pp.
- Dugan, J. E. & D. M. Hubbard, 1996: Local variation in populations of sand crab *Emerita analoga* on sandy beaches in southern California. Rev. Chil. Hist. Nat., **69**: 579–588.
- Dugan, J. E., D. M. Hubbard & A. M. Wenner, 1994: Geographic variation in life history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: relationships to environmental variables. J. Exp. Mar. Biol. Ecol., **181**: 255–278.
- Dugan, J. E., A. M. Wenner & D. M. Hubbard, 1991: Geographic variation in reproductive biology of the sand crab, *Emerita analoga* (Stimpson) on the California coast. J. Exp. Mar. Biol. Ecol., **150**: 63–81.
- Dye, A. H. & L. E. McGwynne, 1980: The effect of temperature and season on the respiratory rates of three psammolittoral gastropods. Comp. Biochem. Physiol. A, **66**: 107–111.
- Efford, I. E., 1969: Aggregation in the sand crab *Emerita analoga* (Stimpson). J. Anim. Ecol., **34**: 63–75.
- Eleftheriou, A. & A. D. McIntyre, 1976: The intertidal fauna of sandy beaches – a survey of the Scottish coast. Department of Agriculture and Fisheries for Scotland. Scott. Fish. Res. Rep., **6**: 1–61.
- Emery, K. O., 1938: Rapid method of mechanical analysis of sand. J. Sediment. Petrol., **8**: 105–111.
- Emery, K. O., 1961: A simple method of measuring beach profiles. Limnol. Oceanogr., **6**: 90–93.
- Fusaro, C., 1980: Diel distribution differences in the sand crab, *Emerita analoga* (Stimpson) (Decapoda Hippidae). Crustaceana, **39**: 287–300.
- Gibbs, R. J., M. D. Mathews & D. A. Link, 1971: The relationship between sphere size and settling velocity. J. Sediment. Petrol., **41**: 7–18.
- Jaramillo, E., 1987: Community ecology of Chilean sandy beaches. Ph.D. dissertation. University of New Hampshire, Durham, NH, USA; 216 pp.
- Jaramillo, E. & A. McLachlan, 1993: Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. Estuarine Coastal Shelf Sci., **37**: 615–624.
- Jaramillo, E., A. McLachlan & P. Coetzee, 1993: Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. Mar. Ecol. Prog. Ser., **101**: 105–118.
- Kensley, B., 1974: Aspects of the biology and ecology of the genus *Tylos* Latrielle. Ann. S. Afr. Mus., **65**: 401–471.
- MacGinitie, G. E., 1938: Movements and mating habits of the sand crab *Emerita analoga*. Am. Midl. Nat., **19**: 471–481.
- McArdle, S. B. & A. McLachlan, 1991: Dynamics of the swash zone and effluent line on sandy beaches. Mar. Ecol. Prog. Ser., **76**: 91–99.
- McArdle, S. B. & A. McLachlan, 1992: Sandy beach ecology: swash features relevant to the macrofauna. J. Coastal Res., **8**: 3987–407.
- McGwynne, L. E. & A. McLachlan, 1985: Spatial and temporal distribution and overlap of three species of *Bullia* (Gastropoda, Nassariidae) on exposed sandy beaches. Veliger, **28**: 28–36.
- McLachlan, A., 1980: Intertidal zonation of macrofauna and stratification of meiofauna on high energy sandy beaches in the eastern Cape, South Africa. Trans. R. Soc. S. Afr., **44**: 213–223.
- McLachlan, A., 1985: The biomass of macro and interstitial fauna on clean and wrack-covered beaches in western Australia. Estuarine Coastal Shelf Sci., **21**: 587–599.
- McLachlan, A. & P. Hesp, 1984: Faunal response to morphology and water circulation of a sandy beach with cusps. Mar. Ecol. Prog. Ser., **19**: 133–144.
- McLachlan, A., E. Jaramillo, T. E. Donn & F. Wessels, 1993: Sandy beach macroinfauna communities and their control by the physical environment: a geographical comparison. J. Coastal Res., **15** (special issue): 27–38.
- McLachlan, A., T. Wooldridge & G. van der Horst, 1979: Tidal movements of the macrofauna on an exposed sandy beach in South Africa. J. Zool., **188**: 433–442.
- Núñez, J., O. Aracena & M. T. Lopez, 1974: *Emerita analoga* en Llico, Provincia de Curicó (Crustacea, Decapoda, Hippidae). Bol. Soc. Biol. Concepción (Chile), **48**: 11–22.

- Pequeño, G., 1979: Antecedentes alimentarios de *Eleginops maclovinus* (Valenciennes, 1830) (Teleostomi, Nototheniidae) en Mehuín, Chile. Acta Zool. Lilloana (Argentina), **35**: 207–230.
- Pino, M. & E. Jaramillo, 1992: Morphology, texture and mineralogical composition of sandy beaches in the South of Chile. J. Coastal Res., **8**: 593–602.
- Seward-Thompson, B. & J. Hails, 1973: An appraisal on the computation of statistical parameters in grain size analysis. Sedimentology, **11**: 83–98.
- Shepherd, R. A., B. Knott & I. G. Eliot, 1988: The relationship of juvenile southern mole crabs *Hippa australis* Hale (Crustacea: Anomura: Hippidae) to superficial swash water-circulation over several diurnal spring-tide cycles during winter conditions on a micro-tidal sandy beach. J. Exp. Mar. Biol., **121**: 209–225.
- Short, A. D., 1983: Sediments and structures in beach-nearshore environments, South East Australia. In: A. McLachlan & T. Erasmus (Eds.), Sandy Beaches as Ecosystems. Dr. W. Junk, The Hague, The Netherlands: 145–155.
- Short, A. D., 1996: The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. Rev. Chil. Hist. Nat., **69**: 589–604.
- Short, A. D. & L. D. Wright, 1983: Physical variability of sandy beaches In: A. McLachlan & T. Erasmus (Eds.), Sandy Beaches as Ecosystems. Dr. W. Junk, The Hague, The Netherlands: 133–144.
- Tiffany, W. J., 1972: The tidal migration of *Donax variabilis* Say. Veliger, **14**: 82–85.
- Wright, L. D., J. Chappel, B. G. Thom, M. P. Bradshaw & P. Cowell, 1979: Morphodynamic states of beaches and surfzones: an empirical predictive model. Mar. Geol., **62**: 339–364.
- Wright, L. D., A. S. Short & M. O. Gree, 1985: Short-term changes in the morphodynamic states of beaches and surf zones: an empirical predictive model. Mar. Geol., **62**: 339–364.