CHAPTER 4

IS THE BURROWING PERFORMANCE OF A SANDY BEACH SURFING GASTROPOD LIMITING FOR ITS MACROSCALE DISTRIBUTION?

Vanagt T., Vincx M., Degraer S.

Abstract

The burrowing capacity of the gastropod *Olivella semistriata*, an extremely abundant surfer on exposed sandy beaches in the tropical East Pacific, was investigated in terms of shell length and sediment grain size. For all investigated sand classes there was a significant increase in burial time with size. Burrowing was fastest in sand with grain size between 150 and 355 µm, as well as in native sediment (median grain size: 209 µm) and in field conditions (median grain size: 223 µm). Values of the Burrowing Rate Index (BRI) were found between 3 and 7, valuing the burrowing capacity of *O. semistriata* as fast to very fast.

Data from previous qualitative and quantitative sampling campaigns were used to identify the distribution of *Olivella semistriata* in terms of sediment grain size and swash conditions. Swash period was shorter than burial time, excluding this as a limiting factor. Swash standstill time (the time between uprush and backwash), however, was just long enough on the beaches were *O. semistriata* was present to allow for securing anchorage. On reflective beaches the swash standstill time is as short as one or two seconds, denying *O. semistriata* the time to burry itself before being swept away by the backwash. As such, swash standstill time is advocated as a valuable part of the swash exclusion hypothesis.

A survey of the available literature on the burrowing of surfers shows that mole crabs are by far the fastest burrowers, and the only surfers that burrow sufficiently fast to withstand the extremely short swash standstill time on reflective beaches. Burrowing ability of surfing gastropods is found in the same range as surfing bivalves, both being insufficient to cope with coarse sediment on steep beaches.

Finally, we suggest that not burial time nor BRI, yet the *minimal burial time* – the time needed to anchor securely in a certain sand at a given swash velocity – should be used to judge the limitations of burial in terms of sediment and swash conditions.

3.4.1 Introduction

Olivella semistriata is a surfing gastropod that lives on exposed sandy beaches along the Ecuadorian Pacific coast. With densities up to almost 100,000 individuals per meter strip transect (Chapter 3) it is one of, if not the most abundant sandy beach gastropod species worldwide. Large aggregates migrate cross-shore at the upper boundary of the swash, traveling distances of up to 100 meter per tidal cycle. The surfing behaviour consists of three different movements. Upon inundation of a surfable wave, the animals crawl actively out of the sediment (1). Timing of this movement is crucial to maintain or regain position on the beach (Ellers, 1995a,b), and can be initiated by wave sounds (Ellers, 1995b), changes in light conditions, thixotrophy or hydrostatic pressure (Brown and McLachlan, 1990) and is often regulated by an endogenous clock (Warman *et al.,* 1993; Ellers, 1995b). The exact trigger for migration of *Olivella semistriata* is not known, although in Chapter 5 we showed the presence of an endogenous circatidal clock and hinted on mechanical agitation of the sediment as the initiator of a surfing movement. After the animals emerge from the sediment they passively ride the swash wave (2). In *O. semistriata* this seems to be controlled by using the extended metapodium as an underwater sail (Olsson, 1956; personal observations), as was also described for *Bullia digitalis* (Brown *et al.,* 1989). Distance traveled per surfing movement is optimally around 3.75 m (Chapter 6). The surfing ends by anchoring to the sediment through rapid burrowing (3).

Fast burrowing has repeatedly been reported as a crucial characteristic for survival on exposed sandy beaches (e.g. Brown *et al.,* 1989; Brown and McLachlan, 1990; Nel *et al.,* 2001; Lastra *et al.,* 2002). The limits of a species' burrowing capacity is often considered to restrict the distribution, mainly towards the reflective end of the beach spectrum, where rapid burrowing is necessary to withstand the harsh swash conditions (Brown *et al.,* 1989; McLachlan *et al.,* 1995; Nel *et al.,* 2001; de la Huz *et al.,* 2002). Many species, especially bivalves and gastropods, are incapable of fast burrowing in the coarse sediment that is found on reflective beaches. Nel *et al.* (2001) showed a clear increase in burial time of two intertidal *Donax*-species from fine to coarse sand. Similar results were obtained by Alexander *et al.* (1993) for a wide range of bivalves.

Although burial time is undoubtedly very important for the mobile fauna of exposed beaches, it remains debatable whether the burrowing performance in certain sediment types has a direct influence on the distribution of species or not. While Nel *et al.* (2001) ascribed the absence of *Donax* on reflective beaches to the slow burrowing of the taxa in coarse sediment, McLachlan (1990) hypothesized that the total swash climate -

including grain size – regulates the presence of species on different beach types. Subsequently, McArdle and McLachlan (1991, 1992) proposed the 'swash exclusion hypothesis', which states that swash climate is the key factor controlling macrofaunal sandy beach communities. The swash climate on fine-grained dissipative beaches was described to be more suited for macrofauna, and only few species could cope with the harsh swash conditions on reflective beaches (McLachlan *et al.*, 1993).

The goals we set for this paper were to identify the burrowing capacity of *Olivella semistriata* over a range of sediment types, to test if this is reflected by or possibly influences the distribution of the species in terms of swash and sediment and to compare the burrowing performance of *O. semistriata* to other sandy beach surfers.

3.4.2 Material and Methods

3.4.2.1 Study site and period for burial time

For field measurements and collection of *Olivella semistriata*, the sandy beach of San Pedro de Manglaralto, Ecuador (1°59'S and 80°45'W) was chosen. The macrofaunal zonation of this beach is described in Addendum 1. Swash zonation of *Olivella semistriata* from this location is discussed in Chapter 2 and 3, as are the beach characteristics (intermediate beach with fine, well sorted sediment and a gentle slope which steepens at the high tide cusps).

3.4.2.2 Field data collection

For the field measurements, one specimen at a time was followed during a surfing movement. Burial time was assessed by means of a hand stopwatch, and was clocked from the start of the burrowing (after the surfing movement) till the apex of the shell disappeared under the sediment. After the burrowing, the animal was collected and shell length was measured with callipers to the nearest 0.05 mm. Animals that were helped in their burrowing by sediment movement were excluded from the dataset, as were animals that turned around 180º while burrowing. 26 measures were retained for further analyses.

The swash was monitored at several occasions, during upcoming and falling tide. Data were collected by filming the swash with a 50 Hz video camera during 10 to 15 minutes. Plastic reference poles were placed in the swash at two meter intervals. *Swash standstill time* was the period at maximum swash run-up when no cross-shore swash current was visible on videotape.

3.4.2.3 Laboratory data collection

Seven different sets of sediment were prepared: six according to grain size class and one with sediment from the collection site. To obtain sediment with a wide variety of grain sizes, sand was collected from several beaches, dried for 24 hours at 70ºC and sieved through a series of sieves. The six size classes that were obtained were very fine (<150 μm), fine (150-250 μm), medium 1 (250-355 μm), medium 2 (355-500 μm), coarse (500-1000 μm) and very coarse (>1000 μm) sand, according to the Wentworth scale (Buchanan, 1984). Transparent plastic 1 litre bottles were filled with 5 cm of sand and 2 cm of sea water.

Animals were collected from the beach by sieving the upper sediment layer of the swash zone through a 1 mm mesh-sized sieve. The collected specimens were then transported to the laboratory (average transport time of 5 min), where they were placed in plastic trays (30x20x4 cm) filled with 1 cm of sediment and 1 cm of sea water. To measure burial time, one specimen was placed per bottle filled with selected sand, and given the time to burrow. Sediment was then agitated to stimulated emergence, as happens in the swash zone, and burial time was measured in a similar way as in the field. This procedure was repeated twice for each specimen (three times with the mixed sediment). A total of 20 specimens per sand class and 39 for the mixed sediment were measured. Again, burrowing movements involving a 180º turn and vertical burrowing movements (compared to the normal burrowing angle of 25º) were neglected. Subsequent specimens were chosen to obtain data from the full shell length range of the species; individual specimens were only used once.

Water temperature was kept constant at 24 ± 1 ºC, which was equal to the swash water temperature in the field.

3.4.2.4 Sediment characterisation

A sediment sample was taken at the site of field data collection. A subsample was also taken from the sediment that was used for the mixed sand laboratory experiment. Both samples were analysed with a laser COULTER LS. Median grain size for the field sample was 223 μm and 209 μm for the sand used in the laboratory.

3.4.2.5 Distribution of *Olivella semistriata*

The distribution and population size of *O. semistriata* was investigated quantitatively on seven sandy beaches with different morphodynamics along the Pacific coast of Ecuador. Details about the sampling can be found in Chapter 1. Additional unpublished data from pilot studies were used to complete the picture. Since sampling was not always done in a similar way, these data were only treated for qualitative investigation. Quantitative data are expressed in density (ind/m^2) and in abundance as individuals per meter strip transect (IST; ind/m), which is a good measure of the total populations size independent of the beach type (Defeo, 1996). To describe the beach type, the Beach index (BI) was used (McLachlan and Dorvlo, 2005). Values increase from reflective to dissipative beaches.

3.4.2.6 Statistical analyses

For field measurements and per sand class (laboratory experiment) a first order linear regression with burial time as dependent variable and shell length as explanatory variable was performed. Differences in slope between the regression lines was checked with a mixed model (proc mixed statement in SAS 9.1) with interaction term shell length*sand class. Where the slope was not significantly different, a Tukey post-hoc test was calculated to find differences in intercept.

Biomass data were retrieved from the shell length data, using the following equation:

$$\text{Wet weight} = 10^{-0.61076 + 2.7873 * \log (\text{Shell Length})}$$

(see Chapter 3 for the description of this regression).

This was used to calculate the burrowing rate index (BRI), defined as the cube root of the wet weight (g), divided by the burial time (s) and multiplied by 100 (Stanley, 1970):

$$\text{BRI} = [\text{ Wet mass (g)}^{0.33} / \text{ Burrowing time (s) }] \times 100$$

The burrowing rate can, therefore, be defined as the mass (g) per second. Values below 2 indicate slow burrowers, between 2 and 5 fast burrowers and above 6 very fast burrowers (Stanley, 1970). BRI was expressed in terms of shell length with a first-order linear regression.

McArdle and McLachlan (1992) found that swash period, beach type (expressed as Dean's parameter) and sediment grain size were highly correlated on exposed sandy

beaches. From the data they list, a second-order linear regression of *swash period* as a function of *sediment grain size* was calculated. Likewise, from the present study, the *swash standstill time* was expressed as a function of *sediment grain size* (for the data, see Table 3.4.4) with a second order linear regression. Both regression lines were superimposed on Fig. 3.4.2. This graph shows the burial time of *Olivella semistriata* in the different sand classes, but divided into three shell length groups (<6mm; 6-9mm and >9mm; chosen to divide the data in three equal groups). To plot the regression, the median value of every sand class was used as sediment grain size value (x-value in the second order regressions).

3.4.3 Results

3.4.3.1 Burial time in relation to size and sand characteristics

For all laboratory experiments as well as for the field data, there was a significant (p<0.0001) increase in burial time with increasing shell length (Fig. 3.4.1; Table 3.4.1), indicating that larger animals take more time to achieve complete burial. The rate of increase in burial time with size was similar in all but the coarsest sand, which showed a much steeper slope of burial time as a function of size (Tukey's post hoc test for comparison of slopes – not shown). Burial time ranged from 2.4 s to just under 24 s (Fig. 3.4.2). Burrowing was fastest in the fine and medium 1 sand (between 150 and 355); in the very coarse sediment burial time was markedly longer than in the other sands (14.26 s compared to between 6.84 and 11.05 s). For the remaining sand, three significantly different groups existed (Table 3.4.2): fine and medium 1 sand (average burial time of 6.84 s); very fine (8.66 s) and medium 2 sand (8.98 s) and coarse sand (11.05 s). The mixed sand and field data lied between the fine / medium 1 and very fine / medium 2 group.

A generalized linear model of the relation between swash period and sediment grain size was calculated based on data from McArdle and McLachlan (1992). The burrowing of *O. semistriata* takes longer than the average swash period where coarse or very coarse sediment occurs (Fig. 3.4.2). For the medium 2 sand, the larger animals burrow, on average, slower than the time between two swash waves.

The burrowing rate index (BRI) ranged from 2.13 to 10.13. There was no correlation between shell length and BRI (Fig. 3.4.3), except for the medium 2 and coarse sand, where BRI significantly increased with size (p=0.001 and p=0.008 respectively). BRI was highest, and thus burrowing fastest, in fine and medium 1 sand. Lowest BRI was found in the very coarse sediment. Burrowing was fast for all sands and very fast for the fine, medium 1 and mixed sand, as well as for the field data (Fig. 3.4.3).

Table 3.4.1 - Linear regressions of burial time (t) in terms of shell length (*L*) for the six different sand classes, mixed sand and field measurements

Sediment class	Sand (µm)	Burial time (s) vs. shell length (mm)	Adj. R^2	n	F-value	p-value
1	Very fine (<150)	$t = 1.69 + 0.84L$	0.52	40	43.37	p<0.0001
2	Fine (150-250)	$t = -0.29 + 0.87L$	0.67	40	81.37	p<0.0001
3	Medium 1 (250-355)	$t = 0.19 + 0.83L$	0.75	40	118.19	p<0.0001
4	Medium 2 (355-500)	$t = 3.48 + 0.69L$	0.52	40	42.83	p<0.0001
5	Coarse (500-1000)	$t = 4.43 + 0.82L$	0.50	40	39.95	p<0.0001
6	Very coarse (>1000)	$t = -0.16 + 1.75L$	0.66	40	77.85	p<0.0001
7	mixed (209)	$t = 0.76 + 0.88L$	0.37	107	62.01	p<0.0001
8	field (223)	$t = 1.15 + 0.77L$	0.62	26	41.97	p<0.0001

Table 3.4.2 - Significance level (p-value) of the Tukey's post hoc comparison indicating differences in intercept of burial times (BT) vs. shell length regressions (see table 3.4.1) of *O. semistriata* individuals between different sands. Slope was not different, except for very coarse sand

| Sediment class	Sand type	Mean Length (mm)	Mean BT (s)	Fine	Medium 1	Medium 2	Coarse	Mixed	Field	Very coarse
1	Very fine	8.32	8.66	<0.0001	<0.0001	0.55 (NS)	<0.0001	0.42 (NS)	0.10 (NS)	Different slope
2	Fine	8.24	6.84		<0.0001	<0.0001	<0.0001	<0.0001	0.56 (NS)	Different slope
3	Medium 1	8.06	6.84			<0.0001	<0.0001	0.0074	0.80 (NS)	Different slope
4	Medium 2	7.95	8.98				<0.0001	0.0009	0.0004	Different slope
5	Coarse	8.07	11.05					<0.0001	<0.0001	Different slope
7	Mixed	8.62	8.34						0.79 (NS)	Different slope
8	Field	8.22	7.52							Different slope
6	Very coarse	8.26	14.26							
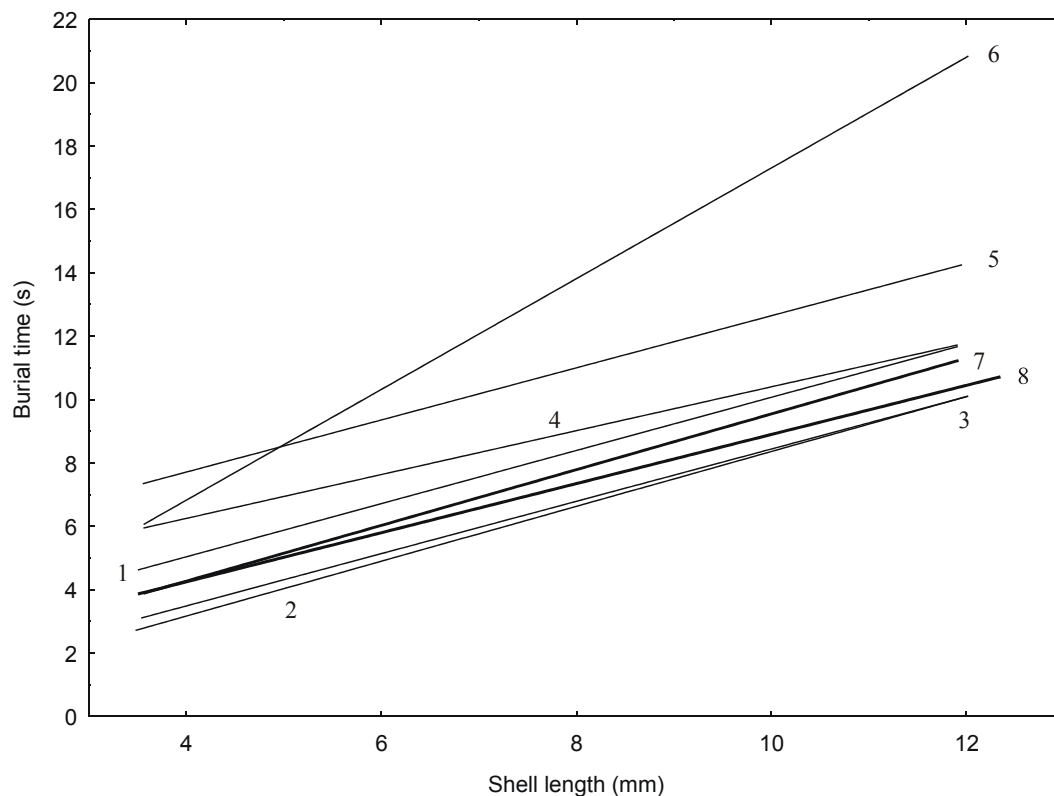
Fig. 3.4.1 – Regressions of burial time as a function of shell length of *O. semistriata* in a series of well-sorted sands. For regression equations see Table 3.4.1.
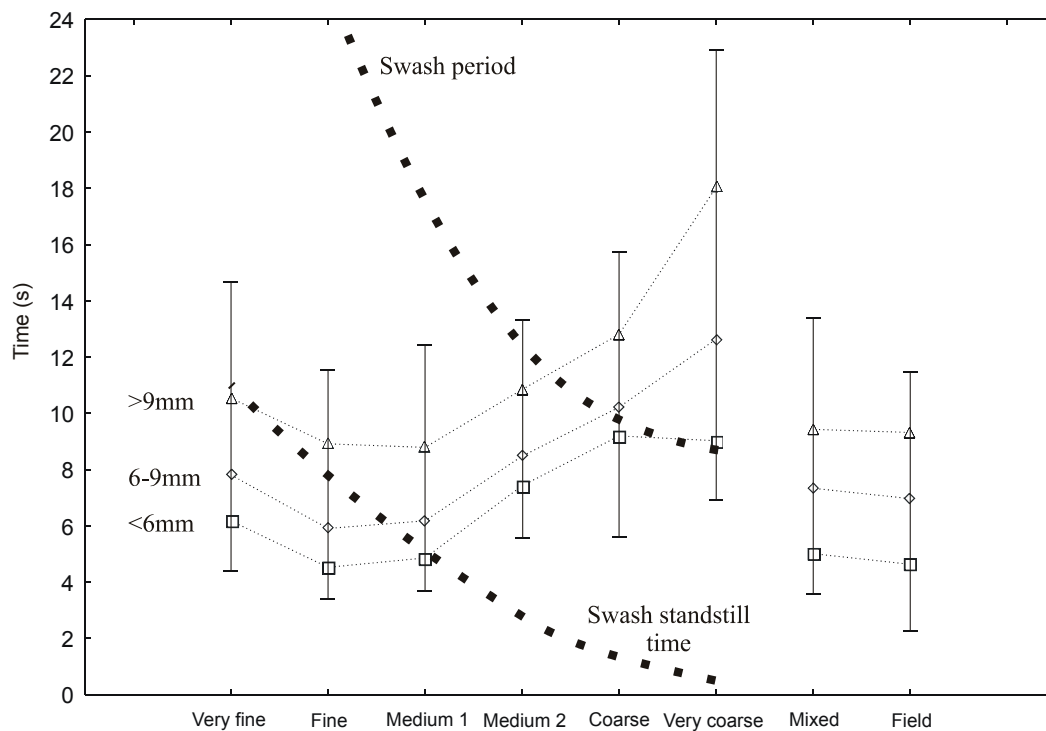

Fig. 3.4.2 - Changes in burial time (Y-axis) with changing sand class (X-axis) for three *O. semistriata* shell length classes. Values are means per size class, with indication of the minimum and maximum range for all animals per sand type. The regression line for swash period (Y-axis) as a function of sediment grain size is based on data from McArdle and McLachlan (1992). The regression for swash standstill time (Y-axis) as a function of sediment grain size is based on data from this paper. Both regression lines are shown as bold dotted lines.

3.4.3.2 Burrowing of *Olivella semistriata* compared to other sandy beach surfers

From the many records in literature on burrowing behaviour of sandy beach macrofauna, those were selected that describe the relation between size and burial time for surfing species (Fig 3.4.4; Table 3.4.3). Twenty-one series of 14 species (two gastropods, four hippid crabs and eight bivalves) were added to the data from this paper. All experiments were done in approximately the same sand size class (around 300 µm, see Table 3.4.3). Most species live in temperate regions, but inhabit a wide range of beach types, from dissipative to reflective. For all species there is a positive relation between size and burial time. Hippid crabs are the fastest burrowers (Fig. 3.4.4). Their burial time lies far below the average swash period on reflective beaches. Except for two slow-burrowing bivalve species (*Tivela stultorum* and *Atactodea striata*) all gastropod and bivalve species seem to have similar burial times or at least comparable relations between burial time and shell length. For all species burrowing is fast (BRI > 2) to very fast (BRI > 6). Highest BRI values for molluscs were found in surfing *Donax*-species. BRI of the mole crabs is in a completely different league, with values up to 140.

3.4.3.3 Distribution of *Olivella semistriata* in relation to sediment

The seven beaches that were sampled quantitatively have different morphodynamics, from highly reflective to almost dissipative, and from very coarse to very find sand (Table 3.4.4). *Olivella semistriata* was found on six of the seven beaches, although the presence of two juveniles on the reflective beach of Ballenita can be regarded as erratic. The population density and abundance increased with increasing sediment grain size to peak at 31,189 ind/m or 520 ind/m^2 on the beach of San Pablo (median grain size 229 µm) and drop to zero from sediment with median grain size of 300 µm on (Fig. 3.4.5). This was more or less the inverse pattern of the burial time, which dropped after the finest sediment class, and raised again from 355 µm on (Fig. 3.4.5).

The six additional beaches that were sampled qualitatively confirm these trends, with the exception of Pedernales (Table 3.4.4). On this beach, no *Olivella semistriata* was recorded, although beach slope and sediment grain size seem to be well within the tolerance range of the species. The bay of Ayangue (Ayangue 1) hosted an extremely large population of *Olivella semistriata* at the south side, whereas the species was absent at the north end of the bay (not shown; distance between sampling transects: 250 m).

Table 3.4.3 - Regression lines of length vs. burial time for different sandy beach surfers, retrieved from literature. Type G = gastropod; B = bivalve and C = crustacean. * Surfing status unclear. ‡ data from Trueman and Brown, 1989. † calculated from regressions for the largest specimens.

| Type	Genus	Species	Paper	Size range (mm)	Sediment class (μm)	BRI	Location	Climate	Beach type	Remarks
G	*Bullia*	*digitalis*	McLachlan &Young, 1982	9-46	± 300	4.6‡	South Africa	warm – temperate	intermediate	at 20°C
G	*Bullia*	*rhodostoma*	McLachlan &Young, 1982	6-49	± 300	4.6‡	South Africa	warm – temperate	intermediate	at 20°C
B	*Donax*	*serra*	McLachlan &Young, 1982	11-64	± 300	-	South Africa	warm – temperate	intermediate	at 20°C
B	*Donax*	*sordidus*	McLachlan &Young, 1982	10-29	± 300	-	South Africa	warm – temperate	intermediate	at 20°C
B	*Donax*	*serra*	Nel et al, 2001	10-65	250-355	±10	South Africa	warm – temperate	intermediate	
B	*Donax*	*sordidus*	Nel et al, 2001	11-26	250-355	±11	South Africa	warm – temperate	intermediate	
C	*Emerita*	*analoga*	Lastra et al, 2004	7-31	250-500	-	Chile	cold – temperate	high intermediate	
C	*Emerita*	*analoga*	Lastra et al, 2004	7-31	250-500	-	Chile	cold – temperate	reflective	
C	*Hippa*	*pacifica*	Lastra et al, 2002	4-22	250-500	-	Hawaii, USA	tropical	very reflective	
G	*Olivella*	*semistriata*	this paper	3.5-11.5	250-355	6.5	Ecuador	tropical	intermediate - reflective	
B	*Donax*	*faba*	McLachlan et al, 1995	? - 24	?	7	Western Australia	cold – temperate	reflective	
B	*Donacilla*	*angusta*	McLachlan et al, 1995	? - 23	?	6	Western Australia	cold – temperate	reflective	
B	*Donax*	*serra*	McLachlan et al, 1995	? - 66	?	11	South Africa	warm – temperate	dissipative - intermediate	
B	*Donax*	*sordidus*	McLachlan et al, 1995	? - 22	?	6	South Africa	warm – temperate	intermediate	
B	*Mesodesma*	*mactroides*	McLachlan et al, 1995	? - 76	?	4	Uruguay	warm – temperate	dissipative	*
B	*Donax*	*hanleyanus*	McLachlan et al, 1995	? - 24	?	15	Uruguay	warm – temperate	dissipative	
B	*Tivela*	*stultorum*	McLachlan et al, 1995	? - 113	?	6	California, USA	temperate	dissipative	*
B	*Atactodea*	*striata*	McLachlan et al, 1995	? - 36	?	2	Queensland, Australia	warm – temperate	intermediate	*
B	*Paphies*	*subtriangulata*	McLachlan et al, 1995	? - 30	?	-	New Zealand	warm – temperate	dissipative	*
C	*Emerita*	*analoga*	Dugan et al, 2000	6 - 34	"medium"	40†	California, USA	temperate	dissipative - intermediate	
C	*Lepidopa*	*californica*	Dugan et al, 2000	10 - 20	"medium"	140†	California, USA	temperate	dissipative - intermediate	
C	*Blepharipoda*	*occidentalis*	Dugan et al, 2000	25 - 65	"medium"	83†	California, USA	temperate	Dissipative - intermediate	
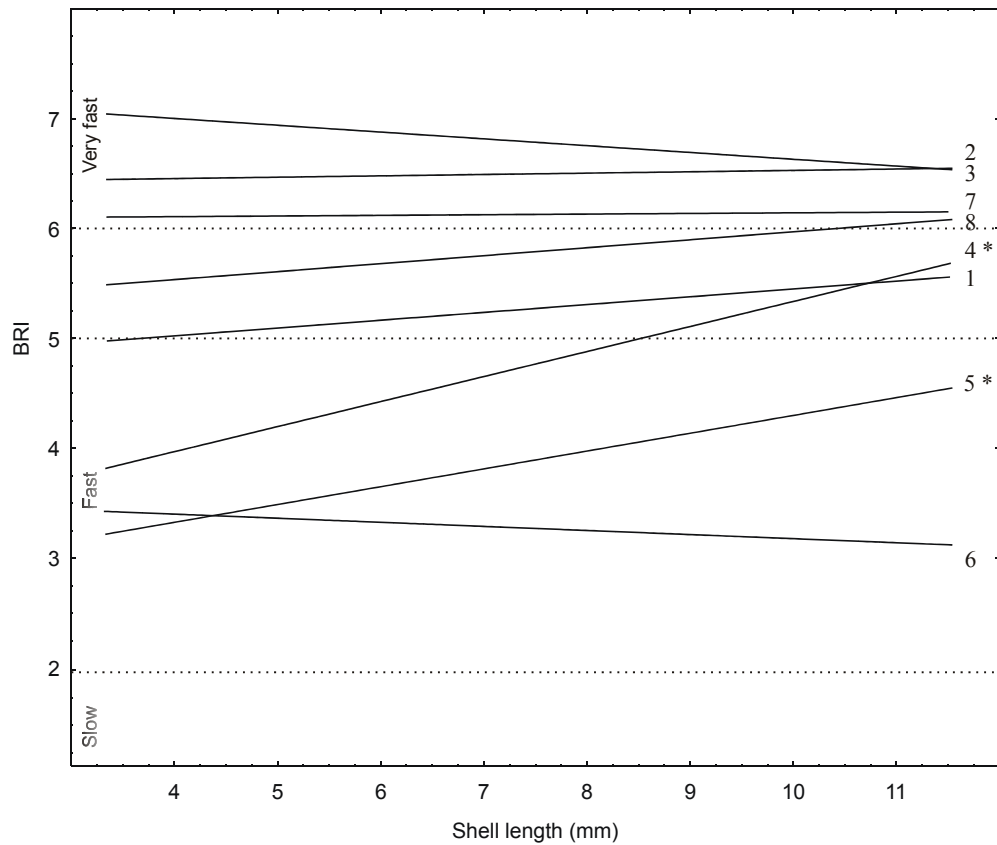
Fig. 3.4.3 - Regression lines for Burrowing Rate Index (BRI) as a function of shell length. Numbers of lines refer to Table 3.4.1; * indicates a significant regression, other regression are not significant. Dotted lines mark the margins between slow, fast and very fast burrowers.
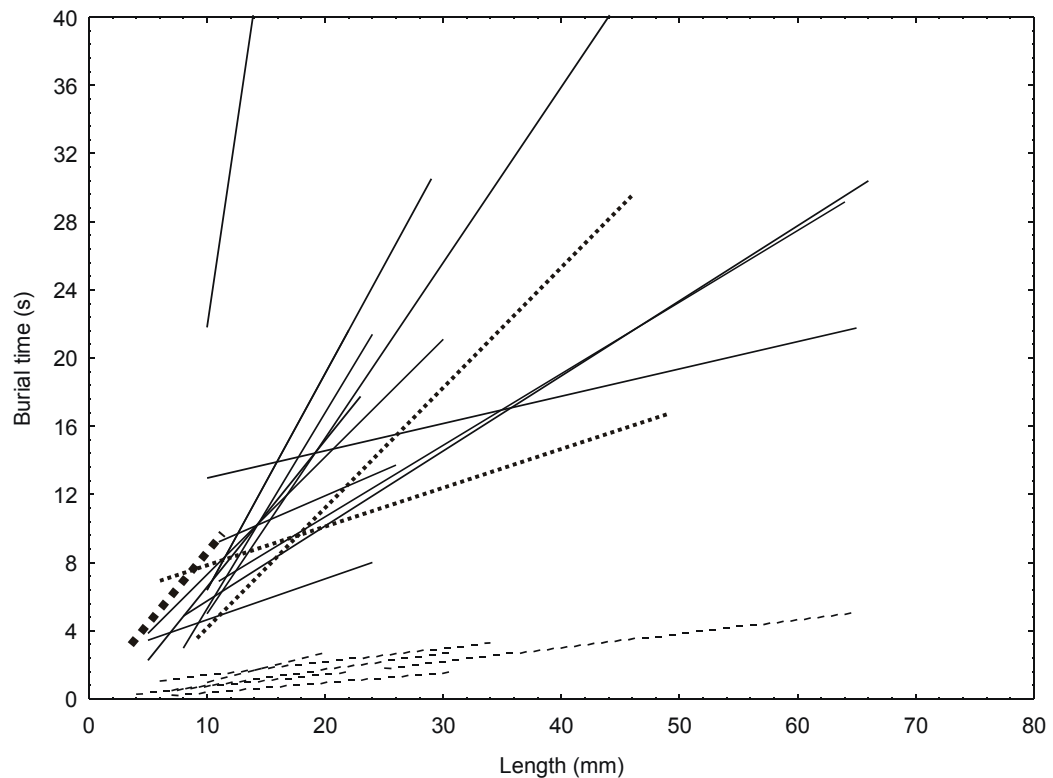

Fig. 3.4.4 – Burial time as a function of length of several surfing species, retrieved from literature and own research. Solid lines indicate bivalves, dotted lines gastropods and striped line indicate crustaceans. The bold dotted line is *O. semistriata*. Y-axis is cut off at 40 seconds. For regression equations, see Table 3.4.3.
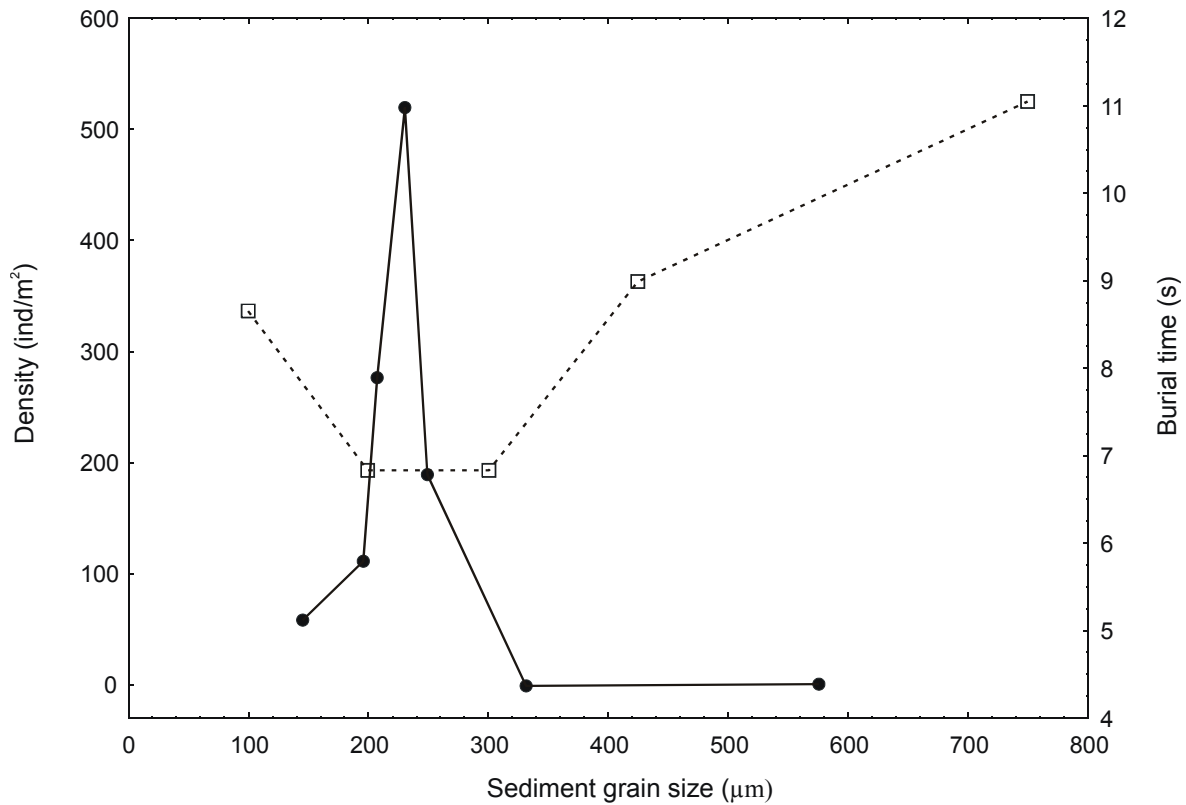
Fig. 3.4.5 – Average density (ind/m^2) of *Olivella semistriata* (Y$_1$-axis; solid line) and burial time of *O. semistriata* (Y$_2$-axis; dotted line) versus sediment grain size (X-axis). Sediment grain size for the density data is the average median grain size per beach (see Table 3.4.4); for the burial time it is the median value of each sediment grain size class.

Table 3.4.4 - Distribution of *Olivella semistriata* along the Ecuadorian Pacific coast. * indicates erratic values (see text).

	Beach	BI	Median grain size (µm)	Slope	Swash standstill time (s)	Average density (ind/m^2)	IST (ind/m)	Remarks
Quantitative	Ballenita	1.56	575	1/7	1.0	*1.66 **	*40.76 **	Very reflective beach
	Briceno	2.74	194	1/63	7.8	111.64	12459.33	Wide beach
	Olon	2.80	144	1/59	7.3	59.29	5650.50	Wide beach, some tourism
	Portete	2.12	331	1/19	2.1	Absent	Absent	Steep pocket beach
	San Clemente	2.48	248	1/38	/	190.06	14482.46	Very touristy beach
	San Pablo	2.46	229	1/34	5.6	519.82	31189.08	Very exposed
	San Pedro	2.50	207	1/36	6.1	277.08	16015.32	Artisan beach fisheries
Qualitative	Ayangue 1	2.48	165	1/32	-	Very abundant		Artisan fisheries and tourism; sheltered bay
	Ayangue 2	1.71	604	1/11	-	No *Olivella*		Steep pocket beach
	Crucita	2.33	261	1/29	-	Abundant		Touristy beach
	Pedernales	2.41	218	1/27	-	No *Olivella*		Pristine, undisturbed
	Playas	2.27	275	1/24	-	Abundant		Very touristy; in Guayas River mouth
	Punta Prieta	2.16	243	1/19	-	Scarce		Undisturbed, steep upper beach

3.4.4 Discussion

3.4.4.1 Burrowing performance of *Olivella semistriata*

Burrowing abilities of the surfing gastropod *Olivella semistriata* were clearly affected by the sediment grain size, yet remained fast (<20 s) even in the coarsest sand we tested. Burrowing was fastest in fine to median sands as well as in the mixed sand and in field conditions. For all tested sediments burial time significantly increased with shell length. Similar results are reported in numerous studies for *Donax* (McLachlan *et al.*, 1995; Net *et al.*, 2001; de la Huz *et al.*, 2002) and mole crabs (Dugan *et al.*, 2000; Lastra *et al.*, 2004). Values of the burrowing rate index (BRI) ranged between three and seven and did not vary with size, suggesting that burrowing is fast to very fast from an early age on and does not improve with age. This was also found in *Donax sordidus*, while BRI increased with shell length in *D. serra* (Nel *et al.*, 2001). The authors ascribed this to the large size of *D. serra*.

The only other known information on the burrowing of *Olivella semistriata* showed BRI values that where much lower than in this study (Dudley and Vermeij, 1989). They found a BRI of 0.57 ± 0.11 or 0.95 ± 0.18 when expressed in seconds (minutes were used by Dudley and Vermeij, 1989), whereas we found values of 3 to 7. So, even though their experiments were done in coarse sediments, there remains a big difference. This could be due to the temperature at which the experiments were conducted (24ºC in this study; not mentioned by Dudley and Vermeij, 1989). McLachlan and Young (1982) demonstrated a clear negative impact of low temperature on the burial time of molluscs. Another difference between the two studies is that we worked with freshly caught animals, where Dudley and Vermeij (1989) kept the animals in the laboratory up to two days, which might have caused starvation and consequently a lower burrowing performance.

The burrowing performance of a mollusc is a function of shell form and structure, density of the animal, burrowing behaviour and sediment characteristics (grain size, thixotrophy and sorting). The relatively good burrowing performance of *Olivella semistriata* could be thanks to the smooth shell, strong foot muscle and large aperture (Vermeij and Zipser, 1986; Dudley and Vermeij, 1989).

Whereas bivalves are infaunal by origin and thus burrowing molluscs *par excellence*, gastropods are primarily adapted to rocky shores (Brown *et al.*, 1989). This might suggest that intertidal sandy beach bivalves are better burrowers than their gastropod counterparts. As far as burial time is concerned, this is contradicted by the results in Fig. 3.4.4: all three surfing gastropod species have burial times that are very similar to or even lower than the surfing bivalves. Taking biomass into account (BRI, see

Table 3.4.3) bivalves indeed seem to have the edge, although their burrowing mode (vertical and deep) is much more energetically costly than the oblique and superficial burrowing of gastropods (Brown *et al.*, 1989).

3.4.4.2 Burial time and distribution of *Olivella semistriata*

Although the distribution pattern of *Olivella semistriata* along the beach type spectrum follows the inverse curve as the burial time (Fig. 3.4.4), it is very difficult to identify a cause-and-effect relation. The species is absent from beaches with median grain size above 300 μm. This is more or less the sediment class present on beaches where the swash period starts to enter the burial time interval (Fig. 3.4.2: medium 2 sand). Swash period, however, is derived from the lower swash boundary (McArdle and McLachlan, 1992), whereas *O. semistriata* occupies the upper swash zone (Chapter 2 and 3). More important to the species is thus the swash interval at the position where they actually sit. Even on very reflective beaches the swash interval at the upper swash boundary is longer than the burial time of *Olivella semistriata*. Towards the dissipative end burial time likewise increases, while swash period and swash interval are much longer than on the intermediate beaches (McArdle and McLachlan, 1991 and 1992) where *O. semistriata* is very abundant. It thus seems unlikely that the low numbers or even absence of *Olivella semistriata* at both reflective and dissipative beaches is limited by their burial time.

3.4.4.3 Burrowing performance of surfers

It is clear from Fig. 3.4.4 that all investigated sandy beach surfers are fast to very fast burrowers. This is indeed a crucial requirement to survive on the exposed sandy beaches where surfers flourish (e.g. Brown *et al.*, 1989; Brown and McLachlan, 1990; Nel *et al.*, 2001; Lastra *et al.*, 2002). After riding a swash wave the animals have to be anchored to the sediment as soon as possible to prevent from being swept away by the next swash wave. This inspired Nel *et al.* (2001) and de la Huz *et al.* (2002) to name the swash period as a limiting factor for survival on sandy beaches. During downward migration the time they have to secure their position is indeed dependent on the swash period or swash interval. Swash interval decreases with increasing slope and from dissipative to reflective beaches, but increases shoreward within the swash zone (Short, 1999). During upward migration, however, the animals have to burrow themselves in the short period of swash standstill, in order to not be carried down the beach again by the same wave. Ellers (1995c), for instance, observed that *Donax variabilis* gains foothold

during or just after swash standstill, when the backwash starts to gain speed. Swash wave standstill is logically much shorter than swash interval. We thus hypothesize that not swash period or swash interval but swash wave standstill time combined with backwash velocity most probably is a limiting factor for the distribution of sandy beach surfers. Swash wave standstill generally decreases and backwash velocity increases towards the reflective beach spectrum (Short, 1999) and is, as such, a valuable part of the swash exclusion hypothesis (McLachlan *et al.*, 1993).

When the swash standstill time (of the upper swash limit) is plotted on the burial time/sediment class graph (Fig. 3.4.2), we can now see that, except for very fine and fine sands, burrowing is not fast enough to be completed while the swash wave is fully extended. If we assume that *Olivella semistriata* can still burrow at low currents, the time they have to burrow could be lengthened (both before and after swash standstill) by a few seconds, bringing medium 1 sand (<350 μm) into the choice of sediment they could live on. Coarser sands in combination with steeper beaches are well outside the tolerance range of the species. So, the burrowing capacity of *O. semistriata* indeed is probably a limiting factor for the distribution towards the reflective end of the beach spectrum.

However, burrowing performance does not explain the low number we found on flat beaches with fine sands. Cubit (1969) hypothesized that surfers require a certain swash action, not reached on dissipative beaches, to be able to surf. This is possibly because a minimum swash velocity is necessary to orientate in the swash (Ellers, 1995c). In Chapter 6 we added that intertidal distance is becoming so long on dissipative beaches that surfing is not an energy efficient strategy anymore.

3.4.4.4 Measuring burrowing performance: some complexities

It has to be noted that burial time itself might not be a good measure for the capability to cope with certain swash conditions. Burial time is generally considered as the time between start of the burrowing movement till the animal is completely covered by sand, and is generally measured in stagnant water (McLachlan and Young, 1982; McLachlan *et al.*, 1995; Dugan *et al.* 2000 and many others). Gaining foothold in the substratum, however, can be secured before the animal is completely covered, especially in bivalves and gastropods, substantially reducing what could be called the *minimal burial time*. Trueman (1971), for instance, found that *Donax* had to be burried at least 2/3 to be anchored securely. This is ecologically more relevant than burial time itself. Note that the *minimal burial time* is dependent on the swash velocity and hence the beach morphodynamics. Additionally, we have observed in the field that burrowing can be speed

up by several second due to sediment transportation in the swash (data not shown). Unfortunately, it is very difficult to investigate the direct influence of wave standstill and sediment transportation on the burrowing or more important the anchoring of swash fauna. Detailed information could be obtained by combining field measurements and experiments in a swash rig (Chapter 5) or a flume tank. To our knowledge, the only attempt to measure burrowing capacity in running water conditions was done by Yannicelli *et al.* (2002) on two *Excirolana* species. They did not find an influence of current. Unfortunately the highest water velocity they used (0.3 m/s) is 10 times lower than the highest swash velocity we measured in the field.

Just as burial time is maybe ecologically not as relevant as previously argued, the same could be said about the Burrowing Rate Index (see also Brown and Trueman, 1994). The BRI was intended to compare different species by calculating the burial time per unit of mass (Stanley, 1970). High values indicate fast burrowers. Large species, however, can be categorized as very fast burrowers because of their weight, although their burial time is very high. And in perspective of withstanding swash conditions, it is the burial time – or minimal burial time as advocated earlier – that is crucial. A large bivalve, for instance, can have a BRI value of 6, just as a lighter and smaller species, yet its burial time will be two or three times higher. This could exactly make the difference between securing position before the next wave comes in or not. Still, the absolute mass of an animal does influence its capacity to cope with certain wave conditions: lighter animals will be carried away at lower swash velocity than heavier species. So weight is important in the ecological relevance of burrowing. Since the *minimal burial time* should be measured in running water, it will automatically inflict the impact of weight.

Another complicating factor in the burrowing of surfers is orientation. Surfers that filter the backwash have to be orientated correctly to do so. *Emerita*-species, for instance, burry themselves seaward (Caine, 1975), whereas *Olivella semistriata* is oriented with the shell mouth shoreward (own observations) and *Donax* burries vertically, anterior end first (Brown *et al.*, 1989; Ellers, 1995c). The correct orientation can be obtained while surfing, just before burrowing of during burrowing. *Donax variabilis* generally burrows in the backwash, even when moving upshore, and is – due to the shell shape - passively orientated with the anterior end shoreward, ready to burrow (Ellers, 1995c). It is thus unlikely that orientation will lengthen the burial time. The same is true for *Emerita*, which turns around before starting to burrow (own observations). *Olivella semistriata*, in contrast, turns around while burrowing during downward migration. We have noted in the field that this can elongate the burial time by several seconds. They only start to turn, however,

after they are burried for about 2/3, so we can assume that this has no effect on the *minimal burial time*.

3.4.5 Conclusions

1) Burial time of *Olivella semistriata* is dependent on sediment grain size and shell length, and lengthens with increasing grain size and shell length.

2) BRI values were found between 3 and 7, indicating that burrowing is fast to very fast.

3) Apart from a few exceptions all macrobenthic surfers show fast to very fast burrowing, with by far the best performances for the mole crabs.

4) Bivalves and gastropods have comparable burrowing capacities.

5) Burial time was not found shorter than the swash period, even under very reflective conditions.

6) We hypothesize that not swash period but swash standstill time at maximum run-up is a limiting factor for *Olivella semistriata* and other mollusc surfers.

7) Swash standstill time on reflective beaches was found to be much shorter (< 4 s) than burial time, and is thus in agreement with the swash exclusion hypothesis. We can conclude that the burrowing capacity of surfing molluscs is indeed very likely limiting for their macroscale distribution.