

CHAPTER 3

SIZE DISTRIBUTION OF THE SURFING GASTROPOD

OLIVELLA SEMISTRIATA ALONG A CROSS-SHORE

GRADIENT IN AN ECUADORIAN SANDY BEACH

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Abstract

The gastropod *Olivella semistriata* is by far the most dominant taxon on mesotidal, intermediate sandy beaches in Ecuador. Its surfing behaviour, in which the snails follow the swash with the tide, makes it very difficult to determine the distribution pattern of this species. In this paper, transect sampling of the swash at different stages in the tidal cycles and at both upcoming and falling tide was used to obtain swash and cross-shore zonation patterns of *O. semistriata*. The swash zonation showed a uniform unimodal curve, independent of the tidal state and of ebb sampling or flood sampling. Maximum densities were typically found in the upper half of the swash zone. Although the swash zonation pattern did not change towards the low intertidal, densities dropped dramatically. A large part of the population, mainly small individuals, remained stranded on the dry intertidal. Hence, there was a clear increase in shell length towards the subtidal, with only animals larger than 4 mm on the low beach. The same trend of increasing length was also found within the swash: the closer to the surf, the larger the snails.

Along with density data, biomass distribution was calculated. This allowed for population size estimation in terms of both abundance and biomass. Therefore, two measures were compared: IST (individuals per strip transect) and IPE (integration population size estimation). Although no significant differences were found, IPE is proposed as the more precise approach. With abundance values of up to 96257 ind./m beach length, *Olivella semistriata* seems to be an extremely abundant species for sandy beaches.

2.3.1 Introduction

Surfing or swash-riding is a behaviour in which animals use the swash to migrate over the beach face. Several molluscs, such as beach clams of the genus *Donax* (Eilers 1995a) and whelks of the genus *Bullia* (Trueman and Brown, 1976; Brown, 2001), as well as crustaceans, mainly mole crabs of the genera *Emerita* (Cubit, 1969), *Hippa* (Lastra *et al.*, 2002) and *Lepidopa* (Dugan *et al.*, 2000), have developed adaptations to surfing. Filter feeders (e.g. *Donax*, mole crabs) use surfing to find optimal feeding conditions in the swash; *Bullia* rides swash waves in pursuit of its prey (Brown, 2001). They all share several characteristics: (1) they actively emerge from the sediment; (2) they ride the swash - uprush when migrating upshore and backwash when migrating downshore - in a mainly passive though (partially) controlled way; and (3) they are fast burrowers.

Olivella semistriata is a dominant surfing species on exposed Ecuadorian sandy beaches (Chapter 1, Addendum 1): they actively crawl out of the sediment, float with the swash, using their extended metapodium to control the movement (Olsson, 1956; Chapter 6), and actively burrow after surfing. The backwash is filtered by use of a mucus net between the extended tentacles. Extensive field observations have shown that *O. semistriata* surfs in a similar way as other filter feeders such as *Donax* (Eilers, 1995a) and *Emerita* (Cubit, 1969; Caine, 1975), but to date detailed information about its behaviour and distribution are lacking.

Where present, the species is very prominent on the beach, densely packed in a narrow band at the upper swash zone. However, the surfing behaviour of *Olivella semistriata*, with the population shifting cross-shore with the tide, makes it very difficult to identify its zonation pattern as well as to estimate its population size. A strategy to sample the swash zonation of surfing species was described in Chapter 2. Instead of working with transects mapped out over the entire intertidal, for studying surfers a swash zone transect is used. To ensure no migration takes places while sampling one transect, wooden boxes are placed at each level prior to sampling (see also Material & Methods and discussion of Chapter 2).

Where the previous study in Chapter 2 focused on how to sample swash zonation, with the surfers *Olivella semistriata* and *Emerita rathbunae* as examples, the present study aims to identify in detail the zonation patterns of *O. semistriata* in the swash zone and over the full intertidal width (cross-shore) during both rising and falling tide. If assumed that swash zonation is caused by feeding conditions (Chapter 2), we expect to find a similar swash zonation pattern at any time of the tidal cycle. Also zonation by size, well described for rocky intertidal shores (Vermeij, 1972), was investigated. The

hypothesis was that smaller specimens live higher in the swash, where swash conditions are physically less stressful.

In general macrofauna on sandy beaches are rather inconspicuous. *Olivella semistriata*, however, is very noticeable in its behaviour, and the very dense band of snails in the swash tends to label the species as dominant. The detailed swash zonation, in combination with the length data, allowed us to estimate the population size in both numbers and biomass, and thus validate the prediction that *O. semistriata* is a very abundant and dominant species for sandy beaches.

2.3.2 Material and Methods

2.3.2.1 Study site and period

The study site was the sandy beach of San Pedro de Manglaralto, Ecuador (1°59'S and 80°45'W). This beach is dominated by *Olivella semistriata* (Chapter 1; Addendum 1) and can be considered representative for reflective to intermediate, exposed beaches in Ecuador (Chapter 1). The tidal regime is semi-diurnal, mesotidal (Davies, 1964), and ranges between 1.0 and 2.6 m. Modal breaker height varies from 0.1 to 2.0 m (average = 0.49 m), with a wave period of about 14 s. In Addendum 1 we found Ω -values around 1.5 for this beach, with a RTR of 5.3, classifying the beach as a low tide terrace and rip, reflective to intermediate beach (Masselink and Short, 1993; Short 1996). The beach is, using the scale of McLachlan (1980), 'exposed'.

2.3.2.2 Sampling strategy

Two samplings took place: one during ebb and one during flood tide. The sampling with falling tide (further referred to as 'ebb sampling') took place on August 23rd of 2003, with upcoming tide ('flood sampling') on August 27th of 2003. Given the time needed to sample half a tidal cycle (around 7 hours) and the short daytime in Ecuador (11 hours), ebb and flood sampling could not be done on the same day. Per sampling, 3x2 transects over time were sampled: two at high tide (HW1 and HW2), two at mid tide (MW1 and MW2) and two at low tide (LW1 and LW2; one at low tide on August 23rd: LW). Each transect consisted of 5-8 sampling levels in the swash 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. At low tide, 4 (August 23rd) and 10 (August 27th) extra levels were sampled between the upper swash limit at low tide and the high tide mark, on

the drying part of the intertidal. Before setting out the position of the levels, the swash was monitored during 10 minutes to find the upper and lower swash limit (Chapter 2).

At each level, three replicate samples were taken by forcing a plastic core with 10 cm diameter (sampling surface area: 0.0079 m²) to a depth of 15 cm. Preliminary trials proved this to be an adequate sampling technique for *Olivella semistriata* (Vanagt, unpublished data). To prevent migration of *O. semistriata* during sampling of a transect, levels were sheltered by placing a wooden box (plywood, 100 x 50 x 50 cm l x h x w) at each level. For more details about the use of these wooden boxes and the sampling procedure, see Chapter 2. The samples were sieved alive over a 1 mm mesh-sized sieve; the retained organisms were stored in an 8 % formaldehyde-seawater solution.

One sediment sample was collected at each level for grain size analysis, using a core with diameter of 3.6 cm, to a depth of 5 cm. Beach profile was assessed using a leveller, taking measurements every 2 meter.

2.3.2.3 Laboratory treatment

Olivella semistriata specimens were counted. A minimum of 50 specimens per sample were measured to the nearest 0.05 mm shell length (SL = base of mouth to apex) using callipers.

The sediment grain size distribution between 2 and 850 µm was determined with a laser COULTER LS (volume percentage of sediment grain size classes) and classified according to the Wentworth scale (Buchanan, 1984).

2.3.2.4 Biomass / Length regression

Length scale between 2 mm and 13.5 mm was divided in 0.5 mm intervals. Per interval, the biomass of 2 – 18 specimens (depending on availability; n = 209) was measured. Animals were dried at 110 °C for 18 hours, weighed (DW), burned at 550 °C for 2 hours and weighed again for shell dry weight (SDW). Ash-free dry weight (AFDW) was calculated as DW – SDW.

Polynomial regression (4th order) of the data resulted in the following equation (p<0.0001; r²=0.9970):

$$\text{AFDW (mg)} = 1.2238 - 8.8625 \cdot \text{SL (mm)} + 26.8964 \cdot \text{SL}^2 - 25.1324 \cdot \text{SL}^3 + 13.8039 \cdot \text{SL}^4$$

2.3.2.5 Statistical analyses

Beach profiles were calculated from the relative height differences between levels, together with tide predictions for the nearby port of La Libertad. 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. 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.

Since the swash zone widens towards the low tide level on beaches with a concave slope, such as the investigated beach, 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. Relative densities are in reference to total densities of one transect.

Regression fitting of the swash zonation 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* of *Olivella semistriata*, with *relative swash position* as explanatory variable. The Proc Genmod syntax was applied with SAS 9.1.3 software.

Two methods to estimate the total population size (i.e. abundance in ind/m) were used and compared. The first method is the calculation of densities per running meter based on the average density and the transect width (IST: individuals per strip transect; Defeo 1996). The second method, introduced in this paper, uses integration of the separate pieces of the distribution curves (IPE: integrated population estimate). Calculations were made for the high water transects and for the sum of the air-exposed intertidal and low water transects.

Differences in shell length between the dry beach samples and the swash samples were tested with a Generalized Linear Mixed Model (GLMM), with *shell length* as dependent variable in function of *cross-shore position* and *dry beach/swash* as predictors and *transect* as random factor (McCullagh and Nelder, 1989). Pairwise comparison between IST and IPE-estimation and between the high tide vs. 'dry beach + LW' was done with the t-test for dependent samples (Zar, 1999). The relation between shell length and swash position or cross-shore position was tested with first-order linear regression. For non-linear fitting, distance weighted least square estimates were used (Statsoft, 1996).

2.3.3 Results

2.3.3.1 Beach characterisation

The sediments consisted of well-sorted fine to very fine sands, with an average median grain size of 217 μm (191 – 254 μm). There was no zonation in sediment particle size. Intertidal distance was 32 m on the 23rd of August (ebb sampling) with a tidal range of 1.0 m, and 60 m on the 27th of August (flood sampling) with a tidal range of 1.7 m. The beach slope was 1/32 during ebb sampling, 1/35 during flood sampling (Fig 2.3.8).

2.3.3.2 Densities: zonation in the swash

As shown in Fig. 2.3.1a (ebb sampling) and 2.3.1b (flood sampling), there is a remarkable similarity in distribution pattern amongst the different transects. Except for two transects during ebb sampling (LW and MW1) the shape of the distribution pattern is consistently a symmetric to slightly negatively skewed unimodal curve, with densities peaking between 18 and 45% of the swash position (Table 2.3.1; except for flood sampling MW2, which peaks at 9%, and the non-significant LW curve). Around 30% of the sampled animals are found at the peak (with a highest average density of over 25,000 ind./m² at high tide during the ebb sampling). GLM parameters are very similar for all transects, with positive α and β and negative γ (all significant), with ebb LW as the only exception (Table 2.3.1). These values confirm the unimodal shape of the density curves.

2.3.3.3 Densities: cross-shore change in zonation

Figures 2.3.2a (ebb sampling) and 2.3.2b (flood sampling) clearly demonstrate that only part of the population migrates downshore (see dotted lines). Especially during the ebb sampling, densities dramatically drop after high tide, with even lower densities at low tide. The high numbers that are not migrating downshore, are mainly found again just below the high tide position (dry beach transects in Fig. 2.3.2a and 2.3.2b). Note the big difference in peak density between transects sampled at similar tidal position ('a' versus 'b' transects).

Table 2.3.1 - Generalized linear model for density and biomass data. Model structure: $y = e^{\alpha + \beta \cdot x + \gamma \cdot x^2}$ with y as the (absolute) swash density or biomass and x as the relative swash position. * indicates where a third order model was more appropriate. Max (%) is the relative swash position at which the density or biomass was maximal.

| Transect | $\alpha \pm SE$ | X^2 (p-level) | $\beta \pm SE$ | X^2 (p-level) | $\gamma \pm SE$ | X^2 (p-level) | N | Max (%) |
|----------------|---------------------|------------------------------|---------------------|----------------------------|----------------------|----------------------------|------------|-----------|
| DENSITY | | | | | | | | |
| Ebb | | | | | | | | |
| HW1 | 7.57 ± 0.34 | 504.49 (p<0.0001) | 13.81 ± 2.93 | 22.21 (p<0.0001) | -31.04 ± 6.26 | 24.63 (p<0.0001) | 27 | 22 |
| HW2 | 5.00 ± 0.65 | 59.48 (p<0.0001) | 30.14 ± 4.01 | 56.57 (p<0.0001) | -46.08 ± 6.03 | 58.49 (p<0.0001) | 30 | 33 |
| MW1 | 7.11 ± 0.25 | 809.13 (p<0.0001) | 7.08 ± 2.44 | 8.44 (p=0.0037) | -20.13 ± 4.81 | 17.54 (p<0.0001) | 24 | 18 |
| MW2 | 4.13 ± 0.69 | 35.75 (p<0.0001) | 10.72 ± 3.49 | 9.46 (p=0.0021) | -11.97 ± 4.05 | 8.74 (p=0.0031) | 24 | 45 |
| Lw * | 6.17 ± 0.27 | 527.98 (p<0.0001) | -7.40 ± 3.29 | 5.03 (p=0.0249) | 5.50 ± 5.71 | 0.93 (NS) | 19 | -20 * |
| Total | 6.38 ± 0.42 | 230.14 (p<0.0001) | 16.92 ± 3.08 | 30.16 (p=0.0002) | -30.29 ± 5.37 | 31.77 (p<0.0001) | 124 | 28 |
| Flood | | | | | | | | |
| HW1 | 6.20 ± 0.54 | 131.67 (p<0.0001) | 18.17 ± 4.63 | 15.37 (p<0.0001) | -36.94 ± 9.36 | 15.56 (p<0.0001) | 21 | 25 |
| HW2 | 7.86 ± 0.49 | 255.01 (p<0.0001) | 7.64 ± 3.75 | 4.15 (p=0.0417) | -15.87 ± 6.46 | 6.03 (p=0.0141) | 21 | 24 |
| MW1 | 3.88 ± 0.81 | 23.23 (p<0.0001) | 25.74 ± 5.94 | 18.80 (p<0.0001) | -46.39 ± 10.43 | 19.77 (p<0.0001) | 24 | 28 |
| MW2 | 7.93 ± 0.20 | 1594.48 (p<0.0001) | 17.89 ± 3.85 | 21.62 (p<0.0001) | -95.29 ± 16.98 | 31.51 (p<0.0001) | 18 | 9 |
| LW1 | 5.31 ± 0.39 | 188.17 (p<0.0001) | 16.55 ± 3.13 | 28.01 (p<0.0001) | -32.45 ± 5.89 | 30.35 (p<0.0001) | 21 | 26 |
| LW2 | 4.72 ± 0.49 | 94.04 (p<0.0001) | 18.94 ± 4.62 | 16.83 (p<0.0001) | -44.07 ± 10.41 | 17.93 (p<0.0001) | 21 | 21 |
| Total | 7.02 ± 0.26 | 735.34 (p<0.0001) | 8.13 ± 2.27 | 12.86 (p=0.0003) | -18.59 ± 4.42 | 17.66 (p<0.0001) | 124 | 22 |
| BIOMASS | | | | | | | | |
| Ebb | | | | | | | | |
| HW1 | 10.93 ± 0.43 | 632.45 (p<0.0001) | 13.80 ± 3.79 | 13.25 (p=0.0003) | -31.12 ± 8.11 | 14.72 (p=0.0001) | 27 | 22 |
| HW2 | 8.17 ± 0.72 | 129.02 (p<0.0001) | 30.07 ± 4.18 | 51.76 (p<0.0001) | -43.28 ± 5.90 | 53.87 (p<0.0001) | 30 | 35 |
| MW1 | 11.37 ± 0.23 | 2439.38 (p<0.0001) | 7.18 ± 2.38 | 9.09 (p=0.0026) | -21.55 ± 4.90 | 19.38 (p<0.0001) | 24 | 17 |
| MW2 | 6.55 ± 0.87 | 56.79 (p<0.0001) | 16.23 ± 3.97 | 16.75 (p<0.0001) | -16.80 ± 4.27 | 15.52 (p<0.0001) | 24 | 48 |
| Lw * | 10.20 ± 0.32 | 1040.51 (p<0.0001) | -5.69 ± 4.67 | 1.48 (NS) | -0.24 ± 9.77 | 0.00 (NS) | 19 | -20 * |
| Total | 10.16 ± 0.38 | 728.73 (p<0.0001) | 14.10 ± 2.67 | 27.83 (p=0.0025) | -24.72 ± 4.51 | 29.99 (p<0.0001) | 124 | 29 |
| Flood | | | | | | | | |
| HW1 | 9.04 ± 0.64 | 200.32 (p<0.0001) | 21.32 ± 4.73 | 20.30 (p<0.0001) | -37.55 ± 8.42 | 19.91 (p<0.0001) | 21 | 29 |
| HW2 | 11.09 ± 0.55 | 404.24 (p<0.0001) | 7.06 ± 3.82 | 3.41 (NS) | -12.04 ± 5.99 | 4.04 (p=0.0444) | 21 | 29 |
| MW1 | 2.09 ± 2.61 | 0.64 (NS) | 61.18 ± 17.84 | 11.75 (p=0.0006) | -99.72 ± 29.01 | 11.81 (p=0.0006) | 24 | 31 |
| MW2 | 11.06 ± 0.27 | 1690.28 (p<0.0001) | 25.82 ± 4.63 | 31.06 (p<0.0001) | -113.09 ± 18.67 | 36.68 (p<0.0001) | 18 | 11 |
| LW1 | 9.41 ± 0.43 | 488.85 (p<0.0001) | 16.33 ± 3.34 | 23.86 (p<0.0001) | -30.98 ± 6.12 | 25.65 (p<0.0001) | 21 | 26 |
| LW2 | 8.50 ± 0.60 | 200.20 (p<0.0001) | 17.37 ± 5.38 | 10.41 (p=0.0013) | -38.08 ± 11.41 | 11.15 (p=0.0008) | 21 | 23 |
| Total | 10.40 ± 0.28 | 1430.12 (p<0.0001) | 8.90 ± 2.21 | 16.14 (p<0.0001) | -17.60 ± 4.01 | 19.29 (p<0.0001) | 124 | 25 |

2.3.3.4 Length distribution: zonation in the swash and cross-shore zonation

Only two ebb sampling (HW2 and MW2) transects showed a significant relationship between shell length and distance: both indicated an increase in length from high to low swash (Fig. 2.3.3a). However, during flood sampling, there was a significant increase in length from high to low swash for all six transects (Fig. 2.3.3b). Furthermore, moving downshore seems to correspond to an increase in shell length. Indeed, Fig. 2.3.4a (ebb sampling) and 2.3.4b (flood sampling) show a significant increase of average shell from the high to the low intertidal. This increase is clearly caused by the reduction in number of small individuals, with no change in maximum shell length (Fig. 2.3.4a and b). It can easily be seen that no shells smaller than 4 mm are found at low tide (Fig. 2.3.3b).

Comparing the average shell length within the swash zone and on the air-exposed intertidal, both cases show a significant increase towards the low tide level (Fig. 2.3.5a and b). The average shell length is significantly lower on the air-exposed intertidal than in the swash (Flood sampling: 5.9 mm vs. 4.7 mm; GLMM: $DF=117$, $F=5.24$, $p=0.0239$; Ebb sampling: 5.7 mm vs. 4.6 mm; GLMM: $DF=99$, $F=13.34$, $p=0.0004$).

2.3.3.5 Biomass: zonation in the swash and cross-shore zonation

Swash zonation of *Olivella semistriata* in terms of densities has a very distinct pattern. There is, however, a clear zonation in size as well. Since biomass data are calculated from shell length, a different zonation pattern is expected for biomass than for densities. However, very similar trends were found for biomass as for densities: a symmetric to negatively skewed unimodal shaped curve with peak biomass between 10 and 35% of the swash position (Fig. 2.3.6a for ebb sampling and 2.3.6b for flood sampling). The highest recorded average biomass at one level was 492 g AFDW/m² (high tide during ebb sampling). With the exception of ebb LW, model parameters are very similar to those for density data (Table 2.3.1), with positive α and β and negative γ (all but two significant), confirming the unimodal shaped curve. Also the position of the maxima is very similar.

Cross-shore zonation in terms of biomass is very similar to cross-shore density zonation (not shown).

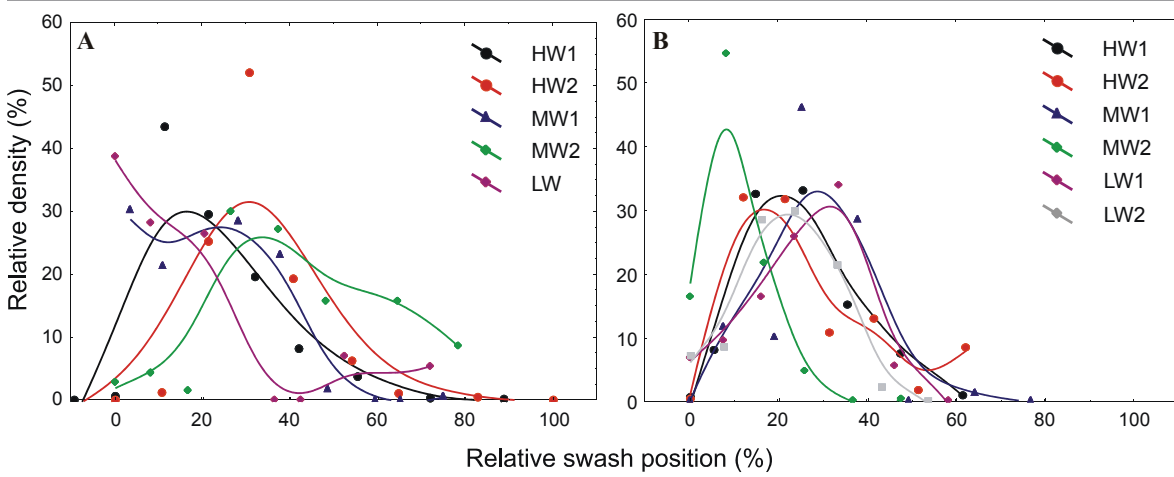


Fig 2.3.1 - Relative densities per swash transect (for abbreviations, see text) of *Olivella semistriata* plotted against relative swash position. Fitting by distance weighted least square estimates. A) Ebb; B) Flood.

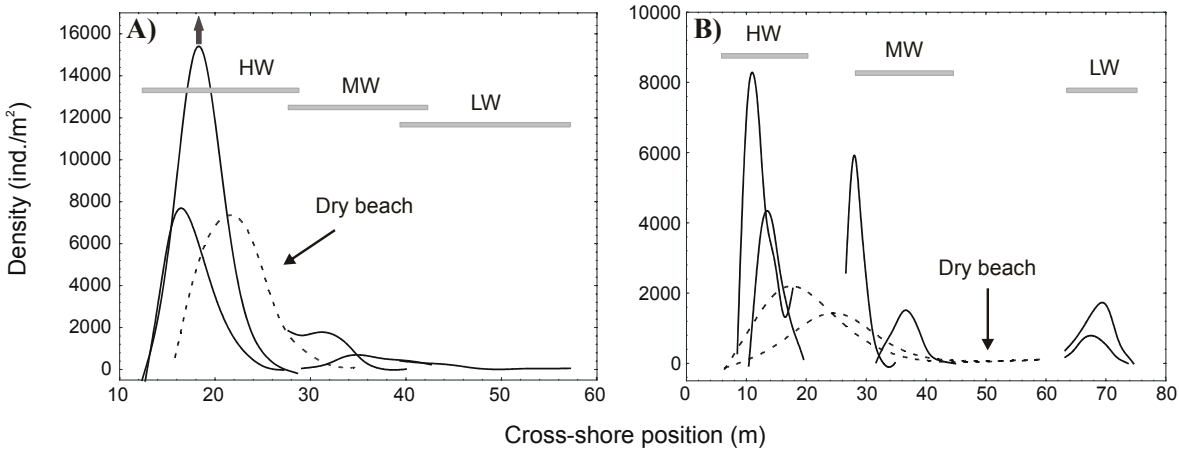


Fig 2.3.2 - Cross-shore distribution of absolute densities of *Olivella semistriata*. Each line represents the pooled data of on transect. The dotted lines are the samples taken on the drying intertidal ('dry beach'). X-axis is the distance from a reference point on the high beach. Fitting by distance weighted least square estimates. A) Ebb, bold arrow indicates 3 values between 23,000 and 28,000 ind/m²; B) Flood.

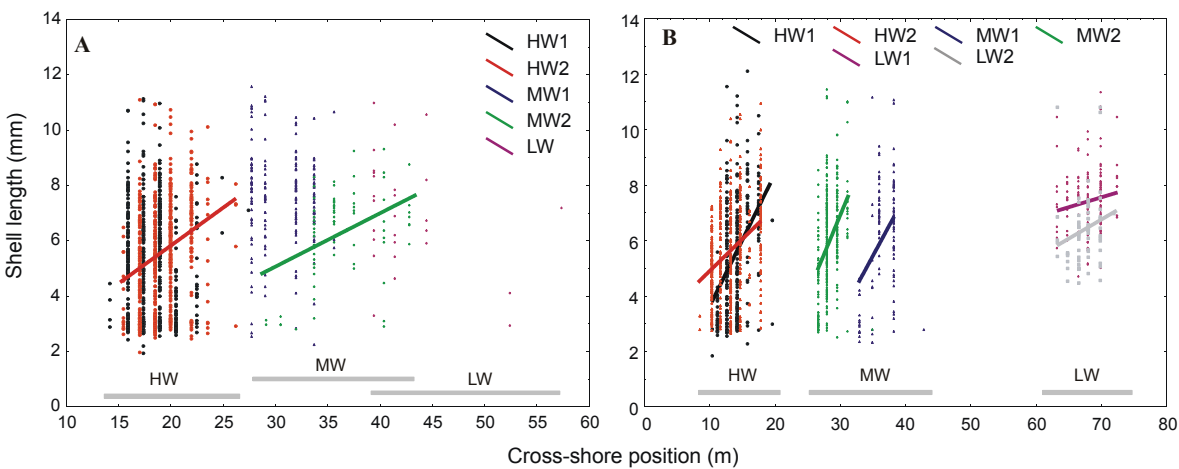


Fig 2.3.3 - Shell length per transect of *Olivella semistriata* plotted against intertidal (i.e. cross-shore) distance from reference point on the high beach. Solid lines indicate a significant linear regression. A) Ebb: shell length for HW2 and MW2 is positively correlated with distance; B) Flood: positive correlation between shell length and distance for all transects.

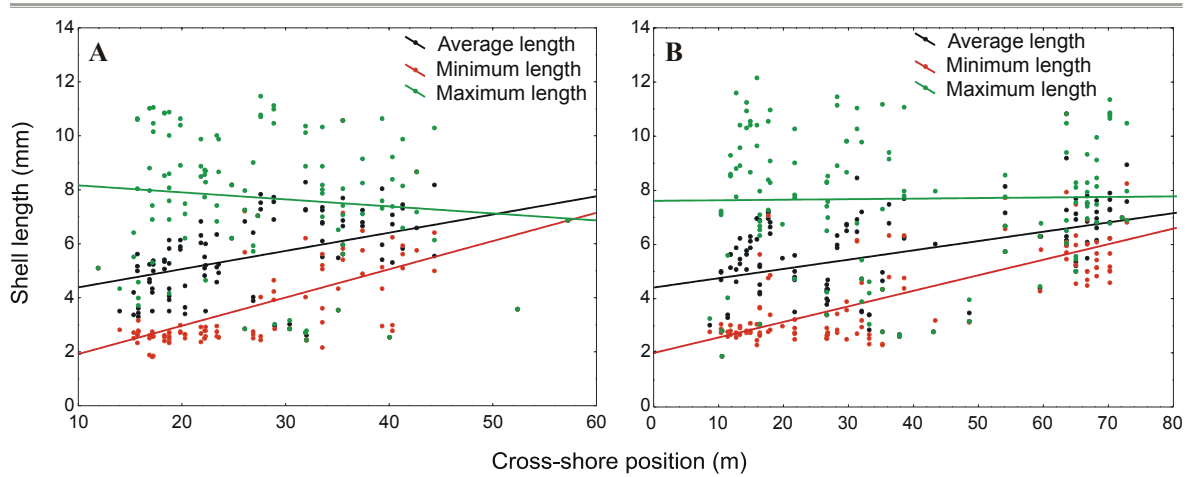


Fig 2.3.4 - Minimum, maximum and average shell length plotted against intertidal distance from reference point on the high beach. Lines indicate simple linear regression. A) Ebb, minimum length: $p < 0.05$ with $r = 0.49$; maximum length: NS; average length: $p < 0.05$ with $r = 0.31$. B) Flood, minimum length: $p < 0.05$ with $r = 0.73$; maximum length: NS; average length: $p < 0.05$ with $r = 0.46$.

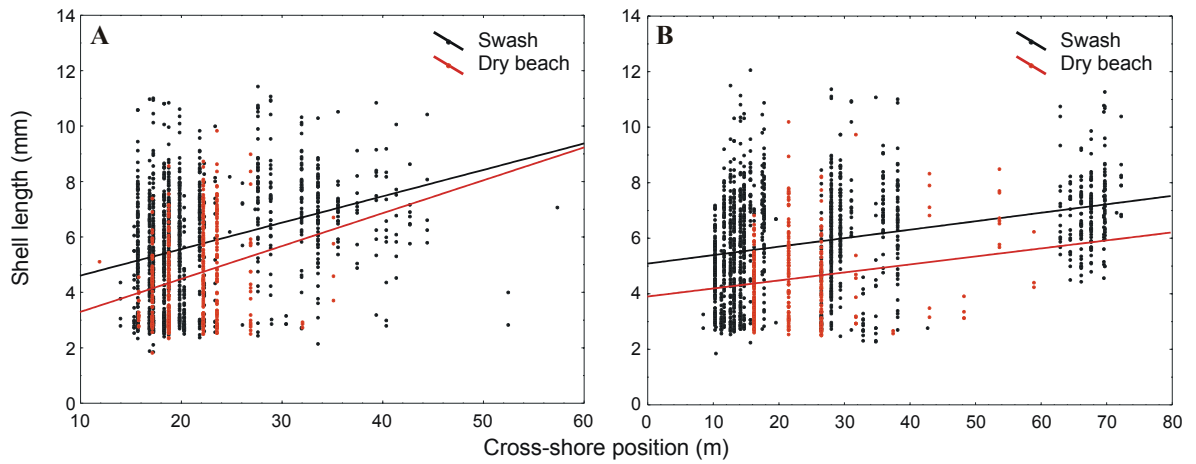


Fig 2.3.5 - Shell length plotted against intertidal distance from reference point on the high beach. Dark line is the linear regression for the swash transects, grey line the linear regression for the dry beach samples. A) Ebb, swash length: $p < 0.05$ with $r = 0.32$; dry beach length: $p < 0.05$ with $r = 0.23$. B) Flood, swash length: $p < 0.05$ with $r = 0.31$; dry beach length: $p < 0.05$ with $r = 0.17$.

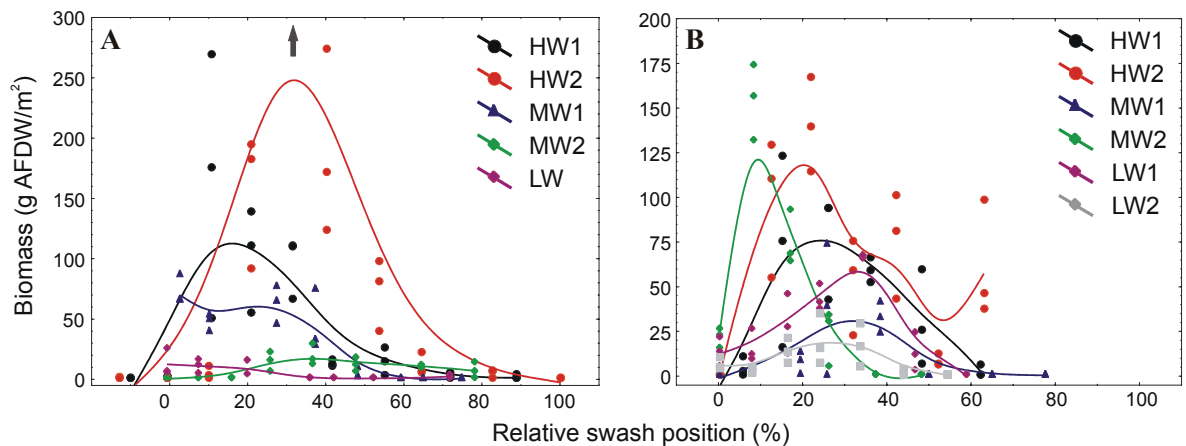


Fig 2.3.6 - Biomass per swash transect plotted against the relative swash position. Fitting by distance weighted least square estimates. A) Ebb, arrow indicates three values between 350 and 500 g/m²; B) Flood.

2.3.3.6 Ebb sampling versus Flood sampling

Although differences exist in both densities and zonation, the average pattern is very similar for both sampling series (Figs. 2.3.1 - 2.3.6). The within-swash zonation of the ebb sampling series seems to be spread over a wider relative position (Fig. 2.3.7a), but the pattern is almost identical. The cross-shore zonation, however, does show some differences (Fig. 2.3.7b): during flood sampling, the six sampling transects are much more distinct and the intertidal width is larger (intertidal range of 1.7 m compared to 1.0 m at ebb sampling), with a wider distribution as a consequence.

2.3.3.7 Population estimation

Population estimates in abundance range between 19,077 and 96,257 individuals per meter of beach length; biomass estimates go from 82.22 to 185.17 gram AFDW per meter of beach length (Table 2.3.2). Though not significant, differences exist between using IST or IPE. The same holds true when using the high water series or the combination of the air-exposed intertidal and low water series for population estimation: the differences are not significant.

Table 2.3.2 - Population estimation over the total beach width for abundance (ind/m) and biomass (g/m) during ebb and flood. IST = individuals per strip transect; IPE = integration population estimation. p-values from t-test for dependent samples.

| | | EBB | | | FLOOD | | | | HW vs. 'Dry beach' + LW | IST vs. IPE |
|------------------|------------|-------|--------|------------------|-------|-------|---------------------|---------------------|-------------------------|-------------|
| | | HW1 | HW2 | 'Dry beach' + LW | HW1 | HW2 | 'Dry beach a' + LW1 | 'Dry beach b' + LW2 | | |
| Abundance | IST | 48802 | 96257 | 77322 | 19077 | 39414 | 55157 | 29842 | p=0.47 | p=0.53 |
| | IPE | 48196 | 88830 | 66634 | 22227 | 43182 | 55840 | 31329 | | |
| Biomass | IST | 83.51 | 185.17 | 111.31 | 42.16 | 73.53 | 123.32 | 63.44 | p=0.99 | p=0.25 |
| | IPE | 82.22 | 173.21 | 99.17 | 50.67 | 78.08 | 98.26 | 62.26 | | |

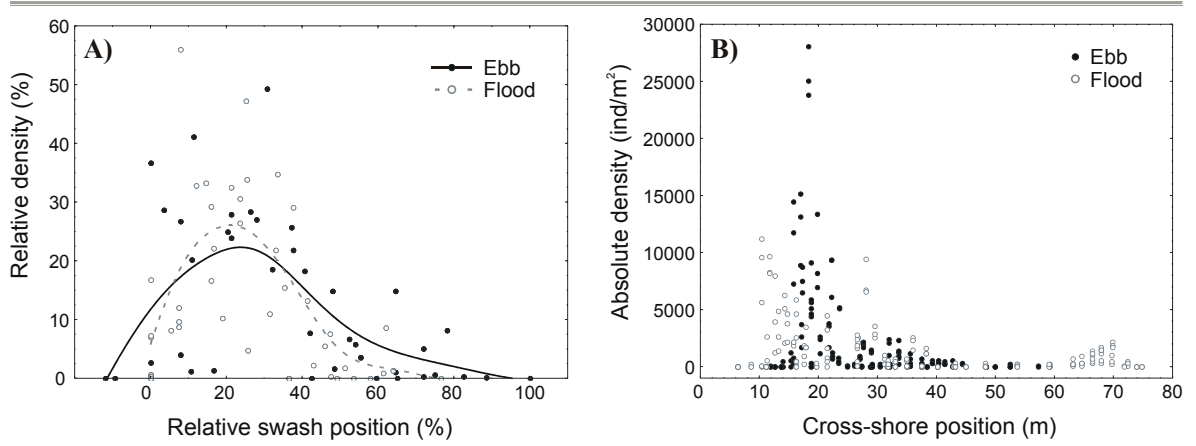


Fig 2.3.7 - A) Average relative densities for ebb (black dots) and flood (grey circles) plotted against the relative swash position. Fitting by distance weighted least square estimates. B) Cross-shore distribution of average absolute densities for ebb and flood. X-axis is the distance from a reference point on the high beach. Fitting by distance weighted least square estimates.

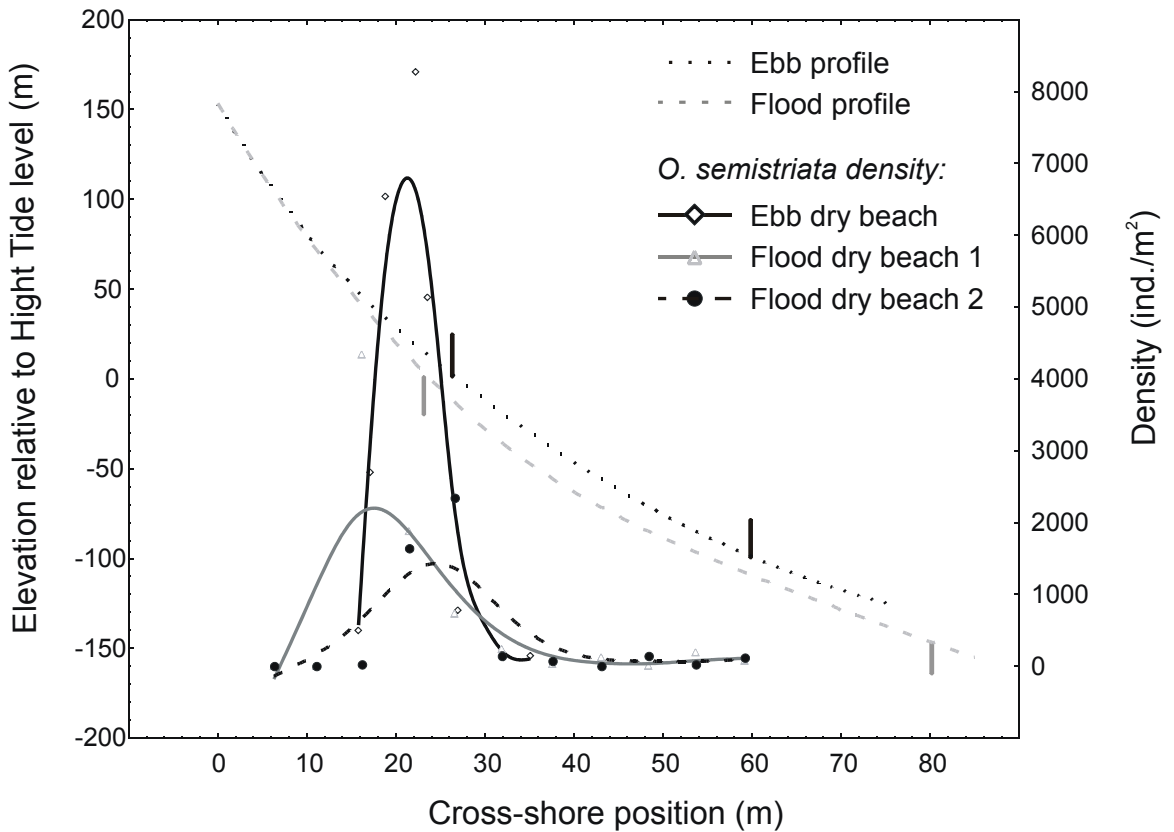


Fig 2.3.8 - Beach profile combined with dry beach density data for ebb and flood. Vertical bars indicate high and low water point. Curves are least square estimates of the density of *Olivella semistriata* at the air-exposed (dry beach) levels.

2.3.4 Discussion

2.3.4.1 Swash zonation of *Olivella semistriata*

The zonation of *Olivella semistriata* within the swash shows a very distinct pattern with a symmetric to slightly skewed unimodal curve, as was described in Chapter 2. This indicates that there is one very narrow zone within the swash, always at 10% to 30% of the upper swash limit, where both densities and biomass are peaking. Given the fact that the distribution pattern is very similar at high, middle and low tide, the population of *O. semistriata* shifts over the beach in a uniform way. If we assume that survival conditions are, on average, optimal where the highest numbers of animals are found (Begon *et al.*, 1996), we can conclude that the upper part of the swash remains, regardless of the tide, the species' optimal zone. We hypothesized this is due to the total feeding time, which must be highest in the upper part of the swash zone and follows a unimodal distribution curve within the swash (Chapter 2).

2.3.4.2 Cross-shore zonation of *Olivella semistriata*

Although the within-swash zonation is very constant over the intertidal, there is a dramatic drop in densities between high and middle tide, with a further drop towards low tide. We found that minimum and average shell length increases towards the low intertidal, while the maximum shell length remains constant. This indicates that mainly small individuals stay behind on the high beach (Fig. 2.3.4). Because surfing is a very complicated behaviour that requires several skills such as timing and judging distance and direction, we hypothesize that the younger – smaller – individuals are not as successful in surfing as the adults and that quantity of good surfing movements, required to move up and down the beach, increases with experience. The very small individuals (<4 mm, with transparent shell) do not migrate beyond the mid tidal level at all. An experience factor in behavioural plasticity of sandy beach fauna, especially on exposed sandy beaches, was already suggested by Brown (1996).

The fact that a large number of snails, also some bigger ones (see Fig. 2.3.5), do not migrate down-shore, raises the question whether migrating all the way down the beach is energetically beneficial or necessary. Brown (1982) measured the energy cost of migration for the surfing gastropod *Bullia digitalis* and concluded that migrating is far more energy consuming than staying in one place. Several swash species, such as *Excrolana braziliensis* and *Eurydice pulchra*, remain burrowed on the high beach at middle and low

tide (*Excirolana*: Yannicelli *et al.*, 2001; *Eurydice*: Alheit and Naylor, 1976), suggesting that feeding for a short period of time and then waiting for a long period of time is more interesting than having to adjust their position all the time to ensure good feeding conditions. Moreover, it is not unlikely that the individuals of *Olivella semistriata* that remain stranded on the high beach, but below the low tide effluent line - no burrowing is possible above the effluent line, can obtain food in a different way than filter feeding the backwash. It is commonly seen that stranded snails crawl about in a haphazardous way, just below the sediment surface (personal observations). This could be a foraging behaviour in which they graze on diatoms that are attached to the sand particles, using their radula. On the other hand, they could be in search of the swash zone, though a more directional movement would then be expected. It might well be, however, that they are clueless for orientation without a water current. Staying behind does seem to increase the predation risk – the animals are very easily seen when crawling about, questioning the foraging hypothesis.

2.3.4.3 Length zonation

As mentioned above, *Olivella semistriata* is zoned according to length, with smaller individuals higher on the beach and higher in the swash. Length zonation is a well-known phenomenon amongst intertidal species. This can be a response to an environmental or a biological gradient (Vermeij, 1972). Swash zonation by size is known for species of the genus *Emerita*. As for *O. semistriata*, smaller animals of *Emerita* live higher in the swash and higher on the beach (Efford, 1965 and references herein; Forward *et al.*, 2005). *Olivella biplicata*, however, was found to be zoned in the opposite way: smaller animals were found closer to the surf zone (Edwards, 1969), possibly because larger animals can better withstand desiccation. Since *O. semistriata* surfs down the beach, desiccation is not an important factor for the species. Length zonation for intertidal gastropods from rocky shores was reviewed by Vermeij (1972). He clearly found two patterns, with increasing length upshore for animals from the littoral fringe and increasing length downshore for animals from the lower intertidal. He ascribed these patterns to a different response to gradients in the intensity and nature of postlarval prereproductive mortality on the shore. Although the length zonation of *O. semistriata* logically falls in the group of gastropods living in the low intertidal, the explanation that for these animals biotic interactions and predation is more intense at low levels, does not seem to fit. It is rather the more severe physical conditions lower in the swash that will cause length zonation. This seems to hold true for several surfing species, such as *O. semistriata* and *Emerita*. This could possibly be explained by a physically driven force:

sand particles settle according to water currents with an increase in particle size from calm to harsh conditions. Since the migration of *O. semistriata* is mainly a passive floating in the swash, the same rules as for sand particles apply: the lower in the swash, the higher the water currents, the bigger the specimens.

2.3.4.4 Population estimation

Because of its very high densities in the swash zone, *Olivella semistriata* is by far the most conspicuous animal on intermediate Ecuadorian beaches. The zone in which they occur at one time, however, is limited to a few meters. To know just how abundant the species is, several ways of estimating the population size were applied. The final goal of these calculations was to have the population size over the full intertidal per meter beach length (i.e. abundance), a measure that allows for straightforward comparison with other species and locations. Population was estimated in both numbers and biomass (ash-free dry weight).

Defeo (1996) proposed IST (individuals per strip transect), with $IST (ind/m) = \text{average sample density } (ind/m^2) * \text{distribution width of the species (cross-shore)}$, as a good proxy for population estimation (for biomass, it is also named BST: biomass per strip transect). This method is based on the assumption that a population is zoned in a perfect bell-shaped way, since the average number (density or biomass) per level is multiplied by the beach width in which the animals occur. Additionally, we estimated abundance by integrating the zonation curve. Each straight line between two levels in the zonation curve was integrated over the distance between the two levels. The sum of all these integrals gives the population. It was expected that this IPE (integrated population size estimation) would render a more precise population size estimate than IST, especially for non-symmetrical distribution curves. Although differences exist (Table 2.3.2), pairwise comparison did not show a significant result for IST versus IPE. Still, we tend to prefer IPE as a general population size estimation tool. It is almost as straightforward to compute as IST, but is logically more precise.

If assumed that the total population of *Olivella semistriata* migrates with the tide and remains zoned in the swash, sampling a swash transect should yield a good population proxy, independent of the current tidal state. However, as we have discussed above, it is clear that a major part of the population does not migrate beyond the high

beach. Since distribution curves within the high tide transect start at zero and end with zero, we can still conclude that the total population is present in the swash at high tide. Consequently, transect sampling within the swash at high tide should thus render a good estimate of the population size.

At low tide only part of the population is found in the active swash. The rest of the animals remain stranded on the air-exposed intertidal. The sum of the snails found in the low tide swash and on the air-exposed intertidal at the time of low tide, should also give a good estimate of the population size.

Both calculations, high tide and low tide swash and air-exposed intertidal, were compared (Table 2.3.2). No significant difference could be found, although numbers did vary substantially. The variation between the parallel transects, however, was also very large, suggesting strong alongshore patchiness in the distribution of *Olivella semistriata*. At flood sampling, for instance, IPE for the HW1 transect was 22,227 ind/m beach length, compared to 43,182 ind/m beach length for the adjacent HW2 transect. Similar differences were found during ebb sampling. It is very likely that this alongshore patchiness is caused by small-scale morpho- and consequently hydrodynamic effects, since migration of *O. semistriata* is mainly a passive floating in the swash. It seems that sampling several parallel transects is necessary to get a good abundance estimate of the species (James and Fairweather, 1996). Whether this is done at high tide or at low tide, does not play such an important role. Since the sampling effort at high tide is much lower, this will generally be the preferred approach. Note that especially the distribution of the left-behind specimens on the air-exposed intertidal is extremely patchy: almost all individuals were found in a very narrow cross-shore zone (Fig. 2.3.8). It is thus crucial to sample enough levels if these animals are not to be missed.

2.3.4.5 Population size of *Olivella semistriata*

For correct comparison of the abundance in numbers and biomass of *Olivella semistriata* with other species, a value in terms of meter per beach length (see above) is needed. Unfortunately, only few studies mention abundance or biomass in this scale. Nevertheless, it is clear that *O. semistriata* is a very abundant species for a sandy beach, both in population size and in biomass. The maximum recorded abundance of almost 100,000 ind/m (ebb sampling HW2) is higher than any other population size number found in literature, even for total sandy beach macrobenthic communities. The maximum biomass (185.17 g AFDW/m) is also rather high for a single species on an intermediate beach. Brazeiro and Defeo (1996) found a total average abundance of 72,890 ind/m and

biomass of 2,081 g Dry Weight/m on an exposed, microtidal dissipative beach in Uruguay, with *Excirolana armata* as the most densely distributed species (59,831 ind/m) and *Mesodesma mactroides* as the most dominant species in terms of biomass (1,657 g DW/m), but the latter is a very large and heavy species, and known for its high productivity (McLachlan *et al.*, 1996). The highest macrobenthic abundance found on Chilean beaches by McLachlan *et al.* (1993) was 66,783 ind/m on an intermediate beach ($\Omega = 4.1$). The highest macrobenthic biomass they found was 3,087 g DW/m ($\Omega = 5.4$). High biomasses (up to 3,504 g DW/m) were found for *Emerita analoga* in California, United States, but in abundances less than 15,000 ind/m (Dugan and Hubbard, 1996). However, no mention is made whether the biomass values are dry weight or ash-free dry weight (the latter being used for *Olivella semistriata*). All high values retrieved from literature were from beaches with a Dean's parameter much higher (i.e. more dissipative) than from the beach investigated in this study ($\Omega < 2$). Abundance and biomass tends to increase with increasing Ω (McLachlan and Dorvlo, 2005). This makes the extremely high population size found for *Olivella semistriata* even more spectacular.

2.3.5 Conclusions

- 1) The zonation of *Olivella semistriata* within the swash showed a uniform unimodal curve, independent of the tidal state.
- 2) No major differences existed between ebb or flood sampling.
- 3) Maximum densities were typically found close to the higher swash limit.
- 4) A large part of the population, mainly small individuals, remained stranded on the air-exposed intertidal, which might be due to a lack of surfing experience.
- 5) Shell length increased towards the subtidal, with only animals larger than 4 mm on the lower part of the beach.
- 6) The same trend of increasing length was also found within the swash: the lower in the swash zone, the larger the snails.
- 7) Abundance estimates ranged from 19,000 to 97,000 ind/m; biomass estimates were found between 42 and 185 g AFDW/m.
- 8) With densities of up to 96,257 ind/m, *Olivella semistriata* is considered to be an extremely abundant species for sandy beach standards.