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IMPACT OF CONSPECIFICS ON RECRUITMENT AND BEHAVIOUR OF *DREISSENA POLYMORPHA* (PALLAS, 1771)

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ABSTRACT: Behaviour of larvae, juveniles and adults of *Dreissena polymorpha* in the presence of the conspecifics was investigated in field and laboratory experiments. Mussel recruitment was studied in plastic chambers containing living conspecifics, their empty shells or calcareous, mussel-sized stones. The objects were glued to the chamber bottom and covered by nylon mesh. The experiment was carried out in the channel connecting the Port Zimowy harbour with the Vistula River (Toruń, Poland). Total mussel densities in the above treatments were the same as in the empty chambers. However, the distribution of the new settlers depended on the quality of the glued objects, with the vicinity of living mussels and empty shells being preferred to stones. This suggests that mussels responded to conspecifics after settling on substrate. Migration of juvenile and adult mussels in the presence of the same stimuli was then studied in a laboratory experiment. Both groups preferred the vicinity of living conspecifics, but any kind of the firmly attached objects decreased the number of individuals leaving the substrate, compared to the flat surfaces.

KEYWORDS: *Dreissena polymorpha*, behaviour, site selection, settlement, conspecifics

INTRODUCTION

Dreissena polymorpha, the zebra mussel, is a gregarious, invasive bivalve, attaching itself to various hard substrates with byssal threads (STAŃCZYKOWSKA 1977, ACKERMAN 1995). High colonisation success of this species is often attributed to its relatively low substrate selectivity (LEVINTON 1994). However, when given a choice among various environmental conditions, zebra mussels do prefer certain sites while rejecting others. For instance, they do not settle on copper or zinc containing materials (WALZ 1973, 1975, LEWANDOWSKI 1982, KILGOUR & MACKIE 1993, KOBAK & WIŚNIEWSKI 1998, MARSDEN & LANSKY 2000), avoid places exposed to excessive water current (ZHANG et al. 1998) and illuminated sites (HANSON & MOCCO 1994, KOBAK 2001, TOOMEY et al. 2002). They can also discriminate among other artificial substrates, preferring e.g. polyvinyl chloride to other plastics (WALZ 1973, 1975). Furthermore, hard surfaces are preferred to soft sediments (LEWANDOWSKI 1982, KARATAYEV 1995), and biofilm-covered sites to clean ones (WAINMAN et al. 1996, GU et al. 1997). Besides, mussel locomotion is influenced by gravity (KOBAK 2001, 2002) and a position within a colony (BURKS et al. 2002).

An important environmental cue, influencing recruitment of many invertebrates, is the presence of adult conspecifics, which may indicate that a site is suitable for growth and maturation. For instance, larval responses to conspecifics were found in a polychaete *Phragmatopoma californica* Fewkes (JENSEN & MORSE 1988), a crab *Rhithropanopeus harrisii* Gould (FITZGERALD et al. 1998) and an oyster *Crassostrea virginica* Gmelin (BROWNE et al. 1998). Settling larvae may respond to waterborne substances (e.g.: FITZGERALD et al. 1998), or factors acting during a direct contact with the surface (JENSEN & MORSE 1988, ZIMMER & BUTMAN 2000).

Some evidence exists that site selection behaviour of zebra mussels is also influenced by conspecifics (LEWANDOWSKI 1976, CHASE & BAILEY 1996, WAINMAN

et al. 1996). TOCZYLOWSKI & HUNTER (1997) found higher settlement on unionid shells overgrown by adult zebra mussels, compared to bare shells and artificial substrates. However, above results are not always consistent. For instance, TOCZYLOWSKI & HUNTER (1997) observed the above-mentioned preferences only in certain years, while in the others they were not shown. Besides, they found no mussel selectivity in their laboratory experiments. On the other hand, CHASE & BAILEY (1996) reported a faster growth of individuals settled outside large adult aggregations, which shows that, at least sometimes, avoiding dense cospecific assemblages might be a better strategy.

Some problems related to larval preferences remain unsolved. For instance, it is difficult to distinguish between responses of settling larvae and metamorphosed individuals crawling over substrate. It is also not known, whether conspecific influence is associated with substances released to water column or shell structure. Moreover, one should note that preferences to some substrate types, observed in the field, in fact might be caused by the poor quality of the surrounding bottom (e.g. soft sediments). Actually, to study mussel preferences, the shells should be compared with other hard substrates of similar size, shape and availability to the tested individuals.

In the present study, I investigated behaviour of settling mussels in the field as well as juvenile and adult preferences in the laboratory. I tested the hypothesis that larvae would recruit preferentially in the presence of conspecifics, compared to mussel-sized stones or empty, flat surfaces. Besides, I checked whether the new settlers would attach to the mussel shells rather than to the stones. Furthermore, I checked if the migration of juveniles and adults crawling over substrate would decrease in the presence of obstacles, especially other living mussels.

METHODS

LARVAL RECRUITMENT (FIELD STUDY)

The study was carried out in the channel connecting the Port Zimowy harbour with the Vistula River (Toruń, Poland, Fig. 1). This is a shallow (ca. 3 m), lenitic site, characterised by high water level fluctuations due to the activity of Włocławek Hydropower Station located ca. 50 km upstream.

Resocart (phenoplast: a thermosetting plastic based on phenol-formaldehyde resin, with paper as the filler) 100 × 100 × 5 mm plates were used to study mussel settlement. Previous study showed that it was a good substrate for *D. polymorpha* recruitment (KOBAK & WIŚNIEWSKI 1998). Four 69 × 5 × 5 mm resocart bars were glued to one of the plate surfaces (Fig. 2) to create a 64 × 64 × 5 mm chamber (area: 40.96 cm^2). Eight living mussels (mean shell length ±SD: 15.38 ±1.260 mm), empty mussel shells (15.42 ±2.044 mm) or mussel-sized calcareous stones (15.10 ±1.015 mm) were then glued to the chamber bottom with aquarium silicone sealant (Fig. 2). The chambers were covered with 1-mm nylon mesh. Due to this procedure, the object distribution was the same in all the treatments, and during the entire exposition period. In addition, empty chambers were also applied. The mussels were collected by a diver several months earlier at the same site, and kept in an aerated, 500-L tank. Empty shells were obtained from the mussels which died in the tank for natural reasons (i.e. they were neither used in other experiments nor killed deliberately). Both valves of the empty shells were glued together to imitate the living mussel shape. The mussels and shells were glued by the bottom surface of one of their valves, so that living animals could protract their feet. Limestone was chosen for comparison with the shells because it is a good substrate for *D. polymorpha* (ACKERMAN et al. 1996, MARSDEN & LANSKY 2000) and its repellent activity could be precluded. Otherwise, it would be difficult to discriminate between a possible avoidance of stones and preference to shells. The stones were kept in the aquarium water for one month before the experiment, to allow biofilm development. After gluing the objects, the plates were left in the moist place for 7–8 hours to let the glue dry, and then put into the tank. No mussel mortality due to this procedure was observed. On the next day, the

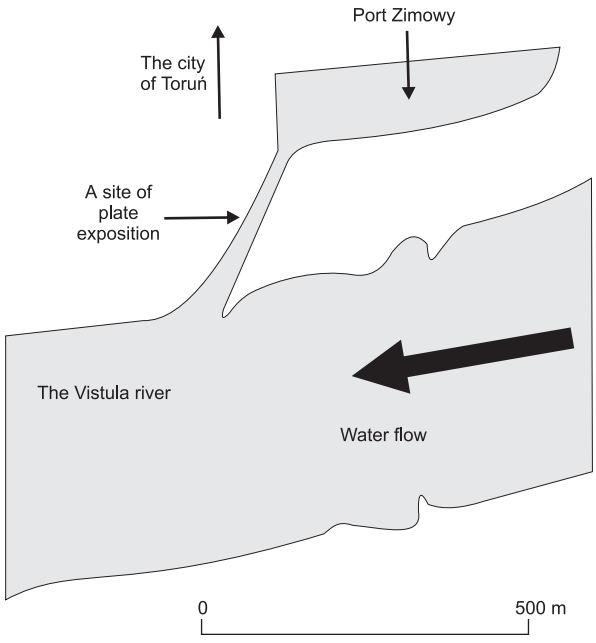

Fig. 1. The study site

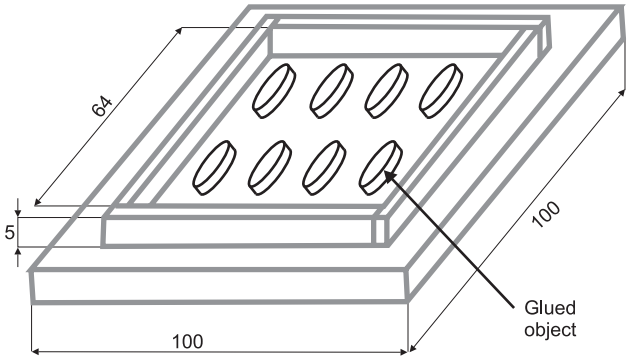

Fig. 2. Experimental set used in the field study (dimensions in mm)

plates were transported to the field. Four plates from each group were exposed on a steel frame for two weeks in June 1998, at a depth of ca. 2 m. The plates were attached to the frame in the vertical position, with the chambers directed to the water column, and the other plate sides to the steel-coated channel bank. The plates were arranged in four rows on the frame, with one plate from each experimental group in a single row. Within a row, the arrangement of the groups was random.

After collecting the plates, all settled plantigrades were counted under a stereomicroscope (magnification 32×) on the covering mesh, inside the chambers, and directly on the object surface. The following parameters were calculated for further analysis: 1) total mussel density (number of all individuals per entire area of the studied surface, including the objects and the covering mesh, without taking into account the holes in the mesh); 2) ratio of mussel density inside the chambers (including individuals settled on the objects) to the total density (further referred to as "relative internal density"); 3) ratio of mussel density on the object surface to their density inside the chambers ("relative object density"). The last two parameters allowed analysing an impact of various objects upon mussel distribution. Values above and below 1 indicated mussel preference or avoidance of a particular part of the chamber, respectively. The object areas were determined by wrapping them with aluminium foil, which, after stretching out, was scanned and processed by the UTHSCSA ImageTool 2.0 image analysis software (University of Texas, Health Science Center at San Antonio). Areas of individual objects did not differ among treatments (mean ±SD: 2.27 ±0.354 cm^2, 2.39 ±0.574 cm^2 and 2.37 ±0.834 cm^2 for stones, shells and living mussels, respectively).

A single-factor analysis of variance (ANOVA), followed by Tukey test, was carried out for each of the three above-mentioned parameters. The homogeneity of variances and normality assumptions were checked with Levene test and Kolmogorov-Smirnov one-sample test, respectively. No transformations were needed to meet these assumptions. Of course, flat plates were not included in the analysis of the relative object density. The results were regarded as statistically significant at $p < 0.017$ (the Bonferroni correction for three comparisons, SOKAL & ROHLF 1995).

JUVENILE AND ADULT MUSSEL BEHAVIOUR (LABORATORY STUDY)

The experiment was carried out in 1998. Ten living mussels, empty shells and mussel-sized stones (mean length ±SD: 15.97 ±2.362 mm, 15.69 ±2.543 mm, 15.79 ±2.907 mm; area: 2.55 ±0.783 cm^2, 2.35 ±0.687 cm^2, 2.42 ±0.912 cm^2, respectively) were glued to 100 × 100 × 5 mm resocart plates (Fig. 3). The plates, including those without the objects, were placed in the middle of 240 × 240 × 140 mm tanks filled with 8 l of settled (24 h) tap water (mean temperature ±SD: 18.6 ±1.26°C). Ten juvenile mussels (shell length < 10 mm, mean: 7.15 mm, SD: 1.453 mm) were then placed among the objects (Fig. 3). After 24 hours, attached individuals that did not leave the plates were counted.

A similar procedure was applied to test the adult mussel (shell length > 10 mm, mean: 15.87 mm, SD: 2.270 mm) behaviour. Mean lengths and areas (± SD) of the objects were as follows: 15.81 ±2.221 mm, 15.34 ±2.543 mm, 15.52 ±2.362 mm and 2.51 ±0.526 cm^2, 2.36 ±0.469 cm^2, 2.46 ±0.651 cm^2 for the living mussels, shells and stones, respectively. Mean water temperature in this experiment was 19.2 ±1.09°C.

The source and treatment of the objects and mussels were the same as in the field study. Three plates from each treatment were tested simultaneously in a single trial. Eleven trials were carried out for juvenile and adult individuals. The time period among consecutive trials was 2 or 3 days (time necessary to prepare the next trial). The same plates were used in all trials. Before each trial, they were dried, cleaned with sandpaper and randomly assigned to the experimental groups.

The data were tested by two-way ANOVA, separate for juveniles and adults. Object quality was a fixed factor and trial number was a random one. The two age

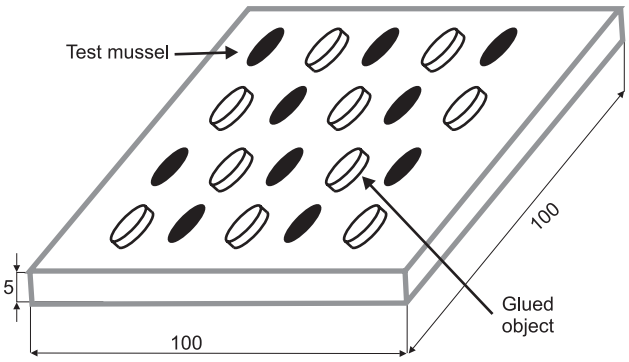

Fig. 3. Experimental set used in the laboratory study and initial positions of the tested mussels (dimensions in mm)

groups were not included in a single analysis because they were not tested simultaneously. The results were regarded as statistically significant at $p < 0.025$ (the Bonferroni correction for two comparisons).

RESULTS

LARVAL RECRUITMENT (FIELD STUDY)

Four of the 32 glued mussels were found dead after collecting the plates. The presence of soft tissue remnants in the shells indicated that mortality happened at the end of the exposition period. Because the number of dead mussels did not exceed two per chamber, and the abundance of plantigrades settled on them did not seem to be different than on the living individuals, they were also included into the further analysis.

Mussel densities in the experimental chambers ranged from 4.4 to 13.6 thousand of individuals per square metre. Various objects glued to the plates did not influence the total density of settling mussels (Fig. 4, ANOVA for total density: $F_{3, 12} = 0.005$, $p = 0.9995$).

The relative internal density was analysed to find out whether the mussels preferred to stay on the covering mesh or to migrate inside a chamber. Comparatively more plantigrades were found inside the chambers in the presence of shells or living conspecifics (Fig. 4). However, the statistical significance of this difference was weak and disappeared after applying the Bonferroni correction (ANOVA for relative internal density: $F_{3, 12} = 3.928$, $p = 0.0364$).

The relative object densities differed among the treatments, indicating that distribution of plantigrades inside the chambers depended on the object quality (ANOVA for relative object density: $F_{2, 9} = 9.696$, $p = 0.0057$). Both living adult mussels and their empty shells attracted significantly more new settlers than mussel-sized stones (Fig. 4). No differences between the two former treatments were found.

JUVENILE AND ADULT MUSSEL BEHAVIOUR (LABORATORY STUDY)

All kinds of the glued objects reduced mussel emigration and increased the number of individuals staying on the plates (Fig. 5, ANOVA: $F_{3, 30} = 28.432$, $p < 0.0001$ and $F_{3, 30} = 15.812$, $p < 0.0001$, for juvenile and adult mussels, respectively). It could be observed that they rarely attached directly to the objects, but usually selected sites in their vicinity. The quality of the objects was also important: juveniles significantly more often stayed on the plates with living conspecifics than on those with empty shells and stones. Adults showed similar preferences, but in this case the difference between the living mussels and shells treatments was insignificant (Fig. 5).

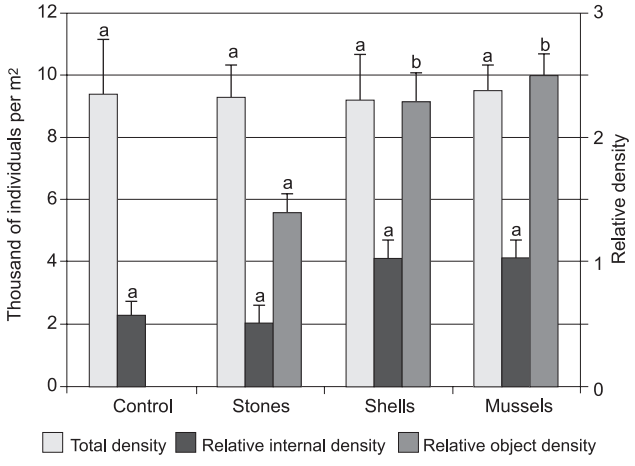

Fig. 4. Plantigrade density in the experimental chambers in the field experiment. Substrates labelled with the same letter did not differ from one another in the Tukey test (separate analyses for each parameter). Error bars indicate standard errors of mean

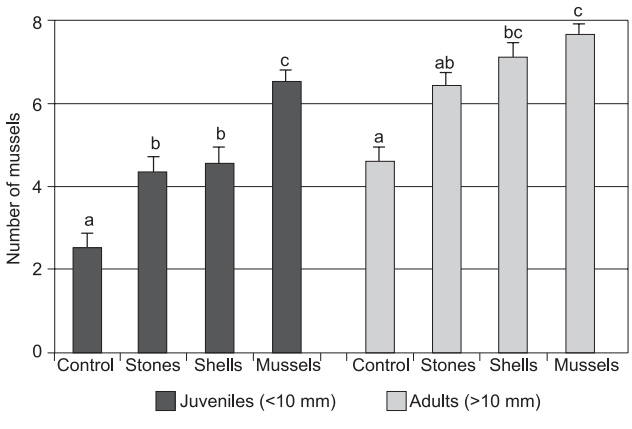

Fig. 5. Numbers of individuals attaching to the plates with various objects glued to their surfaces (the laboratory experiment). Treatments labelled with the same letter did not differ from one another in the Tukey test (separate analyses for juvenile and adult mussels). Error bars indicate standard errors of mean

DISCUSSION

Planktonic larvae usually behave like passive particles, driven by water currents, though some species are able to move in response to chemical or physical stimuli at a very small spatial scale (ZIMMER & BUTMAN 2000). Thus, the first contact of a larva with its potential substrate is probably accidental. Later, it can attach itself or return to the water column, depending on the substrate quality. A site selection made by settled individuals crawling by foot is also possible.

In all of the present experiments, various developmental stages of *D. polymorpha* responded positively to the presence of conspecifics. Although settling larvae did not distinguish between empty and mussel-containing chambers, subsequent plantigrade distribution clearly demonstrated their preferences to the shell surface (Fig. 4). Thus, the observed preferences were most probably associated with post-settlement crawling over substrate by foot. Indiscriminate larval settlement, found in all the treatments of the field experiment, can be explained by limited amount of appropriate substrate, available for zebra mussels in natural conditions. Because the probability of finding a proper attachment site is extremely low (survival at this stage reaches at best ca. 4 % and usually is even lower, LEWANDOWSKI 2001), mussels settle on all, even only marginally suitable hard substrates. For instance, they colonise macrophytes, which die in autumn and the settlers lose their temporary sites (LEWANDOWSKI 1982, 2001). Therefore, empty chambers were also good substrates for the settling mussels in the present study (Fig. 4). On the other hand, the recruits can exhibit the post-settlement movement, allowing for minor corrections of their position (e.g. attaching in crevices, near objects protruding from the surface or, like in this study, to the conspecifics).

In contrast, WAINMAN et al. (1996) observed higher densities of dreissenid larvae settling on plates with living conspecifics and empty shells, compared to mussel-like stones. This discrepancy can be explained by a different experimental design and processing of data. WAINMAN et al. did not count individuals settling on the nylon mesh confining their objects (i.e. mussels, shells and stones), so actually they were unable to discriminate between veliger settlement and later relocation of mussels within a plate. Besides, they used much larger mesh size (5 mm, compared to 1 mm in my study), so that their objects were better exposed to the settling larvae. This supports the hypothesis that mussels responded to the shell surface properties and not to the chemicals released by conspecifics to the water column. Unfortunately, the authors did not test empty, control plates, so it was impossible to check whether the presence of stones on the substrate had any impact on the mussel density in their study.

Many benthic species exhibit a positive thigmotaxis: a preference to sites in crevices and near objects protruding from the flat surfaces (e.g. a freshwater mussel *Limnoperna fortunei* Dunker, URYU et al. 1996). Such behaviour was found also in the present study: the objects (including the stones) increased the probability of mussel staying on the plate (Fig. 5). However, the quality of the objects was also important, with the living conspecifics and their shells being the strongest cues in both laboratory and field studies. Only the juvenile mussels tested in laboratory conditions discriminated between these two object types. Probably mussel responses were age-dependent. On the other hand, in the field study some uncontrolled factors could increase the within-group variability and make the difference between living mussels and shells treatments undetectable.

The fact that in the laboratory experiment juveniles discriminated between living conspecifics and their empty shells (Fig. 5) shows that not only physical shell structure, but also substances produced by living individuals affected the mussels. LEWANDOWSKI (1976) also observed mussel preferences to conspecifics (as well as to unionid clams), compared to empty shells and stones. On the other hand, TOCZYLOWSKI & HUNTER (1997) found no selectivity of zebra mussels in the laboratory, and their field results were ambiguous. However, their experimental design required the mussels to move towards the conspecifics in response to waterborne substances released by them. In contrast, mussels in my experiment responded by staying on the plate or migrating from it. This difference could be responsible for the discrepancy between both studies. Another problem is the fact that a small number of replicates (five) actually precluded obtaining any statistically significant results in the Wilcoxon matched pairs test used by TOCZYLOWSKI & HUNTER (SOKAL & ROHLF 1995).

Dense assemblages of sessile organisms may arise due a number of reasons, including the lack of appropriate substrate (PINEDA & CASWELL 1997), hydrodynamic forces driving planktonic larvae to one, confined site (WALTERS et al. 1997), or larval and juvenile preferences to conspecifics (e.g. ZIMMER & BUTMAN 2000). Contiguous distribution is beneficial because of the vicinity of sexual partners, better anti-predator defence (DJURICICH & JANSSEN 2001, REIMER & HARMSRINGDAHL 2001) and protection from the dislodgement by the water flow (BELL & GOSLINE 1997). Besides, in some bivalves, including zebra mussels, adult individuals enhance juvenile attachment (URYU et al. 1996, KOBAK 2001). On the other hand, new settlers may avoid adult aggregations, escaping from unfavourable effects of life in high density: intraspecific competition, accumulation of faeces and oxygen depletion (BURKS et al. 2002). For instance,

STAŃCZYKOWSKA (1964) observed deteriorating physical condition of mussels living in dense assemblages. CHASE & BAILEY (1996) also found that, although larval settlement was the highest in the areas inhabited by large mussel populations, subsequent growth was better outside those main aggregations. Therefore, two opposite life strategies are possible: selecting sites close to the conspecifics provides better protection at the cost of subsequent growth, while recruiting in empty places, though more hazardous, reduces unfavourable effects of competition and overcrowding.

The experiments presented here showed that, although zebra mussels can attach to a large number of various substrates, they prefer the vicinity of conspecifics, which may influence their distribution in field. It is possible that the observed phenomenon is one of the causes of dense aggregations created by dreissenid mussels (e.g.: STAŃCZYKOWSKA 1964, NALEPA et al. 1993, PROTASOV & SINITSINA 1994).

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