

DISTRIBUTION AND HABITAT STRUCTURE OF
OCYPODE GAUDICHAUDII H. MILNE EDWARDS & LUCAS, 1843,
IN SANDY BEACHES OF NORTHERN CHILE

BY

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ABSTRACT

Ten sandy beaches along the coast of northern Chile (20-23°S) were studied in December 1998, to examine the distribution, abundance, and habitat characteristics of the crab *Ocypode gaudichaudii*. Beach width, slope, and intertidal fringes were identified, and Dean's parameter, describing beach morphodynamic status, was calculated. Crabs were collected and burrows and physical characteristics of the burrow zones analysed. The burrow zone extended primarily across the dry and retention zones. Physical properties across the burrow areas did not influence burrow characteristics. Significant differences in burrow density were detected both within and among the 10 sandy beaches. These differences were not related to morphodynamic beach types, but could be explained by related aspects, such as the height of the drift line, and the width and slope of dry and retention zones. We linked these results to behavioural and not just to physical causes.

RÉSUMÉ

Dix plages de sable le long de la côte nord du Chili (20-23°S) ont été étudiées en décembre 1998, afin d'examiner la distribution, l'abondance et les caractéristiques de l'habitat du crabe *Ocypode gaudichaudii*. La largeur de la plage, la pente et les bordures intertidales ont été définies, et le paramètre de Dean, décrivant le statut morphodynamique de la plage a été calculé. Les crabes ont été récoltés et les terriers ainsi que les caractéristiques physiques des zones de terriers ont été analysés. La zone de terriers s'étend essentiellement sur les zones sèches et de retenue. Les propriétés physiques des zones de terrier n'ont pas d'influence sur les caractéristiques des terriers. Des différences significatives dans la densité des terriers ont été détectées à la fois à l'intérieur et entre les 10 plages sableuses. Ces différences ne sont pas en relation avec le type morphodynamique de la plage, mais pourraient s'expliquer par d'autres aspects comme la hauteur de la ligne de courant, la largeur et la pente des zones de retenue, respectivement. Nous relierons ces résultats au comportement et pas seulement à des causes physiques.

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INTRODUCTION

The community structure of the sandy beach macrofauna is closely related to beach characteristics. Trends of increasing species richness, abundance, and biomass, along a gradient from reflective to dissipative beaches, have been described as the normally occurring patterns (Jaramillo et al., 1993; McLachlan & Jaramillo, 1995). Physical processes associated with beach morphodynamics may also affect population parameters. This has been shown from spatial comparisons of different beach types for isopods (Jaramillo & McLachlan, 1993), the anomuran crab *Emerita analoga* (Stimpson, 1857) (cf. Dugan et al., 1991; Dugan & Hubbard, 1996; Jaramillo & McLachlan, 1993) and several species of bivalves (McLachlan et al., 1995). *E. analoga* and those bivalves are directly exposed to the dynamics of the water, which periodically covers the lower intertidal or swash zone. Those characteristics are integrated in the so called "swash climates" (McArdle & McLachlan, 1992) which includes upwash distance and time, swash speed, frequency of swashes and number of times the upcoming swash cross the effluent line or water table outcrop. It has been argued that swash climates associated with beach types and not beach types by themselves are important for the macroinfauna (McLachlan et al., 1993). It has been also argued that physical variability related to beach morphodynamics can modify food availability and survival of species living in the low tidal levels (surf and swash zones) of exposed sandy beaches (McLachlan, 1980). However, population responses to these changes have not been evaluated in species living higher up in the shore such as ocypodid crabs, talitrid amphipods and tylid isopods.

The brachyuran crab, *Ocyroide gaudichaudii* H. Milne Edwards & Lucas, 1843, is a conspicuous burrower inhabiting sandy beaches of northern Chile (Jaramillo, 1987; Jaramillo et al., 1999). When away from its burrow, this species wanders over the lower levels of the beach surface in search of food and reproductive opportunities (Koepcke & Koepcke, 1953; Trott, 1988). However, its ecology and biology have not yet been described for these habitats. Further north, Koepcke & Koepcke (1952, 1953) studied the role of *O. gaudichaudii* on the degradation of stranded organic wrack on sandy beaches of Peru. In Costa Rica, Trott (1988, 1998) described its feeding behaviour and sex ratios. However, none of these studies related the physical properties of the sandy beaches with any observed population pattern for this species.

This study evaluates if differences in beach type along northern Chile (c. 20-23°S) are associated with any differences in burrow zone characteristics, distribution, abundance, or size of *O. gaudichaudii*.

MATERIALS AND METHODS

Ten sandy beaches were selected along two littoral areas of northern Chile, based on preliminary sampling carried out in April and June 1998. These were: Patache ($20^{\circ}47'S$ $70^{\circ}14'W$); El Aguila ($20^{\circ}50'S$ $70^{\circ}11'W$); Pica ($20^{\circ}53'S$ $70^{\circ}11'W$); Chomache ($21^{\circ}04'S$ $70^{\circ}10'W$); Ike-Ike ($21^{\circ}07'S$ $70^{\circ}10'W$); Guanillos ($21^{\circ}11'S$ $70^{\circ}09'W$); and Chipana ($21^{\circ}18'S$ $70^{\circ}07'W$), around the littoral of Iquique. Also studied were Hornitos ($22^{\circ}54'S$ $70^{\circ}17'W$); Mejillones ($23^{\circ}05'S$ $70^{\circ}26'W$); and La Rinconada ($23^{\circ}28'S$ $70^{\circ}31'W$) around the littoral of Antofagasta. Data reported here come from a major survey carried out during the spring low tides of December 1998.

On each sandy beach, drift and effluent lines, dry, retention and resurgence-swash zones were identified and measured, and the slopes of dry and retention zones estimated (Emery, 1961). The height above the lowest tide level of the drift line and effluent line (water table outcrop), as well as that of each sampling point were measured at each beach (Emery, 1961). Dean's parameter (Ω) was also estimated to characterize morphodynamic beach types, according to Short & Wright (1983). Ω was calculated from the mean wave height (average of $N = 10$ measurements), the wave period (average of $N = 10$ measurements) and the sand fall velocity of sand particles of the swash zone (average of $N = 3$ samples) (see methods in Jaramillo & McLachlan, 1993) as follows:

$$\text{Dean's Parameter } (\Omega) = \text{wave height (cm)} / \text{wave period (s)} \times \text{sand fall velocity (cm s}^{-1}\text{)}$$

The burrow density of *Ocyropsis gaudichaudii* was estimated from transects running between the oldest drift line and the effluent line. At each sandy beach, groups of four transects were analysed in two randomly selected "North" and "South" areas, with total number of fresh burrows per transect being the replicates (thus, there were 8 replicates per beach: 4 transects \times 2 areas). Transects in each area were about 2 m apart from each other, whereas the distance between areas was generally 70 m. Sediment and fresh burrow characteristics were examined along one of these eight transects. The mean sand grain size and water content of the sediment were estimated from surface (0-1 cm depth) samples collected each 5-10 m, according to the width of the crab burrow area. As a measurement of sediment compactness, the in situ shear strength of sediments at each sampling station was determined with 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 are given in kgf.cm^2 . Mean sand grain size was determined using the methods of

Emery (1938) and Seward-Thompson & Hails (1973). Water content was estimated from samples wrapped in pre-weighed aluminum foil bags, dried (80°C, 72 h) and re-weighed. Burrow mouth diameters and depths were measured using calipers and rulers, respectively. Sediment temperature ($\pm 0.1^\circ\text{C}$) was measured with a mercury thermometer at the surface (c. 10 cm from burrow) and at the bottom of the burrows.

A variable number of crabs (c. 15 per beach) were collected to analyse burrow diameter-crab length relationships. The diameter of each burrow and the sex and cephalothorax length from collected individuals were registered. The burrow diameter-crab length relationship was evaluated by adjusting the regression curve to a potential model:

$$\text{length} = a \times (\text{burrow diameter})^b$$

where a and b are coefficients to be estimated by the model. Data from males and females were pooled together, as no differences between sexes for these parameters were detected when preliminary regressions were carried out. This equation was used later to estimate mean crab lengths from burrow diameter data. Burrows were considered specific for individuals, as they were occupied by a single crab (without apparent exchange) in over 97% of the cases studied.

Burrow densities were compared using a two-level nested analysis of variance (Sokal & Rohlf, 1994). This design allowed us to identify the intra-beach variability by comparing the North and South areas for each beach (four transects per area). The design was then used to compare between beaches, to identify any variability over that resulting from the intra-beach comparison. The analysis assumed normality and homocedasticity, which were evaluated using the Kolmogorov-Smirnov and Bartlett tests respectively (Sokal & Rohlf, 1994). Differences in burrow density among beaches were examined with the a posteriori Student-Newman-Keuls's multiple comparison test.

Linear multiple regression analyses were performed to analyze potential relationships between physical data and burrow density (the dependent variable, $N = 10$ sandy beaches). The regression model included up to six of the 13 independent variables presented in tables I and II (in table I Dean's parameter, but not mean grain size, wave height, or wave period was used). The selection of independent variables was based on preliminary correlation analysis (Sokal & Rohlf, 1994) and data met the assumptions of independence and normality.

RESULTS

The height of the drift line (which usually coincided with the lower limit of the dry zone) and the effluent line varied between 141 and 230 cm and from 36

TABLE I
Physical characteristics of the beaches studied. Values of grain size, wave height and wave period are means

	PAT	AGU	PIC	CHO	IKE	GUA	CHI	HOR	MEJ	RIN
Height of drift line above low tide level (cm)	230.0	221.0	141.0	173.0	170.0	222.0	222.0	164.0	161.0	203.0
Height of effluent line above low tide level (cm)	126.0	78.0	36.0	82.0	138.0	114.0	153.0	57.0	126.0	106.0
Grain size of sands from swash zone (μm)	214.1	253.5	285.9	292.2	304.8	275.6	230.3	169.4	476.2	584.7
Wave height (cm)	336	335	104.1	319	92.3	267	130.0	139.7	168.7	82.3
Wave period (s)	15.2	11.9	12.2	16.0	15.8	17.4	18.1	17.4	14.7	11.5
Dean's parameter (Ω)	6.5	8.2	2.2	6.0	1.4	4.6	2.1	4.3	1.6	0.8

The codes for the beaches are: PAT (Patache); AGU (El Aguila); PIC (Pica); CHO (Chomache); IKE (Ike-Ike); GUA (Guanillos); CHI (Chipana); HOR (Hornitos); MEJ (Mejillones); and RIN (La Rinconada).

TABLE II
Physical characteristics of the burrow zone of *O. gaudichaudii* at the beaches studied. Mean values are given for grain size, water content and compactness (shear strength) of the sediments

	PAT	AGU	PIC	CHO	IKE	GUA	CHI	HOR	MEJ	RIN
Dry zone										
Width (m)	22	140	20	70	50	50	20	5	10	15
1/slope	1/34	1/230	1/17	1/35	1/48	1/24	1/48	1/33	1/37	1/14
Grain size (μm)	205.6	247.7	263.7	211.3	258.9	276.6	269.5	192.8	372.6	429.1
Water content (%)	1.3	0.8	0.9	1.0	0.4	1.8	1.6	2.6	1.6	1.2
Shear strength (kgf.cm^{-2})	0.04	0.06	0.03	0.05	0.04	0.03	0.02	0.06	0.04	0.03
Retention zone										
Width (m)	49	10	15	30	20	20	15	50	15	5
1/slope	1/47	1/28	1/14	1/39	1/63	1/19	1/22	1/47	1/43	1/12
Grain size (μm)	208.4	254.4	236.8	217.8	266.9	274.4	209.0	179.1	322.5	458.5
Water content (%)	14.2	9.4	15.3	13.3	2.1	17.8	12.9	13.0	9.4	5.0
Shear strength (kgf.cm^{-2})	0.06	0.06	0.06	0.07	0.04	0.05	0.05	0.11	0.07	0.04

Codes for beaches as in table I.

to 153 cm, respectively (table I). Physical variables determining Dean's parameter (see Material and Methods) varied widely and determined a well-represented range of beach types (table I). Sandy beaches of Ike-Ike, Mejillones, and La Rinconada were reflective ($\Omega \leq 2$), Pica, Guanillos, Chipana, and Hornitos were intermediate ($2 < \Omega < 5$), and Patache, Aguila, and Chomache were dissipative ($\Omega > 5$) (Short & Wright, 1983).

The morphology of the dry zone varied from a narrow (e.g., Hornitos, 5 m) and steep fringe (e.g., La Rinconada, 1/slope = 1/14) to an extremely wide and flat deposit (El Aguila, 140 m, 1/230). Widths and slopes showed narrower ranges of variation in the retention zone (table II). Mean grain size changed little within and between dry and retention zones. Among the beaches, differences in mean grain sizes follow a similar pattern to that described for the sediment of the swash zone (table I): sands in dry and retention zones were coarsest in La Rinconada and finest in Hornitos (table II). Excluding Ike-Ike, water contents changed drastically between dry (0.8%-2.6%) and retention zones (5.0%-17.8%), but were extremely homogeneous within each of these zones. Shear strength values ranged from 0.02 to 0.06 kgf.cm⁻² (dry zone) and between 0.04 and 0.11 kgf.cm⁻² (retention zone) (table II).

Mean burrow diameters varied between 2.3 (Patache) and 4.5 cm (Chipana), with individual burrows ranging from 0.9 to 8.5 cm. Mean burrow depths ranged from 8.1 (Mejillones) to 32.1 cm (Chipana). Temperature differences between the surface and the bottom of the burrow ranged from 5.6°C (La Rinconada) to 23.0°C (Chomache) (table III). For most of the beaches, preliminary correlation analysis identified significant relationships between burrow diameter and depth ($P < 0.05$), but not between these variables and temperature difference or distance from the low tide level ($P > 0.05$). Mean burrow density (from $N = 8$ transects) varied between 0.28 m⁻² (Patache and Ike-Ike) and 1.16 m⁻² (Pica), with an overall mean (all beaches included) of 0.53 burrows m⁻². The crab length-burrow diameter relationship ($N = 155$, $R^2 = 0.78$, $P < 0.01$) can be described as:

$$\text{length} = 10.621 \times (\text{burrow diameter})^{0.829}$$

Mean crab carapace length ranged from 21.04 mm (Patache) to 36.91 mm (Chipana) (table III).

The results of the nested ANOVA for burrow density indicated variability among transects (within areas, c. 19%), between areas (within beaches, c. 15%, $P < 0.001$) and among beaches (c. 65%, $P = 0.002$). The a posteriori test identified one distinctively densely burrowed beach (Pica) and two other groups: four beaches with moderate density of burrows (La Rinconada, El Aguila, Hornitos and Chomache) and five sites with low density of burrows (Patache, Ike-Ike, Mejillones, Chipana and Guanillos). Multiple regression analyses showed that a

TABLE III

Characteristics of the burrows of *O. gaudichaudii*. Temperatures were measured at the bottom of the burrows and at surface (close to the mouth of the burrows), but only temperature differences (surface-bottom) are presented. Mean density of burrows and estimated carapace length (means) are also given

	PAT	AGU	PIC	CHO	IKE	GUA	CHI	HOR	MEJ	RIN
Mean burrow diameter (cm)	2.31	3.91	3.13	3.57	3.28	3.69	4.50	3.07	2.59	2.33
Mean burrow depth (cm)	12.1	31.4	19.6	25.2	26.8	25.4	32.1	18.1	8.1	14.4
Temperature (surface — bottom) (°C)	18.2	14.6	16.2	23.0	7.5	14.9	10.5	5.9	n.d.	5.6
Mean density (burrows.m ⁻²)	0.28	0.57	1.16	0.60	0.28	0.52	0.41	0.59	0.33	0.57
Carapace length (mm)	21.04	32.69	26.94	30.09	28.25	31.16	36.91	26.89	22.49	21.23

Codes for beaches as in table I; n.d. = no data.

TABLE IV

Summary of multiple regression analyses carried out using burrow density ($N = 10$ beaches) as dependent variable. Independent variables included in the multiple regression model and coefficients, t -statistics, and P -values, are also presented

Multiple regression	Independent variables included in the model				
			Coefficient	t -statistic	P -value
Multiple R^2	0.977	Height of drift line above low tide level	-0.007	-7.874	0.000
Adjusted R^2	0.931	Width of the dry zone	0.003	2.915	0.017
Standard error	0.067	Slope of the dry zone	-10.138	-3.135	0.012
P -value (F test)	0.015	Shear strenght at the dry zone	-3.036	-1.153	0.279
Intercept	1.136	Width of the retention zone	0.015	5.492	0.000
		Slope of the retention zone	19.877	6.949	0.000

significant proportion of the burrow density was explained by the independent variables (multiple $R^2 = 0.977$, adjusted multiple $R^2 = 0.931$ and standard error ± 0.067 ; $P = 0.015$) (table IV). The analysis also tested how well each one of the six independent variables used in the model was able to predict the dependent variable. Drift line height, widths of dry and retention zones and slopes of the dry and retention zones were good predictors of burrow density ($P \leq 0.017$, t -test). The predictive equation resulted as follows:

$$\text{burrow density} = 1.136 - 0.007(\text{dl}) + 0.003(\text{wd}) - 10.139(\text{sld}) - 3.036(\text{shd}) + 0.015(\text{wr}) + 19.877(\text{slr})$$

where 1.136 = intercept; dl = drift line height; w = width; sl = slope; sh = shear strength, and d and r, dry and retention zones, respectively. Similar multiple regression analyses were carried out using burrow mean diameter and crab length as dependent variables, but no one combination of independent variables explained their variability with any statistical significance.

DISCUSSION

Burrowing by *Ocypode gaudichaudii* produces characteristic fringe areas, changing in extension and burrow density along the sandy beaches of northern Chile. However, contrary to what had been hypothesized, spatial variability was unrelated to beach morphodynamics as defined by Dean's parameter. As has been shown for community and population parameters, beach types explain spatial differences well at local and regional scales (Jaramillo & McLachlan, 1993; McLachlan & Jaramillo, 1995). From our results, however, it seems that this generalization is restricted to organisms closely related to the tidal action in the mid- and low intertidal levels. Most of the burrow area of *O. gaudichaudii* was located over the drift line, where waves and swash climates define the lower limit for the building

of permanent burrows. Factors such as drift line height, width, and slope of dry and retention zones explained about 97% of density variability. As these are all related to morphodynamic beach types (McLachlan & Jaramillo, 1995), their indirect role cannot be ignored.

O. gaudichaudii disposes of reworked sediments in a typical “kick” pattern (sensu Shober & Christy, 1993) primarily in the dry zone. Since crabs also dig in the wetter sediments of the retention zone, it is evident that they make use of a wide range of physical conditions (Wolcott, 1978; Brown & McLachlan, 1990). However, as damp sediments were found at the bottom of most of the examined burrows, some landward distribution limit may exist. This would explain the negative relationships between drift line height and burrow density (see table IV) and is consistent with what has been reported by Warburg & Shuchman (1979) for *O. cursor* (Linnaeus, 1758) and by Wolcott (1978) for *O. quadrata* (Fabricius, 1787). During the warmer conditions of summer, the burrow area of this last species is displaced to lower tide levels on a barrier sandy beach in North Carolina (Wolcott, 1978). In a comparison of the results presented here and our preliminary surveys carried out in fall and winter, we did not detect this sort of displacement. However, as mentioned before, the location of the lowest limit of the burrow area (near the drift line) seems to be affected by the seasonal changes in wave conditions.

Shear strength and water content changed abruptly between the dry and retention zones, but were extremely homogeneous within each of these zones. These beaches differ in this aspect from what has been described as a continuous gradient of moisture by Shuchman & Warburg (1978) for a sandy beach in northern Israel. These authors described consistent relationships between moisture and distance from low tide levels, and the burrow morphology of *O. cursor*. Along our transects, we found that burrow diameter and depth were usually significantly correlated, but we could not detect any change in that relationship associated with, for example, changes in moisture or compactness of the sands. Similar absence of gradual changes in response to moisture or other physical parameters may be inferred for *O. gaudichaudii* in sandy beaches of Costa Rica. There, daily high tides cover all the burrow areas (Trott, 1998), suggesting that a different set of adaptive forces must be operating in relation to burrow morphology and spatial patterns.

As in other studies on Ocypodidae (e.g., Wolcott, 1978), we found that the size of *O. gaudichaudii* individuals was significantly related to diameter of their burrows. This might be explained by the individual use of burrows by ocypodid crabs (Brown & McLachlan, 1990). In fact, we only found a few burrows occupied by more than one crab (< 3% of total). Thus, although *O. gaudichaudii* is highly gregarious while predating, scavenging or scooping sediments (Trott, 1988), it seems to be quite territorial in using and keeping its burrows (Kurihara et al., 1989;

Wada, 1993). This territoriality in the use of space for burrowing could explain why burrow densities are positive and significantly related to the width of the dry zone.

From the results presented here, further studies on *O. gaudichaudii*, its habitat and related community may be proposed. First of all, our density comparisons detected significant differences among sandy beaches, but interestingly, also within beaches (table IV). Spatial variability has always been addressed in sandy beach ecology (McLachlan & Jaramillo, 1995). However, as James & Fairweather (1996) recognized, most of the studies are still focused on across but not on along-shore variability. This study shows that, for *O. gaudichaudii*, significant along-shore variability exists, but the identification of spatial patterns for this or other sandy beach species remains to be tested. Secondly, tidal, circa-tidal, and seasonal physical cycles have been shown to affect distribution patterns of sandy beach organisms such as peracarids and anomurans. Similar short-term patterns on species such as ocypodids have not been rigorously evaluated, and hence are an open field for linking interactions and behavior. Thirdly, Dean's parameter did not participate in the explanation of the burrow density of *O. gaudichaudii*. Thus, our results could be added to the increasing amount of correlative studies in which biological patterns are not partially or completely explained by Ω . A revision of this parameter might consider the incorporation of variables such as slope, a change that should strongly improve the predictive power of Dean's parameter.

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