

## CHAPTER 2

# SWASH ZONATION PATTERNS OF TWO SURFERS ON EXPOSED TROPICAL SANDY BEACHES.

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## Abstract

Macrofaunal species that show surfing behaviour on tidal sandy beaches use the swash to migrate up and down the beach. When studying the zonation of these surfers, some complications arise which do not occur for sessile organisms or organisms that remain burrowed for some time during the tidal cycle. In this paper, a new approach for sampling mobile swash fauna is proposed. The described method deals with two problems innate to investigating swash zonation of surfing species: setting a reference point independent of the tidal state and taking all the samples of a transect without having migration in due course. The upper swash limit, defined as the highest swash wave during 10 minutes of observation, was chosen as reference point. By placing wooden boxes at every sampling spot prior to sampling, migration while taking the samples was prevented. This allowed us to sample transects in the swash zone, producing swash zonation data for two surfing species on Ecuadorian sandy beaches: the gastropod *Olivella semistriata* and the mole crab *Emerita rathbunae*.

Both species showed a symmetric to negatively skewed unimodal swash distribution curve, independent of the tidal state or sampling location. Peak densities were typically found around 15-60 % of the upper swash limit, with *O. semistriata* living higher and *E. rathbunae* living lower in the swash. It is hypothesized that this zonation is a result of a gradient in feeding time, with optimal feeding conditions around the middle of the swash zone. The different position of peak densities is thought to be caused by differences in morphology and behaviour. The mole crab is a much faster swimmer and burrower than the snail, and its feeding structures seem more robust. This idea is supported by distribution data for both species from beaches with different morphodynamics: where *O. semistriata* is restricted to relatively flat beaches with fine sediment and gentle swash conditions, *E. rathbunae* is mostly present on reflective beaches with coarse sediment and vigorous swash action.

### 2.2.1 Introduction

Zonation is a very important feature in intertidal communities within both hard (Kaiser *et al.*, 2005) and soft substrates (McLachlan and Jaramillo, 1995). Sandy beach zonation has been fairly well studied over a range of beach types and at almost all latitudes. General patterns were reviewed by McLachlan and Jaramillo (1995). Zonation is caused by gradients in environmental and biological factors. Whereas rocky shore zonation is mainly defined biologically (Lewis, 1964), sandy beach zonation is generally thought to be structured by environmental factors (McLachlan and Jaramillo, 1995; Defeo and McLachlan, 2005 and many others), although recent work by Defeo *et al.* (1997) and Dugan *et al.* (2004) suggest that competition cannot be discarded as a structuring force in sandy beach zonation. Knowledge on the zonation pattern of a species is crucial for the understanding of its functioning within the ecosystem, and allows for estimating temporal and spatial variability in population sizes.

Variation in sandy beach zonation of species and communities can be found at different scales, both spatially and temporally (Defeo and McLachlan, 2005). Zonation dynamics can occur on a circatidal, daily, circalunar or seasonal base, as well as because of unpredictable events such as storms or climate cycles (Brazeiro and Defeo, 1996; Gimenez and Yannicelli, 1997; Defeo and Rueda, 2002; Defeo and McLachlan, 2005). On a spatial scale, differences exist at different latitudes, in between beaches, alongshore, cross-shore, within cross-shore zones and at microspatial scale (Dexter, 1992; James and Fairweather, 1996; Jones *et al.*, 1998; Defeo and Rueda, 2002; Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005). Brazeiro and Defeo (1996) showed that on microtidal beaches temporal processes are of predominant importance. These beaches are generally wind-driven, making them vulnerable to erratic changes in morphodynamics (Short, 1999; Brazeiro, 2001). Studying zonation under these conditions requires a proper temporal scale (Brazeiro and Defeo, 1996), especially where there is a clear seasonality.

With increasing tidal range, tide replaces wind as major driving force in the morphodynamics of sandy beaches (Masselink, 1993; Short, 1999). The intertidal width and thus the room for cross-shore spatial differences in zonation likewise increases with tidal range. James and Fairweather (1996) demonstrated that zonation has to be studied on a detailed spatial scale, with a sufficient number of levels per cross-shore zone. One of these zones, the swash zone, plays a crucial part in the functioning of macrofaunal communities on exposed sandy beaches (McLachlan and Brown, 2006). According to McLachlan and Brown (2006) exposed sandy beaches are dominated by a mobile swash fauna and McLachlan *et al.* (1993) hypothesized that swash condition is the major force

limiting the distribution of macrofauna towards reflective beaches (SEH or Swash Exclusion Hypothesis).

Surfing species, such as the beach whelk *Bullia* (Trueman and Brown 1976), clams of the genus *Donax* (Ansell and Trevallion, 1969; Ellers, 1995a), and mole crabs (*Emerita*: Cubit, 1969; *Lepidopa* and *Blepharipoda*: Dugan *et al.*, 2000; Hippa: Lastra *et al.*, 2002), use the swash to migrate over the beach face with the tide (McLachlan and Brown, 2006). Although they can be found over the entire intertidal during the tidal cycle, their actual distribution is restricted to the swash zone, which, on tidal beaches, is narrower than the intertidal. It is thus unlikely that the actual zonation pattern, the 'swash zonation', will be revealed by the sampling strategies generally applied on sandy beaches, i.e. sampling the complete intertidal at low tide, from above the drift line to the lower swash limits (McLachlan and Brown, 2006). Moreover, swash zonation can vary on a circatidal scale. The reference frame to assess swash zonation over the tidal cycle should thus not be the drift line, yet a point relative to the swash. Jones and colleagues (1998) described the 'median-wave technique' to sample tidally migrating amphipods of the genus *Exoedicerus*. Transects are stationed around a swash reference point, resulting in a distribution dataset of swash zonation independent of the tidal state.

A second complicating factor in sampling swash zonation is to obtain, per swash transect, a true snapshot sampling. Surfers use swash waves to migrate over the beach face. While they tend to ride the bigger waves (Ellers, 1995a; Chapter 6) migration can occur in even the smallest waves (Chapter 6). With standard frame or core sampling, it is thus impossible to prevent migration from happening while sampling a transect in the swash. For this study, we tried to develop a sampling strategy that, on the one hand, contained a swash reference point corrected for differences caused by the tidal state or the wave conditions, and on the other hand allowed us to sample a swash transect without migration happening while sampling, i.e. a true snapshot.

On exposed sandy beaches in Ecuador, the snail *Olivella semistriata* and the mole crab *Emerita rathbunae* are dominant surfing species (Chapter 1). Both species inhabit the swash zone and use the backwash for filter feeding (Olsson, 1956; Caine, 1975), apparently occupying an overlapping ecological niche. In this paper, we discuss how these species are distributed at three different spatial scales (*sensu* Defeo and McLachlan, 2005): (1) between beaches with different morphodynamics (macroscale), (2) cross-shore (mesoscale) and (3) in the swash zone (microscale). The hypothesis is that, despite their similar feeding and migrating ecology, *O. semistriata* and *E. rathbunae*

handle swash conditions in a different way, and as such avoid interspecific competition. We expect these differences to be reflected in their distribution and swash zonation pattern.

## **2.2.2 Material and Methods**

### **2.2.2.1 Study sites and period**

Two beaches in the Guayas province of South-western Ecuador were investigated: the beaches of San Pedro de Manglaralto (1°57'11"S and 80°43'28"W) and Playas (2°39'28"S and 80°22'53"W). These are exposed sandy beaches with a maximal tidal range of 2.6 – 3.0 m. Sampling took place on August 21<sup>st</sup> (Playas) and August 22<sup>nd</sup> (San Pedro) of 2003.

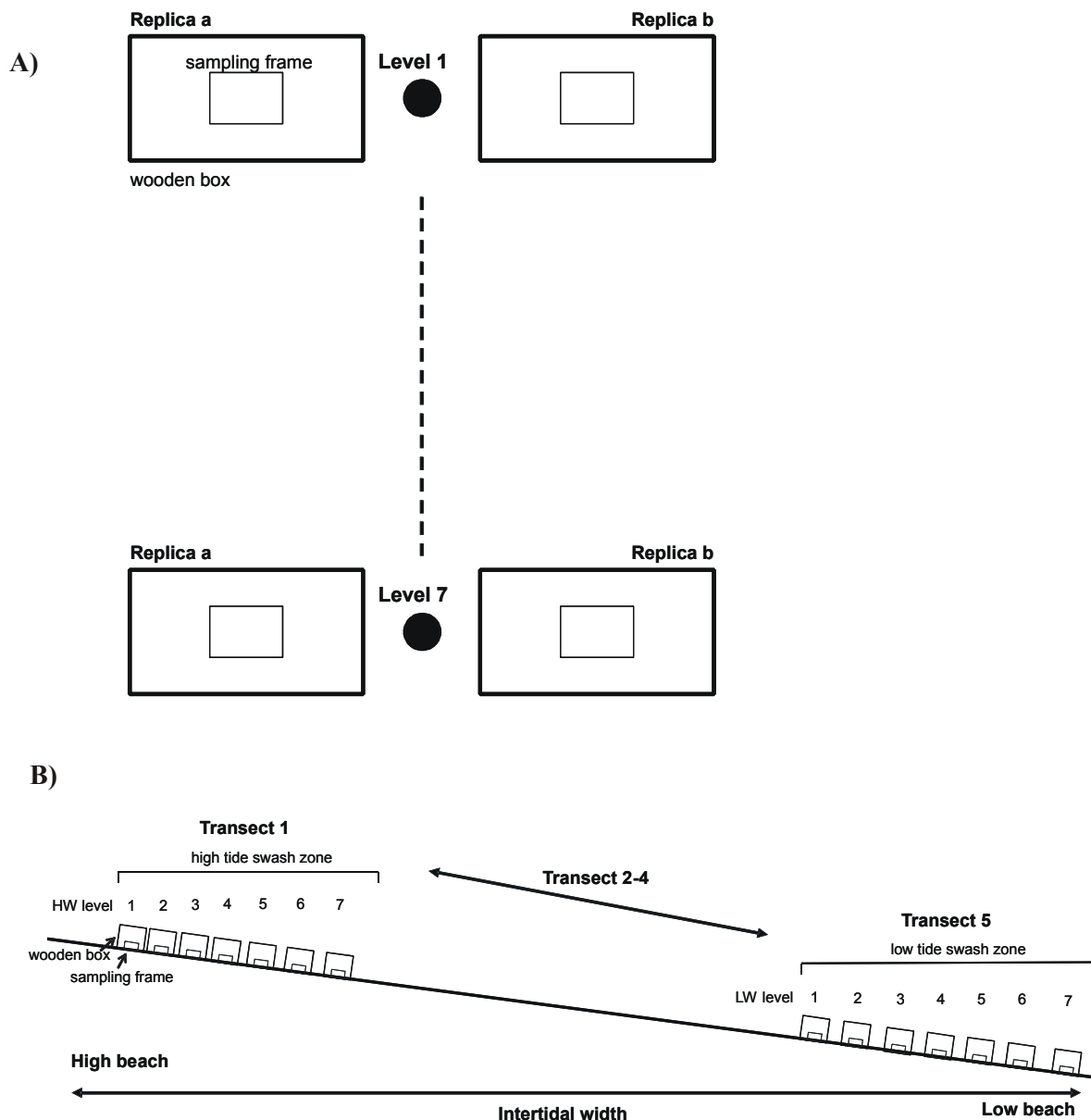
### **2.2.2.2 Sampling strategy**

Per beach five transects were sampled (Fig. 2.2.1). Two transects at high tide (HW1 and HW2), one transect two hours after high tide (MW1), one three hours after high tide (MW2) and one transect at low tide (LW). Each transect consisted of 5-7 levels in the swash zone and one level 1-2 m above the upper swash limit. The levels in the swash were placed at 1 to 3 m intervals between the upper and lower part of the swash. Before setting out the positions of the levels, the swash was monitored during 10 minutes to find the upper and lower limit. At low tide an extra three levels between the upper swash limit at low tide and the high tide level, on the air-exposed part of the intertidal, were sampled.

At each level, two replicate samples were taken by excavating a metal frame with a surface area of 0.1026m<sup>2</sup> to a depth of 15 cm. To prevent migration of the animals during sampling of one transect, levels were isolated by simultaneously placing a wooden box (plywood, 100 x 50 x 50 cm l x h x w) over each sampling spot (Fig. 2.2.1a and b; Picture 2.2.1 and 2.2.2). We had a total of eight boxes, which were put into place after a swash wave fully retreated, beginning with the lowest four levels (4 x 2 boxes for the replicates; see Picture 2.2.1). Firstly, the two replicates of the lowest level were sampled. Then the boxes of this level were moved to lowest level that was not yet protected by boxes. The second lowest level was then the next to be sampled. This procedure was repeated till all samples were taken. More details about the use of these wooden boxes can be found in the discussion section. The samples were sieved alive over a 1 mm

mesh-sized sieve; the retained organisms were stored in an 8 % formaldehyde-seawater solution.

At each level, one sediment sample was collected for grain size analysis, using a core with diameter of 3.6 cm, to a depth of 15 cm. Beach profile was assessed using a leveller, taking measurements every 2 meter. Wave height and period was estimated by monitoring 11 consecutive breaking waves.



**Fig. 2.2.1** - Sampling design, with use of wooden boxes (see text for details). A) View from above of one swash transect with indication of the first and last level and the 2 replicates per level. B) Cross-sectional view of a beach with the first and last swash transect (7 levels per transect). HW = High Water; LW = Low Water.





**Picture 2.2.1** – Sampling protocol (beach of Playas). Wooden boxes are in place to hold the upcoming swash. In total, 8 boxes were used (only 4 shown) so 2x4 levels could be secured at the start of a sampling run (see text).



**Picture 2.2.2** – Sampling protocol. Wooden box with sampling frame.

### 2.2.2.3 Laboratory treatment

Samples were sorted for macrofauna and all specimens of *Olivella semistriata* and *Emerita rathbunae* were identified and counted. The sediment grain size distribution between 2 and 850 µm was determined with a laser COULTER LS and classified according to the Wentworth scale (Buchanan, 1984). Coarser sediment (>850 µm) was not present in a sufficient amount to be quantified.

### 2.2.2.4 Statistical analyses

Beach profiles were calculated from the relative height differences, together with tide predictions for the nearby port of La Libertad (San Pedro) or for Data de Posorja (Playas). Lowest swash point at low tide was assumed to be the low water level (Short, 1999) and is referred to as 0 m of elevation. The highest point of the intertidal was the lowest swash level at high tide. Intertidal distance and beach slope were calculated from this highest point and the 0-point.

Beach characterisation was done using two beach indices: 'Beach Index' (BI) and 'Beach Deposit Index' (BDI) (McLachlan and Dorvlo, 2005). These indices were calculated as:

$$BI = \log\left(\frac{Sand \cdot Tide}{Slope}\right)$$

$$BDI = \left(\frac{1}{\tan B}\right)\left(\frac{a}{Mz}\right)$$

where *Tide* is the maximum spring tide range (meters), *Slope* or  $\tan B$  is the beach slope, *a* is 1.03125 (mm), *Mz* is the mean sand particle size (mm) and *Sand* is the mean sand particle size in phi units +1. BI has dimension  $\log \phi \cdot m$ , BDI is dimensionless. Both indices increase from reflective to dissipative conditions.

Population size (i.e. abundance) estimation was done using the IST (individuals per strip transect; ind/m) technique (Defeo, 1996). IST is calculated by multiplying the average sample density (ind/m<sup>2</sup>) by the intertidal width in which the animals occur. The obtained value gives an estimate of the total population size present over the entire intertidal width (cross-shore) when considering one meter of beach length (along-shore).



Since the swash zone widens towards the low tide level on beaches with a concave slope, such as the investigated beaches in this study, using a relative scale for the swash position allows for a better comparison between transects. Relative swash position was calculated from the measured swash position. The zero value indicates the upper swash limit. Negative values represent the level positioned 1-2 m above the upper swash limit. Densities are also expressed in relative numbers in order to facilitate comparison of the density distribution between transects (see Fig. 2.2.3, 2.2.4, 2.2.5 and 2.2.7). Relative densities are in reference to total densities of one transect.

Regression fitting of the swash zonation per transect was done using second order generalized linear models (GLM) with Poisson distribution, log-link function and correction for overdispersion (McCullagh and Nelder, 1989). Dependent variable was the *absolute density*, the *relative swash position* was used as explanatory variable. The Proc Genmod syntax was applied with SAS 9.1.3 software. To identify the average zonation pattern per beach and per species, *transect* was added as random factor.

To compare the swash zonation between beaches (per species), a generalized linear mixed model (GLMM) was computed. *Absolute density* was the dependent variable, *relative swash position* (second order) and *beach* were the independent variables. *Transect* nested in *beach* (*transect(beach)*) was the random factor. The computations were performed with the proc GLIMMIX statement in SAS 9.1.3 (with Poisson distribution and log-link function). Differences in cross-shore zonation of the two species were tested with a GLMM, with *absolute densities* as dependent variables, *cross-shore position*, *species*, *beach* and *species\*beach* as independent variables and *transect(beach)* as random factor. For comparison of the densities of the two species between the two beaches, a non-parametric Mann Whitney-U test was used, after rejecting the assumptions for parametric tests. Statistical analyses were performed using Statistica 6.0 software package (StatSoft, 1996).

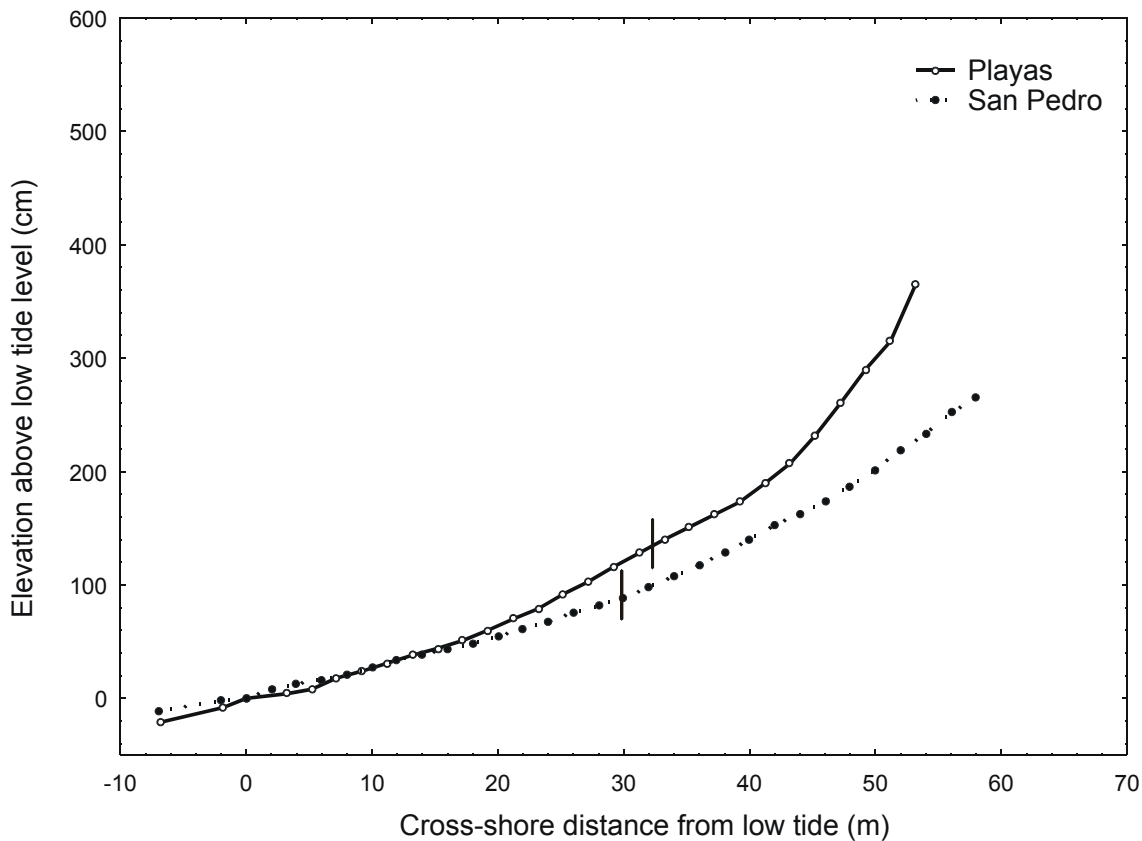
#### 2.2.2.5 Macroscale distribution of the two species

The density distribution (ind/m<sup>2</sup>) and abundance (ind/m) of *Emerita rathbunae* and *Olivella semistriata* was investigated on seven sandy beaches with contrasting morphodynamics along the Pacific coast of Ecuador. Details about the sampling can be found in Chapter 1. The abundance of both species was expressed in terms of the Beach Index (BI, see Chapter 1) by second order linear regression.

## 2.2.3 Results

### 2.2.3.1 Physical environment

Both the beach at Playas and the beach at San Pedro are exposed sandy beaches with a similar tidal regime. The beach profiles are plotted in Fig. 2.2.2. Playas is the most reflective of the two beaches, with a steeper slope, coarser sediment and lower BI and BDI (Table 2.2.1).



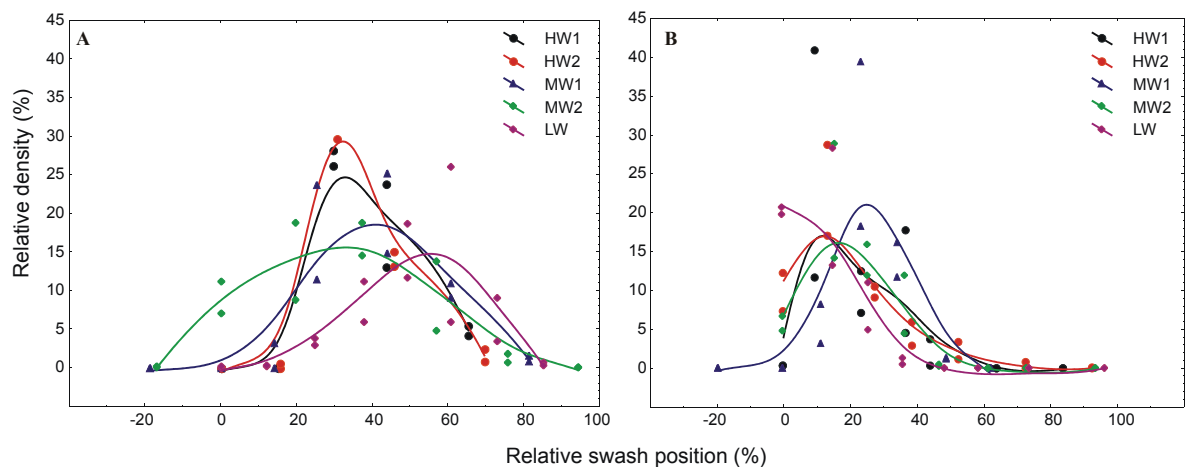
**Fig. 2.2.2** - Beach profiles of Playas and San Pedro. X-axis is intertidal distance from the low tide level; Y-axis indicates elevation above low tide level. Vertical bars mark the high tide level.

**Table 2.2.1** - Environmental parameters for both investigated beaches. Tidal range is the maximum spring tidal range for the sampling month; wave height and wave period are the average of 11 consecutive waves at low tide; BI is Beach index; BDI is Beach deposit index.

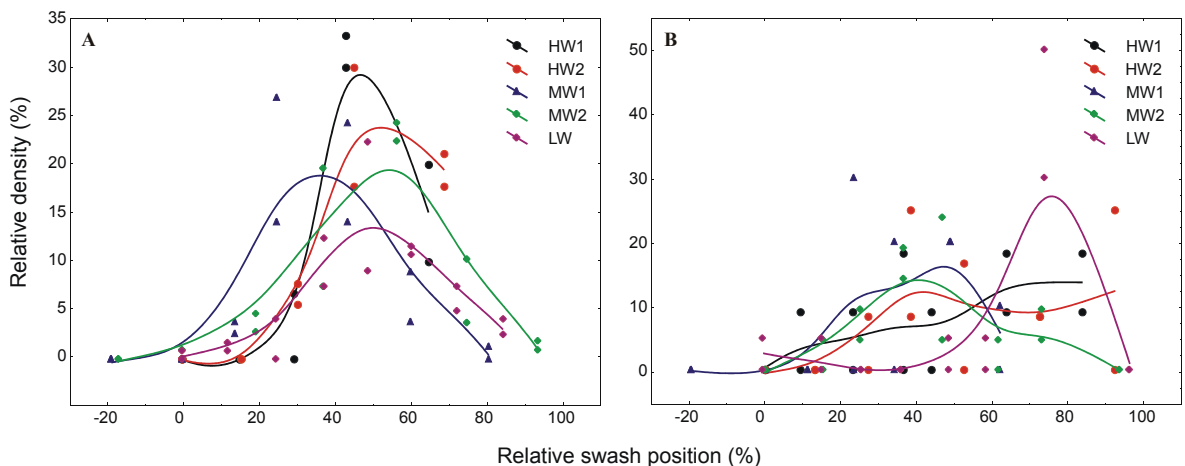
	Intertidal distance	Slope	Median grainsize	Tidal range	Wave height	Wave period	BI	BDI
<b>Playas</b>	31.2 m	1/24	275.3 $\mu\text{m}$	2.69 m	1.0 m	14.5 s	2.27	89.90
<b>San Pedro</b>	30.0 m	1/34	222.4 $\mu\text{m}$	2.74 m	0.8 m	16.5 s	2.47	156.30

### 2.2.3.2 Swash zonation of *Olivella semistriata* and *Emerita rathbunae*

Swash zonation per sampled transect is presented in Fig. 2.2.3 for *O. semistriata* and in Fig. 2.2.4 for *E. rathbunae*. Both species show a remarkably similar distribution pattern, independent of the beach or tidal state. Densities rise from zero at or just above the upper limit of the swash zone to peak around the middle of the swash (between 8 and 52% of the upper limit for *O. semistriata* and between 38 and 83% for *E. rathbunae*) and drop back to zero towards the surf zone. Except for the low tide transect in San Pedro for *Olivella semistriata*, the distribution curve has a symmetric to negatively skewed unimodal shape. Except for *E. rathbunae* in San Pedro, most second order regressions are significant, with  $\alpha$ -values around 0, positive  $\beta$ -values and negative  $\gamma$ -values (Table 2.2.2), confirming the unimodal shape of the distribution curves. All but two  $\alpha$ -parameters of the total regressions are significant. However,  $\alpha$  does not change the shape of the curve, only the height of the peak.



**Fig. 2.2.3** - Relative densities per swash transect of *Olivella semistriata* plotted against the relative swash position. Fitting by distance weighted least square estimates. A) Playas; B) San Pedro.



**Fig. 2.2.4** - Relative densities per swash transect of *Emerita rathbunae* plotted against the relative swash position. Fitting by distance weighted least square estimates. A) Playas; B) San Pedro.

**Table 2.2.2** - Generalized linear model for density data from Playas and San Pedro. Model structure:  $y = e^{\alpha + \beta \cdot x + \gamma \cdot x^2}$  with y as the swash density and x as the relative swash position. Max (%) is the relative position at which the densities peak.

SAN PEDRO							
Transect	$\alpha \pm SE$	$X^2$ (p-level)	$\beta \pm SE$	$X^2$ (p-level)	$\gamma \pm SE$	$X^2$ (p-level)	N Max (%)
<i>Olivella</i>	HW1	4.95 $\pm$ 0.67	54.35 (p<0.0001)	13.77 $\pm$ 7.05	3.83 (p=0.0500)	-35.55 $\pm$ 16.19	4.82 (p=0.0281) 14 19
	HW2	8.17 $\pm$ 2.37	1174.16 (p<0.0001)	3.82 $\pm$ 2.37	2.60 (NS)	-14.46 $\pm$ 5.09	8.09 (p=0.0045) 14 13
	MW1	3.22 $\pm$ 0.78	17.19 (p<0.0001)	36.81 $\pm$ 6.19	35.40 (p<0.0001)	-71.32 $\pm$ 12.08	34.88 (p<0.0001) 14 26
	MW2	6.62 $\pm$ 0.28	540.47 (p<0.0001)	13.43 $\pm$ 2.68	25.06 (p<0.0001)	-36.81 $\pm$ 6.25	34.65 (p<0.0001) 16 18
	LW	6.80 $\pm$ 0.12	3046.89 (p<0.0001)	6.27 $\pm$ 2.03	9.54 (p=0.0020)	-40.47 $\pm$ 7.64	28.04 (p<0.0001) 16 8
	<b>Total</b>	<b>6.85 <math>\pm</math> 0.26</b>	<b>708.87 (p&lt;0.0001)</b>	<b>8.78 <math>\pm</math> 2.46</b>	<b>12.73 (p=0.0004)</b>	<b>-24.75 <math>\pm</math> 5.56</b>	<b>19.82 (p&lt;0.0001) 74 18</b>
<i>Emerita</i>	HW1	0.50 $\pm$ 1.08	0.22 (NS)	5.28 $\pm$ 4.66	1.28 (NS)	-3.18 $\pm$ 4.54	0.49 (NS) 14 83
	HW2	-0.40 $\pm$ 1.68	0.06 (NS)	9.42 $\pm$ 6.24	2.28 (NS)	-6.92 $\pm$ 5.35	1.68 (NS) 14 68
	MW1	-1.86 $\pm$ 2.31	0.65 (NS)	23.51 $\pm$ 12.17	3.73 (NS)	-28.58 $\pm$ 15.18	3.55 (NS) 14 41
	MW1	-0.33 $\pm$ 1.23	0.07 (NS)	16.71 $\pm$ 5.68	8.65 (p=0.0033)	-18.68 $\pm$ 6.25	8.93 (p=0.0028) 16 45
	LW	-1.67 $\pm$ 3.21	0.27 (NS)	13.47 $\pm$ 10.27	1.72 (NS)	-9.03 $\pm$ 7.84	1.33 (NS) 16 75
	<b>Total</b>	<b>0.15 <math>\pm</math> 0.66</b>	<b>0.05 (NS)</b>	<b>8.90 <math>\pm</math> 2.58</b>	<b>11.86 (p=0.0006)</b>	<b>-7.13 <math>\pm</math> 2.38</b>	<b>8.95 (p=0.0028) 74 62</b>
PLAYAS							
Transect	$\alpha \pm SE$	$X^2$ (p-level)	$\beta \pm SE$	$X^2$ (p-level)	$\gamma \pm SE$	$X^2$ (p-level)	N Max (%)
<i>Olivella</i>	HW1	2.51 $\pm$ 1.62	2.41 (NS)	28.38 $\pm$ 8.22	11.93 (p=0.0006)	-35.41 $\pm$ 10.24	11.95 (p=0.0005) 10 40
	HW2	1.37 $\pm$ 2.39	0.33 (NS)	37.63 $\pm$ 14.01	7.21 (p=0.0072)	-51.62 $\pm$ 19.96	6.69 (p=0.0097) 10 36
	MW1	3.94 $\pm$ 0.77	26.26 (p<0.0001)	19.82 $\pm$ 4.00	24.61 (p<0.0001)	-23.89 $\pm$ 4.92	23.59 (p<0.0001) 14 41
	MW2	6.36 $\pm$ 0.25	630.53 (p<0.0001)	7.25 $\pm$ 1.49	23.69 (p<0.0001)	-12.03 $\pm$ 2.22	29.39 (p<0.0001) 14 30
	LW	0.07 $\pm$ 1.35	0.00 (NS)	26.08 $\pm$ 5.29	24.34 (p<0.0001)	-25.11 $\pm$ 5.03	24.84 (p<0.0001) 16 52
	<b>Total</b>	<b>4.47 <math>\pm</math> 0.50</b>	<b>79.50 (p&lt;0.0001)</b>	<b>16.41 <math>\pm</math> 2.63</b>	<b>38.96 (p&lt;0.0001)</b>	<b>-20.87 <math>\pm</math> 3.29</b>	<b>40.20 (p&lt;0.0001) 64 39</b>
<i>Emerita</i>	HW1	-9.95 $\pm$ 3.18	9.75 (p=0.0018)	58.21 $\pm$ 12.84	20.53 (p<0.0001)	-57.17 $\pm$ 12.45	21.08 (p<0.0001) 10 51
	HW2	-3.07 $\pm$ 1.32	5.39 (p=0.0202)	31.66 $\pm$ 5.29	35.81 (p<0.0001)	-28.68 $\pm$ 5.02	32.61 (p<0.0001) 10 55
	MW1	1.24 $\pm$ 0.72	2.94 (NS)	21.06 $\pm$ 4.13	25.99 (p<0.0001)	-27.75 $\pm$ 5.51	25.35 (p<0.0001) 14 38
	MW2	1.27 $\pm$ 0.67	3.63 (NS)	16.11 $\pm$ 2.67	36.36 (p<0.0001)	-15.74 $\pm$ 2.56	37.71 (p<0.0001) 14 51
	LW	0.64 $\pm$ 0.87	0.55 (NS)	16.87 $\pm$ 3.49	23.32 (p<0.0001)	-16.05 $\pm$ 3.37	22.70 (p<0.0001) 16 53
	<b>Total</b>	<b>0.78 <math>\pm</math> 0.54</b>	<b>2.05 (NS)</b>	<b>16.89 <math>\pm</math> 2.31</b>	<b>53.39 (p&lt;0.0001)</b>	<b>-16.54 <math>\pm</math> 2.34</b>	<b>49.81 (p&lt;0.0001) 64 51</b>

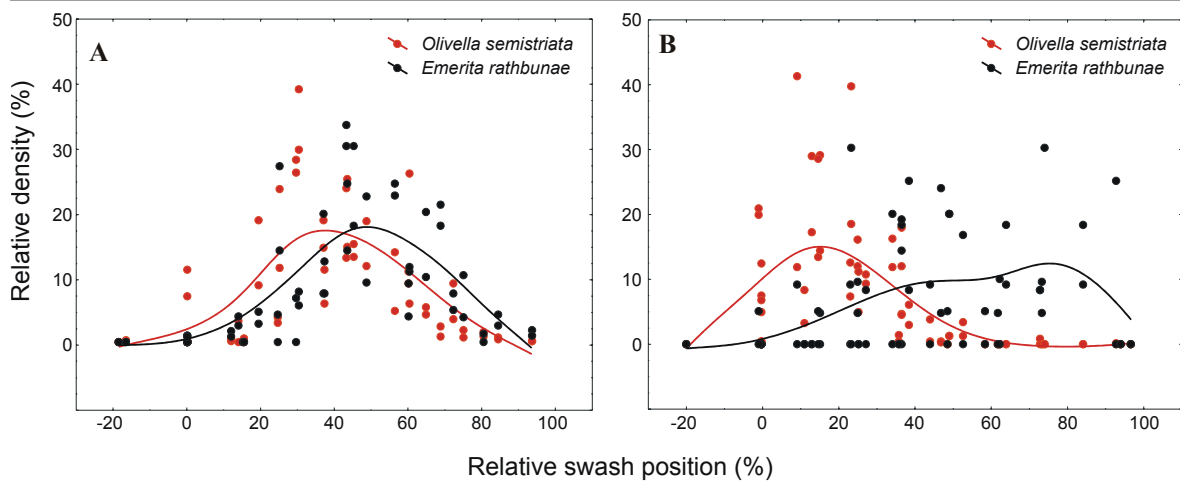
### 2.2.3.3 Comparison between swash and cross-shore zonation of *Olivella semistriata* and *Emerita rathbunae*

The distribution pattern in the swash of both investigated species was compared for Playas and San Pedro. Fig. 2.2.5a and b shows the average swash zonation curve, in relative numbers, for *O. semistriata* and *E. rathbunae*. Although the shape of the curves is very similar, the peak density of *O. semistriata* occurs higher in the swash than the peak density of *E. rathbunae* for all but one transect (Table 2.2.2).

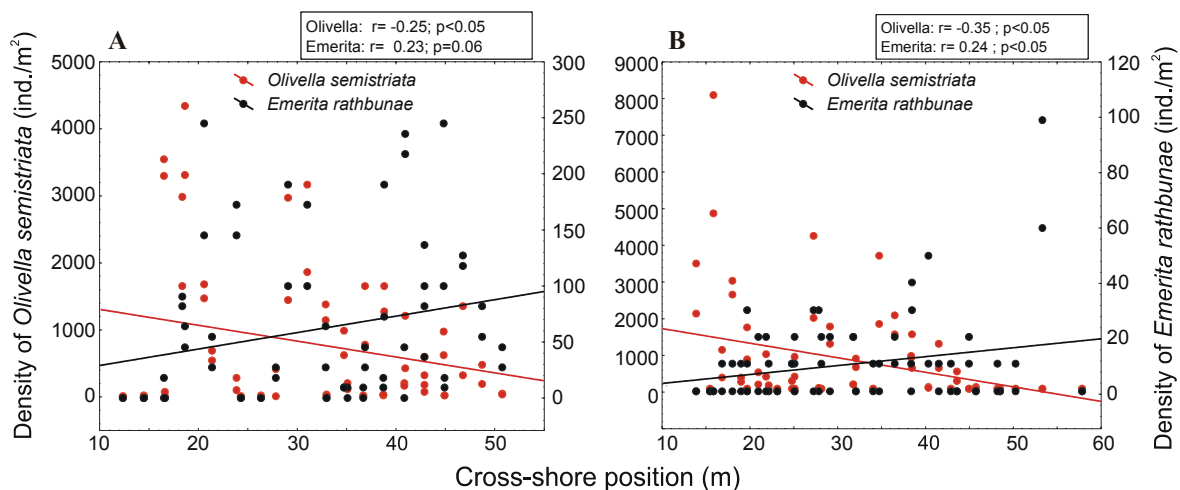
The cross-shore zonation (presented as the sum of all swash transects over the entire intertidal) is completely the opposite for *O. semistriata* and *E. rathbunae* (Fig. 2.2.6a and b; GLMM:  $DF=263$ ,  $F\text{-value}=55.35$ ;  $p<0.0001$ ). Where *O. semistriata* reaches its highest densities high in the intertidal and significantly drops towards the low intertidal, the densities of *E. rathbunae* gradually increase when moving down-shore; cross-shore pattern was not different between beaches (GLMM:  $DF=8$ ;  $F\text{-value}=0.15$ ;  $p=0.7098$ ).

Only very few specimens were found in the three extra samples collected on the air-exposed intertidal at low tide: 0.4 % of the *Emerita rathbunae*-population and 0.0 % of the *Olivella semistriata*-population in Playas, and 0.0 % for *E. rathbunae* and 22.1 % for *O. semistriata* in San Pedro.

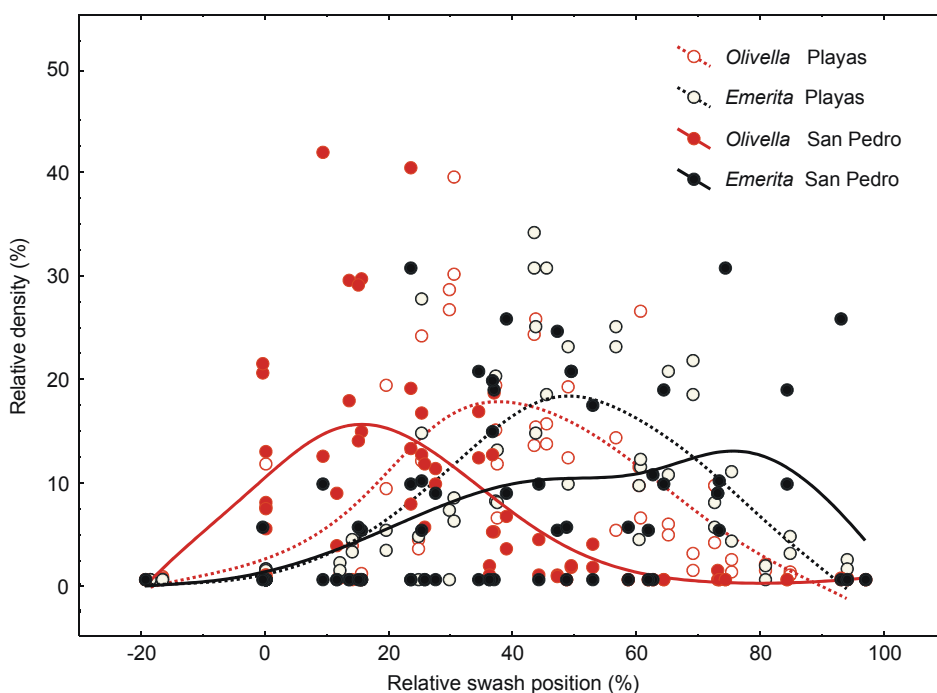




**Fig. 2.2.5** - Relative densities of both *Olivella semistriata* (red) and *Emerita rathbunae* (black), pooled per beach and plotted against the relative swash position. Fitting by distance weighted least square estimates. A) Playas; B) San Pedro.



**Fig. 2.2.6** - Cross-shore distribution (absolute densities) of *Olivella semistriata* (red) and *Emerita rathbunae* (black). Position (X-axis) from high beach to low beach. Fitted line is a simple linear regression. A) Playas ; B) San Pedro.



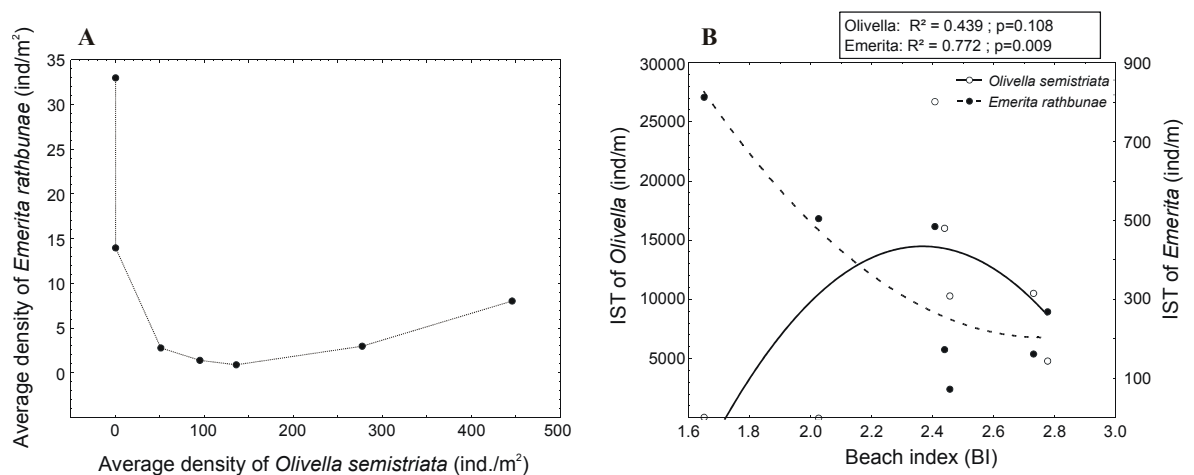
**Fig. 2.2.7** - Relative swash zonation for both species, pooled per beach. Fitting by distance weighted least square estimates.

#### 2.2.3.4 Comparison between the two study sites

If the average of all swash zonation curves is plotted (Fig. 2.2.7), it can be seen that the peak density of *Olivella semistriata* in San Pedro is positioned higher in the swash than in Playas (15 versus 35 %), whereas the peak for *Emerita rathbunae* is situated more towards the surf in San Pedro (75 versus 45 %). Relative peak densities are also lower for both species in San Pedro. Average density ( $\pm$ SE) of *O. semistriata* does not differ between the two beaches ( $849 \pm 76$  ind/m<sup>2</sup> for Playas compared to  $777 \pm 16$  ind/m<sup>2</sup> for San Pedro; GLMM:  $DF=8$ ,  $F\text{-value}=0.77$ ,  $p=0.4049$ ). For *E. rathbunae*, the average density at Playas ( $65 \pm 9$  ind/m<sup>2</sup>) is more than six times higher than at San Pedro ( $10 \pm 2$  ind/m<sup>2</sup>; GLMM:  $DF=8$ ,  $F\text{-value}=62.32$ ,  $p<0.0001$ ).

#### 2.2.3.5 Occurrence of the two species on seven beaches with different morphodynamics

Seven beaches with different morphodynamics, from highly reflective to almost dissipative, along the Ecuadorian coast were sampled during another campaign. In Fig. 2.2.8a, the average densities of *E. rathbunae* and *O. semistriata* are plotted against each other. Where *O. semistriata* is absent, *E. rathbunae* reaches its highest average densities. Abundance (expressed as ind/m) of *E. rathbunae* drops significantly with increasing BI, although the trend weakens around BI of 2.4 (Fig. 2.2.8b). The opposite is found for *O. semistriata*: at low values of BI, the species is not present. Largest populations are found around a BI of 2.4, but they drop again towards the more dissipative beaches (Fig. 2.2.8b).



**Fig. 2.2.8** - A) Average density per sample for *Olivella semistriata* (X-axis) and *Emerita rathbunae* (Y-axis) on 7 beaches with different morphodynamics. B) Abundance (IST, in ind/m) of *Olivella semistriata* (Y<sub>1</sub>-axis, circles) and *Emerita rathbunae* (Y<sub>2</sub>-axis, filled dots) compared to the Beach Index (BI) of 7 beaches. Lines represent second order linear regressions.

## 2.2.4 Discussion

### 2.2.4.1 Sampling mobile swash fauna

Species showing surfing behaviour on tidal sandy beaches use the swash to migrate up and down the beach (McLachlan and Brown, 2006). When studying the zonation of these surfers, some complications arise which are not encountered for organisms with limited mobility. For those non-surfing species, sampling a transect over the intertidal at low tide should be sufficient (McLachlan and Brown, 2006; Jaramillo *et al.*, 1993). Surfers, however, are more likely to be zoned within the swash, and their high mobility, inherent to their lifestyle, implies some sampling strategy difficulties.

Brown and McLachlan (1990) discussed the problem of sampling highly mobile fauna on exposed sandy beaches and proposed integration of samples over the beach width (IST: individuals per strip transect, as defined by Defeo, 1996) as a tool for comparing whole populations, including mobile fauna, between tidal states, seasons or beaches. This, however, does not solve the problem of how to correctly sample very mobile animals, such as surfers, over a swash transect. When sampling along transects migration of a part of the population to or away from the next sampling point is very likely, leading to an over- or underestimation of the population size.

This methodological trap was acknowledged by Jones *et al.* (1998), stating: '*faunal mobility (...) can pose problems in estimation distribution and abundance. For example, it may cause a single population to be sampled in more than one locality or not sampled at all depending on the spatio-temporal pattern of sampling*'. Their solution comprised the identification of the 'median wave level of the swash' (the median of 10 consecutive swash waves), after which the sampling levels were positioned around this reference point. This way, zonation can be assessed independently of the tidal state or wave regime. Whether this method provides a satisfactory solution to the problem of migration in between the taking of two samples depends on the migration rate of the sampled species and the environmental conditions. It might be appropriate for the species studied by Jones *et al.* (1998), amphipods from the genus *Exoediceros* on sheltered beaches, but it is definitely not suitable for investigating *Olivella semistriata* and *Emerita rathbunae*, the two most important surfers on exposed Ecuadorian sandy beaches. For both species, migration can occur with every wave (Chapter 6). The average wave period is between 14 and 16 seconds, which is much less than the time needed to take one sample. It is therefore impossible to sample a full transect in the swash while excluding the possibility of migration, unless all samples are taken simultaneously. This would require as many people as the number of samples one wants to take. And even then,

working with a frame as sampling device (as in this study and numerous others where low densities are expected; see also McLachlan and Brown, 2006) in the lower swash zone would remain impossible, since the frame has to be fully excavated before it is submerged by a next swash wave.

Hence, there was a need for a new sampling strategy, dealing with both methodological shortcomings discussed above: (1) to have a reference point allowing for comparison independent of the tidal state or wave regime at the time of sampling, and (2) to prevent migration while sampling a transect in the swash. For the first issue, we used a modified version of the idea proposed by Jones *et al.* (1998): instead of monitoring 10 consecutive waves, which proved to be insufficient to deal with the very high variability in swash waves on the investigated beaches, the swash was monitored during ten minutes (i.e. about 40 waves). The most shoreward position reached by a swash wave during this period was used as a reference point for sampling.

To solve the second problem, migration while sampling, we designed wooden boxes (as a protective support for the sampling frames) which were positioned at the different levels, prior to sampling (Fig. 2.2.1). Immediately after placing the boxes, the sampling frames were placed within the boxes and excavated, starting with the lowest swash level. Hence, because of the protective boxes, waves that entered the swash zone while sampling could not reach the sediment of the sampling spots, preventing animals from migrating. Due to the high current speed and impact of waves entering the swash zone at some locations (especially during high tide), sampling in the lowest part of the swash zone was not always possible; the boxes were swept away.

The combination of the swash reference point and the wooden boxes allowed us to sample true snapshot swash transects at different times during the tidal cycle, suitable to analyse possible changes in swash zonation on a circatidal scale.

#### **2.2.4.2 Swash zonation of two surfers on Ecuadorian sandy beaches**

The swash zonation pattern of surfing species *Olivella semistriata* and *Emerita rathbunae* showed a very distinct unimodal curve, with the majority of the population positioned around the middle of the distribution range. This unimodal pattern was found at almost all transects, proving to be independent of the tidal state or sampling location. Similar unimodal distribution curves were found for other sandy beach species, such as the beach clam, *Mesodesma mactroides* (Defeo *et al.*, 1986) and the cirrolanid isopod, *Excirolana armata* (Defeo and Rueda, 2002).

A unimodal distribution is present where a species is confronted with a gradient from a central source (Whittaker, 1967; Begon *et al.*, 1996). The gradient most likely to cause the unimodal distribution of filter feeding surfers is the backwash feeding time. Since both species use the backwash for filter feeding (with modified antennae for *Emerita*: Caine, 1975; Ruppert and Barnes, 1994; modified tentacles for *Olivella*: own field observations), backwash time in relation to swash interval probably influences their choice of position. Close to the upper swash limit, swash interval is very long and backwash time very short, resulting in few and short feeding opportunities. Moving lower in the swash, swash interval will gradually decrease and backwash time will increase. At a certain point, incoming swash waves will overrun the backwash of the previous wave, reducing feeding time. Hence, we could hypothesize that feeding opportunity follows a unimodal curve over the swash zone, enhancing a similar distribution pattern for mobile sandy beach filter feeders. Although swash width varies with tide (because of the concave beach slope), we could assume that the relative feeding opportunity pattern remains constant, explaining the similar distribution curve of both surfing species at different tidal states.

In Playas, 0% of the *Olivella*-population and 0.4% of the *Emerita*-population was found on the part of the intertidal that was not covered by the swash at low tide. In San Pedro, these numbers were 22.1% (of which all but one individual at the same level) for *Olivella* and 0% for *Emerita*. This suggests that both species are very efficient surfers, and the numbers are comparable to what McLachlan *et al.* (1979) found for *Bullia digitalis*, although an earlier study reported only 12% of this species' population to be surfing down the beach (Brown, 1971). Brown *et al.* (1989) ascribe this high variability in surfing success to factors such as the nutritional state of the animals, food availability, beach slope and wave action.

#### **2.2.4.3 Comparison of zonation patterns in *Olivella semistriata* and *Emerita rathbunae***

As discussed above, the swash zonation curve of both species is roughly the same, yet peak densities on both beaches occur higher in the swash for *Olivella semistriata* than for *Emerita rathbunae*. On a cross-shore scale, highest numbers of the snail are found around high tide, whereas for the mole crab densities increase towards the subtidal. In San Pedro, the more dissipative beach, peak densities of the two species are further apart than in Playas. Because of the low densities of *E. rathbunae* in San Pedro, this observation should be treated with caution.



A possible explanation for the differences in peak density distribution and different cross-shore zonation patterns could be that these species, where occurring on one beach, try to avoid competition for a common source: backwash feeding opportunities. Using the hypothesis stated earlier, this would imply that *O. semistriata* and *E. rathbunae* use the shared source in a different way, resulting in a shifted unimodal distribution curve of the feeding time and thus densities in the swash zone. The mole crab, living lower in the swash, should therefore be adapted to the stronger swash conditions of the lower swash zone (Short, 1999): faster backwash current speeds to feed upon and less time between waves to burrow after surfing.

The burrowing rate of *Emerita* species was found to be amongst the fastest ever recorded for any sandy beach species (Ansell and Trueman, 1973; Dugan *et al.*, 2000; Lastra *et al.*, 2004): adult crabs of *Emerita analoga* have shown to burrow in less than 4 s and small animals as fast as 0.3 s. No data exist for *E. rathbunae*, but all species of the genus are very similar, so we can assume that *E. rathbunae* is a very fast burrower as well. From field observations and laboratory experiments, we know that the burial time of *O. semistriata* is much slower, ranging from 4 to 15 s (Chapter 4). In general, molluscs have a much lower burrowing rate than crustaceans (McLachlan and Brown, 2006; Chapter 4). These observations support our hypothesis that *E. rathbunae* is adapted to live under harsher swash conditions, such as low in the swash, than *O. semistriata*.

Further evidence comes from the swimming ability of both species. *Emerita* is known to be a very good swimmer and surfing is - at least partially - an active movement (Cubit, 1969). The surfing of *Olivella semistriata* is merely a passive floating in the swash, only enhanced and possibly controlled by extending the wing-like flaps of the metapodium (Olsson, 1956; Chapter 6). The mole crab will therefore have a better control over its surfing in the lower and harsher swash zone, a mandatory capacity for keeping position with the changing tide.

Although no empirical data exist, we also noted that the feeding habit and apparatus of *Emerita* seems more suitable for filter feeding at higher backwash speeds. For instance, *Emerita* burries itself seaward (Caine, 1975), with the feeding structures (second antennae) following the current. *Olivella semistriata* buries shoreward (own field observations), so the feeding structures (mucous net hanging between the tentacles) have to be directed against the backwash current.

It should be noted that the data presented here were sampled on two days during the same season. Zonation, however, is known to vary in time (Brazeiro and Defeo, 1996; Gimenez and Yannicelli, 1997) and Dugan *et al.* (2004) showed that the relative

distribution of two species (the beach clam *Mesodesma donacium* and the mole crab *Emerita analoga*) can also be highly variable. Contrary to our findings, they also described a circatidal shift in relative zonation of the two investigated species. Where we worked with two true swash species, *Mesodesma donacium* does not show consistent tidal migrations, which probably explains why the relative position of *M. donacium* and *E. analoga* changes with the tide (see Fig. 2.2.5 in Dugan *et al.*, 2004).

#### 2.2.4.4 Distribution on the macroscale

The hypothesis that *Emerita rathbunae* is better adapted to the harsher conditions of the lower swash zone than *Olivella semistriata* could be further extended to the spatial distribution of both species on the macroscale. To test this, seven beaches along the Ecuadorian coast from a range of morphodynamic states were sampled for macrofauna. Both *E. rathbunae* and *O. semistriata* were dominant species, the former occurring on all beaches, the latter on all but two beaches.

It is very clear that where the snail is absent, the mole crab reaches its highest average densities. Remarkable is that the beach with the highest densities of *O. semistriata* also has reasonable densities of *E. rathbunae*, suggesting both species are not avoiding each other entirely. Population size of *E. rathbunae* drops significantly with increasing BI, although the trend weakens around BI of 2.4. The opposite is found for *O. semistriata*: at low values of BI, the species is not present. Largest populations are found around a BI of 2.4, but densities drop again towards the more dissipative beaches.

Obviously, the mole crab is able to colonize reflective beaches, but is present throughout the whole morphodynamic range. As previous research has shown, *Emerita*-species are sediment generalists (Dugan *et al.*, 2000; Jaramillo *et al.*, 2000a) and dominate in reflective conditions (Dugan and Hubbard, 1996). *Olivella semistriata* is completely absent from beaches with coarse sediment and steep slopes. Where *Emerita* can survive on beaches with very harsh swash conditions, *Olivella* is clearly incapable of coping with very reflective conditions. This is in accordance with the predictions from the swash exclusion hypothesis (McLachlan *et al.*, 1993) which says that many macrofaunal taxa, especially molluscs (McLachlan *et al.*, 1995), are excluded for reflective beaches because of the harsh swash conditions.

It is interesting to note that populations of especially *O. semistriata* decrease once conditions are too dissipative. This is probably due to the large beach and swash width at those beaches: i.e. when the ratio 'feeding / migrating to maintain position' becomes too

small, surfing behaviour seems to be a less successful strategy. In some cases, swash conditions at dissipative beaches might also be too gentle to be used for surfing (Cubit, 1969).

#### 2.2.4.5 Swash exclusion

As discussed in the previous section our findings on the macroscale are supported by the predictions of the swash exclusion hypothesis (McLachlan *et al.*, 1993). Where the swash exclusion hypothesis was intended to describe the distribution patterns of species along the range of beach types, swash exclusion can also be extended to a smaller spatial scale (i.e. the microscale): within the swash zone swash conditions become harsher from the upper to the lower swash limit. The observation that the mole crab *Emerita rathbunae*, dominating on reflective beaches under harsh swash conditions, lives lower in the swash under more benign conditions than *Olivella semistriata*, supports the idea of swash conditions as a limiting factor in the distribution of species, both on a large and small spatial scales. As such, this is an interesting addition to the original concept of swash exclusion.

#### 2.2.4.6 Implications for interpreting zonation data

In this study, we have demonstrated the existence of a clear zonation pattern of surfing species on a very small cross-shore scale, i.e. the swash zone. Almost the entire population can be concentrated in the 10 to 15 m of the swash zone at any time of the tidal cycle (e.g. Playas). It is obvious that, when one wants to study populations of surfers, the swash zone should be sampled carefully and extensively. However, when a beach is sampled for all macrofauna, as is the case in many studies, the presence of surfers should be checked. If present, at least two, but preferably more, swash levels should be sampled.

Since the distribution pattern of the investigated species follows a unimodal pattern within the swash, high densities are only present in a very narrow band. Thus, when too few swash levels are sampled, it is very likely that no levels are sampled in this narrow densely populated zone, resulting in an underestimation of the population size. On the other hand, when the receding tide is followed as a sampling strategy (Addendum 1; Degraer *et al.*, 1999, 2003), the same population of surfers could be sampled several times, overrating the population size. Both obstacles should be considered when interpreting existing data on sandy beach macrofaunal zonation.

### 2.2.5 Conclusions

- 1) By monitoring the swash limits for 10 minutes, a reference point relative to the swash and independent of the beach or tidal state can be obtained. This is necessary to sample swash zonation.
- 2) Placing the sampling device within protective boxes allows for sampling a true snapshot.
- 3) *Olivella semistriata* and *Emerita rathbunae*, the most common surfers from Ecuadorian sandy beaches, show a very similar swash zonation patterns. This patterns has a unimodal shape and remains almost unvaried throughout the tidal cycle.
- 4) Peak density of *O. semistriata* is found higher in the swash than peak density of *E. rathbunae*. It seems that the latter species is better adapted to harsh swash conditions than the former species.
- 5) This is confirmed by the macroscale distribution: *E. rathbunae* is very abundant on reflective beaches, where *O. semistriata* is completely absent.