

A TEST OF RHEOTACTIC BEHAVIOUR OF THE BLUE MUSSEL *MYTILUS EDULIS* L.

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ABSTRACT

Many marine invertebrates show rheotaxis. Marine mussels may orientate the inhalant siphon towards currents to optimize feeding and sanitary conditions thereby improving growth rates. The blue mussel, *Mytilus edulis* L., forms extensive beds on both hard and soft substrata. *M. edulis* is an active filter-feeder showing great mobility by constant reorientation and attachment by aid of a well developed foot and byssus threads. We predicted that mussels would show rheotaxis and orientate uniformly in relation to currents to optimize feeding. To test this hypothesis, orientation of mussels in the field were observed using underwater stereophotography. Furthermore, experiments *in situ* and in a laboratory flume were performed. The results showed that *M. edulis* lack rheotaxis. Movements within a mussel patch were highly dynamic indicating that rheotactic behaviour may be concealed by the difficulty in experimentally separating competition for space from competition for food.

INTRODUCTION

Orientation of marine invertebrates in relation to currents is reported to be advantageous by inducing passive flow for filtration in sponges (Vogel, 1974), gorgonians and leptogorgonians (Wainwright & Dillon, 1980; Leversee, 1976), brachiopods (LaBarbara, 1977), scallops (Hartnoll, 1967), sabellid polychaetes (Merz, 1984), and ascidians (Young & Braithwaite, 1980). Field observations of the infaunal mussel, *Geukensia demissa* (Frey *et al.*, 1987), and *Mya arenaria* (Van Vincent *et al.*, 1988) showed a perpendicular orientation of the siphons relative to flow direction in locations with bidirectional tidal currents and in a model study of bivalve siphons, Monismith & Koseff (1990) showed that a perpendicular orientation in relation to flow direction reduced refiltration of water from the exhalant siphon. Eckman *et al.* (1989) showed that in the bay scallop, *Argopecten irradians concentricus*, changes in orientation relative to currents may provide a significant means of maintaining high growth rates.

The blue mussel, *Mytilus edulis* L., is influenced

by water movement throughout its life cycle affecting dispersal of gametes and larvae, renewal of food resources and oxygen, and removal of metabolic waste products (Frechette & Bourget, 1985; Butman, 1987; Asmus & Asmus, 1991; Shimeta & Jumars, 1991). Mussels living in still water may experience reduced growth rates (e.g. Svane & Ompi, 1993) and *M. edulis* and *M. californianus* living sympatrically are reported to reduce competition from other species by living in wave-swept environments (Suchanek, 1981). There are thus several factors which may influence behavioural adaptations in relation to currents and water flow. The question we want to address is: "Does the blue mussel, *M. edulis*, display rheotactic behaviour?". First, we made field observations by underwater stereophotography in a natural habitat with predictable high water flow. Second, we performed field experiments with orientation of mussels established in pre-fixed positions. Third, we performed experiments in a laboratory flume to study rheotactic behaviour in a unidirectional flow.

MATERIALS AND METHODS

The field observations and experiments were performed at Björnsholmen, a high-flow habitat constituting a man-made channel of 9 meter depth, 30 meter wide and 350 meter long situated in Strömmarna, an area of narrow sounds connecting Gullmarsfjorden with Koljöfjorden on the west coast of Sweden. The bottom of the channel is flat and covered with *M. edulis* coexisting with the small morph of the sea anemone *Metridium senile* (L.). The current in the channel is bidirectional and generated by a relatively small tidal amplitude (30 cm) and changing air-pressures. The current velocity may be as high as 100 cm/sec.

The flume experiments were conducted in a closed circuit flume flow (300 cm long, 48 cm wide, and 21 cm deep) situated at Kristineberg Marine Biological Station. The design of the flume is described by Vogel (1981).

Field observations of mussel orientation

Orientation of *M. edulis* was analysed by use of underwater stereophotography (see Lundälv, 1971; Svane & Gröndahl, 1988). A transect line with 8 regular spaced position marks was haphazardly placed on the bottom parallel to the channel walls in March 1993 and a stereophotograph was taken at each position mark. The stereocamera was equipped with a 50 x 50 cm photographic frame so the resulting photographs represented 8 replicates, each covering 0.25 m² of the mussel bed. The sea-water temperature varied between 2-4 °C.

The orientation of the mussels in the stereophotographs was analysed in two aligned Wild M5 stereomicroscopes where a three-dimensional view of the mussels could be obtained. Only mussels with the umbo pointing downwards, when it was possible to identify the position of the sagittal plane, were included in the analysis. By use of a compass fixed to the photographic frame the orientation of the mussels was determined in relation to the direction of the flow. The orientations of the mussels were ranked in 8 classes of 45° sections out of 360°. Deviation from a random orientation was tested by use of a G-test (Sokal & Rohlf, 1981) comparing the 8 classes

of orientations against an even distribution. Since the mussels occupy a habitat with a bidirectional current the 8 classes were pooled in pairs, so that classes with an equivalent orientation in relation to the two directions of flow were reduced to one class, reducing 8 classes to 4. These 4 classes of orientations were compared to an even distribution by use of a G-test.

Field experiments on mussel orientation

In field experiments with high and low mussel density, the orientation of *M. edulis* was investigated as a function of initial orientation in relation to direction of flow. In both the experiments, plastic trays (36x54 cm) subdivided into 4 sections (18x27 cm), and separated by thin plastic walls, were filled with coarse sandy sediment.

The mussels used in the experiments were collected by scuba divers at the location Björnsholmen on the 16th of March 1993. Mussels in the length interval of 65-85 mm were used in the experiments. The mussels were cleaned of byssus threads and epizoids and kept at the laboratory in running sea-water.

On the 22nd of March 1993, 6 sediment filled plastic trays (24 compartments) were placed on the bottom of Björnssund channel. In each tray section, 24 mussels were placed with the anterior end (umbo) into the sediment and one quarter of the mussel below the sediment surface. In each tray section, the mussels were oriented in the same direction. Four initial orientations were used with the sagittal plane orientated vertically 0, 90, 180, and 270° from the direction of the flow, respectively. The direction 0° was 240° compass reading. All four treatments were thus replicated 6 times in a randomized design. The trays were arranged on the bottom perpendicular to the prevailing direction of the current and buried down into the sediment level of the mussel bed. The trays were then stereophotographed immediately after deployment and subsequently after 24 and 48 hours. The photographs were analysed as described above.

The orientations of the sagittal plane of the mussels were ranked in 8 classes of orientation, and compared after 24 and 48 hours with the start distribu-

tion by use of two separate G-tests (Sokal & Rohlf, 1981). Deviations from initial orientations after 24 and 48 hours were tested using Kruskal-Wallis test (Zar, 1984).

During the field experiment, flow activity was measured by use of the technique described by Muus (1968). Two series of moulded plaster balls each attached to a 2 mm metal wire were fastened 12 cm above the edge of each tray. The subsequent erosion of the plaster balls was measured by weighing and the mean flow velocity calculated by interpolation of a flume calibration curve.

Flume experiments: reorientation as a function of flow

Orientations of mussels arranged in 6 x 4 blocks of mussels were investigated in two separate flume runs with flow velocities adjusted to 0 and 20 cm/sec, respectively. In each run, mussels were placed in a 35x35 cm sediment filled box in the recessed area of the flume, 200 cm from the flume inlet. In each flume run 24 mussels were arranged in identical positions in a 18x24 cm matrix in the center of the sediment box. The mussels were oriented as described for the field experiment with the anterior part (umbo) into the sediment with one quarter of the mussel below the sediment surface. The orientation of the sagittal plane were 0, 90, 180, 270° in relation to the direction of flow. Each treatment was replicated 6 times with different and freshly collected mussels. After 24 hours of exposure the mussels were photographed and the orientations subsequently recorded. Effect of orientation was tested in a one factor ANOVA using the computer package, SuperANOVA (Abacus v.1.11) for Macintosh. Homogeneity of variances was tested by use of the F_{\max} -test (Sokal & Rohlf, 1981).

An identical experiment as described above was performed with only 2 mussels per flume run. The same four start orientations of the mussels were used and all treatments were replicated 6 times.

Flume experiments - gape size as a function of shell orientation and flow

Mussels in the size interval of 50-55 mm were col-

lected in natural mussel beds at Rønbjerg Marine Biological Field Station, Denmark, and placed in a sand filled PVC tube with an inner diameter of 42 mm and a length of 50 mm. Two tubes with individual mussels were positioned parallel and vertically to the flow direction in a sand filled box in the recessed area of the flume with the upper edge of the tubes leveled with the sediment surface. The mussels were placed in the sand of the individual tubes and orientated as described above. Two series of experiments with four shell orientations and two flow speeds were performed in a two-factorial statistical design. Each experiment was replicated 11 to 7 times. Gape sizes were measured on calibrated photographs taken after each flume run. The results were tested statistically using a two-factor ANOVA. Homogeneity of variances was tested by use of the F_{\max} -test.

Flume experiments - byssus tread application as a function of shell orientation and flow

These experiments were conducted as described above. Angle of attachment of byssus threads to the edge of the surrounding tube edge in relation to flow direction was measured after 30 minutes of flow or no flow. The data was tested statistically by use of two-factor ANOVA. Homogeneity of variances was tested by use of the F_{\max} -test.

RESULTS

Field observations of mussel orientation

The orientations of 297 mussels from the 8 transect stereophotographs were recorded. A G-test of orientation of the sagittal plane divided into 8 classes of orientation showed a non-significant deviation from a random distribution ($0.25 < p < 0.50$). When the 8 classes of orientation were pooled in pairs into 4 classes of orientation, considering the bidirectional flow conditions, a G-test also showed a non-significant deviation from a random distribution ($0.1 < p < 0.25$). The classes of orientations and the frequency of mussels in the classes are shown in Table 1.

Field experiments of mussel orientation

The mussels arranged in regular blocks in sediment filled trays deployed on the bottom of the

Table 1. Gape direction of vertically positioned *Mytilus edulis* L. in a natural mussel bed in Björnsund channel. 0 and 180 degrees indicate the main directions of the bi-directional currents. The observed values are not statistically different from a random distribution. Total number of mussels = 297.

	Angle section	Frequency (%)	Angle section	Frequency (%)
1	0-45	12.1	1+5	26.6
2	45-90	15.5	2+6	30.6
3	90-135	15.2	3+7	25.6
4	135-180	8.8	4+8	17.2
5	180-225	14.5		
6	225-270	15.2		
7	270-315	10.4		
8	315-360	8.4		

Table 2. Reorientations of *Mytilus edulis* L. of more than $\pm 22.5^\circ$ deviation from initial orientation after 1 and 2 days. The reorientations are not significantly different from initial orientations (Kruskal-Wallis test; $p > 0.05$).

Day 1	Angle	No. of mussels	%	SD	Day 2	Angle	No. of mussels	%	SD
	0°	6	61.1	15.1		0°	6	82.7	4.9
	90°	4	45.4	21.4		90°	6	68.9	14.1
	180°	5	45.3	4.0		180°	6	71.9	7.0
	270°	5	47.7	7.6		270°	6	73.7	13.1
Total		20	50.7	14.1			24	74.3	11.2

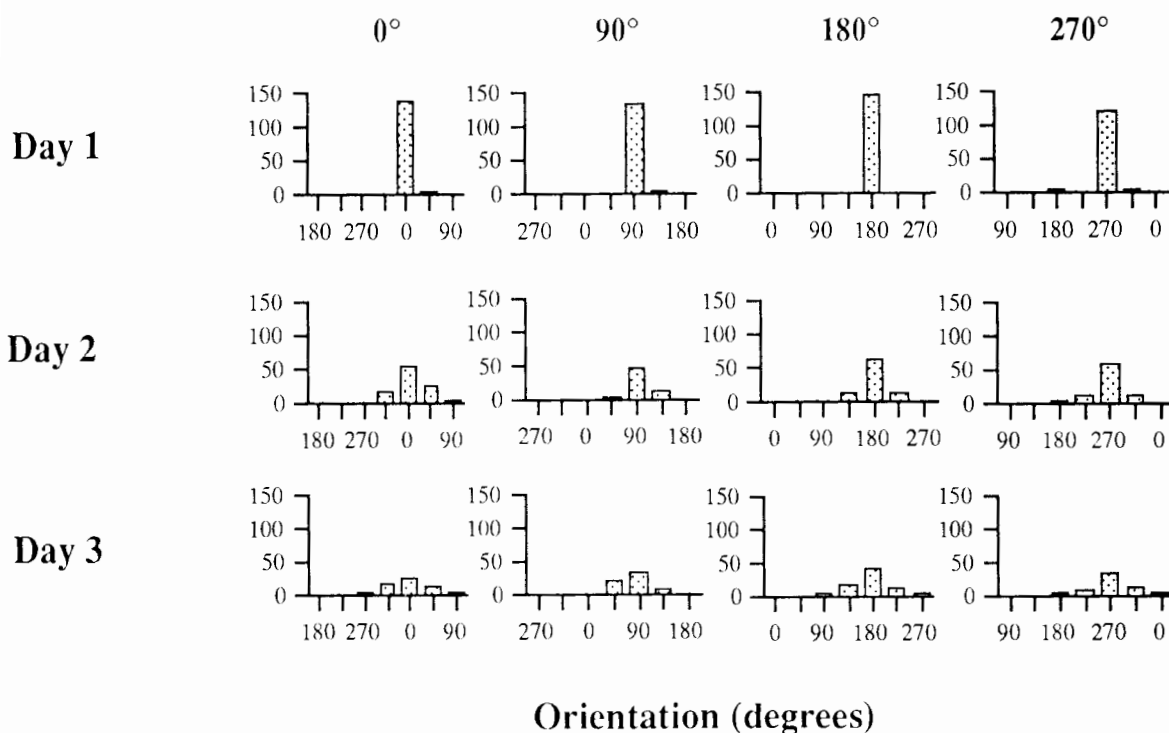


Figure 1. Distribution of orientations during a 48 hours experiment of preset orientated *Mytilus edulis* arranged vertically in blocks of 6x4 mussels in sediment in plastic trays exposed to bidirectional currents on the bottom of Björnsund channel.

Björnsholmen channel, reorientated from a regular preset distribution to a random distribution of orientations within two days. After 24 hours, no significant reorientation was observed (G-test, $p < 0.001$). After 48 hours a random distribution of orientations was obtained indicating that a significant reorientation of mussels took place (G-test, $0.1 < p < 0.5$). Fig. 1 shows the reorientations of the mussels as a function of time and initial orientation. The number of mussels reorientating more than $\pm 22.5^\circ$ from the initial orientations was not significantly dependent of initial orientation after 24 hours (Kruskal-Wallis, $p = 0.38$) or after 48 hours ($p = 0.185$) (Table 2).

During the experiment, the mean flow velocity was calculated to 25 cm/sec ($n=4$) the first 24 hours and 32 cm/sec ($n=2$) the second 24 hours.

It was not possible to perform experiments with solitary mussels distributed in sediment in trays since the individual mussels either moved away to the edges or were lost. In both field experiments, performed in May and later in September 1993 with only two mussels per tray section, most of the sediment was quickly eroded by the flow and most of the mussels were consequently lost.

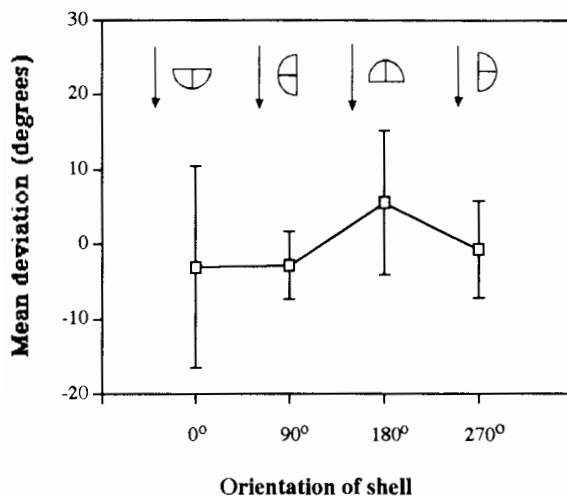


Figure 2. Mean deviation from preset orientations of vertically arranged blocks of 6x4 *Mytilus edulis* exposed to a flow velocity of 20 cm/sec in a laboratory flume. Flow direction and positions of mussel indicated above. Error bars indicate 95% significance level.

Flume experiments: reorientation as a function of flow

The orientations of mussels arranged in blocks at four different directions 24 hours after deployment are shown in Fig. 2. The mussels in each flume run showed only slight movements and fixed themselves to one another by byssus threads. No significant effect of initial orientation was found (one-way ANOVA, $p > 0.05$).

In the flume experiments with two mussels per flume run, none of the mussels exposed to 0 or 20 cm/sec were observed to reorientate from the initial orientation.

Flume experiments - gape size as a function of shell orientation and flow

Gape size in *M. edulis* was found to be independent of flow and initial orientation (Fig. 3). A two-factor ANOVA showed no significant effect of orientation to flow. However, there appears to be a tendency, although not statistically significant ($p = 0.08$), that gape sizes are larger during the flow conditions compared to conditions of no flow irrespective of initial orientations.

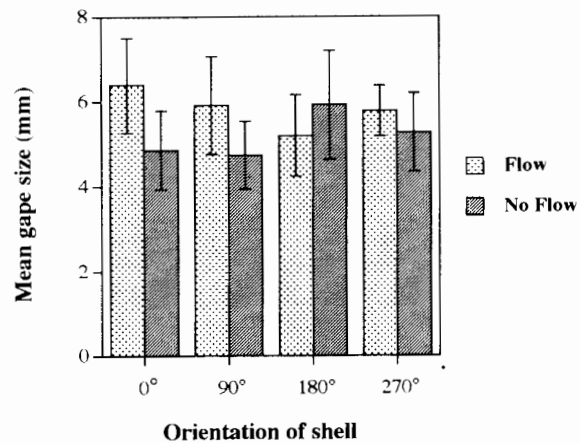


Figure 3. Gape size as a function of flow and preset orientation of *Mytilus edulis* arranged vertically in sediment filled PVC-tubes and exposed to flow of 0 & 20 cm/sec. Flow direction, positions of mussels, and error bars as in Fig. 2.

Flume experiments - byssus thread application as a function of shell orientation and flow

The patterns of directions of byssus thread applications are shown in Fig. 4. Mussels applied byssus

treads randomly irrespective of orientation of the individual mussels and flow conditions. A two-factor ANOVA showed no statistical effects of orientation ($p = 0.652$) or flow ($p = 0.628$).

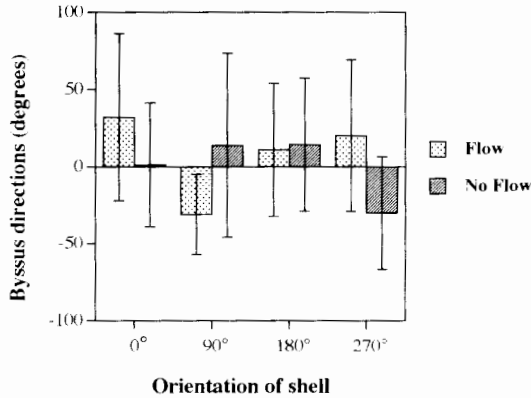


Figure 4. Directions of byssus thread application of pre-set orientated *Mytilus edulis* arranged vertically in sediment filled PVC-tubes and exposed to flow of 0 and 20 cm/sec. Flow direction, position of mussels, and error bars as in Fig.2.

DISCUSSION

There are theoretically several advantages for suspension feeding mussels to show rheotactic behaviour. The most important orientation may be to position the siphons with the inhalant siphon upcurrent and exhalant siphon downcurrent thereby taking advantage of induced passive flow and to release waste products downstream. When mussels are oriented with the inhalant siphon upcurrent, an increased hydrostatic pressure into the siphon can be observed. This increased hydrostatic pressure on the inhalant side of the gills results in a deflation of the demibranchs in *M. edulis* (Jørgensen, 1990). According to Jørgensen (1990), the deflation increases the resistance to water flow and reduce any effect of a passive current. The metabolic cost for active filtration in *M. edulis* has been calculated to be 1.5 % of the total aerobic metabolic rate (Jørgensen *et al.*, 1986) which is low. Hence, any energy gained by a passive flow would be likely to be lost by increased cost of movements to obtain a favorable position. Our results showed that under the experimental conditions in this study no rheotactic behaviour was evident in orientation and gape size thus rejecting the hypothesis.

Growth of scallops, *Placopecten magellanicus*, has been reported to be dependent on flow velocity by Wildish & Saulnier (1992). At high flow velocities (> 13.5 cm/sec) growth decreased. At lower flow velocities no effect was observed. Individual *M. edulis* located at the edge of a mussel bed are generally larger than in the center where mussels experience lower turbulence and flow rates (Suchanck, 1981; Newell, 1990; Svane & Ompi, 1993). The correlation of flow velocity and growth may be explained by favourable feeding conditions at high flow rates simply because more particles pass the siphons per unit time and not due to increased physical performance of the mussels.

In the epibenthic mussel *M. edulis*, the posterior byssal retractor muscle is located directly above the byssus root. This position allows a powerful anchorage to the substratum (Stanley, 1972). Our results showed that directions of byssus thread application was random, independent of flow and initial orientation. Consequently, direction of byssus thread applications were not an indicator of rheotactic behaviour. Young (1983) showed that *M. edulis* do not attach to sediment particles less than 0.85 mm in diameter by use of byssus threads. Assuming that mussels primarily use a byssal attachment and a tightening of the byssus threads controlled by the posterior byssal retractor muscle for movements, the use of sandy sediment may to some extent have prevented reorientation. In the flume experiments with solitary mussels, movements from the original positions were marginal indicating that access to hard substratum may be necessary for movements.

It was not possible to perform field experiments with individual mussels in the different tray compartments since the sediment was partly eroded away, some of the mussels were lost, and some were found attached on the edges. In the experiments with more mussels in the individual compartments, mussels quickly became interconnected by byssus threads which stabilized the blocks and the sediment thereby inhibiting rheotaxis. Witman & Suchanck (1984) observed in a mussel bed established on hard substratum that the byssal attachment was tighter on the edge of a mussel bed than in the center. Byssal threads in *M. edulis* may consequently have evolved for attachment, *per se*, and not for rheotactic orientation.

Our field observations showed that mussels, with respect to a bidirectional current, were distributed randomly. Constant movements and reorientations were observed during the experiments when a batch of mussels was used. In a mussel bed the local microtopography may induce a complex, changing flow field above the mussel bed (Frey *et al.*, 1987) thus obscuring a possible rheotactic pattern. Grant *et al.* (1993) found that passive transport of sea scallops had a behavioural component related to gape that is independent of shell size. Scallop orientation and recessing was explained by physical processes rather than simple behaviour (Grant *et al.*, 1993). The problem of interpreting behavioural movements in mussels is complex and strongly connected with

the problem of separating competition for space from competition for food.

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