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Is the body condition of the invasive zebra mussel (*Dreissena polymorpha*) enhanced through attachment to native freshwater mussels (Bivalvia, Unionidae)?

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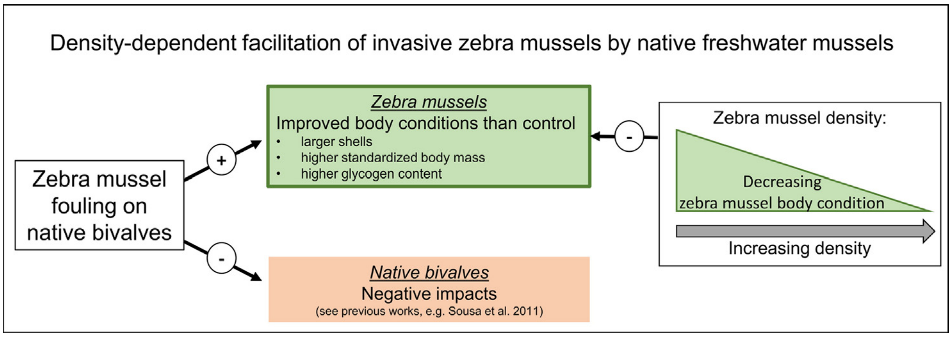
HIGHLIGHTS

- The invasive *Dreissena polymorpha* negatively impacts native unionoid bivalves.
- We studied whether *D. polymorpha* benefits from fouling unionoids.
- *D. polymorpha* had better body condition when attached to unionoids than control.
- Body condition worsened with increasing density on the same unionoid.
- Density-dependent facilitation of *D. polymorpha* by native unionoid.

GRAPHICAL ABSTRACT



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ABSTRACT

The invasion of zebra mussels, *Dreissena polymorpha*, into Western Europe and North America has driven widespread ecological change. Attachment of zebra mussels to the shell of native unionoid mussels has resulted in reductions in unionoid abundance and, in extreme cases, their localised extirpations. While the impacts of zebra mussels on infested unionoids are well documented, the possible benefits of the association to the zebra mussel have been little considered. We collected zebra mussels attached to unionoids and to inanimate structures. Zebra mussels attached to unionoids had significantly larger shells, higher standardized body mass and glycogen content than those attached to inanimate substrates, suggesting that *D. polymorpha* benefits from settling upon unionoids. The body condition of individual zebra mussels was negatively correlated with the number of zebra mussels attached to the unionoid, indicating intraspecific competition. Therefore, zebra mussels seem positively affected through attachment to unionoid mussels, but that these benefits decrease at higher densities of fouling. This association may offer advantages to the spread of zebra mussels within unionoid-rich systems, especially at sites with soft substrates and at the early stages of the invasion process where intraspecific competition is likely to be lower and benefits to the zebra mussels are higher.

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1. Introduction

The establishment and spread of invasive non-native species is recognised as an important and increasing threat to global ecosystems and economies (Simberloff et al., 2013; Gutiérrez et al., 2014). The population dynamics of an invader typically begins with a lag phase, followed by rapid increase in abundance after which populations tend to stabilise (Richardson et al., 2011). The early stage increases are often characterised by particularly rapid growth rates of individuals, and this has been attributed to the ability of the invasive species to exploit resources more efficiently than might be the case for native biota. However, as populations of the invasive species continue to increase, individual and population growth rates may slow as resources become limiting and intraspecific competition increases (Arenas et al., 2002; Marushia and Holt, 2008). Such patterns of density-dependent growth rates are well known in bivalve species, and contribute, for example, to the optimisation of stocking densities in aquaculture systems (Frechette, 2010). In natural systems, the highly invasive zebra mussel, *Dreissena polymorpha* (Pallas, 1771), similarly shows the characteristic patterns of lag, increase and stabilisation (Strayer, 2009), and in some cases may ultimately show a trend for declines in population abundance and individual growth rates (Strayer et al., 2011). Zebra mussels represent one of the world's most prolific invasive species (DAISIE, 2009) and so understanding the drivers of their population dynamics can be important in understanding their potential impacts and developing appropriate management tools.

The ability of zebra mussels to attach to hard substrates by secreting adhesive byssal threads causes considerable economic and ecological harm (Strayer, 2009; Sousa et al., 2014). The removal of biofouling zebra mussels attached to the inside of water pipes and filters cost industry in the US approximately US$300 million for the period 1989–2004 (Connelly et al., 2007) and the UK water industry spends approximately £5 million per year in their management (Oreska and Aldridge, 2011). Zebra mussels can alter the structure of native ecosystems by changing nutrient concentration and water quality, reducing phytoplankton standing stocks and suspended particles; the subsequent increase in water clarity has influences on macrophyte growth and on the benthic community (Griffiths, 1993; MacIsaac, 1996; Sousa et al., 2009; Strayer, 2009). Perhaps the most direct and severe ecological impact of zebra mussels is on native unionoid bivalves. The attachment of zebra mussels to native mussels negatively affects unionoids in different ways: by smothering siphons, preventing closure and opening of valves, interfering with balance, locomotion and burrowing, and competing for food (Mackie, 1991; Baker and Levinton, 2003). These processes lead to a decrease of energy stores and an increase of mortality in the underlying unionoid (Haag et al., 1993; Ricciardi et al., 1996; Sousa et al., 2011). Together with the loss and fragmentation of habitat, declines in host fish, overexploitation, pollution, climate change and flow regulations (Bogan, 1993; Lopes-Lima et al., 2014, in press), zebra mussel fouling may be responsible for the severe decline of native freshwater mussel populations both in Europe (Aldridge et al., 2004; Sousa et al., 2011) and in North America (Schloesser et al., 1996; Ricciardi et al., 1998).

While the negative impact of zebra mussels on native mussels has been extensively documented in previous studies (Schloesser et al., 1996; Ricciardi et al., 1998; Aldridge et al., 2004; Sousa et al., 2011; Bódis et al., 2014), only a few have analysed possible costs or benefits to the zebra mussel and these reported contrasting results. It has generally been considered that zebra mussels benefit from native unionoids simply in terms of gaining a hard substrate on which to attach. However, Hörmann and Maier (2006) reported that zebra mussels attached to the swan mussel (*Anodonta cygnea*; Linnaeus, 1758) in German lakes had a greater growth rate than those attached to rocks, concluding that zebra mussels may benefit from settling on unionoids. The authors hypothesized that zebra mussels could use the food provided by the filter current of the unionoid, since their inhalant siphons were directed towards the siphons of their host. When the bottom is soft or unstable, unionoids may also represent a more favourable attaching substratum than inanimate hard surfaces due to their ability to maintain their positions in the sediment-water interface and thus reduce the risk of burial within accumulating sediments (Toczylowski et al., 1999). In contrast, Baker and Hornbach (2008) found that zebra mussels attached to unionoids in North America had lower energetic stores (as measured by tissue glycogen) than zebra mussels attached to inanimate substrates. The lower body condition was imputed by the authors to physiological costs of attaching to unionoids such as competition for food and disturbance caused by unionoid movements. The causes of these contrasting results may relate to different abiotic and/or biotic features in the study areas such as river flow, type of sediment and the density of zebra mussels on the unionoid's shell. Although it is known that intraspecific competition occurs among zebra mussels in dense colonies (Burks et al., 2002; Tuchman et al., 2004; Wacker and Von Elert, 2008), no studies have investigated the interplay between interspecific (i.e. between zebra mussels and unionoids) and intraspecific (among zebra mussels) interactions in determining the physiological condition of zebra mussels.

In this study, we analysed zebra mussel condition, hypothesizing that zebra mussels should benefit from being attached to unionoids. However, we also hypothesized that when *D. polymorpha* density on native unionoid increases, intraspecific competition would occur and erase this profit. Therefore, the objectives of this study were: i. to investigate if zebra mussels attached to unionoids were in better physiological condition than those attached to other solid inanimate substrates, and ii. to examine if this potential benefit was density-dependent.

2. Materials and methods

2.1. Sampling strategy

Specimens of *Anodonta anatina* (Linnaeus, 1758), *Unio pictorum* (Linnaeus, 1758) and *D. polymorpha* were collected in the River Stour (Cattawade, Suffolk, United Kingdom, 51°57.5N, 01°03.5E). Zebra mussels have been present in the region since the 19th century (Killeen, 1992). The river stretch selected was typical of English lowland rivers, with >10 m width, <2 m maximum depth and with a soft, muddy substratum. Macrophyte assemblages were dominated by *Phragmites australis* (Cav.) Trin. ex Steud at the fringes and *Nuphar lutea* (L.) Sm. in the littoral zone. Mean water chemistry parameters for the River Stour in 2008 were characterised by ammonia (N mg/l) 0.09 ± SD 0.07, dissolved oxygen (% saturation) 98.1 ± 37.0, nitrates (NO_3-N mg/l) 27.1, and phosphates (PO_4 mg/l) 0.27 (data from the UK Environment Agency). *A. anatina* and *U. pictorum* are two common and widely distributed species of native unionoid mussels in Europe and both are listed as Least Concern by IUCN (Lopes-Lima et al., 2016). Both species differ in shell morphology, burrowing behaviour and filtration rate (Sousa et al., 2011; Lorenz et al., 2012). In addition, the reproductive life cycle is quite different in the two species: in U.K. *A. anatina* has a gravid period lasting from August to March-April, and mature glochidia within the outer demibranchs from December to March; *U. pictorum* has a gravid period lasting from April to June and mature glochidia from May to June (Aldridge, 1999).

Sampling was conducted in summer (July 2008) using hand collection at approximately 1.0 m depth, by wading. Eight randomly placed 0.25 m^2 quadrats were searched by two operators within a 25 m reach until no more mussels were found after a continuous 10 min of searching to a sediment depth of 20 cm. In total 24 *A. anatina* and 116 *U. pictorum* were collected. Additionally, 150 zebra mussels were collected from an inanimate substrate (i.e. concrete wall) within the same river reach at approximately 1.0 m depth. There, zebra mussels were found in a layer of only one individual thick. Specimens were transported to the laboratory in buckets filled with aerated river water.