CHAPTER 6

SURFING ON SANDY BEACHES: AN EFFICIENT STRATEGY TO FLOURISH IN A HIGHLY DYNAMIC ENVIRONMENT?

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Abstract

The gastropod *Olivella semistriata* is a dominant surfer on exposed, intermediate beaches in the tropical part of the East-Pacific. The impact of the swash dynamics on the feeding behaviour of the species was studied in order to improve the understanding of the swash zonation pattern of *O. semistriata*, and its general success on beaches.

The feeding activity of dense patch of *Olivella semistriata* was monitored for 5 to 15 min, while simultaneously noting the swash dynamics. *Feeding time* and *feeding rate* (both expressed per wave) were a function of three swash parameters: *swash distance* (i.e. swash run-up above the monitored patch), *swash time* (immersion time of the patch by a swash wave) and *swash interval* (time between two consecutive swash waves). The longer the swash time, the longer species could feed upon the backwash. Large waves were generally less favourable for feeding: the possibility of the next swash wave interrupting the backwash was very high.

With the combination of the swash parameters (distance, time and interval), the feeding parameters could be modelled in terms of the swash position (i.e. the position relative to the swash boundaries). Both feeding time and feeding rate were found to follow a skewed unimodal curve within the swash zone, with highest feeding time and feeding rate in the upper half of the swash zone. Maximal feeding rate was modelled to be 32.25%. The feeding curves over the swash zone show remarkable similarities with the swash zonation of *Olivella semistriata*, suggesting that the zonation of the species is a result of the feeding opportunities.

A migration model was built to calculate the total feeding time of *Olivella semistriata* per 6 hours as a function of distance travelled per surfing movement. The highest feeding time was found at 17 surfing movements per 6 hours, or 3.5 m per movement (on a beach of 60 m wide).

Finally, using the migration model, a time budget for *Olivella semistriata* was calculated. With the optimal surfing distance of 3.5 m, just over 1% of the time has to be spent surfing (0.16% for emerging from the sediment, 0.47% for surfing itself and 0.73% for burrowing). This allows the species to feed during 30.26% of the time. Under the same conditions, a hypothetical non-migratory species would only be able to feed during 5.72% of the time. Thus, spending no more than 1% of the time or around 5% extra energy by surfing increases the feeding time by 529%, clearly demonstrating the benefits of this behaviour.

3.6.1 Introduction

Surfing or ‘swash riding’, a behaviour in which the swash is used to migrate over the beach face, has been a very successful strategy for animals inhabiting exposed sandy beaches. Surfing is found in a range of molluscs and crustaceans. Well-known examples are the beach clams of the genus *Donax* (Ellers 1995a), beach whelks of the genus *Bullia* (Trueman and Brown, 1976; Brown, 2001) and mole crabs of the genera *Emerita* (Cubit, 1969), *Hippa* (Lastra *et al.*, 2002) and *Lepidopa* (Dugan *et al.*, 2000). Filter feeders, such as *Donax* and most of the mole crabs. use surfing to maintain optimal feeding conditions in the swash (McLachlan and Brown, 2006); *Bullia* rides swash waves in pursuit of its prey (Brown, 2001). They all share several characteristics which are necessary for surfing: (1) active emergence from the sediment; (2) mainly passive though partially controlled riding of the swash – wave uprush when migrating upshore and backwash when migrating downshore; and (3) fast burrowing.

Another example of surfing behaviour is found in the olivid gastropod *Olivella semistriata*, a dominant species on exposed sandy beaches of the intermediate type along the East-Pacific coast of Ecuador (Chapter 1; Addendum 1). Its surfing consists of actively crawling out of the sediment, floating with the swash, using its extended metapodium to control the movement (Olsson, 1956; personal observations), and actively burrowing after surfing. A mucus net between the extended tentacles is used to filter the backwash. No empiric information exists about the surfing itself, although field observations suggest *O. semistriata* surfs in a similar way as other swash riders such as *Donax* (Ellers, 1995), *Bullia* (Brown *et al.*, 1989) and *Emerita* (Cubit, 1969; Caine, 1975).

Surfing has been investigated in numerous macrofaunal species (Ansell and Trueman, 1973; Brown, 1982, 2001; Brown *et al.*, 1989; Cubit, 1969; Dugan *et al.*, 2000; Ellers, 1995a,b,c; Forward, 1986; Lastra *et al.*, 2002, 2004; this thesis). Some studies concentrated on the intertidal dynamics of the surfer’s population (Lastra *et al.*, 2004; Dugan *et al.*, 2000; Chapter 2, 3) whereas others focused on the behavioural aspects of surfing (Lastra *et al.*, 2002; Ellers, 1995a,b,c; Brown, 2001; Forward, 1986). Only few attempts, however, have been made to determine the ecological relevance of surfing. Brown (1982) and Ansell and Trueman (1973) calculated the costs in terms of energy expenditure and time allocation that come with surfing in molluscs of the genera *Bullia* and *Donax* and in an *Emerita* mole crab. They found that surfing only adds an extra 3 to 10% to the daily energy cost. Hence, surfing is an energetically very cheap way of locomotion in terms of distance covered, compared with for instance crawling or burrowing.

While the extra costs of surfing have been studied and seem to be rather limited, no attempt has been made to identify the actual benefits of surfing. It is widely accepted that surfing is an interesting predator-avoidance strategy and that it increased the feeding opportunities (Ansell and Trueman, 1973; Dugan *et al.*, 2004; McLachlan and Brown, 2006). This, however, has never actually been demonstrated.

In this paper, feeding of *Olivella semistriata* was analysed in terms of prevailing swash conditions. In Chapters 2 and 3, we demonstrated that the swash zonation pattern of *O. semistriata* shows a very distinct unimodal shape, which remains nearly constant over the complete tidal cycle. We hypothesized that this specific unimodal swash zonation of *Olivella semistriata* might be a reflection of the changing feeding opportunities over the swash zone. Theoretically, backwash feeding time follows a unimodal pattern within the swash, with very low values at the upper swash limit (hardly any waves are coming that high), gradually increasing towards the lower swash and decreasing again where the interval between swash waves becomes too small to allow feeding. Additionally, a short field sampling of feeding activity at different degrees of beach slope was used to show the impact of beach slope on the feeding behaviour of *O. semistriata.*

Based on the field measurements, two theoretical models were constructed to describe: (1) the feeding rate in terms of swash zonation, and (2) the balance between feeding and migration. This last model is used to calculate a time budget of *Olivella semistriata* and to identify the possible advantage of surfing in terms of feeding opportunities.

This paper thus aims to identify the influence of the swash conditions on the feeding behaviour of the surfing gastropod *Olivella semistriata*, to analyse how the swash controls the time management of the species and to see if the surfing behaviour of *O. semistriata* could explain its success on Ecuadorian sandy beaches.

3.6.2 Material and Methods

3.6.2.1 Study site and period

The surveys were conducted on the sandy beach of San Pedro de Manglaralto, Ecuador. This is an intermediate, exposed beach, with fine sands. The macrofaunal zonation of this beach is described in Chapter 1. Swash zonation of *O. semistriata* from this location is discussed in Chapter 2 and 3. Surveys took place in June and July of 2005. The high tide feeding sampling was done on the 2nd of July 2004.

3.6.2.2 Feeding survey (Fig. 3.6.1)

Feeding activity of *Olivella semistriata* in relation to swash climate was monitored by filming a patch of animals in the field using a Sony DV (50Hz) video camera. The start and ending of a feeding bout could be identified on the video images. At the same time, swash data were recorded. Plastic poles placed at 1 m intervals were used as reference frame for monitoring the swash position. Each survey lasted for 10 to 20 minutes. In total, six surveys were filmed during falling tide, four during upcoming tide.

The videotapes were analysed frame by frame and the following activities were timed: start of the flooding of the patch; swash standstill; end of patch flooding; start of feeding; end of feeding. Wave position of every swash wave was also recorded. Where possible, the number of feeding cycles and migration in the patch was noted. From these data, a set of parameters was calculated:

- total time: time between start and end of one survey
- swash distance: swash run-up above the monitored patch; a big wave causes a long swash distance and vice versa
- swash interval (a-g): time between two waves that fully cross the patch
- swash time (a-e): time from the start of flooding till the end of the backwash
- % flooded: ratio of swash time and swash interval
- feeding time at standstill and during backwash: see Fig. 3.6.1
- feeding time: sum of feeding time at standstill and feeding time during backwash
- interrupted swash: when a new incoming wave interrupts the backwash of the previous wave (i.e. when g falls before f, see Fig. 3.6.1)

- time before feeding (a-d): time between the start of the flooding and the start of feeding during backwash
- feeding rate: ratio of the feeding time and the swash interval of one swash wave
- total feeding time: total feeding during one survey
- total feeding rate: ratio of total feeding time and total time of one survey

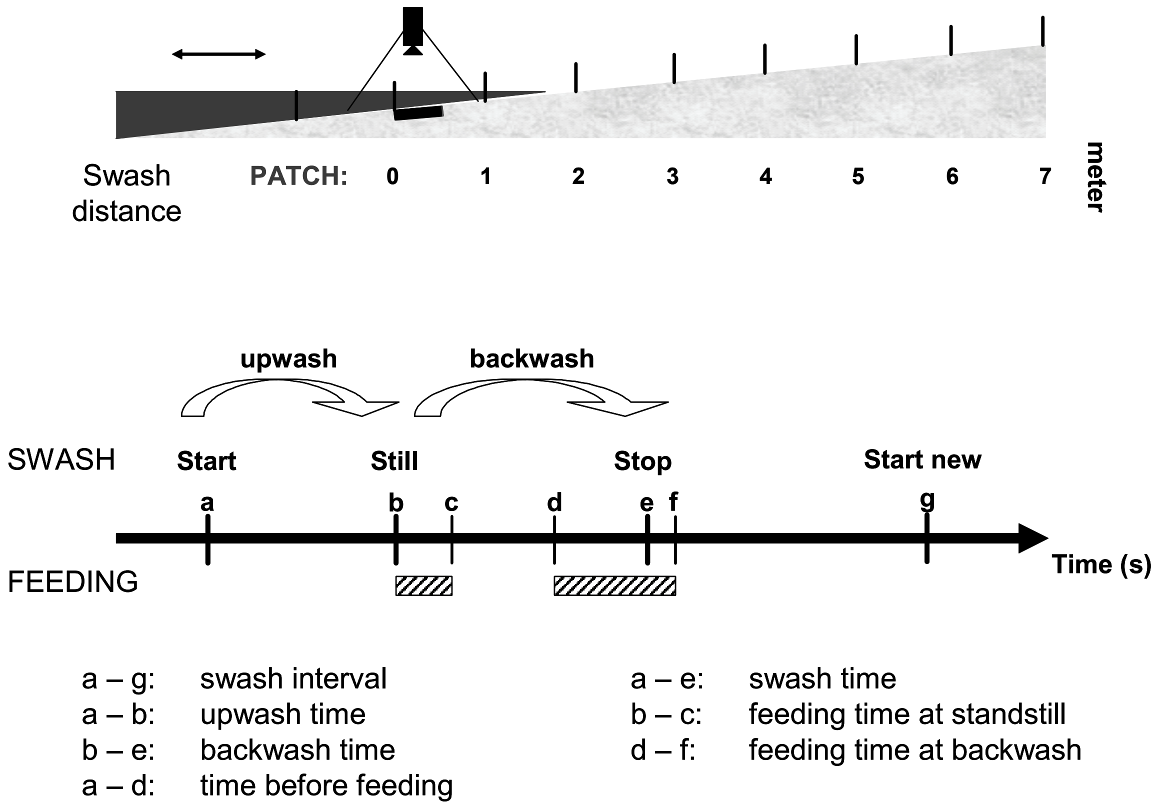


Fig. 3.6.1 - Setup of the feeding survey and schematic overview of the parameters retrieved from the videotapes. Start (a) indicates the start of the flooding of the patch by a swash wave; Still (b) is when there is no visual cross-shore swash movement over the patch. Stop (e) is when the swash wave has completely retreated from the monitored patch.

3.6.2.3 High tide feeding sampling

To test the influence of beach slope on the feeding behaviour of *Olivella semistriata*, two short perpendicular transects were sampled in the high tide swash zone of the San Pedro beach. One transect was situated on the steep slope of a cusp, the other transect was placed on a very flat part of the upper beach (the truck entrance to the beach). The two sites were just 22 m apart (along-shore) and were subjected to the same

wave regime. After a swash wave, feeding activity was recorded by taking two digital pictures (4 megapixel) of a 30 x 30 cm quadrant. Subsequently two replicate core samples (10 cm diameter, to 15 cm depth) were collected - from the photographed spot - to assess the density of *Olivella semistriata*. This was repeated at five different spots for both transects.

Relative beach slope was measured for both transects using a leveller. Breaker height and period were assessed by monitoring 10 consecutive waves. At each transect the position of 10 consecutive swash waves was noted.

The number of feeding specimens was counted from the pictures, and was calculated to individuals per square meter. Densities from the samples were also expressed as ind/m^2.

3.6.2.4 Statistical analyses

Differences in swash and feeding parameters between the surveys sampled during *upcoming* or *falling tide*, and on the *low* or *high beach* were tested with a mixed effects model (*survey* as random effect). Univariate correlation between swash and feeding parameters was executed with Pearson’s correlation test. Feeding parameters (time before feeding, feeding time and feeding rate) were expressed as a function of swash parameters (distance, time and interval) by first or second order linear regression.

For regression analyses of the feeding survey data with several fixed and random factors, Generalized Linear Mixed Models (GLMM) were calculated (McCullagh and Nelder, 1989) using the proc MIXED statement in SAS 9.1 (SAS Institute Inc, 2004). The fixed effects were *time* (per survey, starting at 0 for the first wave of each survey), *swash time*, *swash interval*, *swash distance* and all possible interactions. *Survey* and the interaction *survey*time* were the random factors. Non-significant parameters were eliminated by a backward procedure. The model for feeding time (s) was performed on log-transformed data, the model for feeding rate (%) on acrsin-transformed data (Underwood, 1981).

To detect differences in environmental (swash velocity) and biological (density, feeding and the ratio between density and feeding) variables between the two transects of the feeding sampling, a Student t-test or a non-parametric Mann-Whitney U test was used. The assumption of homogeneity of variances was tested with Levene’s test (Underwood, 1981).

3.6.3 Results

3.6.3.1 Feeding survey

Ten surveys were videotaped and analyzed, four during upcoming tide, six during falling tide (Table 3.6.1). All but two surveys were placed on the low beach (i.e. under the low tide effluent line). Average swash distance (relative to the monitored patch) ranged between 1.3 and 11.4 m; high swash distance indicates a patch low in the swash. Most surveys had around 50% of the swash waves interrupted; two surveys had no interrupted swash waves, two surveys had more than 85% interrupted swash waves. The average feeding rate per wave, i.e. feeding time during one wave against swash interval, was found between 38 and 70%, resulting in a total feeding rate (total feeding time against total time of the survey) of 14 to 40%. Feeding was observed at swash velocities below 0.53 ± 0.03 m/s.

Swash time and swash interval were higher during falling tide than during upcoming tide (Table 3.6.2); swash distance was not significantly different. Feeding time at backwash was much shorter during upcoming tide, resulting in a lower overall feeding time. Feeding rate, however, did not differ significantly. Swash time was significantly lower on the high beach than on the low beach, as were feeding time at backwash and total feeding time. There was no significant difference between feeding rate on the high or low beach.

There was a very strong correlation between the following five parameters: swash distance, swash time, swash interval, time before feeding and feeding time (Table 3.6.3). Only swash distance and swash time were not correlated. The only negative correlations were between swash distance and feeding time and swash distance and swash interval.

Table 3.6.1 - Overview of the feeding survey data.

Survey number	Tide	Location	N (waves)	% interrupted	% flooded	Total time (s)	Average swash distance (m)	Average swash intrerval (s)	Average swash time (s)	Average time before feeding (s)	Average feeding time (s)	Total feeding time (s)	Average feeding rate (%)	Total feeding rate (%)
1	down	Low beach	10	50	54	693	3.9	69	37	14	20	221	60	32
2	down	Low beach	11	45	68	478	3.2	43	29	13	17	187	58	39
3	up	Low beach	20	65	66	773	3.3	39	25	10	15	308	61	40
4	up	High beach	9	0	25	470	1.3	52	13	6	7	65	55	14
5	up	High beach	17	29	75	340	3.2	20	15	9	6	98	38	29
6	down	Low beach	6	50	43	379	3.1	63	27	18	12	75	46	20
7	down	Low beach	18	44	41	840	6.1	47	35	24	13	240	70	29
8	down	Low beach	9	89	89	448	5.6	50	44	16	22	197	50	44
9	down	Low beach	3	0	25	259	2.0	86	22	9	15	44	67	17
10	up	Low beach	39	95	97	806	11.4	21	20	32	7	272	35	34

Table 3.6.2 - Mixed effects models for differences of swash and feeding parameters between surveys (as random factor) monitored at upcoming or falling tide and on the low or high beach. F- and p-values are listed. For the actual data, see Table 3.6.1.

		Upcoming vs. falling tide		Low vs. high beach	
	DF	**F-value**	**p-value**	**F-value**	**p-value**
Swash time (s)	132	14.39	0.0002	7.11	0.0086
Swash distance (s)	131	0.21	0.6470	1.26	0.2635
Swash interval (s)	132	8.00	0.0054	0.88	0.3505
Feeding time at standstill (s)	44	2.34	0.1330	no values for high beach	
Feeding time at backwach (s)	87	7.32	0.0082	12.56	0.0006
Feeding time (s)	132	8.04	0.0053	4.50	0.0357
Feeding rate (%)	132	0.12	0.9052	1.27	0.2624

Table 3.6.3 – Pearson's correlation matrix of the main parameters of the feeding survey. Non-significant correlations are given in italic.

Parameter	N	Range	Average ± S.D.	Swash time	Swash interval	Time before feeding	Feeding time
Swash distance (m)	141	0.5 – 21.5	6.3 ± 5.1	*0.111 p=0.1882*	-0.200 p=0.0173	0.861 p<0.0001	-0.210 p=0.0127
Swash time (s)	142	2 - 84	25 ± 15	---	0.593 0<0.0001	0.720 p<0.0001	0.801 p<0.0001
Swash interval (s)	142	2 - 183	39 ± 34		---	0.205 p=0.0471	0.653 p<0.0001
Time before feeding (s)	94	0 - 39	14 ± 10			---	0.381 p=0.0002
Feeding time (s)	142	0 - 62	12 ± 11				---

There was a particularly significant linear relation between swash distance and time before feeding (Fig. 3.6.2). For feeding time, swash distance (Fig. 3.6.3a), swash interval (Fig. 3.6.3b) and swash time (Fig. 3.6.3c) were significant predictors: the longer the swash time, the longer the feeding time. With both swash distance and swash interval, the relation was parabolic; feeding time peaked at a swash distance of 3 m and a swash interval of 100 s.

Three examples of surveys are shown in Fig. 3.6.4: one survey was placed low in the swash and as such had 95% of the swash waves interrupted (Fig. 3.6.4a), resulting in very few feeding opportunities during the backwash but with a fair amount of feeding during swash standstill. The second survey was positioned on the high beach, around the effluent line (Fig. 3.6.4b). No swash waves were interrupted here, swash distance was

much shorter and there was no feeding at swash standstill. Fig. 3.6.4c shows a survey from the middle of the low beach swash zone, with a clear balance between feeding at swash standstill and feeding during the backwash.

Generalised linear mixed models with feeding time or feeding rate as dependent variables and swash distance, swash interval and swash time as predictors gave highly significant results (Table 3.6.4). Swash interval was not retained as a predictor for feeding time (Table 3.6.4). Feeding time always increased with increasing swash time, but the increase was steeper at short swash distances (Fig. 3.6.5). The feeding that existed with very short but big waves (<20 s and >20 m) was restricted to feeding at standstill (see also Fig. 3.6.4a). The feeding rate was high where waves were small but swash intervals were short or where waves were big and intervals long (Fig. 3.6.6a); the feeding rate was very low to even zero when big waves followed each other rapidly or when small waves were far apart in time (Fig. 3.6.6a). Feeding rate was highest when the swash time was close to the swash interval (Fig. 3.6.6b).

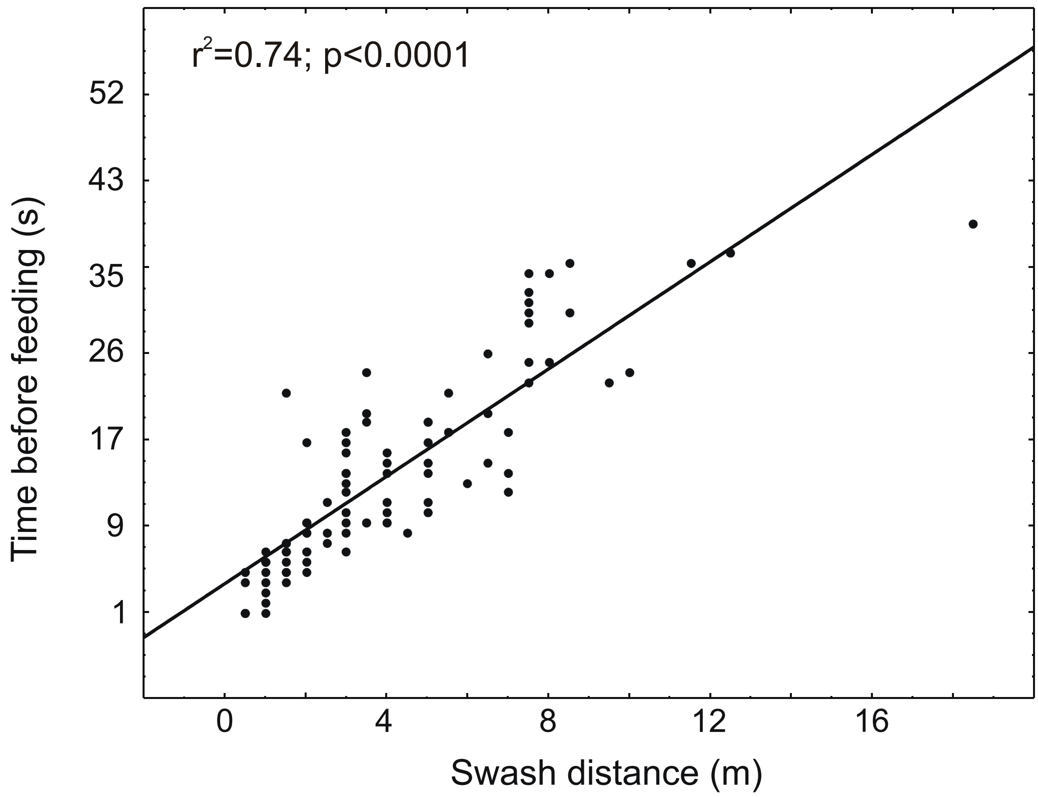
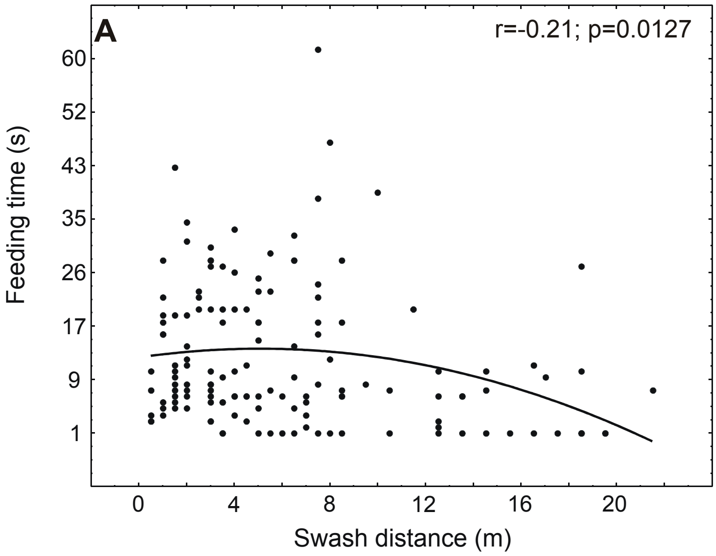
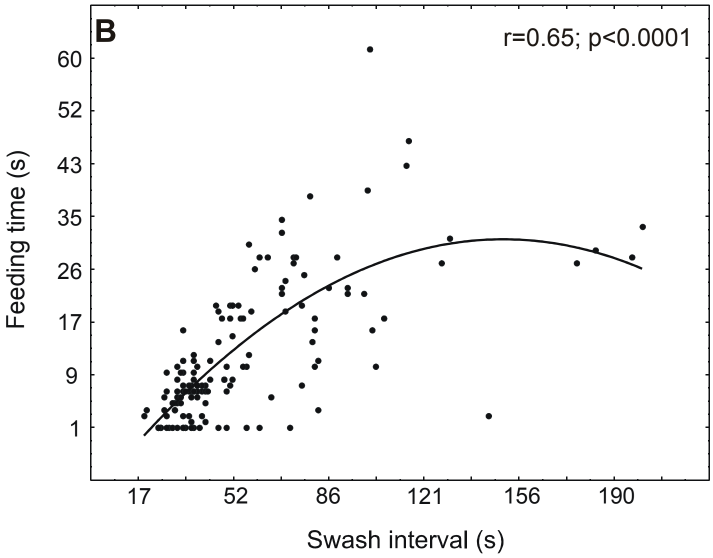


Fig. 3.6.2 - Time before feeding (y-axis) as a function of swash distance (x-axis). Line represents linear regression, with r^2 and p-value





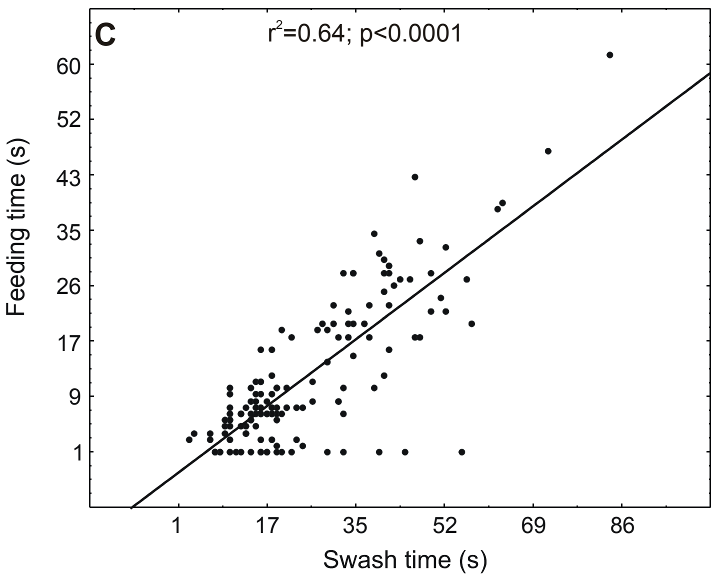


Fig. 3.6.3 – Scatter plots of feeding time (y-axis) as a function of A) swash distance (with second order linear regression), B) swash interval (with second order linear regression) and C) swash time (with first order linear regression).

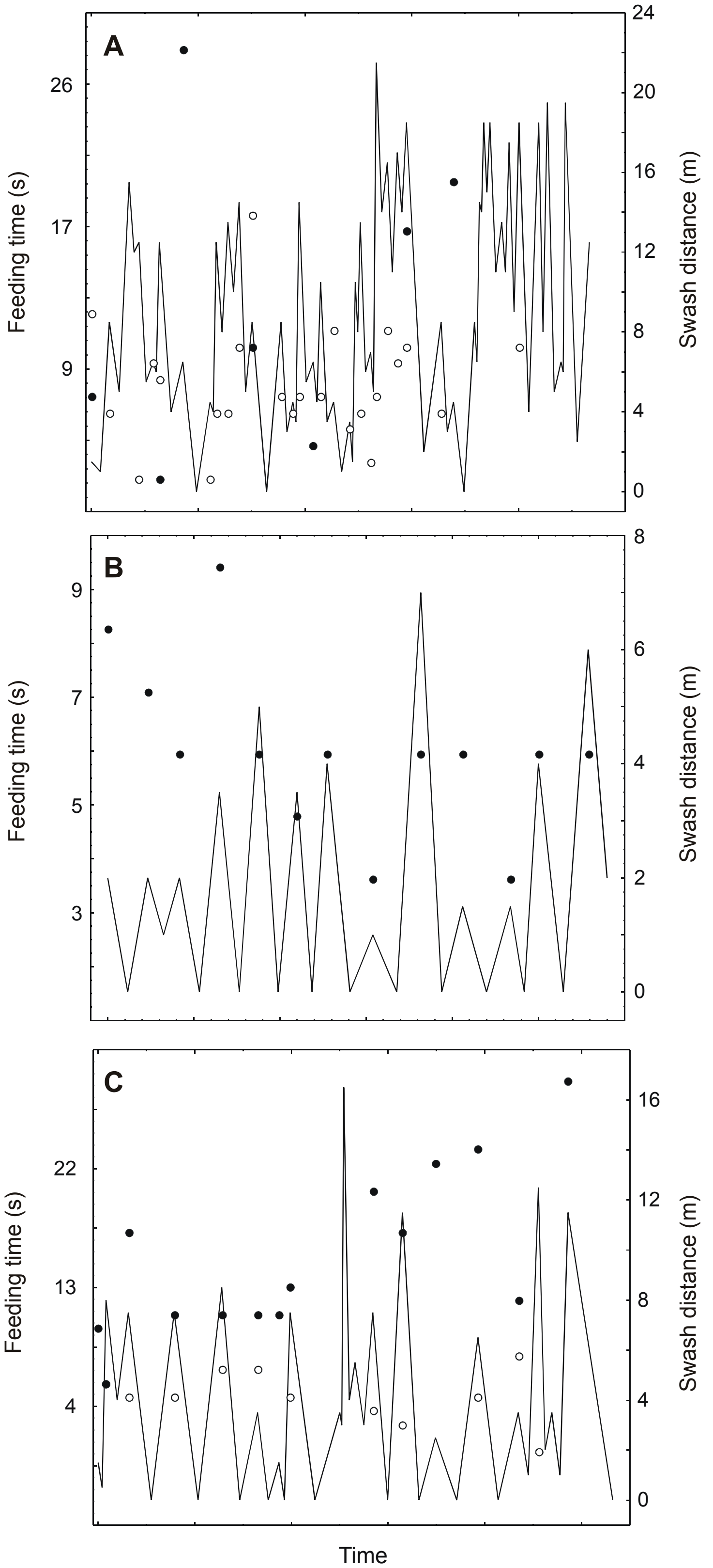


Fig. 3.6.4 – Three examples of the feeding surveys. Closed dots represent the feeding time during backwash and open dots feeding time at swash standstill (feeding time on Y_1-axis). Solid lines illustrate the swash dynamics (swash distance on Y_2-axis; 0-value indicates the monitored patch). A) Survey (number 10) low in the low beach swash with many interrupted waves (solid line not reaching 0-level). B) Survey (number 5) on the high beach (around the Effluent Line). C) Survey (number 7) in the middle of the low beach swash with 44% interrupted waves.

Table 3.6.4 - GLM Models for feeding time (log-transformed data) and feeding rate (arcsin-transformed data)

	Feeding time (s)					Feeding rate				
Parameter	**DF**	**Estimate**	**Standard error**	**t-value**	**p-value**	**DF**	**Estimate**	**Standard error**	**t-value**	**p-value**
Intercept	9	1.1787	0.2485	4.74	0.0011	9	1.0490	0.1000	10.48	<0.0001
Fixed effects										
Time (s)	122			-0.70	0.4853	122			-0.62	0.5392
Swash time (s)	127	0.0877	0.0141	6.24	<0.0001	123			0.62	0.5364
Swash interval (s)	123			1.38	0.1711	124	-0.0125	0.0031	-4.00	0.0001
Swash distance (m)	127	-0.2137	0.0467	-4.57	<0.0001	124	-0.1296	0.0223	-5.81	<0.0001
*Swash time * Swash time*	127	-0.00045	0.00020	-2.28	0.0245	124	0.00031	0.00007	4.57	<0.0001
*Swash distance * Swash distance*	127	0.0050	0.0023	2.19	0.0300	124	0.0029	0.0009	3.32	0.0012
*Swash interval * Swash interval*	124			-0.85	0.3954	124	0.00003	0.00002	2.08	0.0391
Swash interval Swash distance	120			0.15	0.8829	124	0.0025	0.0007	3.68	0.0003
*Swash interval * Swash time*	121				0.8516	121			0.18	0.8580
*Swash time * Swash distance*	126			-0.93	0.3560	120			0.18	0.8571
*Swash time * Swash interval * Swash distance*	125			1.49	0.1383	124	-0.00004	0.00001	-3.16	0.0020
Random effects										
Survey		0.0743	0.0591				0.0101	0.0075		
*Survey * Time*		/	/				/	/		

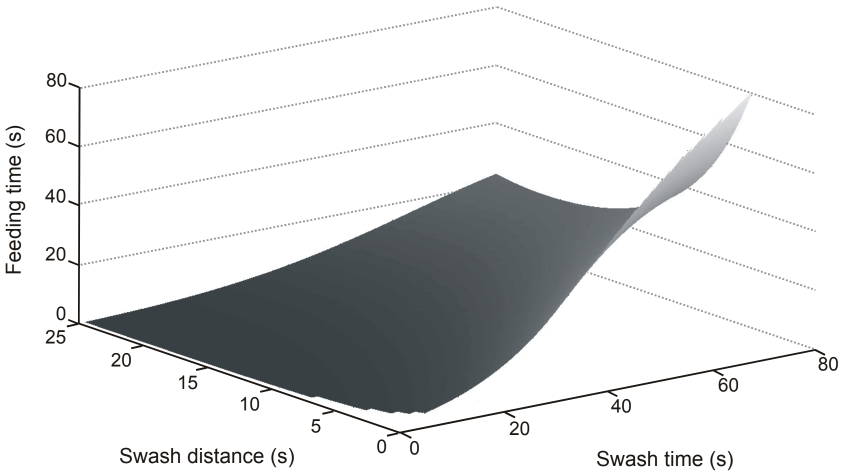


Fig. 3.6.5 – 3D chart based on the GLM Model for feeding time. Feeding time is shown as a function of swash distance and swash time.

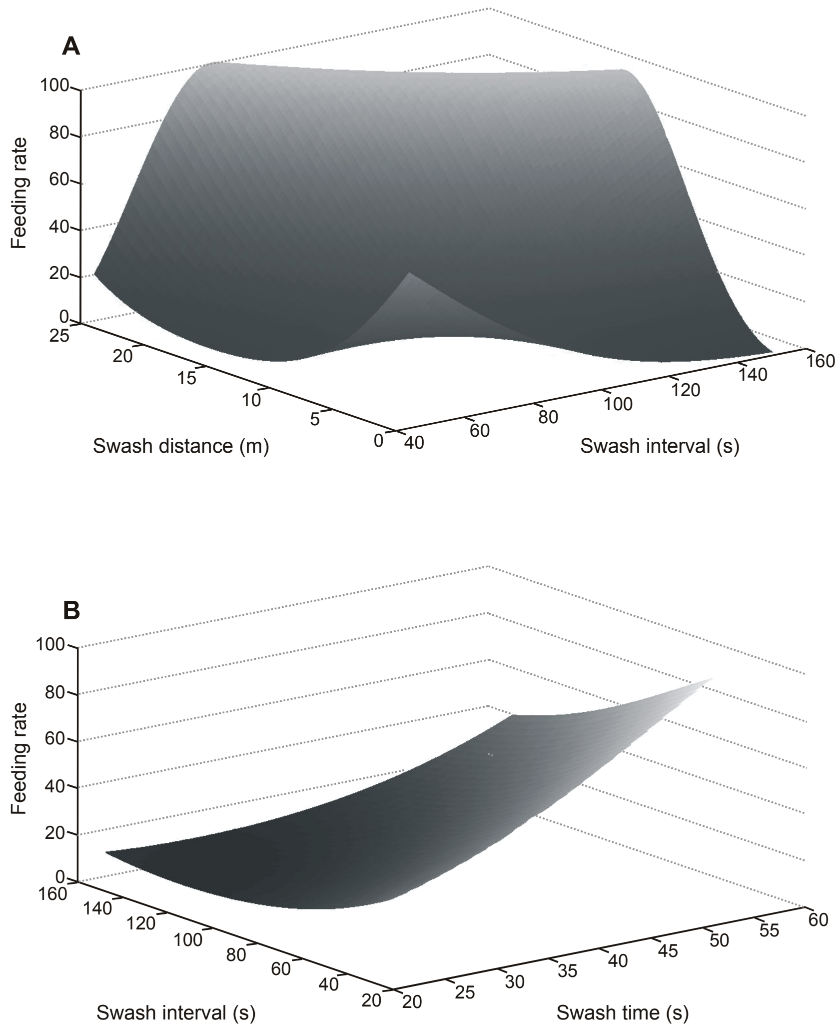


Fig. 3.6.6 - 3D chart based on the GLM Model for feeding rate. Feeding rate is shown as a function of A) swash distance and swash interval (at the modal value of swash time: 25s); B) swash interval and swash time (at the modal value of swash distance: 3m)

3.6.3.3 High tide feeding sampling

The slope of the flat transect was obviously flatter than of the steep transect; this was especially in the part where the samples were taken (sampling area) (Fig. 3.6.7; Table 3.6.5). Both uprush and backwash speeds were lower on the flat transect, though this was only significant ($p<0.05$) for the backwash speed (Table 3.6.5). Sediment grain size was comparable between the two transects; penetrability of the sediment was not measured, however, it was very clear that on the steep slope, most of the backwash ran back through the sediment, whereas on the flat slope the backwash was much more significant.

Although densities were higher on the steep transect, no feeding activity could be observed (Fig. 3.6.8). Yet, all stations on the flat transect had apparent feeding activity, with 22 to 522 ind/m^2 feeding on the backwash. The ratio feeding/density was thus obviously much higher for the flat transect.

Table 3.6.5 - Environmental data of high tide feeding sampling. NS indicates non-significant t-test : *DF*=18, t=1.95 with p=0.067; ** significant t-test: *DF*=18, t=3.23 with p=0.005

	Breaker height (m)	Breaker period (s)	Distance (m)	Elevation drop (m)	Slope	Sampling area (m)	Elevation drop sampling area (m)	Slope sampling area	Upwash speed (m/s)	Backwash speed (m/s)	Sediment grainsize (µm)
Steep	0.78	14.4	40	2.50	1/16	5 – 15	0.96	**1/9**	1.95 (NS)	**1.31** **	241
Flat			40	2.06	1/19	6 – 15	0.47	**1/21**	1.44 (NS)	**0.95** **	228

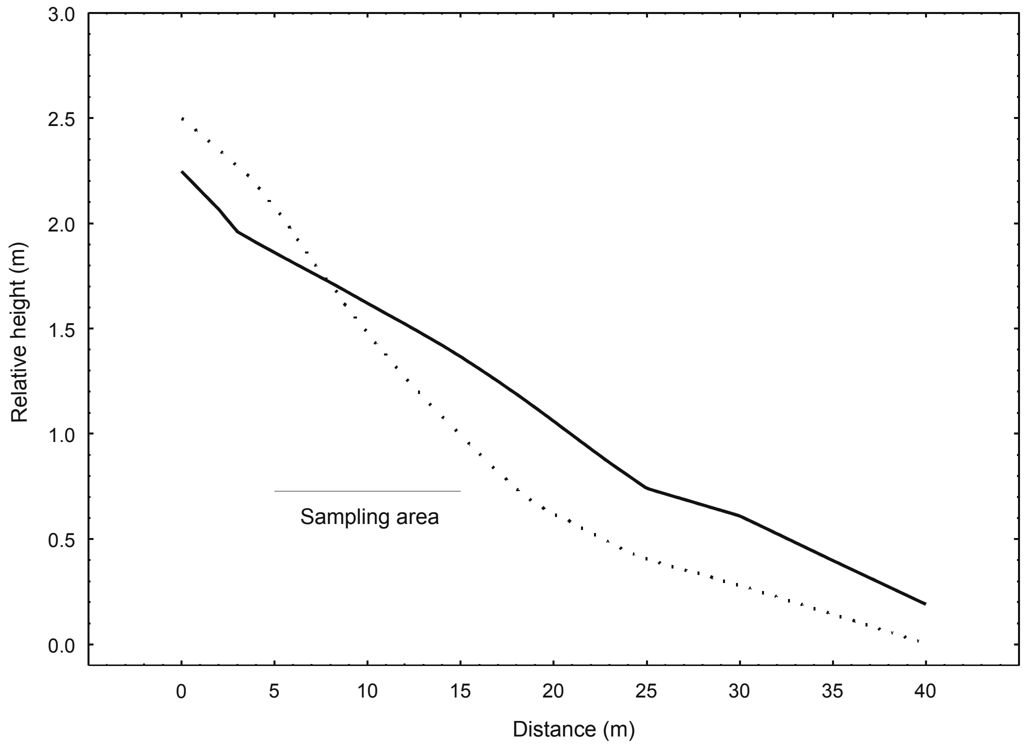


Fig. 3.6.7 - Profile of the two sampled transects. The solid line is the flat transect, the dotted line the steep transect. The part of the transect that was sampled is indicated as 'sampling area'. The 0-point on the X-axis is a fixed reference point on the high beach.

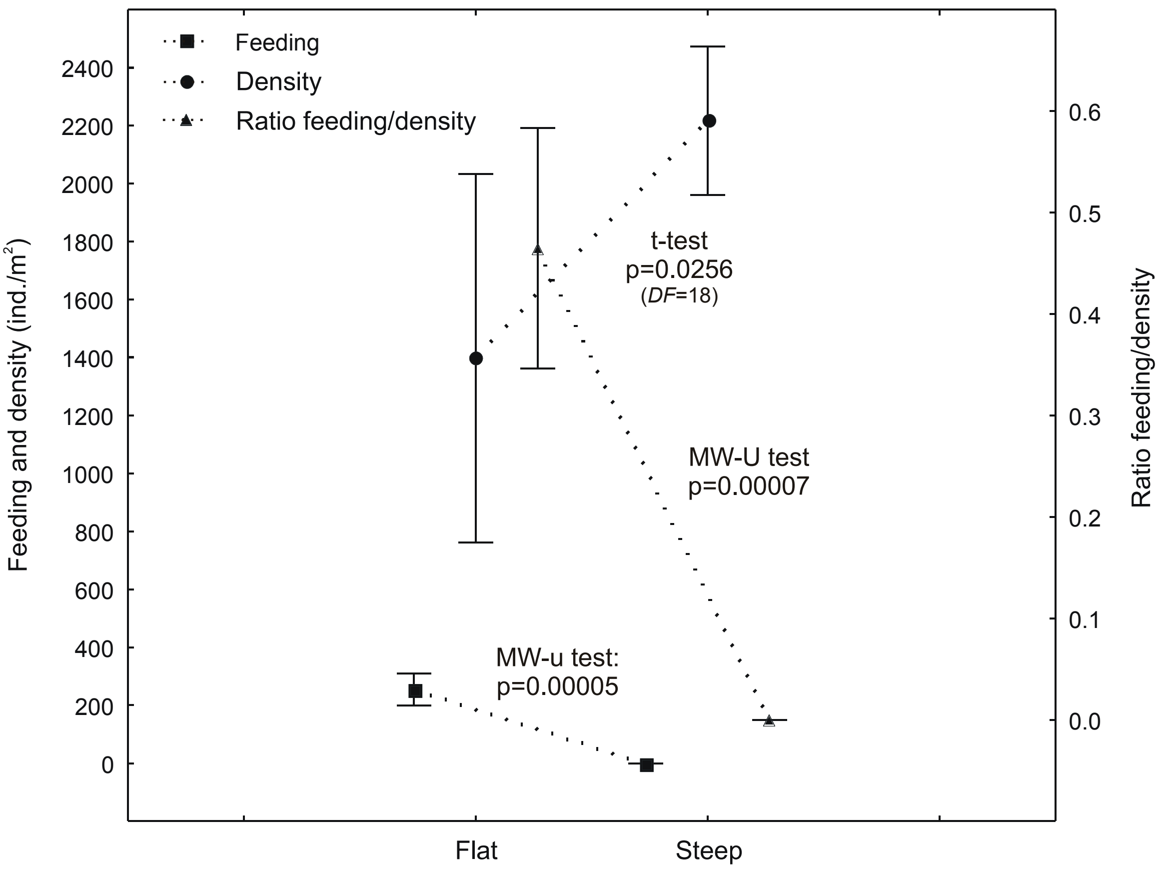


Fig. 3.6.8 - Differences in feeding (Y_1-axis), density (Y_1-axis) and ratio feeding/density (Y_2-axis) between the steep and flat transect, with indication of the p-values.

3.6.4 Theoretical models

3.6.4.1 Feeding (zonation) models

With the information from the feeding survey we modelled the theoretical feeding time (FT) and feeding rate (F) according to position in the swash (S). This is the position relative to the upper and/or lower swash boundary at a given time, with S=0 being the lower swash limit. To do so, the following assumptions had to be made (1) the upper and lower limit of the swash zone stay constant for a certain period of time, and (2) the width of the swash zone is 20 m (see also Chapter 1), so 0 ≤ S ≤ 20.

With the data from the feeding survey (see higher) the feeding time (FT) and feeding rate (F) were modelled in function of the swash distance (D), swash interval (I) and swash time (T) with the following GLM Models (Table 3.6.4):

$$FT = e^{\left(1.1787+0.088\cdot T-0.214\cdot D-0.00045\cdot T^2+0.0050\cdot D^2\right)}$$ **(eq. 1)**

$$F = \left[\sin\left(\begin{array}{l}1.0490\ -0.0125\cdot I\ -0.1296\cdot D+0.0025\cdot \mathrm{I}\cdot \mathrm{D}+\\ 0.0029\cdot \mathrm{D}^2+0.0003\cdot \mathrm{T}^2+0.00003\cdot \mathrm{I}^2\ -0.00003\cdot \mathrm{T}\cdot \mathrm{I}\cdot \mathrm{D}\end{array}\right)\right]^2$$ **(eq. 2)**

Each of the predictors (D,I and T) had to be expressed in terms of position in the swash (S):

- to calculate the swash distance (D) in function of the position in the swash (S), an algorithm was created based on the average swash distance (and its distribution) from a range of field measurements. From the average swash distance and its distribution a hypothetical set of 20 consecutive waves was generated. For each of these waves the swash distance was then determined in function of S, going from 0 to 20 (Appendix 1). This itineration was repeated 1000 times and resulted in the following equation:

$$D = -0.0004\cdot \mathrm{S}^3+0.0404\cdot \mathrm{S}^2-1.289\cdot \mathrm{S}+13.173$$ (eq. 3)

- the distribution of the swash interval (I) in function of swash distance (S) was calculated from field data: the swash period, i.e. the swash interval at S=0, was 17 s. The maximum swash interval (at S=20) was 200 s. This gave the following equation:

$$I = 0.0345\cdot \mathrm{S}^3+0.4055\cdot S^2+3.4289\cdot \mathrm{S}+14.925$$ (eq. 4)

- swash time (T) could be predicted by swash interval (I) and swash distance (D) through a GLM Model (fixed effects: I, D, I^2, D^2 and I*D; random effect: surveys; *DF*=127, p<0.0001 for all parameters) and could thus be described as:

$$T = 7.088 + 0.4333 \cdot I + 0.04895 \cdot I \cdot D - 0.0394 \cdot D^2 - 0.0025 \cdot I^2 \qquad \text{(eq. 5)}$$

The variables I, T and D from eq. 1 and 2 can now be replaced by eq. 3, eq.4 and eq. 5. These are the models of feeding time (FT) and feeding rate (F) in function of position in the swash (S). The resulting graphs for a swash zone of 20 m width are given in Fig. 3.6.9. Longest feeding time is obtained at a swash position of 15.38 m (i.e. at 23.1% from the upper swash limit; for comparison with zonation data from Chapter 3, which are listed relative to the upper swash limit); the feeding rate peaks, with a value of 32.25 %, at a swash position of 11.42 m (i.e. at 42.9% from the upper swash limit). The curve of both models can be described as a skewed unimodal curve.

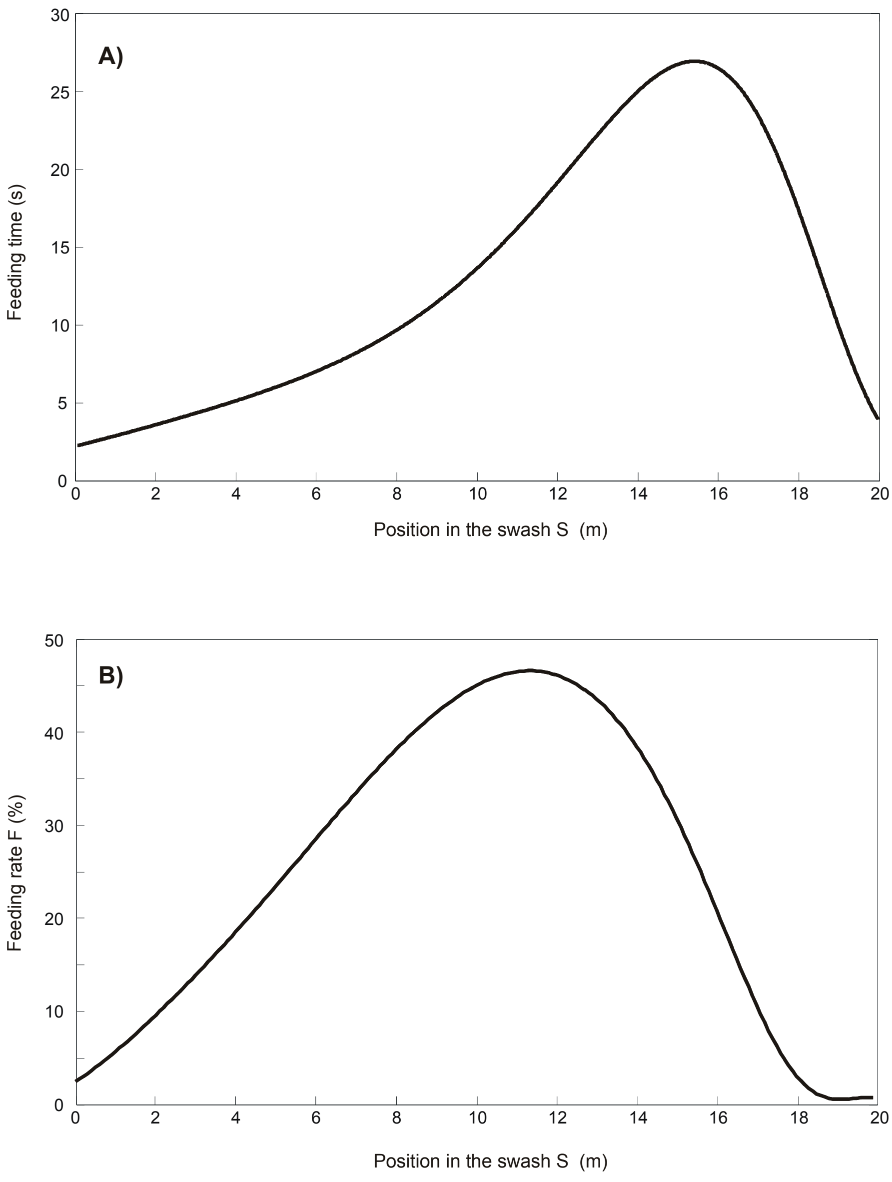


Fig. 3.6.9 - Graph of the feeding model with A) predicted feeding time and B) predicted feeding rate (F) in terms of position in the swash (S). S=0 is the lower swash limit, S=20 is the upper swash limit.

3.6.4.2 Migration model

The feeding rate model is a fixed model and does not include the shift of the swash zone over the beach with the tide. Consequently, this model does not take account of the migration of the animals. To include the loss of feeding time due to migration (i.e. emerging from the sediment, surfing and burrowing) the fixed feeding rate model was extended to a dynamic migration model over time. This migration model covers the total feeding time, based on the feeding rate model, during half a tidal cycle (6h).

The set of assumptions was expanded with the following:

- the beach profile is uniform and so are the environmental and feeding conditions over the intertidal width
- the intertidal zone (W) is 60 m wide (see also Chapter 1)
- the swash zone shifts over the beach in a uniform way (this is not the case in reality: the tide moves slower around low and high tide)
- per surfing movement one wave is lost for feeding (based on extensive field observations); one wave takes 53 s (WT, for the optimal feeding point S=11.42 in eq. 4)
- the animals try to stay as close as possible to the optimal feeding point; as such their migration keeps them in a symmetrical way around the optimal feeding point, i.e. 32.25% of the upper swash limit. For example: a specimen that migrated 2 m per surfing movement will stay till one meter away from the optimal feeding point and subsequently move to a spot one meter beyond the optimal feeding point.

The purpose of the model is to describe the total time a specimen can feed during 6 hours (TFT) in terms of the distance covered per surfing movement (DS). The hypothesis is that with increasing distance covered per surfing movement, the total time lost through surfing decreases, yet the period of the oscillation around the optimal feeding point becomes larger, resulting in a lower average feeding rate. There must be an optimal surfing distance (DS) at which the resulting total feeding time is maximal.

The breakdown of the model can be found in Appendix 2. To obtain the total feeding time over a period of 6 hours (i.e. 21,600 s) a polynomial estimation (ES; power 10) of eq. 2 (feeding rate model) is integrated over a certain swash position interval. The value of this interval is dependent on the distance travelled during one surfing event (DS), with the optimal feeding position (11.42 m) lying in the middle of the interval. The number

of surfing movements (N) can be described by eq. 6, which is then used to calculate the total time spent for surfing during 6 h (TS; eq. 7):

$$N = \frac{W}{DS} \qquad \text{(eq. 6)}$$

$$TS = N \cdot WT \qquad \text{(eq. 7)}$$

The total feeding time (TFT) can now be expressed as:

$$TFT(s) = (21600 - TS) \cdot \int_{11.4-\frac{S}{2}}^{11.4+\frac{S}{2}} ES(F) \qquad \text{(eq. 8)}$$

The solution of eq. 8 with varying distance per surfing movement (DS) is shown in Fig. 3.6.10. The highest total feeding time (TFT) of 6,538 s per 6 hours (i.e. 30.26% of the time) is obtained with a surfing distance (DS) of 3.5 m or 17 surfing movements (N) per 6 hours. TFT rapidly declines with decreasing DS and half the maximal TFT (i.e. 3250 s) is obtained at a surfing distance (DS) of 0.27 m. The drop in total feeding time (TFT) is more gentle with longer surfing distances (DS) and half the maximal TFT is now obtained at surfing distances (DS) of 21 m.

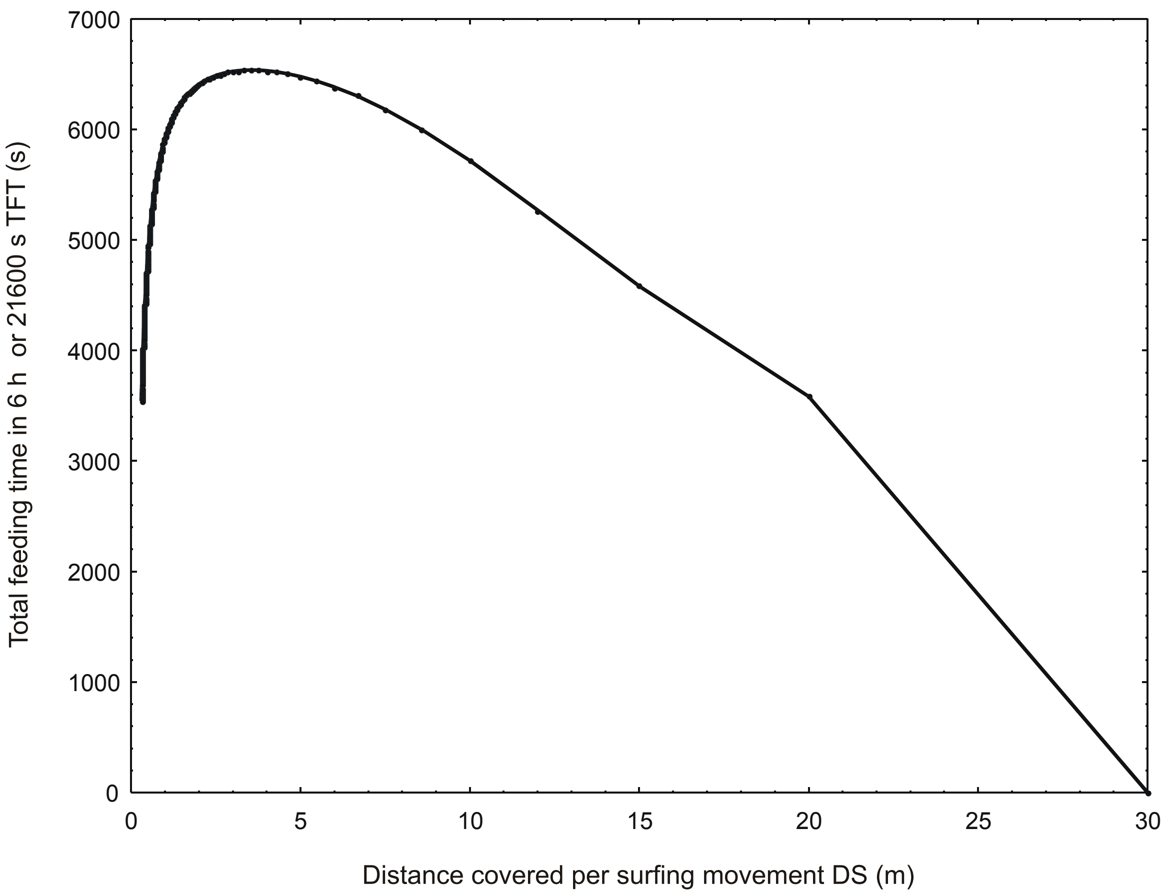


Fig. 3.6.10 - Graph of the migration model with total feeding time during 6 hours (TFT) predicted in terms of distance covered per surfing movement (DS).

3.6.4.3 Time budget

The migration model allows us to construct a time budget distribution for *Olivella semistriata*. The three main activities of the species are (1) surfing, (2) feeding and (3) remaining buried without apparent activity. Surfing can be divided into three different actions: (1.1) emerging from the sediment, (1.2) surfing itself and (1.3) burrowing. For each of these activities the time allocation per 6 hours can be calculated:

- (1) Surfing: the total number of surfing movements per 6 hours (N) is optimally 17.
  - 1.1: emerging from the sediment takes around 2 s (assumption based on laboratory measurements)

    → **34.0 s** or **0.16%**
  - 1.2: if we assume that surfing speed is half the swash velocity (1.24 m/s; Chapter 1), and take 3.5 m as surfing distance, the time spent for surfing itself is 5.95 s

    → **101.2 s** or **0.47%**
  - 1.3: the average burrowing time for an adult specimen in field conditions is 9.3 s (Chapter 4). Note that this value is higher during falling tide, since animals have to turn 180º during burrowing to be ready to feed upon the next wave (Chapter 4)

    → **158.1 s** or **0.73%**

Surfing → **293.3 s** or **1.36%**

- (2) feeding: as calculated from the migration model, the maximal feeding time is:

  → **6,538 s** or **30.26%**
- (3) time buried: the total time animals are waiting to exert one of the active behaviours is thus:

  → 21,600 s – 293.3 s – 6,538 s = **14,768.7 s** or **68.84%**

In theory remarkably little time (1.36%) has to be spent to keep up with the moving tide. Even if the distance travelled per surfing movement is significantly reduced (e.g. 1 m; calculations not shown), still only a mere 3.3% of the total time has to be allocated to surfing.

If *Olivella semistriata* was a sessile species, unable to surf, instead of staying close to the optimal feeding point of the feeding rate model, they would gradually be found at every possible swash position with the changing tide. The average feeding rate would then be 17.17% (integration of ES(F) over the entire swash width, i.e. 0 – 20 m), and the time they would actually be in the swash zone per 6 hours would be 2 hours or 7,200 s (swash zone 1/3 of the intertidal width). This means that the total feeding time in absence of surfing would be 1,236 s or 5.72% of the time. Thus, by surfing 1 – 3% of the time, feeding time can be increased from 5.72% to 30.26%, or an increase of 529%.

3.6.5 Discussion

Surfing or swash-riding is a very complex behaviour for animals living in a dynamic environment such as exposed sandy beaches. It requires detecting certain exogenous cues, analysing them in order to choose the appropriate set of circumstances to take action and respond rapidly yet in a controlled manner. Species that have mastered these difficulties are thought to benefit from a number of assets: they are exposed to the active swash – a zone with excellent feeding conditions for filter feeders and scavengers - throughout most of the tidal cycle and, they maintain position in a zone which provides shelter from both avian and piscine predation (Dugan *et al.*, 2004).

The exogenous factors to which the animals have to respond are ample and include, amongst others, the swash conditions, food supply, biological interactions, insulation, hydration, desiccation and sediment thixotrophy. For animals living in the swash zone, most of these factors are directed by the swash conditions: food, for instance, is brought in by the swash and the swash determines the balance between inundation (hydration) and air exposure (insulation) and therefore affects the changes in sediment thixotrophy. Hence, we could hypothesize that in order to be successful as a surfer, a species must be able to detect and handle the prevailing swash conditions. This idea was tested for the feeding dynamics of the gastropod *Olivella semistriata,* a thriving surfing species from sandy beaches in the tropical East-Pacific (Chapter 1). Feeding was monitored as a function of the following swash parameters: swash distance, swash interval and swash time.

3.6.5.1 Filter feeding and swash conditions

In Chapter 2 we hypothesized that feeding conditions for a swash filter feeder, such as feeding time and feeding rate, follow a unimodal curve within the swash zone. Low in the swash, close to the surf zone, the interval between two swash waves is short, and the swash velocity is very high. Before the backwash velocity has dropped sufficiently to allow for filter feeding, there is a great possibility that the next swash wave will already have entered the swash zone. Feeding conditions are therefore very limited. Moving higher in the swash, the swash interval increases and the swash velocity gradually decreases, adding up to an increase in the feeding opportunities. At a certain point in the swash zone, the swash interval will become so long and the backwash time will become so short that feeding conditions will decrease again. Ultimately at the upper swash limit feeding will be close to zero once more.

Olivella semistriata offers a unique opportunity to study the influence of swash on the feeding behaviour of a surfer. It is present in very high number in the upper swash zone (Chapter 2 and 3) and feeding activity can very easily be seen in the field and on video images. Unfortunately, it is very difficult to directly measure feeding in terms of position in the swash itself. This would require intensive and simultaneous observation of a set of levels within the swash, combined with monitoring of the swash. An alternative method is to use the indirect approach of observing one patch at a time, thereby omitting direct information of swash position. However, three swash parameters – swash distance, swash time and swash interval - could be quantified, which ultimately allowed us to model the position in the swash.

The univariate results of the feeding survey (Table 3.6.3; Figs. 3.6.2 and 3.6.3) are very straightforward to interpret. The longer the swash distance (i.e. the further a swash wave crosses the patch of snails), the shorter the swash interval, the longer before *Olivella semistriata* can start feeding on the backwash and consequently the shorter the feeding time. Feeding time, however, increases with increasing swash time and swash interval. With a big wave, it is thus very likely that a new wave will enter the patch before the backwash speed has dropped sufficiently (below ± 0.5 m/s) for the animals to start feeding; as such, feeding in big waves is predominantly during the few seconds of maximal wave extension that the swash stands still.

In a multivariate approach (GLM Model) it becomes more difficult to understand what happens exactly. The impact of swash time on feeding time is still easily explained (Fig. 3.6.5): the longer the swash takes the longer the animals can feed, especially in

smaller waves (short swash distance). The feeding rate regression, however, gave a much more complex result (Fig. 3.6.6). Feeding rate at short swash intervals is high with small waves, very low with average waves and again higher with big waves, probably because feeding at swash standstill is only noticeable with big waves. At long swash intervals the feeding rate rapidly decreases with decreasing swash distance: even if the wave itself is used very efficiently for feeding, the total feeding time on a small wave will be very low compared to the swash interval. Feeding is only very efficient where swash time is relatively long and equals the swash interval.

Ultimately, the pieces of the puzzle fall into place by modelling the position in the swash as a function of the measured swash parameters (distance, time and interval). For both feeding time and feeding rate a pattern very similar to the hypothesized unimodal curve (Chapter 2) is obtained (Fig. 3.6.9). The curves are not symmetrical, though, yet rather skewed. Most favourable conditions are clearly found in the upper half of the swash, where there is an optimal balance between swash interval, time and distance.

The high tide feeding sampling showed the impact of slope on the distribution of the species through its feeding opportunities. A steep slope results in a higher swash velocity as well as in a faster drainage of the backwash through the sediment (Short, 1999; McLachlan and Brown, 2006). The combination of these two factors hamper the presence of a slow backwash - a laminar stream of water, which is exactly what *Olivella semistriata* feeds upon. The maximum swash velocity at which they can start feeding was found around 0.5 m/s. It is unlikely such low swash velocities are reached on a steep part of the beach – or on a steep beach for that matter. So, even though the animals were present in high numbers on the steep part of the high tide intertidal, and had thus surfed to this place, no feeding activity was observed. Only 20 m further on the beach, at the same elevation level, animals were feeding in high numbers where the slope was much more gentle.

3.6.5.2 Feeding conditions and swash zonation

In a highly dynamic environment, the zonation of a species is caused by its response to one or several environmental and/or biological gradients (autecology hypothesis; Noy-Meir, 1979). Highest densities can be expected where conditions are optimal, with a decrease at either side of this optimum, resulting in a unimodal distribution. The zonation of *Olivella semistriata* was found to be confined to the swash zone and showed to be uniformly of a unimodal (symmetric to negatively skewed) shape,

independent of the tidal state – high, middle or low tide during falling or upcoming tide (Chapter 3) - or location (Chapter 2). Highest densities were typically found in the upper half of the swash zone. The two general swash models based on relative densities and relative swash position, for upcoming and falling tide, from Chapter 3 were combined with the results of the feeding models, also expressed in relative numbers, from this paper (Fig. 3.6.11). The similarities between the zonation data on the one hand and the feeding predictions on the other hand are striking. The shape of the curves is almost identical and the peaks are relatively close to each other.

Although we cannot provide direct evidence, our findings strongly suggest that the zonation of *Olivella semistriata* in the swash zone is a result of the feeding conditions at different positions within the swash and that they actively aggregate in the most suitable areas. As such, this brings the science of sandy beach zonation, which has been stuck at a very descriptive level (McLachlan and Jaramillo, 1995; McLachlan and Brown, 2006), to a point where causal links can be sought. Explaining zonation of species or communities will require a shift from studies of population dynamics and the likes, to behavioural response studies, such as this paper, or experimental studies (e.g. Dugan *et al.*, 2004).

Our findings also question the paradigm in sandy beach ecology that intertidal zonation on sandy beaches is environmentally driven (Defeo and McLachlan, 2005; McLachlan and Brown, 2006). Although feeding conditions are a result of swash dynamics, an environmental factor, the reason why the species shows its typical unimodal zonation in the swash is very likely to be exactly because of the feeding conditions and not the swash dynamics. Where the paradigm of environmentally driven zonation on sandy beaches has already been extended to competition and predation under certain circumstances (Cardoso and Veloso, 2003; Defeo *et al.*, 1997; Dugan *et al.*, 2004), it seems that food availability has to be added as well. Note that swash dynamics do play a crucial role in the formation of the swash zonation pattern of *O. semistriata* through its surfing behaviour. Thus, we could say that the reason for the swash zonation of *Olivella semistriata* is biological (feeding conditions) but the zonation pattern appears because of the environmental conditions (swash action).

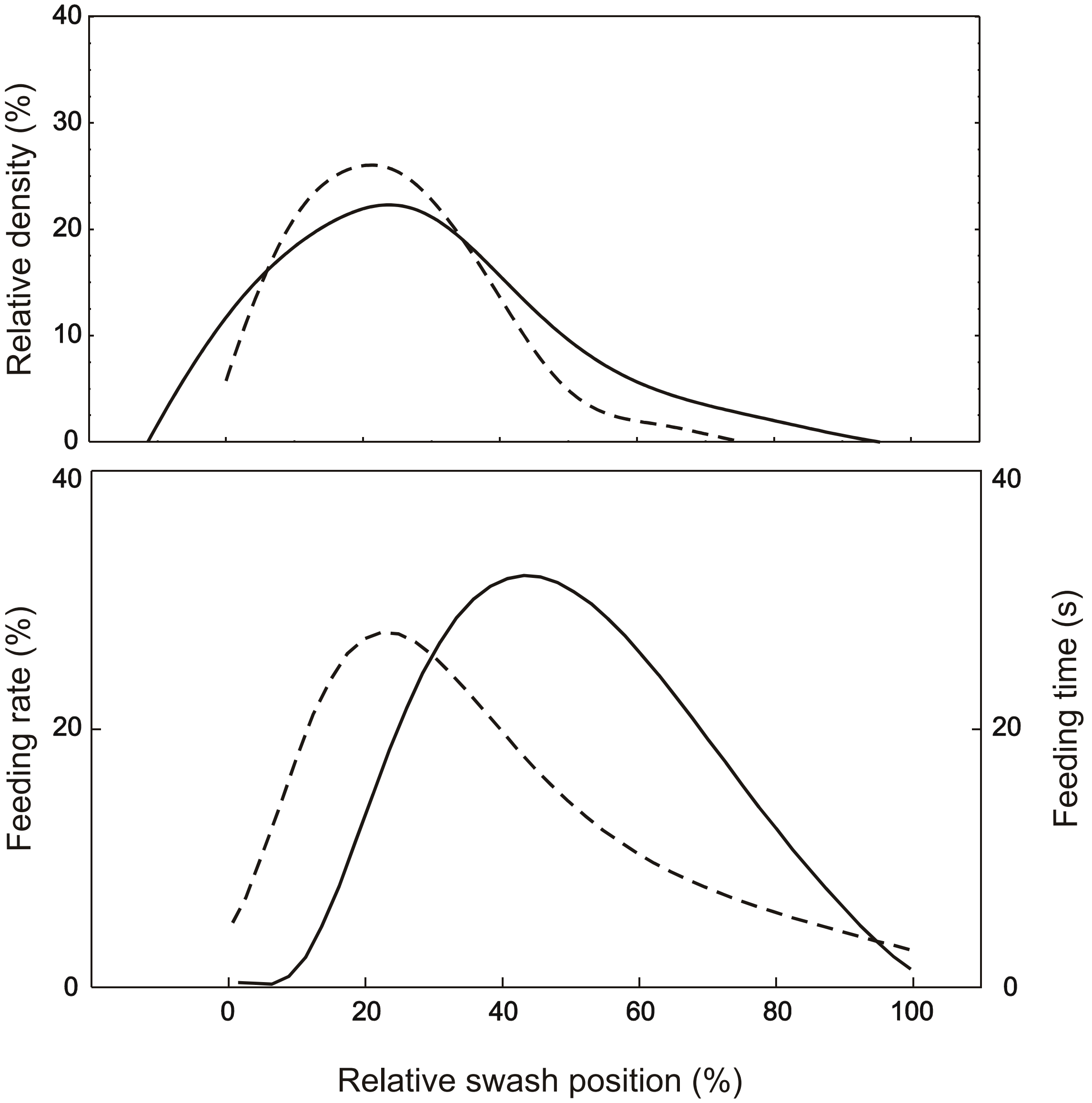


Fig. 3.6.11 - Above (modified from Chapter 3): relative densities in the swash zone during falling (solid line) and upcoming tide (dotted line). Fitting by distance weighted least square estimates.

Below: feeding time model (dotted line) and feeding rate model (solid line) on a relative swash position scale. 0-value on the X-axis indicates the upper swash limit; 100% indicates the lower swash limit.

3.6.5.3 Activity budget and the benefits of surfing

It has been widely demonstrated that surfing is a very successful strategy on exposed beaches, especially of the intermediate type (e.g. Brown, 2001; McLachlan and Brown, 2006; Chapter 1). This has been credited to the advantages of maintaining position in the swash zone: good shelter from predators and continuous feeding opportunities (Ansell, 1983; Dugan *et al.*, 2004; McLachlan and Brown, 2006). There could be a number of ways to demonstrate these benefits of surfing, however, studying feeding behaviour and biological interaction on beaches, and especially in the swash zone, is very challenging (Peterson, 1991; McLachlan, 1998; Dugan *et al.*, 2004). So far, only a limited number of papers about the costs and benefits of surfing have been published. One of the approaches has been to investigate the energetics of surfing. The energy cost of surfing itself is surprisingly high, especially for *Bullia* (Brown, 1982) but also for *Donax* and *Emerita* (Ansell and Trueman, 1973), although it is relatively cheap in terms of distance covered (Brown, 1982). Surfing also requires emerging from the sediment and reburial after floating, both energy-consuming activities as well (Brown, 1982). Combining these energetics with an activity budget of the species can give an idea of how costly surfing is in terms of energy expenditure. Brown (1982) calculated that, where surfing takes up 6.4% of the time budget of *Bullia digitalis*, it requires almost 10% of the daily energy consumption. For *Donax incarnatus* and *Emerita hothuisi* surfing was less costly, with around 3% of the daily energy consumption (Ansell and Trueman, 1973). In this study, however, no account was given for emerging from the sediment and surfing itself, so the actual figure will be higher. Note that neither study mentions time or energy allocation to feeding.

There is no reason to believe that the energy cost of surfing should be much different for *Olivella semistriata*, compared to *Bullia* or *Donax*, given the similarities in their surfing behaviour and dynamics. Moreover, the theoretical calculations of the activity budget of *Olivella semistriata* render numbers that are in the same magnitude as the observation made for *Bullia* (Brown, 1982). For both species emerging and burrowing takes less than 1% of the daily time budget, and surfing itself requires 0.5% (*O. semistriata*) to 5% (*B. digitalis*). This higher number for surfing in *Bullia* is probably due to the feeding nature of this species, consisting of actively pursuing prey. Reaching a food item normally requires several surfing movements (Brown, 2001).

In this study, we have not looked at the costs yet at the possible benefits in terms of feeding rate and feeding time. It seems that, where surfing adds about 3-10% to the daily energy cost, it increases the daily feeding time by 529% compared to a species that would live sedentary and filter feed the backwash in a similar fashion as *Olivella*

semistriata. Even if we change the numbers and increase the total time spent surfing, for instance because several short excursions are needed for fine-tuning the position in the swash, the figures remain undisputable: moving on average 1 m per surfing excursion reduces the maximal total feeding time with 9.3%, which is still 480% higher than when not moving at all. The benefit is further reduced because more surfing movements require a higher energy expenditure, but this does not stand against the very large increase in feeding time. Moreover, filter feeders that do not migrate cross-shore still have to migrate vertically in order to keep their position relative to the sediment surface, which changes continuously through erosion and accretion (Ansell and Trueman, 1973).

Our calculations do not include feeding success nor measurements of the energy uptake through filter feeding and the energy cost of filter feeding, but it seems very clear that for a species that acquires its nutrition through filtering the backwash on intermediate sandy beaches, surfing is a very interesting strategy, probably explaining the dominance of such species under these conditions (Brown, 2001; McLachlan and Brown, 2006; Chapter 1).

3.6.6 Conclusions

1) Feeding time and rate are a function of three swash parameters: swash distance, time and interval.

2) Highest feeding time and rate are reached in the upper half of the swash zone, with a modelled maximum feeding rate of 32.25 %.

3) The curve displayed by both feeding time and feeding rate within the swash zone is very similar to the zonation of the species within the swash.

4) During one tidal cycle, feeding time was modelled to be highest with an average surfing distance of 3.5 m per movement (on a 60 m wide beach) and resulted in a total feeding rate of 30.27% during the tidal cycle.

5) Surfing increases the feeding opportunities with 529% compared to a non-migratory species with similar feeding habits.

6) Surfing is a very interesting strategy for filter feeders inhabiting exposed, intermediate beaches, probably explaining their dominance under these conditions

Appendix 1: Swash distance (D) in function of position in the swash (S)

Swash distance (m)	Position in the swash S (m)																				
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
6	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
5	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0
15	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0
17	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0
14	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0	0
18	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0
11	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0
4	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0
2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0
16	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0
19	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0
19	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	0
3	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	7	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	12	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0
11	11	10	9	8	7	6	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0
D	**12.05**	**11.05**	**10.05**	**9.10**	**8.20**	**7.35**	**6.55**	**5.80**	**5.10**	**4.40**	**3.75**	**3.10**	**2.55**	**2.05**	**1.55**	**1.10**	**0.70**	**0.40**	**0.20**	**0.05**	**0.00**
	Average value of D at each swash position S (m)																				

Appendix 2: Breakdown of the migration model (matlab code)

S=0.01:0.01:20 (*range of swash position)*;

I= 0.0345*S.^3 - 0.4055*S.^2 + 3.4289*S + 14.925 (*I in function of S)*;

D= -0.0004*S.^3 + 0.0404*S.^2 - 1.289*S + 13.173 (*D in function of S)*;

T= 7.0878 + 0.4333*I + 0.04895*I.*D -0.00246*I.*I – 0.03944*D.*D (*T in function of I and D)*;

F= 1.0490- 0.01247 * I - 0.1296*D + 0.002489*I.*D + 0.002906*D.*D + 0.00031*T.*T + 0.00003*I.*I - 0.00004* T.*I.*D *(F in function of I, D and T)*;

F=sin(F);

F=F.*F *(F in function of I, D and T)*;

```
[A,B]=size(F);
Max=0;
Min=1;
for j=1:B
   if F(j)>Max
      Max=F(j);
      Smax=j*0.01;
   end
   if F(j)<Min
      Min=F(j);
      Smin=j*0.01;
   end
end
```

plot(S,F) *(Feeding rate model plot);*

Polynomial fit of feeding rate model:

```
Npoly=10;
p=polyfit(S,F,Npoly);
SP=0.01:0.01:20;
LP=0;
for i=1:(Npoly+1)
   LP=p(i)*SP.^(Npoly+1-i)+LP;
end

for b=1:B
   if F(b)>1
      F(b)=NaN;
   end
end
```

```
plot(S,F,S,LP);

res=LP-F;
MaxErr=max(abs(res));

for i=1:(Npoly+1)
   Pint(i)=p(i)/(Npoly+2-i);
end
```

Migration model:

```
N=200 (maximum number of migration movements N);
MinSpringen=ceil(60/19.2);
Efficientie=zeros(N,1);
for n=MinSpringen:1:N
   Tgraven = 53 (time lost per surfing movement);
   Vgolf = 60/(3600*6);
   TEten=(3600*6)/n-Tgraven (time left for feeding);
   Smax=11.42; (optimal position in the swash)
   VoedingsInterval=Vgolf*TEten;
   IntervalOndergrens=Smax-VoedingsInterval/2;
   IntervalBovengrens=Smax+VoedingsInterval/2;

   LPintB=0;
   LPintO=0;
   for i=1:(Npoly+1)
      LPintB=Pint(i)*IntervalBovengrens.^(Npoly+2-i)+LPintB;
      LPintO=Pint(i)*IntervalOndergrens.^(Npoly+2-i)+LPintO;
   end
   Oppervlakte = LPintB-LPintO;
   Efficientie(n)=Oppervlakte/(IntervalBovengrens-IntervalOndergrens);
   Voedingstijd(n)= Efficientie(n)*Teten (feeding per surfing movement);
   TFT(n)= Efficientie(n)*TEten*n (Total feeding time in 6 hours);
end
plot(TFT);
```