

## CHAPTER 5

# CAN SANDY BEACH MOLLUSCS SHOW AN ENDOGENOUSLY CONTROLLED CIRCATIDAL MIGRATING BEHAVIOUR? HINTS FROM A SWASH RIG EXPERIMENT.

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## Abstract

Many macrofaunal species inhabiting exposed sandy beaches are dependent on the swash for their nutrition and for migration and are highly adapted to the harsh physical conditions of the swash. The most important physical factors that determine the distribution and behaviour of swash related fauna, next to the swash itself, are sediment grain size and beach slope. Crucial swash parameters are swash period and swash velocity. Studying the influence of these factors on the animals in the field is often very difficult and it is almost impossible to identify which factor causes what effect.

Crucial knowledge about the direct role of the swash itself is lacking. Therefore a device that generates swash waves on an artificial beach under laboratory conditions was designed: the swash rig. In the swash rig, full and independent control on sediment grain size, beach slope, swash velocity and swash period is present. This will allow us to do a variety of experiments on the influence of each of these factors, independently or combined, on swash fauna.

In one such experiment, *Olivella semistriata* - a dominant surfing gastropod on Ecuadorian sandy beaches – was placed in the swash rig during rising and falling tide and subjected – under constant conditions - to an equal wave regime. During falling tide, and in absence of any tidal cue, almost all specimens moved downshore, as they would in the field; hardly any specimens moved upshore. During upcoming tide, however, there was noticeable upward migration in the swash rig, and half of the runs showed a net upward migration.. Contrary to the common understanding that the behaviour of sandy beach molluscs is entirely environmentally driven, this experiment hints to the presence of an endogenous circatidal clock which is used to direct the tidal migration of the species.

### 3.5.1 Introduction

Exposed sandy beaches are one of the world's most hostile environments because of the high degree of disturbance. It is mainly the combination of heavy wave action with an unstable substratum that makes life so hard on a sandy beach. The most important adaptations required to survive under these conditions are rapid and powerful burrowing and a high degree of mobility (Brown and McLachlan, 1990). It is also essential that the animals can maintain or regain their position on the shore. Only very few taxa have developed these skills. It is mainly crustaceans, together with some mollusc species, that have been successful on exposed sandy beaches (Brown and McLachlan, 1990; Dexter, 1992; McLachlan and Jaramillo, 1995). Many of these species are 'swash riders' or 'surfers', who use the swash to migrate over the beach (Naylor and Rejeki, 1996). They have also developed several strategies to feed in the swash zone, such as filtering the backwash. Living in the swash zone provides the fauna with an almost unlimited and easily accessible food supply (Brown and McLachlan, 1990). Moreover, the time of exposure to predation is very short. Marine predators such as large crustaceans and surf-zone fish, as well as terrestrial predators such as birds, do not have enough time to find their prey because of the swash (Dugan *et al.*, 2004).

Swash dependent fauna is found on a range of beach types, from intermediate to highly reflective beaches, from beaches with very fine to very coarse sediment. Some species can inhabit a variety of beach types, such as the mole crabs of the genus *Emerita* (Jaramillo *et al.*, 2000a) and *Hippa* (Lastra *et al.*, 2002), whereas other species are limited in their distribution to a specific beach type (Brown *et al.*, 1989). Several interdependent physical factors, e.g., sediment grain size, breaker height and intertidal beach slope may limit the distribution of macrofauna on exposed sandy beaches (reviewed in Brown and McLachlan, 1990). Yet, more recent studies (McLachlan *et al.*, 1993, 1995) suggest that also the swash climate itself, and especially the number of effluent line crossing, plays a crucial part in the distribution of mobile macrofauna on exposed beaches. This theory, known as the 'swash exclusion hypothesis', states that the decrease in number of species and decrease in densities from dissipative to reflective beaches is caused by an increase in swash harshness towards the reflective end of the beach spectrum (McLachlan *et al.*, 1993).

Studying swash fauna *in situ* cannot reveal all information about the mechanisms behind the behaviour and distribution of these animals. To understand the underlying mechanisms, it is crucial to have independent control over the different physical parameters, which explains the need for laboratory experiments. So far experimental work

on swash fauna has always been performed in aquaria (Ellers, 1995a; McLachlan and Young, 1982; Naylor and Rejeki, 1996) or flumes (Warman *et al.*, 1993; Ellers, 1995b; Yannicelli *et al.*, 2002). Although valuable results were obtained, these studies pass by the crucial factor for swash fauna: the presence of swash waves, as was for instance acknowledged by Ellers (1995b). If one wants to investigate the influence of physical factors on the distribution, migration and feeding behaviour of swash fauna, a 'swash simulating device' with independent control of swash period, swash velocity, beach slope and sediment grain size is needed. Based on a design used by Dr. O'Donoghue and colleagues from the University of Aberdeen, Scotland, we built a 'swash rig'. In this paper, we illustrate the functioning and application of this swash rig by means of an experiment on *Olivella semistriata*.

Exposed sandy beaches along the Pacific coast of Ecuador are dominated by the snail *Olivella semistriata* (Chapter 1, Addendum 1). These molluscs live in the upper part of the swash zone, where they filter the backwash (Chapter 6). They maintain their position by surfing. Previous tests showed that in absence of swash waves, experiments of the surfing behaviour of the species were bound to fail. We hypothesized that this could be solved by using the swash rig.

In a first test of the effectiveness of the swash rig, the presence of an endogenous circatidal clock in the migration behaviour of *Olivella semistriata* was investigated. It has been demonstrated for several crustacean swash species that the tidal rhythm in activity is directed by an endogenous clock. Due to this internal clock, the tidal behaviour often remains present in the laboratory for several tidal cycles, even in the absence of a tidal cue. Alheit & Naylor (1976) showed that *Eurydice pulchra*, kept in aquaria without tidal regime, mainly swims at times of high tide, and this behaviour persisted for more than 5 tidal cycles. Similar responses have been described for *Excirolana* and other crustaceans (Enright, 1972; Yannicelli *et al.*, 2001).

Evidence for an internal circatidal clock in sandy beach molluscs, however, is missing. The regulation of the observed tidal migrations have been ascribed to the changing physical conditions during ebb and flow (Ansell, 1983; Brown *et al.*, 1989). For *Donax variabilis* the specific trigger that initiates migration is the sound of incoming waves (Ellers, 1995b), for other *Donax* species it is probably the change in liquefaction of the substratum (Trueman, 1971). Ellers (1995b) noted that the regulation of these environmental-driven triggers, however, could be by an endogenous clock. The swash rig hands us a unique tool to investigate the response of a surfing mollusc to swash under controlled laboratory conditions.

## 3.5.2 Material and Methods

### 3.5.2.1 Description of the swash rig

The concept of generating swash waves by using a gate system was derived from a model used by Dr. O'Donoghue and colleagues from the University of Aberdeen, Scotland (<http://www.eng.abdn.ac.uk/envhrg/facilities/swashrig.hti>). The original design consists of a swash rig with a built-in wave generating device. We made several modifications to that model, which was originally designed to generate just one swash wave per experiment.

#### 3.5.2.1.1 Wave generating device (Fig. 3.5.1)

The wave generating device is a wooden box (18mm water resistant plywood) with two gates, dividing the box in two parts (Fig. 3.5.1). Measures are 80x100x50cm (w $\times$ l $\times$ h), with the inner gate at 20cm from the front and the outer gate at the front of the box. The part behind the inner gate is the reservoir, where the water input (2x 40 l/min) is located. This reservoir is perforated by several holes at different heights. By adding or removing taps in this holes, the maximum water level can be controlled without changing the water input. The front part contains the water that will be released to create a swash wave. By lifting the inner gate, the front part is being filled by water coming from the reservoir (Fig. 3.5.2a). After closing the inner gate, the outer gate can be opened. Lifting this gate at high speed will create a surfing wave (Fig. 3.5.2b). Immediately after releasing the water, the front gate can be closed, and the process can start again (Fig. 3.5.2c). This device can easily be manipulated by one person.

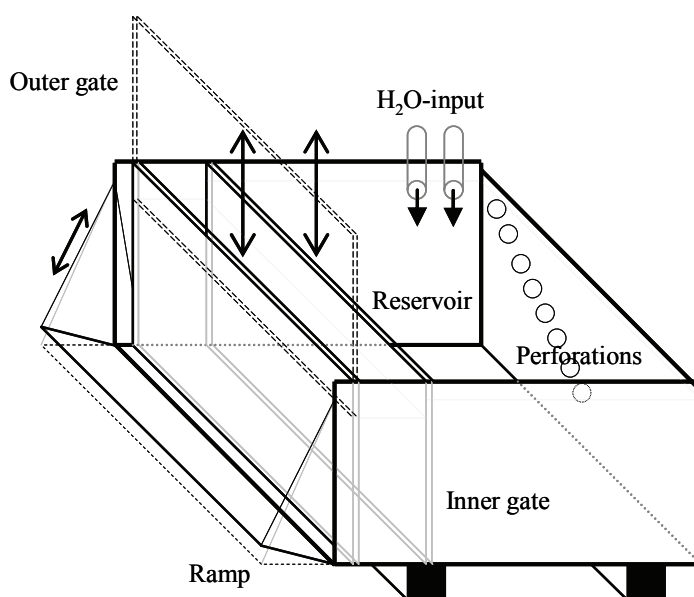
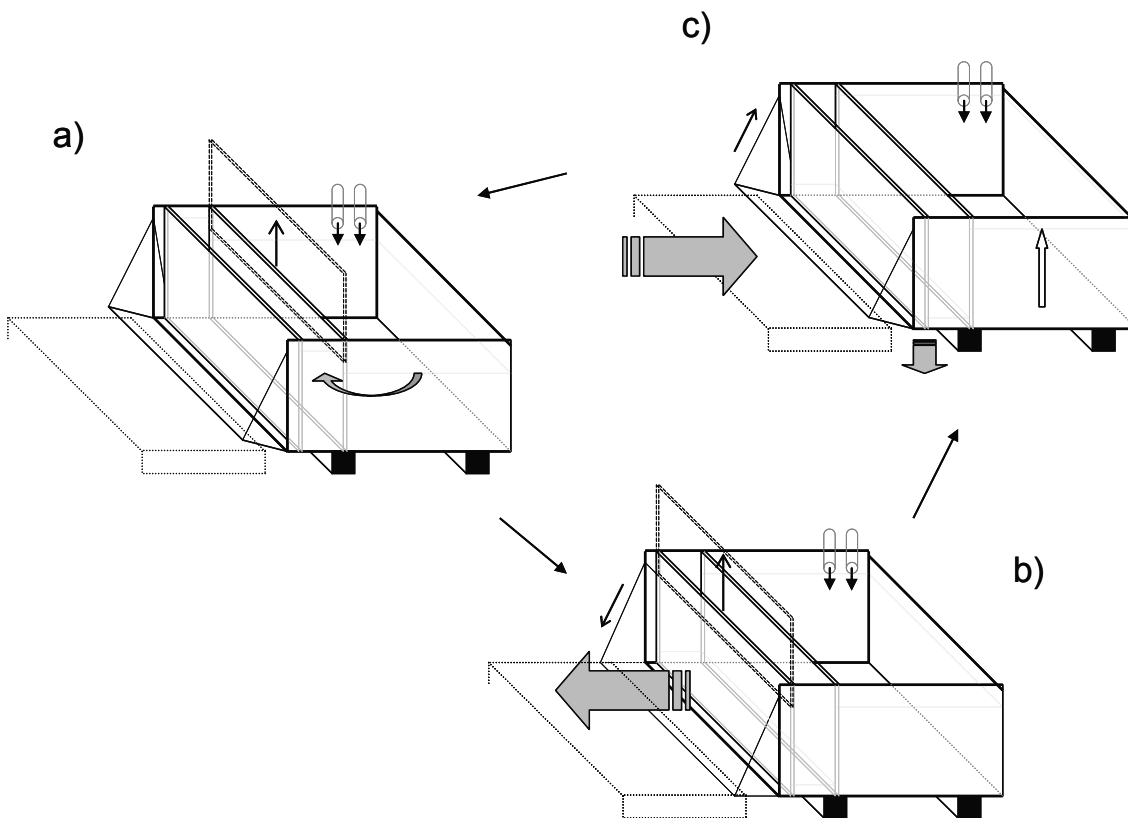


Fig. 3.5.1 - Wave generating device.

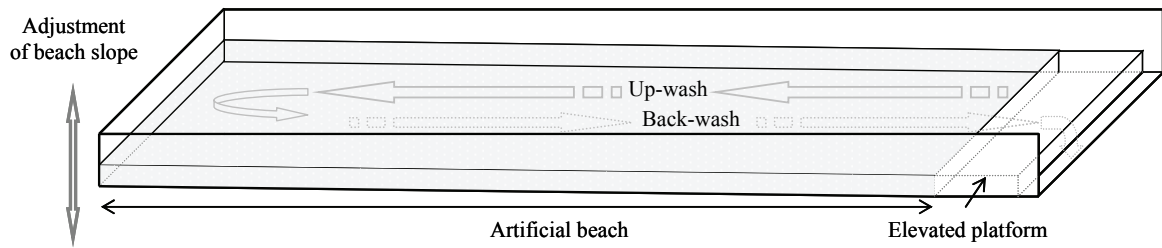
To have the water from the backwash removed from the swash rig, there should be a gap between the swash rig and the wave generating device. The incoming wave, however, should enter the swash rig without finding obstacles such as a gap. To achieve this, we attached a ramp to the front of the wave generating device. This ramp is operated by the front gate, in such a way that the ramp is opened with the front gate closed, and closed by opening the front gate (Fig. 3.5.2b). When opened, the outlet of the swash rig is opened so that the backwash can run away. When closed, the ramp serves as a 'bridge' for the incoming swash wave.



**Fig. 3.5.2** - Working of the wave generating device. a) lifting of the inner gate; b) closing inner gate and lifting outer gate, creation of swash wave; c) closing of outer gate, filling of reservoir.

### 3.5.2.1.2 Artificial beach in the swash rig (Fig. 3.5.3)

The rig containing the beach is made of polyester around a plywood body. Dimensions are 80x450x30cm (w<sub>x</sub>l<sub>x</sub>h). This rig is not attached to the wave generating device, which allows for changing the beach slope. The first 50cm of the tank has a 10cm elevated platform in polyester, on which the incoming swash wave lands (Fig. 3.5.3). This platform also holds the sediment in place. The beach itself is thus 4m long and 80cm wide, with a sediment depth of 10cm.



**Fig. 3.5.3** - Artificial sandy beach. Arrows indicate swash movement.

#### 3.5.2.1.3 Limitations of the experimental setup

For our experiments with *Olivella semistriata*, the dimensions of the swash rig are satisfactory. The distance the animal travels on the beach is generally less than four meters (Chapter 6), so a beach length of four meter was sufficient for the goals we set.

The maximum amount of water that could be released at one time, 80 l, was just sufficient to create a swash wave till the upper part of the artificial beach at a beach slope of 1/10, which is much steeper than the steepest beach where we recorded *Olivella semistriata* in Ecuador (1/19; Chapter 4), and steeper than the slope we used for the endogenous clock experiment (see further). With a double input of 40 l/min, a maximal wave could be generated every minute, which is more frequent than the average interval between two waves entering the swash zone where *Olivella semistriata* lives (75 seconds).

According to the animals one wants to study, the dimensions of the swash rig could easily be changed. We doubt it would be very useful to narrow the beach, but beach length could be adjusted to the needs of the particular research. The maximum swash volume and thus swash speed can be controlled by changing the position of the inner gate and the position of the holes in the reservoir. A higher frequency of swash waves could be achieved by increasing the water input and/or increasing the volume of the reservoir.

#### 3.5.2.1.4 Problems

The only real problem we encountered was erosion. Because of the turbulence created by the entering swash wave, sediment is eroded from the lower part of the beach and deposited higher on the beach. Hence, after a number of waves, an even slope will turn into an S-shaped profile. As a result of this, there will always be some water at the

base of the beach after the wave recedes. This reduces the swash velocity of the next incoming swash wave. The formation of this small water volume takes place after the first swash wave, however, so we think it should not influence the results as long as the very first wave is not included in the experiment. In order to reduce the erosion, which is probably due to the abrupt change in consistency from the elevated platform to the sediment, we placed a rigid plastic net with 1 mm mesh-size over the first 30 cm of the beach. This reduced the erosion process substantially.

The change in beach morphology did not interfere with the kind of experiments that were done so far, but it might become a problem when tackling other aspects of surfing.

### **3.5.2.2 *Olivella semistriata* endogenous rhythm experiment**

#### *3.5.2.2.1 Study site and period*

The experiments were conducted in the Centro de Investigacion Acuicultura y (CENAIM) in San Pedro, Ecuador. Animals were collected from the beach in front of the institute. The macrofaunal zonation of this beach is described in Addendum 1. Swash zonation of *O. semistriata* from this location is discussed in Chapter 2 and 3. The experiments took place between June 6<sup>th</sup> and July 23<sup>rd</sup> of 2005, on 10 different days, during daylight hours. A total of 27 experimental runs were performed.

#### *3.5.2.2.2 Swash rig setup*

The sediment was brought from the intertidal of the same beach as the studied population; sediment was refreshed every two days. Sediment analysis was done using a laser COULTER LS. The slope of the artificial beach was similar to the slope of the San Pedro beach (1/30). Sea water was pumped from the surf zone of the same beach, and had the same temperature as in natural conditions.

#### *3.5.2.2.3 Collecting and treating animals*

Live animals were collected 3 h before and after low tide, using a net with 1 mm mesh-size. Only animals larger than 5 mm were used, since smaller specimens do not show the same migrating behaviour as the larger ones (Chapter 3). The animals were immediately brought to the laboratory (average travelling time of 5') and placed in the artificial beach. About 1000 individuals were placed in a patch of 30x30 cm. Burrowing



was stimulated by creating a gentle water stream, until all animals were fully burrowed. Before the start of the experiment, two gentle swash waves were created to wash out specimens that were not adjusted to the new conditions.

Another 1000 individuals were kept in trays of 30x20x4 cm, filled with 1 cm of sediment and 1 cm of sea water. These individuals were used in the swash rig 6 h after collection. After the experiment, all the animals were collected and placed back in their natural habitat.

#### 3.5.2.2.4 Wave regime

The swash was monitored in the field where densities of *O. semistriata* were very high (easily visible as a dense band). The average recorded wave interval was used in the swash rig. The wave distance and velocity was kept constant over all the experimental runs. Swash waves were filmed using a 50 Hz video camera. Per experimental run, five waves were released. The migrating animals were collected using a net with 1mm mesh-size just above and below the patch. To minimize the influence of the nets on the swash wave, the upper net was only applied during the water up-rush, the lower net during the backwash. After the experiment, the artificial beach was cleared from any remaining specimens by sieving the upper 5 cm of the substratum over a 1 mm sieve.

#### 3.5.2.2.5 Data analyses

Swash velocity was calculated from the time the up-wash and backwash need to cover a fixed distance.

Total number of upward and downward migrating animals was pooled per experimental run, and a ratio of up- and downward migration was calculated as followed:

$$ratio = \frac{\text{number of downward migration} + 1}{\text{number of upward migration} + 1}$$

If ratio >1 there is a net downward migration. Differences in migration ratio between treatments was tested with a Generalized Linear Mixed Model (GLMM), with *tide*, *postponement* (i.e. tide + 6 hours) and *tide\*postponement* interaction as fixed effects. Therefore, the proc GLIMMIX syntax was used in SAS 9.1.3 software (with binomial distribution and logit-link function)(McCullagh and Nelder, 1989).

### 3.5.3 Results

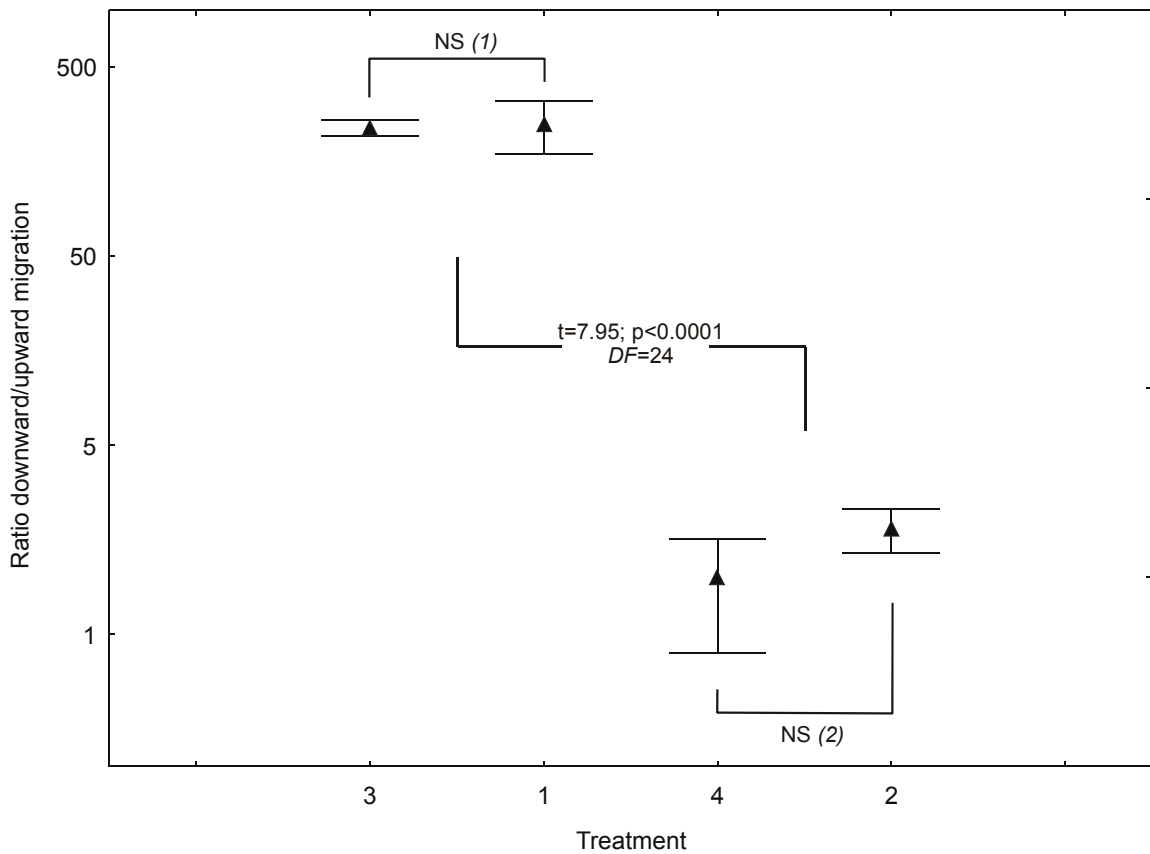
Average swash period at the place where *Olivella semistriata* was present in high densities, was 75 seconds. This swash interval was applied in the swash rig. The sediment that was used in the swash rig consisted mainly of fine to medium sands (125-500  $\mu\text{m}$ ). The median grain size was 212  $\mu\text{m}$ . Swash velocity on the beach ranged from 0.21 to 3.00 m/s (average  $1.22 \pm 0.47$  m/s); in the swash rig we set the swash velocity slightly higher at 2.0 m/s, to stimulate migration.

From the total of 27 experimental runs, 15 were done during falling tide (treatment 1+3) and 12 during upcoming tide (treatment 2+4). Ten runs were done with animals that had been kept in tanks for six hours. Six of these were with animals that were collected during upcoming tide and placed in the swash rig during falling tide (treatment 3); four runs were performed during upcoming tide with specimens that had been collected six hours prior, during falling tide (treatment 4).

None of the runs during falling tide (treatment 1+3) had a net upward migration, the maximum number of individuals migrating upward was 6 (Table 3.5.1). Three out of eight and three out of four of the runs during upcoming tide (treatment 2 and 4 respectively) had a net upward migration, with at least 11 and on average 46 individuals migrating upward (Table 3.5.1; Fig. 3.5.4). The ratio ranged from 0.07 to 3.36 for upcoming tide (treatments 2 and 4) and 41 to 301 for falling tide (treatments 1 and 3). No differences were found between the runs that were tested at the same tidal state, i.e. treatment 1 and 3 and treatment 2 and 4 did not differ statistically. The total number of migrating individuals was much lower during upcoming tide (a maximum of 207) compared to falling tide (a maximum of 822).

**Table 3.5.1** - Number of downward/upward migrating individuals, with the ratio between brackets. Ratio values < 1 indicate a net upward migration.

treatment 1	treatment 2	treatment 3	treatment 4
411/6 (59)	22/40 (0.56)	819/3 (205)	77/28 (2.69)
192/2 (64)	20/62 (0.33)	237/0 (238)	4/71 (0.07)
163/3 (41)	47/17 (2.67)	740/3 (185)	34/64 (0.54)
601/1 (301)	110/32 (3.36)	161/1 (81)	82/125 (0.66)
441/1 (221)	117/36 (3.19)	595/2 (199)	
183/0 (184)	14/11 (1.25)	223/1 (112)	
182/1 (92)	15/48 (0.33)		
284/0 (285)	48/18 (2.58)		
665/2 (222)			



**Fig. 3.5.3** - Average  $\pm$  SE of the downward/upward migration ratio (log-scale) of the four different treatments. Differences between treatments were tested with a GLMM: NS (1):  $t=-0.27$ ;  $p=0.7916$ ;  $DF=23$ . NS (2):  $t=1.95$ ;  $p=0.0629$ ;  $DF=23$ .

### 3.5.4 Discussion

When we started investigating the swash behaviour of the sandy beach snail *Olivella semistriata*, a dominant species on exposed Ecuadorian beaches (Chapter 1; Addendum 1), we were soon confronted with the limitations of using aquaria and flow tanks for experimental work. In the absence of waves, the animals did not behave accordingly to field observations. We thus needed an experimental setup that would enable us to create swash waves in a controlled environment. The swash rig as described in this paper proved to serve the task.

#### 3.5.4.1 Research possibilities

The possibilities a swash rig provides for experimental work are very promising. First of all, the question which of the major physical parameters of sandy beaches has a determining influence on the distribution and the behaviour of sandy beach macrofauna can be addressed. Some authors suggest that it is the sediment size that limits species towards reflective beaches (Nel *et al.*, 2001; de la Huz *et al.*, 2002), whereas others think this is due to the beach slope or the wave action (reviewed in Brown & McLachlan, 1990). McLachlan *et al.* (1993) hypothesized that it is the swash climate itself that makes it impossible for some species to survive on reflective beaches. In the swash rig, each of the physical parameters can be changed in a controlled way, keeping the others constant.

Other possibilities include investigation of endogenous rhythms (see further) or endogenous sense of orientation. The latter could be studied by changing the position of the artificial beach relative to the position of the natural beach. Also more complicated studies on a longer term, for instance to detect circa-tidal, circa-diurnal or circa-lunar cycles lie within the possibilities of a swash rig. This, however, would imply the need for an automatization of the wave generating device.

#### 3.5.4.2 Endogenous rhythm experiment with *Olivella semistriata*

During falling tide, and in absence of any tidal cue, almost all specimens moved downshore, as they would in the field; hardly any specimens moved upshore. During upcoming tide, however, there was noticeable upward migration in the swash rig, and half of the runs showed a net upward migration. We could demonstrate that this rhythm remains present for at least half a tidal cycle: animals that were collected during upcoming tide (mid-tide) and kept under constant laboratory conditions migrated downward six hours later (during falling tide) and vice versa. Since the conditions in the swash rig were

identical during all runs, these results can be best explained by an endogenous circatidal clock.

Two degrees in endogenous circatidal behavioural control exist. The simplest form is an endogenous clock which tells the animals the state of the tide. As a result, the response of species to migration cues ('triggers') such as changes in thixotrophy, light intensity or direction or hydrostatic pressure is different during upcoming and falling tide (Warman *et al.*, 1993; Naylor and Rejeki, 1996). The most common, yet most complex, form is an endogenous rhythm in behaviour: animals show a different degree of activity depending on the tidal state and depending on directional or non-directional cues.

Both types of endogenous behavioural control help intertidal fauna to maintain or regain their position on the beach and are thus important in structuring intertidal zonation (Yannicelli *et al.*, 2001; Thurman, 2004; Forward *et al.*, 2005). Endogenous rhythms have been found in several sandy beach taxa, though mainly crustaceans. When placed in aquaria under constant conditions, cirrolanid isopods of the genus *Excirrolana* and isopods of the genus *Eurydice*, all inhabiting the upper part of the beach, retain their natural activity rhythm: swimming around high tide and remaining burrowed for the rest of the tidal cycle (*E. braziliensis*: Yannicelli *et al.*, 2001; *Eurydice pulchra*: Alheit and Naylor, 1976; Naylor and Rejeki, 1996). Similar results were found for downshore migrants, such as *Talitrus saltator*, and upshore migrants, such as *Crangon crangon* and *Carcinus maenas* (reviewed by Naylor and Rejeki, 1996). Other examples of sandy beach crustaceans showing endogenous tidal behaviour are the amphipod *Bathyporeia pilosa* (Preece, 1971) and the mole crab *Emerita talpoida* (Forward *et al.*, 2005). Along with a circatidal rhythm, these species often possess a circadian and a circalunar rhythm (Alheit and Naylor, 1976; Naylor and Rejeki, 1996; Thurman, 2004). The endogenous response can persist under laboratory conditions for several tidal cycles, and even up to several weeks (Enright, 1972; Forward *et al.*, 2005). Enright (1972) suggested that a long-lasting endogenous response is necessary for species inhabiting a zone on the beach which might only be flooded around spring high tide. For the surfer *O. semistriata*, which migrates over the full intertidal width (Chapter 2, 3) stranding will probably never last longer than half a tidal cycle, so the endogenous response of six hours as demonstrated in this paper seems sufficient. Note that we did not test whether the endogenous response lasts for longer than six hours.

Endogenous circatidal rhythms in tidal migrants are often expressed as changes in response to exogenous non-directional or directional cues, helping the animals to

maintain position on the beach. In other species like the surfing mole crab *Emerita analoga*, however, there is no endogenous rhythm in response to environmental cues and the migratory process is solely regulated by changes in the thixotrophy of the sediment (Cubit, 1969), although this was earlier contradicted by Enright (1963) and Efford (1965). The surfing clam *Donax variabilis* seems to show an endogenous tidal response to sediment agitation, but this response is symmetrical and consequently does not tell the difference between upcoming and falling tide (Eilers, 1995b). Brown *et al.* (1989) stated that nor the surfing clam *Donax serra*, nor the surfing whelk *Bullia digitalis* possess an endogenous clock. Thus, it seems that species that actively swim (amphipods, isopods) need endogenous rhythms for cross-shore migration, whereas in surfers that float with the waves (mole crabs, clams) this is regulated by the interaction between waves and sediment, with a less clear role for circatidal rhythms. *Olivella semistriata*, however, is a surfer but nonetheless shows an endogenous circatidal migration behaviour, which discriminates between upcoming and falling tide.

An endogenous circatidal response to directional cues seems to be a necessary characteristic for the surfing gastropod *Olivella semistriata*. It does not, however, suffice for successful tidal migration since it does not solve the problem of timing of the individual migration movements. The 'trigger' for tidal migration excursions could be changes in temperature, salinity, hydrostatic pressure, inundation, sediment thixotrophy or mechanical agitation (Brown and McLachlan, 1990). For *Donax variabilis*, for example, it is the sound of large incoming waves that gives the animals the cue when to jump out of the sediment and ride a wave (Eilers, 1995b). At this stage, we do not know what the exact trigger is for *O. semistriata* to use a specific wave for surfing. From field observations we know that the species is very sensitive to mechanical agitation of the sediment (they emerge from the sediment upon mechanical pressure), suggesting that sediment thixotrophy could be triggering migration; further investigation, however, is needed to evaluate this. Detection of the swash direction, crucial for cross-shore migration, could be through the siphon, which sticks out of the sediment when they are burrowed. This is in contrast to migrating crustaceans, where current detection is thought to be through phototaxis (Alheit and Naylor, 1976; Forward, 1986; Warman *et al.*, 1993).

With the kind of experiment performed during this study, it is difficult to judge the efficiency of the endogenous clock. During some runs, the number of migrating specimens was quite low. Laboratory experiments concerning endogenous circatidal rhythms may indeed sometimes exhibit contradicting results, with only part of the investigated specimens showing tidal behaviour (Warman *et al.*, 1993; Eilers, 1995b; Palmer, 1995).

This does not explain why downward migration was much more efficient in the swash rig than upward migration. A possible explanation is that the transportation to the laboratory of the animals resets the tidal clock, since it could be considered as being stranded above the high tide level. A longer period without environmental cues, such as waves, has indeed been shown to reset tidal clocks (Warman *et al.*, 1993; Palmer, 1995).

### 3.5.5 Conclusions

- 1) The swash rig as described here is the first experimental tool that allows scientists to investigate swash-related organisms in the presence of possibly their most influencing environmental factor: the swash.
- 2) We demonstrated that the surfing of the sandy beach gastropod *Olivella semistriata* could be controlled by a circatidal endogenous clock.
- 3) The endogenous clock is manifested as a directional control over non-directional triggers for migration, which enables the animals to distinguish between upcoming and falling tide.
- 4) The presence of an endogenous circatidal migration behaviour is crucial in explaining the surfing pattern of this species.