

Shape and surface variations of syphon openings during complete tidal cycles in *Mya arenaria* in the intertidal zone

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Since the degree of syphonal opening can be an index of the pumping activity, the shape and the surface of syphon openings in *Mya arenaria* were filmed with an underwater camera at two stations in the middle of the intertidal zone. The individuals were perpendicularly oriented to the main current direction or parallel with the inhalant syphon upstream during flood tide, causing refiltration risks during ebb tide. The surface of the inhalant opening (SI) was strongly reduced with increasing current speeds. Its shape (XI) varied with the individual's orientation and had a tendency to become more circular with time. The surface of the exhalant opening (SE) decreased and its shape (XE) flattened with increasing current velocity and with time. However, variations of XI and XE were weak. Current direction had no significant effect on SI, SE, and XE, but did cause a strong decrease of the SE/SI ratio during ebb in individuals exposed to important refiltration risks during ebb tide. Significant negative correlations between stomach content in phaeopigments and SI and SE suggest that a syphonal constriction could contribute to more efficient feeding. For parallel oriented individuals, the decreases of SE, SE/SI, and XE during ebb can then be interpreted as an attempt to deviate or increase the excurrent velocity relative to the incurrent so as to limit refiltration. We suggest that decreases in opening surface and shape may serve, above all, to increase syphon current jet velocity in syphonate bivalves.

INTRODUCTION

In the literature, actively pumping bivalves were generally described by extended mantle edges or fully dilated syphon openings, whereas reduced pumping or filtration rates were associated with reduced valve gape, recessed mantle edges, constricted syphon openings, or guard tentacles leaning inward to screen syphon or mantle openings (Ali, 1970; Eaton, 1983; Famme et al., 1986; Foster-Smith, 1975; Jørgensen et al., 1988; Jørgensen & Riisgård, 1988; Newell & Bayne, 1980; Palmer, 1980; Riisgård & Randløv, 1981; Riisgård, 1991). In mussels, the retraction of mantle edges and exhalant aperture with partial closure of the shell gape results in decreasing the width of the interfilament canals which control the pressure pump and the flow rate through the inhalant opening (Jørgensen et al., 1988). Since exhalant aperture in bivalves is generally narrower than the inhalant aperture (Jørgensen, 1966), it was generally presumed that the exhalant syphon controls the flow (Foster-Smith, 1976; Jørgensen, 1966). Newell & Bayne (1980) suggested that much of filtration rate variability may be ascribed to differences in the degree of syphon opening. Eaton (1983), who considered that filtration rates were always correlated with external syphon appearance in *Mya arenaria*, proposed that close visual observations of syphon openings would be a useful field technique for estimating filtration rate without direct measurement.

However, Foster-Smith (1976) suggested that a reduction of 80% in the exhalant aperture would be required to significantly affect the total flow resistance through the

pumping system, smaller aperture reduction rather producing an increase of the exhalant flow velocity for several epi- and endo-benthic species including *M. arenaria*. It can therefore be hypothesized that aperture size could change jet velocity without greatly modifying bivalve pumping rate. This agrees with Grizzle et al. (1992) who suggest that syphonate taxa generally have faster inhalant pumping speeds than non-syphonate taxa because their inhalant opening are more reduced. They also predicted that ambient flow velocities for optimal growth would be several cm s^{-1} greater for syphonate taxa. In epibenthic species, few publications have reported partial closures of valve gapes or syphon openings in response to high flow velocity causing strong pressure gradients across the gills (Wildish et al., 1987; Wildish & Miyares, 1990; Wildish & Saulnier, 1993). To our knowledge, no measure of syphon aperture in relation to ambient flow velocity has been reported in syphonate species. Working on artificial syphons with constant section size, Monismith et al. (1990) showed that pumping velocity may alter the refiltration rate, depending on individual orientation, when a high crossflow severely deflected the exhalant jet of syphonate species. When the exhalant syphon was located upstream of the inhalant, refiltration could be significant if the current speed was stronger than the excurrent velocity, but no refiltration occurred when incurrent was upstream. In the intertidal zone, Vincent et al. (1988) suggested that refiltration can explain the preferential orientation of *M. arenaria* with both syphons side by side, normal to the main tidal current direction, this orientation minimizing refiltration risks during flood as well as

ebb tides. In weak current and depleted fluid conditions, increasing both pumping rate and velocity could have two opposite effects: first, it could increase the flow of phytoplankton-depleted fluid into the boundary layer enhancing refiltration; second, it could increase syphon jet height, increasing mixing in the water column and enhancing food availability (O'Riordan et al., 1993, 1995). Nevertheless, Monismith et al. (1990) and O'Riordan et al. (1993, 1995) altered pumping velocity by varying pumping rate since they had no possibility to change the artificial syphon section size. They did not take into consideration the possibility of bivalves modifying their inhalant and exhalant jet velocities by variations of syphon openings. It can be hypothesised that, without greatly modifying the pumping rate, small variations of syphon section size may permit modifications of jet velocity and jet height according to current velocity fluctuations. Furthermore, separate variations of inhalant and exhalant section size or shape could control jet interactions in response to variations of current direction and refiltration risks.

The aim of this study was to test current velocity and direction effects, with regard to individual orientation, on various characteristics of *M. arenaria's* syphon openings, during complete tidal cycles. Variations of shape and surface of inhalant and exhalant syphons were analysed from a model and from a series of *in situ* video recording experiments covering several tidal cycles at two stations of the intertidal zone.

In the following sections, we used the definition of filtration rate given by Bayne et al. (1976): the volume of water completely cleared of particles per unit of time. This definition is quite 'general' since it did not make a difference with the clearance rate. The filtration rate should not be confused with the pumping rate which is the volume of water flowing through the inhalant aperture without consideration of particle retention (Bayne et al., 1976).

MATERIALS AND METHODS

Experimental design

Using an underwater video camera, syphonal apertures of *Mya arenaria* in the middle of the intertidal zone at 'Anse à l'Original' were filmed, on the south shore of the Saint Lawrence Estuary, Québec (48°21'N 68°47'W). Two stations (B and C) were chosen for their different hydrodynamic conditions. Twelve individuals (IND) were observed at each station (STATION). Individuals had two possible orientations: their sagittal plane perpendicular to the principal axis of the current (90°) or parallel, their inhalant syphon being located upstream during flood (0°). For each station, in August 1995, three individuals of each orientation (ORIENT) were filmed during a first date (DATE) and the six others during a second date three days later, using the same experimental design. Each date corresponded to two tidal cycles (CYCLE) on two consecutive days. A total of eight tidal cycles were studied, cycles and individuals were nested within date and dates were nested within station. During the entire submersion cycles, the current direction and velocity were continuously recorded on a Marsh–McBurney current

meter (Model 511) and video recordings were performed every 15 min for five minute sequences (Thorin et al., 1998). Each cycle, composed of 26 or 27 video sequences, was divided into three phases (PHASE) corresponding to flood, high and ebb tides, phases being centred around the slack of high tide. At the end of each date, individual stomachs were dissected in the field, ground in 90% acetone and kept away from light at 0°C for 24 h. Chlorophyll-*a* (CHL) and phaeopigment (PHE) concentrations were determined according to Thorin et al. (1998), adapted from Parsons et al. (1984).

Model and hypothesis

By considering tidal phases (flood, high tide and ebb) and individual orientations (perpendicular or parallel), the model examined six different cases (PHASE×ORIENT) which permitted to test of effects of current velocity (V), current direction (D) and time (T) variations on syphon opening characteristics (Figure 1). In this model, we assumed that current direction effect was positive and equal when the current arrived from the left (A1), right (A3) or from the side of the inhalant syphon (B1). This assumption can be tested by comparing A1 with B1 cases. The effect of current direction was negative, however, when it came from the side of the exhalant syphon since it carried, in this case, an important refiltration risk (Monismith et al., 1990). We also assumed that the two orientations during high tide (A2 and B2) were equal, as the current was weak and its direction was extremely variable; this assumption can be checked by comparing A2 and B2. Lastly, we considered that effect amplitudes of either velocity or time between Phases 1 and 2 were the same as between Phases 2 and 3, since mean current speeds were similar in Phases 1 and 3 and since high tide corresponded to the middle time of submersion period. We also assumed that the effects of velocity and time were additive. The effect of time (T) can then be tested by comparing A1 and A3 and the effect of direction (D) can be tested by comparing A3 and B3 (Figure 1). Velocity effect (V) can then be deduced from time and direction effects by comparing several cases from A1 to B3.

Measures of syphonal opening characteristics

The variations of eight syphonal opening characteristics (Table 1) were studied. The opening surface (mm²) of the inhalant (SI) and exhalant (SE) syphons were estimated from measures of the two ellipse axes (Wildish & Saulnier, 1993). Since the mean shell length (\pm SD) of all individuals was 63.2 \pm 4.4 mm, SI and SE were adjusted to a shell length of 60 mm. The short term variations of syphon surfaces were measured during events of simultaneous closures followed by simultaneous openings of the two syphons to determine the influential period of these events on the longer term variations of SI and SE. This type of closure/opening represented 87.8% of all behavioural sequences in *M. arenaria* (Thorin et al., 1998). Twenty-four events were randomly selected from all the video recordings and were viewed at low speed (5 images s⁻¹). The variations of SI and SE within a tidal cycle were then measured only once per 5-min video

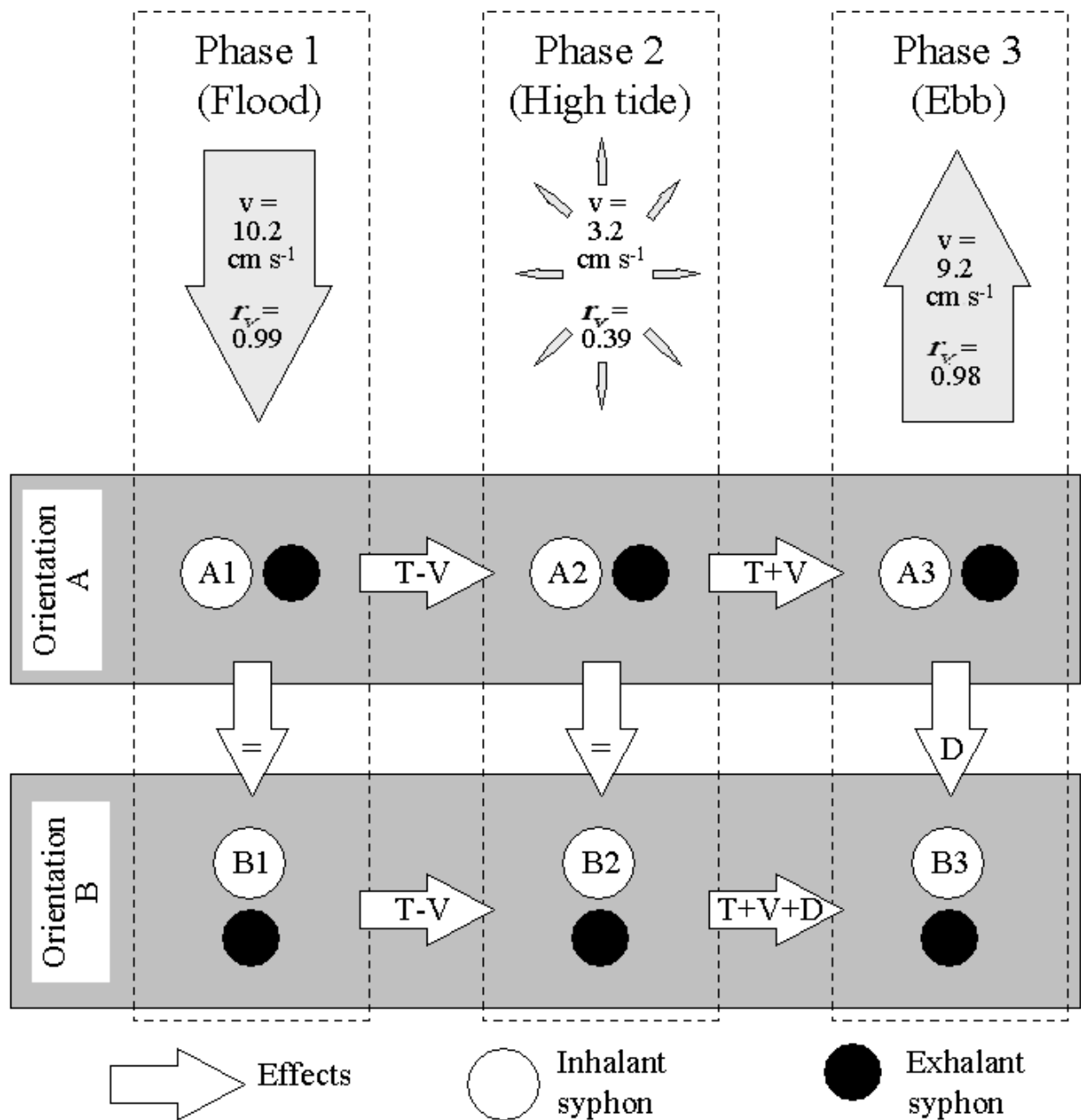


Figure 1. Model of time (T), current velocity (V) and current direction (D) effects on the syphon surface and shape relative to the individual orientations (A, perpendicular; B, parallel) and the tidal phases (1, flood tide; 2, high tide; 3, ebb tide). v, mean current velocity measured for each phase; r_v, measure of concentration of the current direction.

Table 1. Definitions and means for opening syphon characteristics for all dates and individuals.

Symbols	Definitions	Units	Mean	CV (%)
SI	Opening surface of the inhalant syphon	mm ²	69.34	36.7
SE	Opening surface of the exhalant syphon	mm ²	45.23	38.3
SE/SI	Ratio of the two surfaces	–	0.66	15.2
XI	Index of the inhalant opening shape	–	0.79	7.6
XE	Index of the exhalant opening shape	–	0.77	7.8
OPE	Length of time the two syphons are open	s min ⁻¹	51.09	9.7
IF	Inhaled flux index (SI×OPE)	mm ² s min ⁻¹	3854.03	40.5
EF	Exhaled flux index (SE×OPE)	mm ² s min ⁻¹	2514.33	42.0

CV, coefficient of variation between individuals.

sequence during periods which were not influenced by the closure/opening events; SE/SI ratio was then calculated. In order to define an index representing the syphon shape, the ratio between the two perpendicular diameters (height/width) of the ellipse of each syphon (XI and XE) was calculated, giving a measure of the eccentricity of the ellipse. This ratio will be equal to one for a perfectly circular syphon and will decrease as the syphon flattens. Lastly, the variations of the angle of the vector passing through the two syphon surface centres was measured to test the individual's ability to reorient their syphon axis by torsion (TOR) in order to decrease refiltration rate, as suggested by Vincent et al. (1988). However, these angle variations during a tidal cycle were extremely low for almost all individuals. The concentration indices of the vectors (corresponding to the norm r_v , see Zar, 1984) varied between 0.97 and 1.00, according to individuals, giving a mean angular deviation of 4.73° . Because the

torsion was so low and probably close to the measurement error, its analysis was abandoned. In *Ruditapes philippinarum*, Defossey & Daguzan (1996) have also observed that shell orientation was similar to the direction given by the alignment of the two syphons of individuals. In order to simplify the statistical analysis, intra-date variations (between cycles) were not considered, and the means of the behavioural variables per phase, per date and per individual were analysed.

Data analysis

The studied current characteristics were the mean current velocity (v) and the mean length (r_v) of the current vector during each 5 min-video sequence of a given date. r_v can vary from 0 when the dispersion is maximum to 1 when all the current directions are the same; r_v is therefore a measure of concentration of the

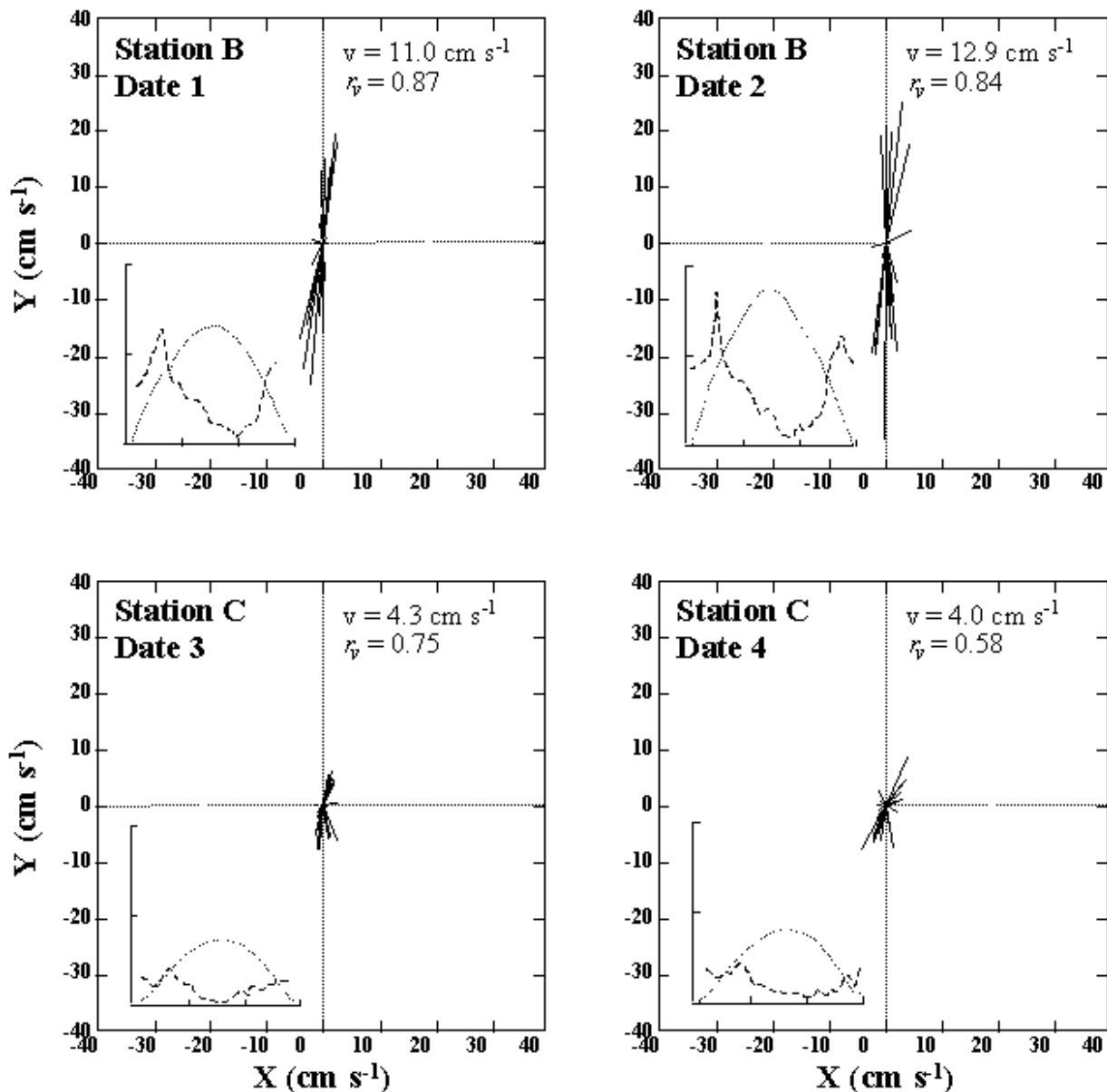


Figure 2. Bimodal distribution of current vectors and tidal variations of current velocity (dotted line) and water height (solid line) for each date. The units of speed and of water height are not given but the scale is the same for all dates; v , mean current velocity; r_v , mean length of current vectors calculated for each phase.

directions (Zar, 1984). Mean v and mean r_v were calculated for each date (Figure 2) and for each phase (all dates merged, Figure 1).

The correlations between the opening characteristics were calculated using a Spearman test completed by principal component analysis (PCA). Relationships between the behavioural variables and the stomach pigment content were tested with Spearman's r calculated on the means of the opening characteristics for each individual during the second tidal cycle of each date (cycle corresponding to the stomachs' dissection).

A four-way partially-hierarchical analysis of variance (ANOVA) without replication (DATE, ORIENT, IND and PHASE) was performed on the syphon opening characteristics. The station was not taken into account since: (i) this factor is already integrated in interdate variations, (ii) variations between stations were equivalent or weaker than intrastation (between dates) variations, limiting a possible interpretation of this factor; and (iii) a preliminary five-way ANOVA including the station showed that this factor did not have any significant effect. Moreover, the date was considered as a random factor. The assumptions of the analysis were respected as the residuals met the conditions of normality (Shapiro–Wilk test: $W=0.98$; $N=69$; $P \geq 0.448$) and of independence with the estimates (visual checking). When the null hypothesis was rejected, protected Least Significant Differences multiple comparison tests were used. Statistical analyses were performed on SAS software.

RESULTS

Current characteristics

During phases of flood and ebb tides, the current velocity (v) was high and the vector dispersion (r_v) was low, values being similar between phases 1 and 3 (Figure 1). By contrast, during the slack of the high tide, the mean current velocity was much reduced, and in more variable directions. Furthermore, mean current velocity was much greater at station B (dates 1 and 2) than at station C (dates 3 and 4) (Figure 2). Station B showed mean velocity approaching 12 cm s^{-1} with maxima exceeding 35 cm s^{-1} while station C had speeds of the order of 4 cm s^{-1} increasing to maxima of 10 cm s^{-1} . The current vectors calculated for each 5-min video sequence of observation during the four dates (Figure 2) showed that the current direction was more variable in station C (higher vector dispersion, r_v) than in station B.

Short-term variations of the syphonal surface

The duration of a closure event was defined as the time interval between the last value exceeding 85% of the maximal surface measured before each closure and the moment when the surface becomes zero. In the same way, the end of the syphonal opening events was established as the first value to exceed 85% of the maximal surface defined before the syphon closure. According to the analysis of 24 simultaneous two syphon closure and opening events, randomly chosen, the mean duration of a closure event of the inhalant syphon was of 1.2 s (Figure 3). The syphon remained closed for a mean of

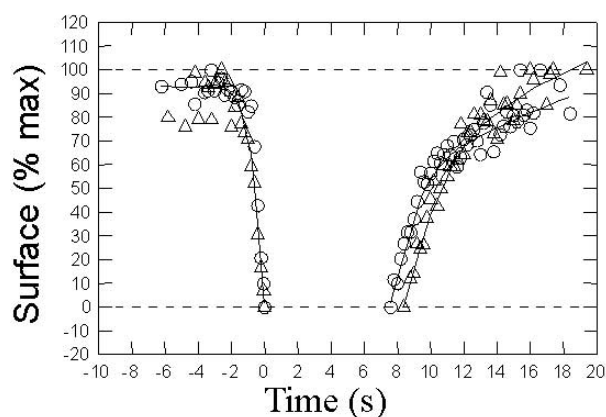


Figure 3. Short-term variations of inhalant and exhalant syphon surfaces during simultaneous closures and openings of the two syphons. The surface of the inhalant syphon is symbolized by a circle and that of the exhalant by a triangle.

7.6 s then opened for a mean of 5.8 s. The exhalant syphon closed in a mean of 1.6 s, stayed closed for a mean of 8.4 s then opened for a mean of 5.2 s. The exhalant syphon remained closed slightly longer (a difference of 0.8 s), but opened more rapidly (0.6 s) reaching 85% of its maximal surface in the same amount of time as the inhalant syphon. At opening, the increase in the surface area of the two syphons appeared to take place in two steps: beginning with a quick growth until 50–70% of the maximal surface before closure, followed by a slower growth period (Figure 3). Ten seconds after the beginning of the opening events, the variations in the syphonal surfaces became weak and difficult to observe. However, the surface of the inhalant syphon could attain a value slightly less than its maximum value before closure. A small difference between the periods before and after syphonal closure/opening could then exist which was not taken into account during the statistical analysis. During the time periods without closure events the syphon surfaces were considered stable and a single measure was taken per 5-min video sequence for the variation analysis within the tidal cycles.

Correlations between behavioural variables

SI and SE were strongly correlated ($r=0.95$; $P<0.001$) showing similar variations during the submersion cycles. XI and XE were correlated respectively to SI ($r=0.58$; $P<0.001$) and SE ($r=0.76$; $P<0.001$) showing that the syphonal surface decrease came with a flattening of the openings. The PCA confirmed the majority of these results (Figure 4). The SE/SI variable was clearly distinguished from the other behavioural variables and it contributed to the second factor of the PCA (Figure 4). This suggests that SE/SI tidal variations may respond differently to environmental variables than the other behaviour patterns.

Chlorophyll-*a* was not linked to any behavioural variable ($r \leq 0.38$; $P > 0.05$), however phaeopigments were negatively correlated to SI ($r = -0.54$; $P < 0.01$; $N = 23$) and SE ($r = -0.49$; $P < 0.05$; $N = 23$). SI and SE were then the two variables that could explain the best the stomach content of individuals.

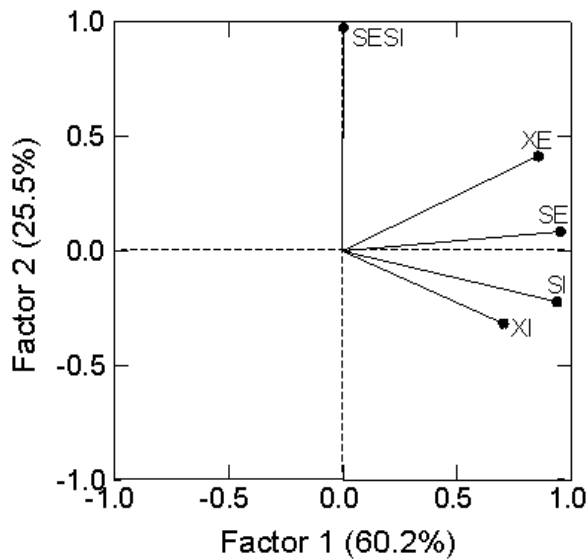


Figure 4. A two-factor principal component analysis for all syphon opening characteristics. For abbreviations, see Table 1.

The effects of individual orientations and different tidal phases

The r^2 coefficients obtained by ANOVA on SI (0.95), SE (0.90), SE/SI (0.83), XI (0.86) and XE (0.75)

variables showed that the percent variance explained by DATE, ORIENT, IND and PHASE variables was very large. The date had an extremely significant effect on SI, SE and XE (Table 2). However, for each date, the means of the various syphon opening characteristics were not clearly differentiated between stations B (dates 1 and 2) and C (dates 3 and 4), and the date effect was therefore difficult to interpret. For this reason, the details of this random factor were not studied and, in Figure 5, the tidal variations of syphonal characteristics for all the dates were merged.

There was an extremely significant effect of date, of individuals, and of phase upon SI and SE (Table 2). The absence of the orientation effect alone, or in interaction with phase confirmed that in the A1 and B1 cases, as well as in the A2 and B2 cases, situations were equivalent. Moreover, it indicated that there was no current direction effect ($A3=B3$; $D=0$). The multiple comparison tests for SI showed that phase 2 was different from phases 1 and 3 ($P<0.001$). There was therefore no time effect ($A1=A3$; $2T=0$), yet there was an important velocity effect ($AB1\neq AB2$; $T-V=-V$). The negative effect of velocity on SI produced a difference of 23.5% between values during high tide and values during flood and ebb (Figures 5 & 6). Multiple comparison tests for SE showed that phases were all different one from the other ($P\leq 0.008$),

Table 2. Partially-hierarchic four factors ANOVA testing date (DATE), individual orientation (ORIENT), individuals (IND) and phase (PHASE) effects on the inhalant and exhalant syphon opening characteristics.

Variables	Sources	SS	df	MS	F-ratio	P
SI	DATE	33577.5	3	11192.5	32.45	0.000
	ORIENT	134.8	1	134.8	0.38	0.543
	IND(DATE×ORIENT)	7318.0	20	365.9	5.87	0.000
	PHASE	4438.8	2	2219.4	35.63	0.000
	ORIENT×PHASE	20.6	2	10.3	0.16	0.849
SE	DATE	13750.2	3	4583.4	23.73	0.000
	ORIENT	31.9	1	31.9	0.16	0.691
	IND(DATE×ORIENT)	4068.0	20	203.4	3.70	0.000
	PHASE	2018.4	2	1009.2	18.34	0.000
	ORIENT×PHASE	247.0	2	123.5	2.24	0.119
SE/SI	DATE	0.018	3	0.006	0.22	0.884
	ORIENT	0.075	1	0.075	2.61	0.122
	IND(DATE×ORIENT)	0.600	20	0.030	6.87	0.000
	PHASE	0.084	2	0.042	9.60	0.000
	ORIENT×PHASE	0.080	2	0.040	9.21	0.001
XI	DATE	0.057	3	0.019	3.05	0.052
	ORIENT	0.038	1	0.038	5.85	0.025
	IND(DATE×ORIENT)	0.140	20	0.007	6.54	0.000
	PHASE	0.010	2	0.005	4.49	0.017
	ORIENT×PHASE	0.004	2	0.002	1.80	0.178
XE	DATE	0.099	3	0.033	5.84	0.005
	ORIENT	0.015	1	0.015	2.59	0.122
	IND(DATE×ORIENT)	0.120	20	0.006	2.37	0.010
	PHASE	0.050	2	0.025	10.31	0.000
	ORIENT×PHASE	0.014	2	0.007	2.64	0.083

The crossed factors are separated by an asterisk. The IND factor is nested in DATE×ORIENT. Interactions with DATE and IND were not taken into account since these factors were considered as random factors. The error term of DATE and ORIENT is IND and the error term of IND and PHASE (alone or in interaction) is the residuals. One individual was eliminated as its orientation was wrong, N=23.

indicating a time effect ($A1 \neq A3$; $2T \neq 0$; $P=0.008$) as well as a combined effect of time and velocity ($AB1 \neq AB2$; $T - V \neq 0$; $P=0.002$). For all individuals, time was linked with a 16.0% decrease of SE between phases 1 and 3 (2T). Given that time effect was assumed to be linear, the increase of 14.6% between phases 1 and 2 (T - V) must be due to decreasing velocity which was responsible for 6.6% of SE variations (Figure 5).

The ANOVA indicated no date effect for the SE/SI ratio, an extremely significant effect of individuals and an extremely significant effect of phase which varied with orientation since $ORIENT \times PHASE$ was significant (Table 2). Multiple comparison tests showed that the interaction $ORIENT \times PHASE$ was primarily due to the B3 case which differed from all the others ($P \leq 0.008$), and was also due to the B2 case which differed from A1, A3, and B1 ($P \leq 0.007$), but not from A2 ($P=0.114$)

(Figure 5). The A1, A2, and A3 cases were not different ($P \geq 0.124$), no significant variation occurring in perpendicular oriented individuals. Therefore, there was no time effect ($A1 = A3$; $2T = 0$; $P=0.929$), and an important negative effect of current direction ($A3 \neq B3$; $D \neq 0$; $P < 0.001$) which was responsible for a difference of 24.3% in SE/SI between the B3 case, and the A1, A2, and A3 group (Figure 5). Our model assumptions ($A1 = B1$; $P=0.818$ and $A2 = B2$; $P=0.114$) were therefore verified. In parallel oriented individuals, the difference between B1 and B2 (distance of 10.9%; $P=0.004$) suggested an eventual positive current velocity effect on SE/SI variations.

The ANOVA showed a significant to extremely significant principal effect of orientation, of individuals and of phase upon XI (Table 2). The $ORIENT \times PHASE$ interaction was not significant, and the inhalant syphon had a more circular shape for perpendicular oriented

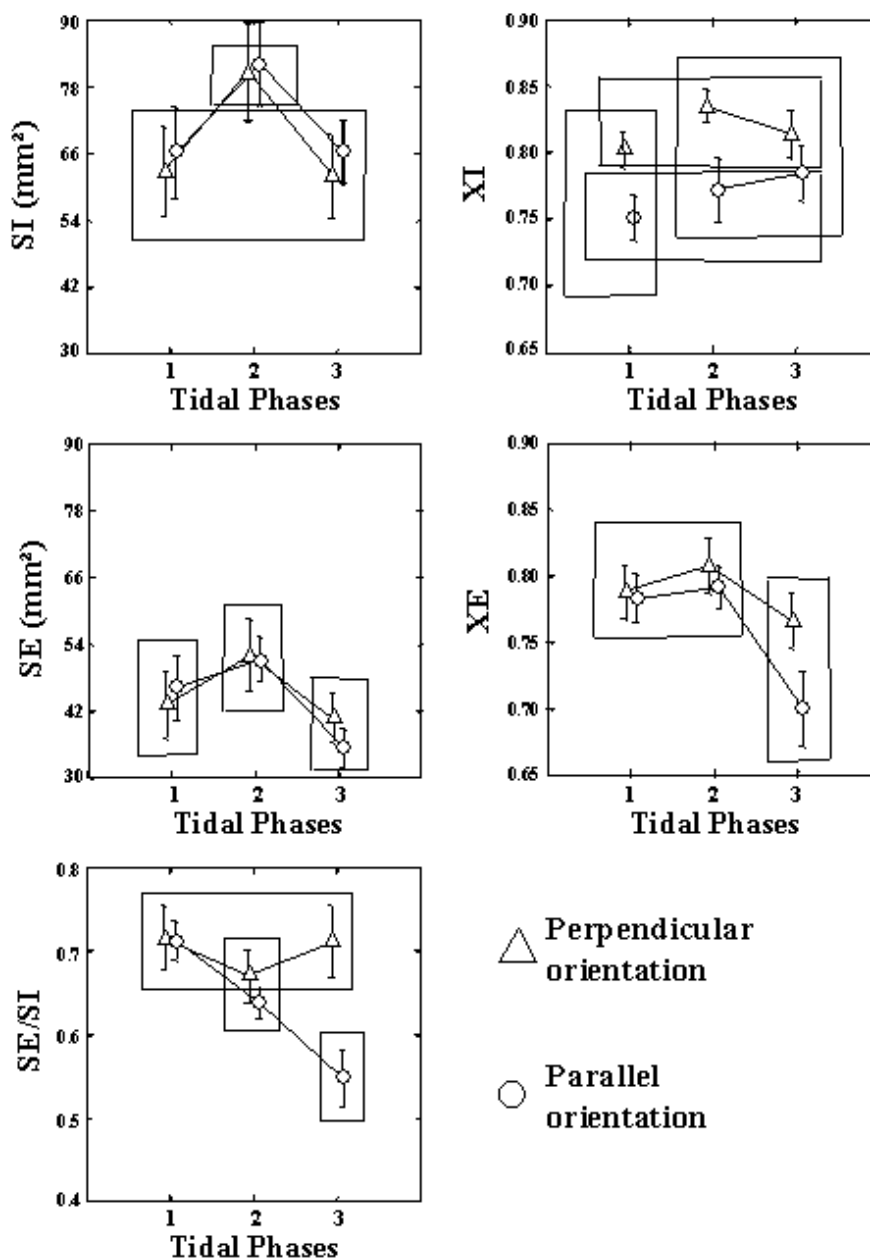


Figure 5. Mean values of syphon opening characteristics for the three tidal phases, and the two individual orientations (\pm SE). Phase 1, flood tide; phase 2, high tide; phase 3, ebb tide; the rectangles regroup values which have no significant difference after analysis of variance.

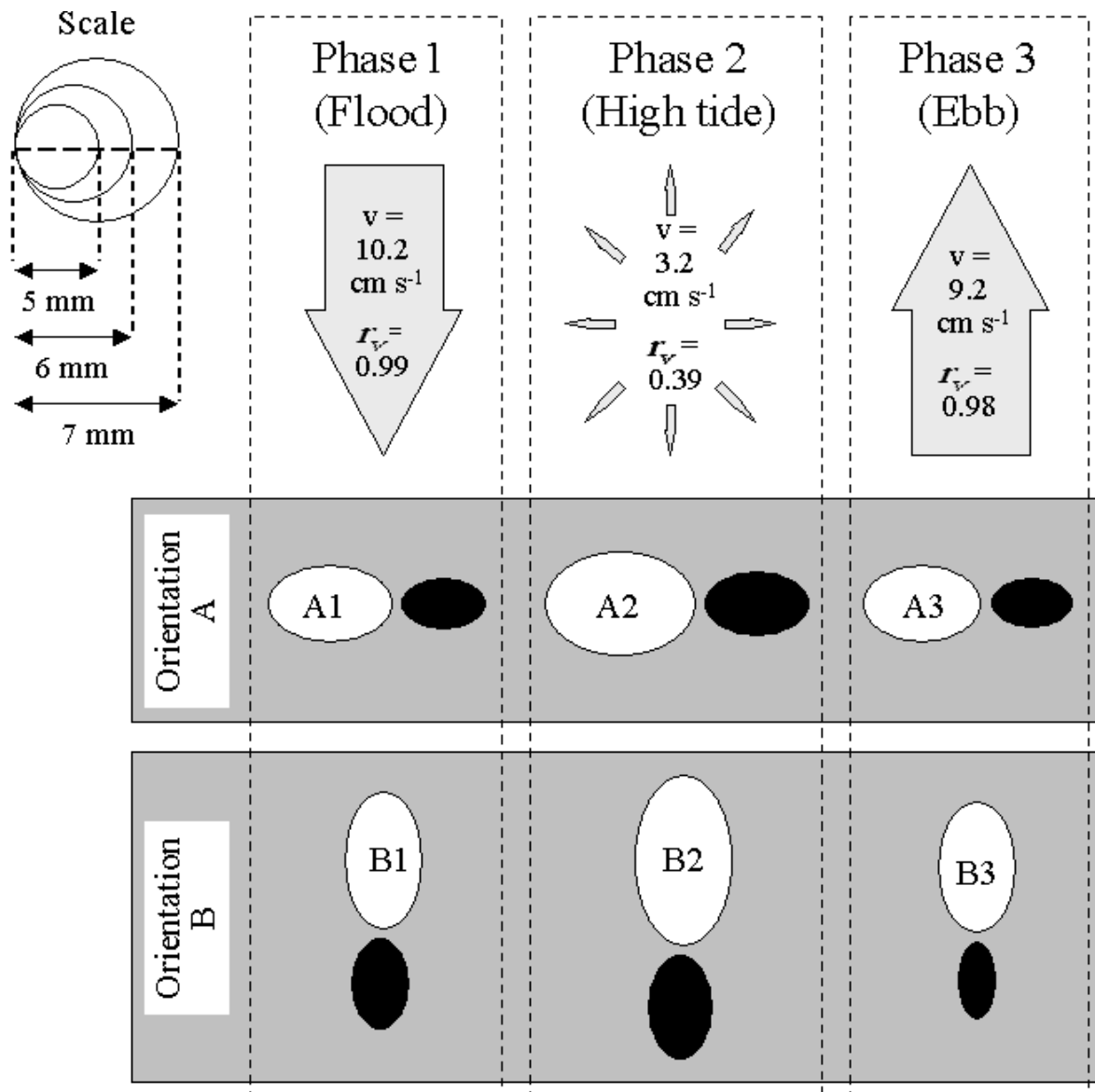


Figure 6. Comparisons of the observed shape and syphon surface during each of the A1 to B3 cases. The syphon surface and shape were obtained by squaring the mean height and width to bring out differences between syphon characteristics; v , mean current velocity measured for each phase; r_v , measure of concentration of the current direction.

individuals than for parallel oriented individuals during the entire submersion time (Figures 5 & 6). It is therefore impossible to interpret the difference between A3 and B3 from current direction since the results also showed significant differences between A1 and B1 as well as A2 and B2. For both orientations, multiple comparison tests indicated that XI values were smaller during phase 1 compared to phases 2 ($P=0.010$) and 3 ($P=0.018$). There was, therefore, a positive time effect ($A1 \neq A3$; $2T \neq 0$) and a combined effect of time and velocity ($AB1 \neq AB2$; $T-V \neq 0$) on XI. For all individuals, time was responsible for an increase of 3.2% in XI between phases 1 and 3 (2T). The increase in XI was of the same order of magnitude between phases 1 and 2 (T-V) indicating a 1.6% negative velocity effect upon variations of inhalant opening shape.

There was a very to extremely significant effect of date, of individuals and of phase for XE (Table 2). The absence of a principal effect or interaction for orientation suggested that current direction had no significant effect

on XE ($A3=B3$; $D=0$) and that the model's restrictions were validated ($A1=B1$ and $A2=B2$). Multiple comparison tests showed that phase 3 was different from phases 1 ($P=0.002$) and 2 ($P<0.001$). There was, therefore, a time effect ($A1 \neq A3$; $T \neq 0$), but no combined effect of time and velocity ($AB1 \neq AB2$; $T-V=0$; $P=0.345$). For all individuals, time produced a 7.8% decrease of XE between phases 1 and 3 (2T), while the same XE decrease between phases 2 and 3 (T+V) indicated a negative velocity effect by 3.9% (Figure 5).

DISCUSSION

Variations in syphon opening

SI and SE varied within the tidal cycles but remained stable on a short-term scale ($t < 5$ min) outside the closed periods of syphon opening/closure events ($t < 10$ s). However, the tidal current velocity may double, in a 5-min time interval, and the mean coefficient of variation

for velocity within a sequence was 20.6% for the whole studied cycles. Then, *Mya arenaria* only modified its syphon openings to current variations in the medium term (within a submersion cycle). Increasing current velocity caused a reduction in both syphon surfaces during flood and ebb tides compared to the slack of the high tide (Figures 5 & 6). The effect was stronger on SI than on SE, suggesting that the exhalant syphon may not always be the single adjustment system for water transportation in bivalves as stated by Jørgensen (1966) and Foster-Smith (1976). However, there was a decrease of SE in function of time which did not exist for SI. The term 'time effect' was used in the absence of immediate interpretation of difference between A1 and A3. However, it is obvious that the time was certainly not directly involved but represented other environmental factors or physiological states of individuals. Indeed, decrease of SE and XE between A1 and A3 may be due to differences in food availability or quality between flood and ebb tide or a state of tiredness or bivalves' fill, as examples. Unfortunately, if our model allowed us to quantify such an effect of time, it did not provide us an obvious interpretation.

The decrease of SE/SI in parallel oriented individuals during ebb clearly indicated an important effect of current direction on this variable (Figures 5 & 6). The difference between SI and SE was then maximal when the angle between the current direction and the axis of the two syphons reached a maximum value during ebb tide (close to 180°), in other words, when the exhalant syphon was situated upstream (B3). The SE/SI ratio seems to hold an important role in clam feeding behaviour as it was the only syphon opening characteristic which was entirely independent of DATE ($P \geq 0.05$). Furthermore, despite a strong individual effect, mean variations of SE/SI repeated themselves in a similar way for each date.

The difference between inhalant syphon shapes (XI) for perpendicular and parallel oriented individuals is difficult to explain as it remained significant for the entire submersion period and therefore it cannot be interpretable by a current direction effect due to refiltration risk. Our model also showed a slight increase in XI as a function of time, combined with a weak and negative effect of current speed. The inhalant syphon had then a tendency to flatten as current speed increased and to become more and more circular during submersion time (Figures 5 & 6). These effects were very weak, however. XE variations showed that the negative effects of both time and current speed were relatively weak, but highly significant (Figures 5 & 6). The exhalant syphon had a tendency to flatten with increasing current and time. XI and XE variations with time were then in opposite directions. In spite of the lack of significant difference (possibly due to a high interindividual variability), XE values strongly differed between A3 and B3, being probably meaningful in terms of behavioural reaction. Indeed, parallel oriented individuals had their exhalant syphon constricted and flattened whereas their inhalant syphon was more opened and circular. This behavioural pattern can be interpreted as an effort to deviate the exhaled flow away from the radius of particle capture surrounding the inhalant syphon. According to Amouroux (1976) and Ansell (1961), membranes, strongly developed on the end of syphons in some species, could canalize and regularize

the rejected water discharge. *Mya arenaria* possesses a membrane around the tip of the exhalant syphon which would be able to fulfil such a function. While SCUBA-diving, this behaviour of excurrent deviation by the syphonal membrane in some individuals has been verified in the field. We can also interpret the circular shape of SI as an effort of parallel oriented individuals to capture particules getting round from one side or the other side of the exhalant jet.

Adaptations to the current fluctuations

The maximal aperture size during high tide could result from favourable environmental conditions since large apertures in bivalves were often associated with optimal conditions of food availability, water temperature and absence of individual disturbance (Jørgensen et al., 1986; Jørgensen et al., 1988; Riisgård & Møhlenberg, 1979; Riisgård, 1991). As well, the negative effect of current speed on the inhalant syphon surface (and to a lesser way on the exhalant syphon) could be interpreted by an inhibition on both pumping rate and feeding activity induced by current velocity. Actually, current speeds higher than 6 or 10 cm s⁻¹ may cause partial valve or syphon closures limiting filtration in certain epibenthic species (Wildish et al., 1987; Wildish & Miyares, 1990; Wildish & Saulnier, 1993). The inhibiting mechanisms can come from: (i) a decrease in the particle capture radius around the inhalant syphon (Ertman & Jumars, 1988); (ii) an increase in the individual's refiltration rate (Monismith et al., 1990; O'Riordan et al., 1993, 1995); (iii) unfavourable pressure gradients between inhalant and exhalant syphons (Wildish et al., 1987; Wildish & Miyares, 1990; Wildish & Saulnier, 1993); or (iv) a mechanical stress linked to local turbulence phenomena (Grizzle et al., 1992). If increasing current decreases the particle capture radius around the inhalant syphon (Ertman & Jumars, 1988), it also increases the particle flux near the bottom. However, we need to test how these two opposite effects can respectively influence the rate of particle capture in syphonate species. As well, in our study, SI variations were independent of current direction, showing that the syphon constriction was not an answer to refiltration problems. Finally, for syphonate species that have their opening surface in the same plane as the surrounding flow, it is difficult to attribute an inhibiting effect of speed with unfavourable pressure gradients as has been proposed for epibenthic species (Wildish et al., 1987; Wildish & Miyares, 1990; Wildish & Saulnier, 1993). Furthermore, in the syphonate species *Mercenaria mercenaria*, Judge et al. (1992) did not observe any inhibitory effect of current speed on individual growth. By contrast, in a laboratory flume, *Mya arenaria* growth seemed to be enhanced by increasing free-stream (U) and shear (U*) velocity except when the superficial layer of sediment was hardly disturbed (Emerson, 1990). In favourably positioned individuals, current inhibition would then be mostly explained by very high velocity and shear stress. However, the path of the particles in suspension, observable in our video, did not reveal important erosion or turbulence phenomena even when the current was maximal. In *M. arenaria*, few elements can then clearly explain SI and SE decreases with current speed.

It is generally accepted in the literature that a reduction of the valve or syphon opening causes a decrease in filtration or pumping rates (Ali, 1970; Eaton, 1983; Famme et al., 1986; Foster-Smith, 1975; Jørgensen et al., 1986; Jørgensen et al., 1988; Jørgensen & Riisgård, 1988; Newell & Bayne, 1980; Riisgård & Randløv, 1981; Riisgård, 1991). These studies are counter to Foster-Smith (1976) who showed that a reduction less than 80% of the exhalant syphon opening could increase the excurrent velocity without causing important resistance on the bivalve's pump. In our study, the mean syphon surface variations between the three phases did not exceed 30.4% (SE decrease between phases 2 and 3). Considering the study of Foster-Smith (1976), we suggest that SI and SE Aperture surface variations could serve to adjust the incurrent and excurrent velocities in relation to the tidal fluctuations of current velocity and direction. Indeed, in parallel individuals, the decrease of SE/SI at ebb tide could be more logically interpreted as a certain effort to increase the excurrent velocity compared to the incurrent velocity, rather than being a decrease in pumping rate linked to the exhalant syphon's partial closure, since syphons surfaces were negatively correlated with stomach contents. These correlations suggest that surface variations of inhalant and exhalant syphons did not affect the pumping rate of individuals. In this way, in parallel oriented individuals, the exhalant flow could escape the influence of the inhalant syphon and thus avoid a strong refiltration, in accordance with the conclusions of Monismith et al. (1990) and O'Riordan et al. (1993, 1995). It would then explain why, in spite of high refiltration risk, parallel oriented individuals had similar stomach content as perpendicular oriented individuals. We find then justified to suggest that, considering our results in *M. arenaria* and those of Foster-Smith (1976), certain surface and shape variations of syphon openings in bivalves may modify the syphon jet velocity (mainly the exhalant one) and improve the feeding efficiency according to tidal current velocity and direction variations. This suggestion, however, only applies to syphonate endobenthic species.

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