



IMPACT OF LIGHT CONDITIONS ON GEOTAXIS BEHAVIOUR OF JUVENILE *DREISSENA POLYMORPHA*

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ABSTRACT: Zebra mussel (*Dreissena polymorpha*) strongly affects aquatic ecosystems and underwater hydro-technical equipment. In this study, movement direction of juvenile mussels (< 10 mm) was studied on a glass plate inclined against an aquarium wall (at angle of 16.5° to the bottom), or on the flat bottom, in various light conditions. In the darkness, the mussels exhibited a negative geotaxis, while in uniform light the numbers of specimens moving up and down the plate were similar. On the flat bottom, the mussels displayed a negative phototaxis. When only the upper part of the inclined plate was illuminated, most of the individuals moved downwards, indicating that light was a stronger signal than gravity. On the inclined plate with its lower part illuminated, more mussels moved upwards (like in the darkness), but this tendency was not statistically significant. Due to the observed behaviour, mussels could counteract adverse effects of conspecific competition by selecting sites on the top of a colony (due to the negative geotaxis in the darkness), and avoid dangers associated with water surface, such as increased probability of air exposure or predator attacks (due to the negative phototaxis in the light).

KEY WORDS: *Dreissena polymorpha*, juvenile, behaviour, phototaxis, geotaxis, locomotion

INTRODUCTION

Dreissena polymorpha (Pallas, 1771), the zebra mussel, is an invasive, freshwater bivalve, capable of reaching high density (WIKTOR 1963, ARNOTT & VANNI 1996) and filtration capacity (STAŃCZYKOWSKA et al. 1976, STAŃCZYKOWSKA 1977, KARATAYEV 1994) in suitable conditions. For this reason it strongly influences freshwater ecosystems in Europe (e.g.: KARATAYEV 1994, LEWANDOWSKI 2001) and North America (MILLER et al. 1992, RICCIARDI et al. 1998). Furthermore, *D. polymorpha* often colonizes hydrotechnical devices, increasing costs of their maintenance, and is regarded as a nuisance (SHEVTSOVA 1994).

Apart from substratum selection by planktonic larvae (LEWANDOWSKI 1982, WAINMAN et al. 1996, KOBAK & WIŚNIEWSKI 1998, MARSDEN & LANSKY 2000), selection of suitable sites by metamorphosed juveniles is another important factor determining adult mussel distribution. Detached young mussels often drift over long distances, using byssal threads to prevent sinking (MARTEL 1993, BAKER & MANN 1997 for review). They can also travel attached to pieces

of macrophytes, wood, etc. (HORVATH & LAMBERTI 1997). Moreover, mussels settled on macrophytes lose their temporary sites in autumn, when green parts of plants decay (LEWANDOWSKI 1982, 2001). Such mussels, when they finally reach the bottom, have to find an appropriate site of attachment by crawling over substratum.

Environmental cues used by juvenile and adult mussels in their site selection behaviour are not well known. Especially, investigations of interactions among various factors influencing mussel locomotion are uncommon. Light and gravity are factors which potentially can have an impact upon such behaviour because they provide valuable information about distance to the surface and mussel's position in a vertical direction (i.e. whether it moves up or down). Field observations reporting mussel responses to these stimuli are often ambiguous. For instance, THORP et al. (1994) found that mussels attached themselves preferentially to the underside of cobbles in the Ohio River. A similar behaviour was observed by WALZ

(1973) on artificial plates in Lake Constance and by LEWANDOWSKI (2001) on glass microscope slides in the Mazurian Lakes. MARSDEN & LANSKY (2000), on the other hand, noted a preference of mussels to the upper side of the plates. Higher numbers of post-veligers settled on the upper surface of artificial substrates were also observed in my own field studies in the Włocławek Dam Reservoir (unpublished data). The above distributions could be a result of both photo- and geotaxis, as well as water currents or predator activity (DJURICICH & JANSSEN 2001). According to HANSON & MOCCO (1994), minimal depth for zebra mussel recruitment was greater in the sun than in shaded places. Again, factors other than light, for instance temperature, could bring about the observed distribution of mussels.

MATERIAL AND METHODS

Mussels were collected in November 1999 by a diver from a dam wall in the Włocławek Dam Reservoir (the Vistula River, Poland). They were kept in an aerated 40-L aquarium filled with settled tap water. The temperature in the aquarium was about 20°C.

The study was carried out in March and April 2000. Preliminary experiments showed that small mussels (<10 mm) displayed a higher mobility, thus they were chosen for further investigations. Only mussels found attached to the substratum in the aquarium were used.

The experiment was conducted in a glass aquarium (480 × 230 mm, water level: 240 mm, volume: 26.5 l) filled with tap water which was settled and aerated for 24 h before trials (Fig. 1). During the experiments water was not aerated, because its circulation could affect the mussel behaviour. Given a large amount of water per individual, and the high tolerance of mussels, living usually in much greater densities than used in this study, oxygen conditions were unlikely to influence the results. Besides, these conditions were equal in all treatments, so they could not cause any differences among them. A glass plate, 400 × 240 mm, was placed in the aquarium. One of the longer edges of the plate rested on the bottom of the aquarium, while the other leaned against its vertical wall, 68 mm above the bottom. Thus, an angle between the plate and the aquarium bottom was about 16.5°. The tested mussels were put onto the central line of the plate, along its longer edge, and covered with rectangular glass tunnels (width and height: 25 mm, length: 230 mm) to separate animals from each other (Fig. 1). The tunnels consisted of two side walls and a roof. Their outlets were closed with a nylon net (diameter: 1 mm). The position of the mussels' siphons relative to the slope (up or down) was alternated in adjacent specimens. The direction of the

My previous experiments, conducted in laboratory conditions (KOBAK 2001), revealed that zebra mussels exhibited a strong negative phototaxis. Besides, almost 50% of young (< 10 mm) individuals moved up the vertical wall of a test-tube, which was an evidence of negative geotaxis. It should be noted, however, that under natural conditions these two types of behaviour would be contradictory – moving upwards would mean moving at the same time to the light source. This suggests that the mussel responses to gravity and light are much more complex. This paper describes geotaxis of zebra mussels and modifying effects of light on this behaviour in laboratory conditions, allowing for separation of these stimuli and investigation of various interactions between them.

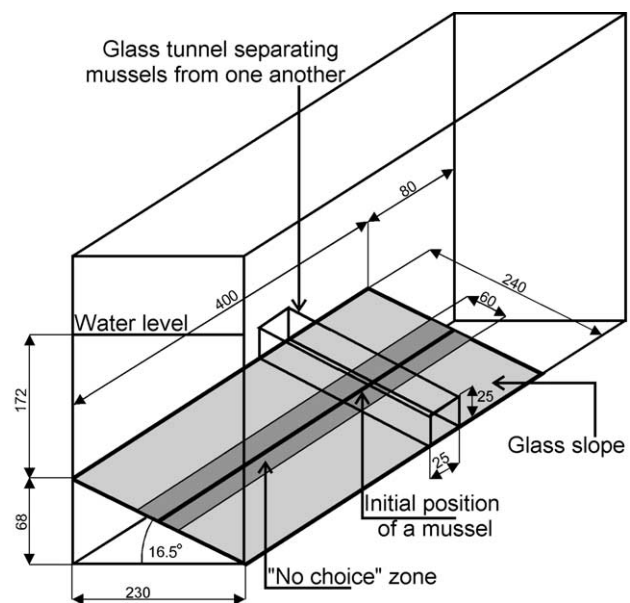


Fig. 1. Experimental design used in the study. Dimensions are given in mm

slope relative to the laboratory room was also changed in consecutive trials.

The mussels were tested in the following light conditions: (1) total darkness (86 individuals; mean water temperature during trials: 19.8°C); (2) uniform light (81; 19.6°C); (3) the upper half of each tunnel illuminated, the lower one darkened (82; 19.4°C); (4) the lower half of each tunnel illuminated, the upper one darkened (79; 19.4°C). Additionally, the mussels were tested on the flat bottom, with one half of each tunnel darkened and the other one – illuminated (86; 20.0°C). In all the treatments the experimental aquarium was put onto a white cloth, so that the bottom colour was always light. Seven trials, 13 mussels in each,



were carried out. The above numbers differ from the expected value of 91 mussels in each trial, because some individuals turned out to be dead or in a poor physiological condition – they neither moved nor attached themselves in their initial position. Such specimens were not included into further analysis.

Darkening was obtained by covering the external surface of the glass tunnels with aluminium foil. This metal was found to be a good substratum for *D. polymorpha* recruitment (e.g. KOBAK & WIŚNIEWSKI 1998, MARSDEN & LANSKY 2000), so adverse effects on the mussel behaviour were unlikely. Furthermore, the tested animals had no direct contact with its surface. Except for the first treatment, electric light (60 W, distance 0.5 m from the water surface) was provided overnight during the experiment.

After 20–24 hours, site selection made by the mussels was determined. It should be noted that, instead of actively choosing the movement direction, the animals could passively slide down the slope. To check for this possibility, 20 empty shells of the same size as individuals used in the experiment, filled with aquarium silicon glue to imitate live mussel's shape and weight, were put on the slope in various positions (laying on the ventral or lateral surface, and with the

front, back, or side pointing down). This preliminary test showed that any changes of mussel position on the slope should be regarded as a result of active locomotion. Individuals were regarded as making a clear selection, if they moved at least 30 mm away from their initial position in a direction parallel to the tunnel's long side. Otherwise, they were assumed to be "undecided". Finally, water temperature was measured and length of all individuals was estimated with callipers to the nearest 0.1 mm.

A G-test of goodness of fit (SOKAL & ROHLF 1995) was applied to check whether the numbers of mussels in the two halves of the plate differed from the expected ratio 1:1. The results of all trials were pooled together for this analysis. The "undecided" individuals were not analysed in order to avoid including random movements, not related to the directional locomotion, into the test. Because five G-tests were carried out, Bonferroni correction for multiple comparisons was applied to avoid an increased probability of making type I error (SOKAL & ROHLF 1995) – an intended p-level, at which the null hypothesis was rejected (0.05), was divided by the number of comparisons. Thus, the results were regarded as statistically significant if p-level was lower than 0.01.

RESULTS

Both light conditions and bottom inclination influenced the mussel behaviour (Table 1). In the uniform light mussels did not prefer any direction of movement, while individuals tested in the darkness significantly more often climbed up the slope (68% of moving animals were found in the upper half of the plate), which can be regarded as a consequence of negative geotaxis. When only the lower halves of the tunnels were darkened, an opposite response was ob-

served (65% of mussels moved downwards). This result, however, was not significant after applying the Bonferroni correction for multiple comparisons. If the upper half of the slope was darkened, more mussels moved upwards (60%), but this tendency was not statistically significant. On the flat bottom, mussels exhibited a strong negative phototaxis (75% of individuals selected the dark parts of the tunnels).

Table 1. Movement direction of mussels in various conditions. Integers denote numbers of mussels. N – number of individuals. Position on the plate: L/I – lower part of the slope or illuminated half of the flat bottom, U/D – upper part of the slope or dark half of the flat bottom, NC – no choice. Statistically significant differences ($p < 0.01$ after Bonferroni correction) are indicated by an asterisk

Treatment	N	Mean shell length \pm SE	Position on the plate			G-test (df = 1)	
			L/I	U/D	NC	G	p
Darkened slope	86	7.1 \pm 0.13	21	45	20	8.931	0.0028*
Uniformly illuminated slope	81	7.0 \pm 0.14	26	24	31	0.080	0.7773
Lower half of the slope dark	82	7.2 \pm 0.15	36	19	27	5.342	0.0208
Upper half of the slope dark	79	7.0 \pm 0.15	22	33	24	2.215	0.1367
Flat bottom	86	7.0 \pm 0.13	14	43	29	15.468	0.0001*

DISCUSSION

Geotaxis of bivalves is often investigated by putting an animal onto the bottom of a vertical cylinder or tank (e.g. URYU et al. 1996, KOBAK 2001). However, in such an arrangement two stimuli are provided to the mussel simultaneously. One is encountering an appropriate substratum when the animal touches the tank wall. The other is gravity, which can make the mussel move up the wall or stay at the bottom. Thus, staying at the bottom may be an evidence of positive geotaxis, but may also indicate a preference to attach to the first suitable material encountered (angles between the bottom and vertical walls are often preferred by the mussels; URYU et al. 1996). Therefore a glass plate inclined against an aquarium wall was applied to investigate geotactic behaviour of the zebra mussels in this study.

Selection of shaded places by the zebra mussels looking for an appropriate site of attachment was often observed both in laboratory (ZHANG et al. 1998, KOBAK 2001) and in the field (e.g. HANSON & MOCCO 1994). Besides, mussels tested in the darkness attached firmly to the substrate more often than in the treatment in which light was provided (KOBAK 2001), indicating that such conditions were more suitable for them. Another interesting factor related to light and influencing zebra mussel site selection behaviour is substrate colour – in my previous studies (KOBAK 2001) the animals were found to choose black surfaces significantly more often than white ones. Preference for dark sites rather than illuminated ones was detected also in other bivalves, such as juveniles of *Limnoperna fortunei* (Dunker, 1857) (URYU et al. 1996) or larvae of *Crassostrea virginica* Gmelin, 1791 (BAKER & MANN 1998) and various aquatic invertebrates, e.g. didemnid ascidians (OREN & BENAYAHU 1998) or spirorbid polychaetes (SAUNDERS & CONNELL 2001).

A negative phototaxis was exhibited by the zebra mussels also in this study. Furthermore, the results showed that light, apart from being a separate cue in locomotion of mussels, influenced also their geotactic movement. While in the darkness the animals moved up the slope, no geotaxis was detected in uniform light. The most interesting results were obtained in the treatments with partial illumination of the slope. When given a choice between moving upwards (as they would in the darkness), or down to the darkened parts of the tunnels, the mussels selected the latter, indicating that light was a stronger cue than gravity. However, this tendency was significant only without applying the Bonferroni correction. Probably a weaker response of the mussels in this treatment was caused by incomplete darkening of the lower half of the slope, due to dissipated light coming from the illuminated part of the experimental set. The results of the opposite treatment (i.e. with the upper halves of

the tunnels darkened) were rather surprising. One could expect that, when both stimuli (light and substratum inclination) are arranged to act together in the same direction, the mussels would exhibit much stronger (or at least not weaker) movement upwards and to the dark zone, than they did in the treatments with only one of these cues present. In fact, the number of mussels crawling up the slope, though larger, was not significantly different from the number of specimens moving in the opposite direction. Illuminating the lower part of the slope created an artificial situation, uncommon in the field. Hence, the mussels might have been confused in their response to this treatment. Otherwise, it was possible that light in this case acted not as a directional cue. Instead, detection of light in itself was a stimulus modifying the geotactic behaviour. One should remember that in this treatment the mussels were initially placed on the border between the illuminated and dark zones of the plate, thus they could detect light in their environment at the start of the trial.

Geotaxis is a cue used by many aquatic invertebrates. For instance, BAKER (1997) found larvae of the oyster *C. virginica* to settle preferentially on lower surfaces of oyster shell substratum because of their strong positive geotaxis. The geotactic response of oyster larvae appeared to be stronger than their phototaxis, which was in contrast with the results of the present study. MORTON (1977) described an opposite situation in larvae of *L. fortunei*, which tended to exhibit negative geotaxis. This behaviour was not confirmed in juvenile and adult *L. fortunei*, which selected sites close to the bottom (URYU et al. 1996).

Negative geotaxis, exhibited by small zebra mussels in the darkness, may be beneficial in overcrowded colonies, when competition of large conspecifics becomes too strong for new settlers – according to STAŃCZYKOWSKA (1964), physical condition of zebra mussels in dense aggregations deteriorates. Moreover, small specimens are endangered by siltation, caused by biosedimentation of faeces and pseudo-faeces produced by conspecifics. Climbing up, a mussel could find sites rich in oxygen and valuable food but would also become more vulnerable to predators and desiccation. Detection of light usually indicates that individuals are in the vicinity of the surface, where dangers mentioned above become more realistic and may overcome benefits obtained from negative geotaxis. Therefore, when light is detected, the behaviour of the mussels should change, as it was shown in this study.

It is possible that negative geotaxis is responsible for the distribution of mussels on substratum – juveniles often aggregate on the edges of vertically orientated experimental plates (especially on the top



edge), deployed in the field to investigate larval settlement, leaving their middle parts empty (KOBAK & WIŚNIEWSKI 1998). Such a pattern may be a result of geotactic movement, which ceases after reaching the edge of the plate.

Avoidance of illuminated sites by mussels, detected in the present study, may be helpful in designing underwater equipment which should be protected from biofouling. Perhaps, in certain conditions, light could be used as a factor repelling mussels from substrate. Besides, the results presented here may be useful in designing artificial reefs serving as an additional, valuable substrate for mussels in those water bodies, where their influence would be beneficial (e.g. as filtrators increasing water transparency). For

instance, quality of such constructions would be enhanced if settling sites within them were protected from light.

The behaviour of zebra mussels turned out to be very complex, involving interactions among various stimuli, the effects of which were difficult to predict from experiments dealing with single factors. Therefore, further studies on mutual interactions of environmental cues influencing active locomotion of zebra mussels are necessary to understand their behaviour in the field. The knowledge of the zebra mussel site selection behaviour will allow the researchers to develop better methods of controlling this species and preventing its appearance in places where it could be harmful.

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