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# Environmental factors affecting behavioural responses of an invasive bivalve to conspecific alarm cues

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Antipredator defences of aquatic animals depend on various environmental parameters. We studied behavioural responses of a Ponto-Caspian invasive bivalve, the zebra mussel, *Dreissena polymorpha*, to conspecific alarm cues. We hypothesized that mussels would change their locomotion and aggregation in response to alarm signals. We also hypothesized that body size, light, substratum quality (suitable or unsuitable for attachment) and inclination would affect mussel defences. Changes in horizontal movement of mussels exposed to the alarm substance depended on light. In the presence of crushed conspecifics illuminated mussels (all sizes) moved longer distances than control individuals, whereas in darkness their reaction was the opposite. The response of small mussels was the strongest. Furthermore, the alarm substance reduced upward relocations of all size groups on an inclined surface but at the same time stimulated their downward movement. Large and medium mussels (but not small individuals) exposed to alarm signals formed aggregations more often than control individuals. This effect was only exhibited on sand, unsuitable for mussel attachment. Mussels were generally more clumped on sand than on hard substratum, suggesting that they did not prefer conspecific shells as attachment sites when alternative substrata were available. All responses of mussels to alarm cues tended to be stronger in light, which is an indirect indication of danger. Our study shows that the responses of the zebra mussel to conspecific alarm cues are not limited to activity reduction, as previously thought. They are adjusted to particular environmental conditions and may also involve increased locomotion when relocation to a safer site gives a better chance of survival.

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Predators shape their environment not only by killing prey, but also by frightening their potential victims (Brown, Laundré, & Gurung, 1999). This increases the level of stress in prey populations, affecting their behaviour and physiology, which in turn exerts prolonged, multidirectional effects on reproduction and survival (Clinchy, Sheriff, & Zanette, 2013). Prey organisms exhibit a number of antipredator strategies, most of them being energetically costly and negatively affecting living conditions and/or fecundity (De Meester, Dawidowicz, Van Gool, & Loose, 1999).

Defences of prey organisms induced by predation cues are common in the aquatic environment (Gliwicz, 2005). They include changes in behaviour (De Meester et al., 1999), morphology (Dzialowski, Lennon, O'Brien, & Smith, 2003) and life histories (Ślusarczyk, Dawidowicz, & Rygielska, 2005) and may substantially affect ecosystem functioning by modifying habitat selection by animals, their reproductive success or foraging intensity (De Meester et al., 1999; Naddafi, Eklöv, & Pettersson, 2007). As behavioural defences are very efficient, predation success may be greatly limited, although predators are often able to overcome prey defences (Gliwicz, 2005). None the less, predator–prey interactions shape the functioning of communities and evolution of both prey and predator species to a large extent. Responses to predation cues may be modified by numerous environmental factors, such as light (De Meester et al., 1999) or substratum type (Baumgärtner, Koch, & Rothhaupt, 2003), which influence the risk level perceived by prey under particular conditions and provide different possibilities for hiding or escape.

The relationship between zooplankton and planktivorous fish is the best known model of a system of behavioural antipredator defences in the aquatic environment (Lass & Spaak, 2003), but strong evidence for similar mechanisms in bottom-dwelling animals also exists (Baumgärtner et al., 2003; Koperski, 1997; Krist, 2002). An interesting case is that of sessile species with limited mobility, such as bivalves (Côté & Jelnikar, 1999; Zardi, Nicastro, McQuaid, Rius, & Porri, 2006). They cannot escape from their enemies, but decrease the risk of predation by reducing their activity, selecting sheltered sites, adjusting attachment strength (Ishida &

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Iwasaki, 2003; Naddafi & Rudstam, 2013; Reimer & Harms-Ringdahl, 2001; Reimer & Tedengren, 1997) and, over a longer period, developing heavier shells (Naddafi & Rudstam, 2014) or stronger adductor muscles (Reimer & Harms-Ringdahl, 2001).

Various types of antipredator defences have been observed in the freshwater zebra mussel, *Dreissena polymorpha* (Czarnołęski, Müller, Adamus, Ogorzelska, & Sog, 2010; Kobak & Kakareko, 2009; Naddafi et al., 2007). This Ponto-Caspian species is alien in most of its present range in Europe and North America (Karatayev, Burlakova, & Padilla, 2002), but responds to both sympatric predators and those with a very short coexistence time, such as crayfish and fish of American origin (Naddafi & Rudstam, 2013). The ability to adjust quickly to new predators may contribute to the impressive invasion success of this species (Karatayev et al., 2002), given the large number of its potential enemies in novel areas (Molloy, Karatayev, Burlakova, Kurandina, & Laruelle, 1997). Interestingly, responses of the zebra mussel to the presence of predators and alarm substances produced by injured conspecifics seem to differ from each other. The presence of predators makes mussels attach more strongly, select safer sites, form aggregations and reduce upward climbing (Houghton & Janssen, 2013; Kobak, Kakareko & Poznańska, 2010; Kobak & Kakareko, 2009; Naddafi & Rudstam, 2013). Moreover, predators induce reduced but more selective feeding (Naddafi et al., 2007), shell thickening and lower growth rate (Naddafi & Rudstam, 2014). In contrast, injured conspecifics inhibit overall activity, including byssogenesis, thus reducing both adhesion and locomotion (Czarnołęski et al., 2010; Czarnołęski, Müller, Kierat, Gryczkowski, & Chybowski, 2011; Toomey, McCabe, & Marsden, 2002). Despite these findings, the effect of abiotic environmental factors upon the variability of mussel responses to conspecific alarm cues has not yet been studied, although they are likely to change the vulnerability of mussels to potential predators and affect their defence mechanisms (Czarnołęski et al., 2006; Gownaris & Commito, 2008; Kobak & Nowacki, 2007).

To address the gaps in our knowledge of zebra mussel responses to alarm stimuli, we studied their horizontal and vertical relocations as well as aggregation forming in the presence of crushed conspecifics. So far, the latter two behaviours have not been investigated in the light of responses to conspecific alarm cues. We expected inhibition of mussel activity in the perceived presence of danger from predation. Furthermore, we hypothesized that the defensive behaviour of mussels would be affected by their body size and by several environmental factors, such as light, substratum type and gravity. We expected a stronger response of mussels in light, an indirect sign of exposure to predation risk (Kobak & Nowacki, 2007), and on soft substratum, unsuitable for attachment. We assumed that endangered mussels would more often move downwards and that smaller individuals, vulnerable to a wider range of predators (Czarnołęski et al., 2006), would be more responsive than the largest specimens.

## METHODS

Mussels (ca. 10 000–12 000 individuals) were collected by a diver from the Włocławek Reservoir, a dam reservoir on the lower River Vistula (Central Poland) from a depth of ca. 2 m. They were transported to the laboratory (2 h transport time) in 10-litre food-grade plastic containers (ca. 3000 individuals per container) in aerated water. We kept them in two 350-litre stock tanks on hard plastic trays, to which they could attach themselves. Their density was ca. 7000–8000 individuals per square metre, which is a common density at which this species occurs in the wild (Karatayev et al., 2002). They were fed every second day with ca. 2 g of dried *Chlorella* sp. per 1000 mussels (Kilgour & Baker, 1994). However, mussels were not fed during the experiments. Water was aerated and filtered, the temperature was 16–18 °C, and the photoperiod was 9:15 h light:dark. We did not observe any negative effects of transport and stocking conditions on mussel survival. The mussels were used in the experiments within 3 months of collecting. After the experiments, the mussels were humanely killed by freezing.

We conducted our experiments in tap water, aerated and filtered for at least 24 h in a 100-litre tank without any animals before use. We checked water quality during the experiments with a multimeter Multi340i (WTW GmbH, Weilheim, Germany). Water temperature (mean ± SD) was 19.1 ± 1.9 °C, oxygen concentration 7.5 ± 1.5 mg/litre (saturation: 78.1 ± 14.8%), pH 8.2 ± 0.3 and conductivity 525 ± 100 μS/cm. We conducted the experiments in darkness obtained by using Styrofoam curtains, or under constant fluorescent light (550–650 lx) at the water surface (determined with a luxometer L-20A, Sonopan Ltd., Białystok, Poland).

The mussels were divided into three size classes: small (mean length: 8.7 mm; range 7.3–9.5 mm), medium (14.5; 10.9–18.3 mm) and large (26.4; 22.8–32.5 mm). These groups differ from one another in their mobility (Toomey et al., 2002) and antipredator defences (Kobak & Kakareko, 2009).

We prepared the alarm substance according to Toomey et al. (2002), by crushing living mussels (all sizes mixed) in water (volumetric proportion of mussels to water: 3:7) and adding 1–2 ml of this solution to treated experimental dishes, depending on their size. The number of crushed individuals was kept at the minimum necessary for a given set of trials. Altogether, we used ca. 1000 individuals for crushing. The final concentration of the crushed mussel extract in the treated dishes was 2.2–2.6 ml per 1 litre of water. Czarnołęski et al. (2010) and Toomey et al. (2002) have shown that this amount of extract does affect mussel behaviour. It was necessary to use living mussels to prepare the extract, as we needed the active alarm substance, produced by living prey individuals attacked by a predator (Czarnołęski et al., 2010; Toomey et al., 2002).

In all experiments, trials with different treatments (with regard to the presence of the alarm substance, mussel size, light and substratum type) were carried out in a random sequence.

All experimental procedures applied in our study were carried out in accordance with the Polish law and ethical guidelines of the Polish National Ethics Committee for Experiments on Animals.

### *Experiment 1: Horizontal Migration*

We put a single mussel in the centre of a glass circular dish with a thin layer of fine sand (ca. 1–2 mm) on the bottom (Fig. 1a). Immediately after placing the mussels in the dishes, we added 1 ml of the alarm substance to the treated dishes. After 24 h of exposure in darkness or under constant illumination, we photographed the trails left in the sand by crawling mussels and measured them using ImageJ 1.48a (freeware by W. S. Rasband, U.S. National Institutes of Health, Bethesda, MD, U.S.A., http://rsb.info.nih.gov/i) according to the procedure described by Toomey et al. (2002). Unfortunately, it was impossible to test groups of mussels in this experiment, which would be a more natural situation for this gregarious species, as they would obscure one another's trails in the dish. We replicated this experiment 20 times.

### *Experiment 2: Vertical Migration*

We studied mussel behaviour on a glass slope, inclined at 6 degrees to the bottom of an experimental tank (Fig. 1b). This inclination can be detected by mussels but does not make them slip

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