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# Fouling of European freshwater bivalves (Unionidae) by the invasive zebra mussel (*Dreissena polymorpha*)

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## SUMMARY

1. The zebra mussel (*Dreissena polymorpha*) is well known for its invasive success and its ecological and economic impacts. Of particular concern has been the regional extinction of North American freshwater mussels (Order Unionoida) on whose exposed shells the zebra mussels settle. Surprisingly, relatively little attention has been given to the fouling of European unionoids.
2. We investigated interspecific patterns in fouling at six United Kingdom localities between 1998 and 2008. To quantify the effect on two pan-European unionoids (*Anodonta anatina* and *Unio pictorum*), we used two measures of physiological status: tissue mass : shell mass and tissue glycogen content.
3. The proportion of fouled mussels increased between 1998 and 2008, reflecting the recent, rapid increase in zebra mussels in the U.K. *Anodonta anatina* was consistently more heavily fouled than *U. pictorum* and had a greater surface area of shell exposed in the water column.
4. Fouled mussels had a lower physiological condition than unfouled mussels. Unlike tissue mass : shell mass ratio, tissue glycogen content was independent of mussel size, making it a particularly useful measure of condition. *Unio pictorum* showed a stronger decline in glycogen with increasing zebra mussel load, but had a broadly higher condition than *A. anatina* at the time of study (July).
5. Given the high conservation status and important ecological roles of unionoids, the increased spatial distribution and fouling rates by *D. polymorpha* in Europe should receive more attention.

*Keywords*: *Dreissena polymorpha*, fouling, glycogen, interspecific and intraspecific patterns, non-indigenous invasive species, unionoid mussels

## Introduction

The zebra mussel *Dreissena polymorpha* (Pallas, 1771) is the most intensively studied invasive species world-wide, as a result of its rapid expansion and serious

ecological and economic impacts (Pyšek *et al.*, 2008). *Dreissena* was once distributed widely throughout Europe (Stanczykowska, 1977), but retreated during the last glaciations, becoming restricted to the areas around the Black, Azov, Caspian and Aral seas, and the lower River Volga. This distribution remained until the 18th century, when *Dreissena* again extended its European distribution because of human activities (Olenin, Orlova & Minchin, 1999 and references therein). It appeared in Rotterdam in 1826, Hamburg

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in 1830 and Copenhagen in 1840 (Kerney & Morton, 1970). In Great Britain, it was described for the first time in the London Docks in 1824 and became quite widespread over the next 10 years (Aldridge, Elliot & Moggridge, 2004). After 1835, new records were frequent in Great Britain but, after 1850, the species distribution stabilised for more than a century (Kerney & Morton, 1970; Kerney, 1999).

The impacts of the *D. polymorpha* invasion received renewed attention when it was discovered in the North American Great Lakes in the 1980s, from where it has spread widely through the U.S.A. and southern Canada (MacIsaac, 1996). In Europe, Ireland and Spain were invaded recently (Araujo & Alvarez, 2001; Minchin, Lucy & Sullivan, 2002; Pollux *et al.*, 2003). In Great Britain, the species has increased rapidly over the last decade in both abundance and distribution (Aldridge *et al.*, 2004). The reasons for this newly invasive pulse in Great Britain are unclear, but improvement in water quality, increased dispersal by boats and interconnectivity of waterways and the introduction of new genes are possible explanations (Aldridge *et al.*, 2004).

Established populations of *D. polymorpha* can have wide-ranging direct and indirect impacts on invaded ecosystems. Commonly observed changes include reductions in phytoplankton and zooplankton (MacIsaac, Lonnee & Leach, 1995; Caraco *et al.*, 1997; Pace, Findlay & Fischer, 1998; Strayer *et al.*, 2008), increased water clarity (Effler *et al.*, 1996; Caraco *et al.*, 1997), an increase in submersed vegetation and periphyton (Hecky *et al.*, 2004; Strayer *et al.*, 2008), changes to fish populations (Karatayev, Burlakova & Padilla, 1997; Strayer, Hattala & Kahnle, 2004b) and changes to the benthos (Strayer *et al.*, 1999; Sousa, Gutiérrez & Aldridge, 2009). A particularly notable impact on the benthos is the extinction of native mussels of the Order Unionoida (Ricciardi, Whoriskey & Rasmussen, 1995; Strayer & Malcom, 2006). Unionoids live partially buried in the sediment, usually with the posterior part of their shells exposed to the water column to enable filtration (Jokela & Ricciardi, 2008). Exposed unionoid shells can therefore serve as a substratum for *D. polymorpha*, and many negative effects of such fouling on native bivalves have been described. For example, encrusting of the posterior end hinders locomotion and burrowing, disrupts balance and equilibrium and can deform unionoid valves, resulting in valve occlusion and consequent suffocation (Mackie, 1991). Growth of zebra mussels prevents normal functioning of siphons, and zebra mussels can compete for available food (Ricciardi *et al.*, 1995; Schloesser, Nalepa & Mackie, 1996; Hörmann & Maier, 2006). These mechanisms can contribute to unionoid mortality or at least reduction in their physiological condition. Several North American studies reported that unionoids were heavily colonised by zebra mussels soon after the latter's arrival (MacIsaac, 1996 and references therein). This fouling may decrease the energy reserves of the infested unionoids, which can lead to high mortality. In extreme cases, all unionoids may disappear within a few years (Strayer & Malcom, 2007). The life habits of different North American unionoids are thought to explain interspecific patterns in fouling intensity, with species exposing a greater shell area into the water column typically becoming more fouled (Burlakova, Karatayev & Padilla, 2000).

While considerable attention has been paid to the conservation implications of zebra mussel fouling on North American unionoids, remarkably little attention has been paid in Europe. A number of European unionoid species show Ponto-Caspian sympatry with *D. polymorpha* and so it is possible that some degree of coevolution took place during their previous coexistence. However, the majority of Europe's unionoid populations have been recently sympatric with *D. polymorpha* for much less than 200 years and so it is possible that they are as vulnerable to the impacts of zebra mussel fouling as many of the North American species.

The European unionoids showing the strongest distributional overlap with *D. polymorpha* belong to the subfamily Unioninae, the two most widely dispersed and common representatives of which are *Anodonta anatina* (Linnaeus, 1758) and *Unio pictorum* (Linnaeus, 1758). The main objectives of this study were to look for interspecific and intraspecific patterns of fouling of U.K. populations of unioniods (principally on *A. anatina* and *U. pictorum*) by *D. polymorpha*. We assessed whether the fouling was harmful and asked whether it might lead to changes in community structure and/or to ecosystem processes.

## Methods

### Study area

Mussel populations were surveyed from six sites across central, eastern and southern England: (1)

River Witham, Woodhall Spa, Lincolnshire (53°09.2N, 00°12.7W); (2) River Nene, March, Cambridgeshire (52°33.1N, 00°05.4E); (3) River Great Ouse, Ely, Cambridgeshire (52°20.9N, 00°13.1E); (4) River Stour, Cattawade, Suffolk (51°57.5N, 01°03.5E); (5) River Thames, Clifton Hampden, Oxfordshire (51°39.4N, 01°12.6W) and (6) Barden Lake, Tonbridge, Kent (51°11.8N, 00°16.5E). The river sites selected were typical English lowland rivers with >10 m width, with >2 m maximum depth and with a soft, muddy substratum. Barden Lake is a disused gravel pit with a gravel substratum.

### Sampling strategy

The sites were known to have large populations of unionoids. At each site, the abundance of unionoid mussels and the degree of zebra mussel infestation were assessed. Sampling was conducted in summer (June to August) between 1998 and 2008 (see Table 1 for years in which samples at each site were taken) using hand collection at approximately 1.0 m depth. On each sampling occasion, a minimum of eight randomly placed 0.25 m$^2$ quadrats were searched until no more mussels were found after a continuous 10 min of searching to a sediment depth of 20 cm.

Aldridge, Fayle & Jackson (2007) showed that eight 0.25 m$^2$ quadrats were sufficient to provide a reliable estimate of unionoid populations in U.K. lowland rivers. In Barden Lake, we used a different method since the abundance of unionoids in this lentic system turned out to be low. All unionoids encountered along two 20 × 1 m transects were collected from at least five different locations. Sampling of each transect lasted >10 min and transects ran parallel to the shore at 1.0 m depth. To ensure comparability between the quadrat and transect surveys, in all instances all mussels encountered were removed from a sediment depth of up to 20 cm, a water depth of 1.0 m and sampling ceased only after a continuous 10 min yielded no further mussels.

All unionoids were identified to species, and maximum length was measured with Vernier calipers (±1 mm) before being returned to the collection site. Each unionoid was inspected visually to determine whether or not it was fouled with *Dreissena*. Fouled unionoids were those which carried at least one *Dreissena*. Unfouled unionoids were those with no live *Dreissena* or presence of any byssal threads. Unionoids, which carried byssus but no live *Dreissena*, were excluded from this analysis.

**Table 1** Percentage of unionoid infestation by zebra mussels in the Rivers Thames, Great Ouse, Witham, Nene and Stour and in Barden Lake over the last 10 years

| | Aa (%) | Ac (%) | Up (%) | Ut (%) | Pc (%) | Total (%) | N | χ$^2$ test |
|---|---|---|---|---|---|---|---|---|
| Thames 1998 | 1.6 | x | 0.3 | 0.3 | 2.9 | 0.9 | 1675 | – |
| Thames 2003 | 12.6 | x | 5.1 | 3.3 | 4.7 | 8.0 | 2481 | 56.52* |
| Thames 2006 | 11.5 | x | 3.7 | 4.0 | 15.4 | 5.9 | 421 | 0.60 ns |
| Barden lake 2002 | 60.0 | 0.0 | 68.3 | 66.7 | x | 67.2 | 119 | – |
| Barden lake 2003 | 50.0 | x | 100.0 | 100.0 | x | 91.6 | 83 | 27.01* |
| Barden lake 2008 | 100.0 | x | 92.3 | 83.3 | x | 88.5 | 26 | 1.25 ns |
| Ouse 1999 | 0.0 | x | 0.0 | 0.0 | 0.0 | 0.0 | 1110 | – |
| Ouse 2003 | 11.6 | x | 5.5 | 16.7 | x | 8.7 | 300 | 0.76 ns |
| Ouse 2008 | 50.6 | x | 7.0 | 14.1 | 0.0 | 17.6 | 720 | 9.97* |
| Witham 2001 | 88.9 | 100.0 | 53.1 | 81.8 | 0.0 | 78.9 | 190 | – |
| Witham 2004 | 95.9 | 53.8 | 93.2 | 79.3 | 50.0 | 92.2 | 424 | 10.63* |
| Nene 2001 | 4.5 | x | 2.8 | 5.7 | x | 4.1 | 831 | – |
| Stour 2005 | 0.0 | x | 25.4 | x | x | 25.4 | 59 | – |
| Stour 2008 | 60.7 | x | 37.6 | x | x | 40.4 | 230 | 11.87* |

Values of the χ$^2$ test for temporal differences in the infestation rate of unionoids at each site between successive years are presented. *N.B.* abundance of *A. cygnea* and *P. complanata* was low at survey sites and so percentage values must be interpreted with caution. Aa, *Anodonta anatina*; Ac, *Anodonta cygnea* (Linnaeus, 1758); Up, *Unio pictorum*; Ut, *Unio tumidus* (Philipsson, 1788); Pc, *Pseudanodonta complanata*; *N*, total number of unionoids sampled; x, absent.
Statistical significance: $P < 0.001$ (*), $P > 0.05$ (ns, not significant).

*Physiological status*

*Anodonta anatina* and *U. pictorum* were collected by hand from the River Stour, Suffolk (i.e. Site 4), in July 2008 and split into three classes: uninfested (no zebra mussels and no attached byssus); lightly infested (<5 zebra mussels attached); and highly infested (≥5 zebra mussels). Thirty *U. pictorum* were collected for each of the three classes. For *A. anatina*, sample sizes were seven, seven and 10, respectively. Mussels were transported to the laboratory in buckets of aerated water, and zebra mussels were allowed to remain attached. The maximum length of each unionoid was measured and the wet mass recorded after blotting dry to remove surface water. For each infested unionoid, we recorded the number and wet mass of attached zebra mussels. In addition, all the *U. pictorum* specimens were sexed based on microscopic inspection of gonad smears (following McIvor & Aldridge, 2007).

The exposed area of each unionoid collected in the River Stour was clearly visible by the presence of algae and calcareous deposits, and this area was estimated by covering the exposed part of the shell with aluminium foil, the foil subsequently being weighted and converted to area using a standard area-mass ratio (following Ricciardi *et al.*, 1995).

A standard condition index [condition index = dry tissue mass (g)/dry shell mass (g)] was used to measure the physiological status of each unionoid. In addition, we determined the glycogen content to compare the energy stores in infested and uninfested unionoids. The soft tissue (whole body) was dried to constant mass at 60 °C in an oven and then ground to a fine powder. Glycogen was measured colorimetrically using the phenol-sulphuric acid method (following Baker & Hornbach, 2000).

*Statistical analysis*

Statistical analyses were performed using R version 2.5.0. (http://www.r-project.org).

Data distributions were tested for normality using Shapiro-Wilk W tests, and log-transformation was applied to non-normal data. F tests were used to compare the variances of two samples from normal populations.

The proportion of unionids fouled and unfouled by zebra mussels was compared between sampling occasions (Table 1) in each site by $\chi^2$ tests. Such analysis on temporal data assumed that different individuals were sampled on the two occasions. Similarly, we tested for differences in the infestation rate of male and female *U. pictorum* in the River Stour. A paired *t*-test was used to check possible differences in the degree of infestation between *A. anatina* and *U. pictorum* using the most recent data for each of the six sites surveyed (after arcsin transformation to account for the use of proportional data). Generalised linear models were used (i) to test the relationship between the length of mussel and exposed area, (ii) whether there were differences in the condition index and glycogen content of infested and uninfested mussels and, if so, (iii) whether this differed between the two species (*A. anatina* and *U. pictorum*). Pearson's correlation coefficients between glycogen content of unionoids and the wet mass of attached zebra mussels were calculated for *A. anatina* and *U. pictorum*. Physiological condition (measured by glycogen content) of *A. anatina* and *U. pictorum* was compared using ANCOVA with the wet mass of attached zebra mussels as covariate.

**Results**

In all six locations, both *A. anatina* and *U. pictorum* were encrusted by *D. polymorpha* on the exposed posterior end of the shell (Fig. 1a,b) and, in general, the proportion of unionoids carrying zebra mussels has increased over time (Table 1).

Using the most recent data for each of the six sites surveyed, a greater proportion of *A. anatina* was fouled than *U. pictorum* (paired *t*-test = 2.90, $P = 0.034$). This is also true for the River Stour, where *A. anatina* also carried a greater number of zebra mussels than *U. pictorum* (ANCOVA with length as covariate: $F = 3.95$, $P = 0.049$; Fig. 2). Using the wet mass instead of the number of attached zebra mussels, the results are very similar (data not shown). However, we found no difference in the degree of infestation between males and females of *U. pictorum* in the River Stour ($\chi^2 = 0.095$, $P = 0.76$).

*Anodonta anatina* had a significantly greater surface area exposed than *U. pictorum* ($F = 26.40$, $P < 0.001$), longer mussels had larger exposed areas ($F = 178.48$, $P < 0.001$), and more infested mussels had a greater exposed shell area ($F = 10.08$, $P < 0.001$) (Fig. 3a,b).

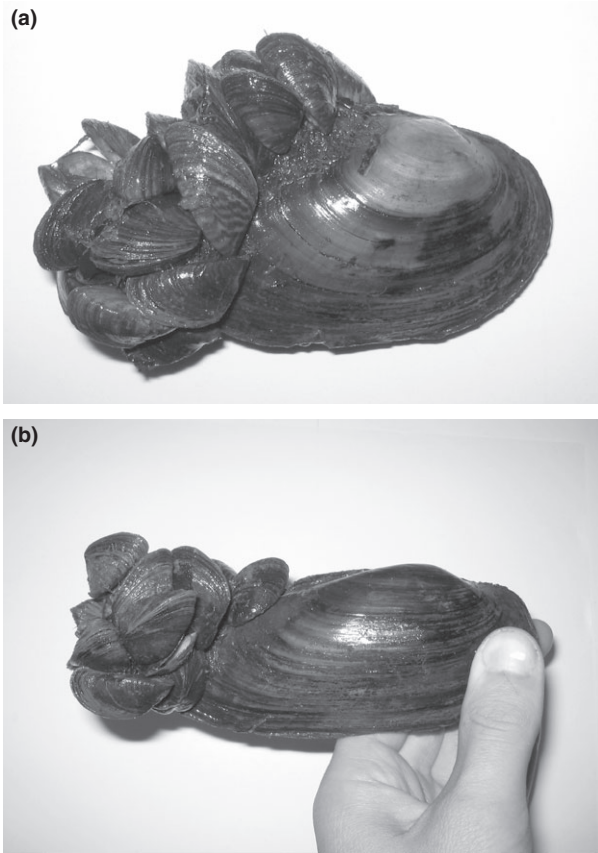A comparison of the condition index, measured as the tissue mass : shell mass ratio, between species and

**Fig. 1** Zebra mussels infesting the posterior parts of the shells (a) *Anodonta anatina* and (b) *Unio pictorum*.
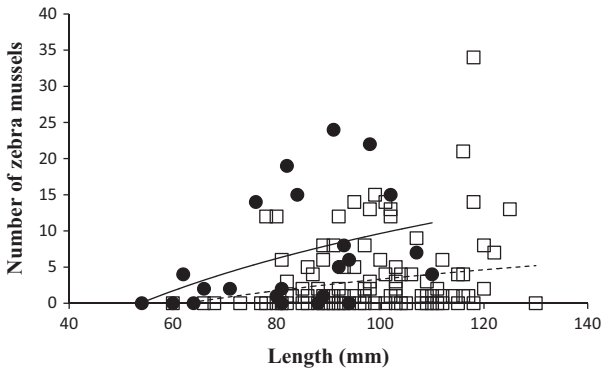


**Fig. 2** Regressions of the number of zebra mussels attached to *Anodonta anatina* (black circles, solid line) and *Unio pictorum* (white squares, dashed line) on shell length. *Anodonta anatina*: $y = 15.52\mathrm{Ln}(x) - 61.84$ ($R^2 = 0.18$, $P < 0.05$) and *U. pictorum*: $y = 7.15\mathrm{Ln}(x) - 29.61$ ($R^2 = 0.04$, $P < 0.05$).



**Fig. 3** Regressions of (a) exposed area of *Anodonta anatina* and (b) *Unio pictorum* from the River Stour on shell length for uninfested, lightly infested and highly infested unionoids. *Anodonta anatina* uninfested: $y = 3.00x - 6.27$ ($R^2 = 0.94$, $P < 0.01$); *A. anatina* lightly infested: $y = 1.79x - 0.90$ ($R^2 = 0.67$, $P < 0.05$); *A. anatina* highly infested: $y = 2.88x - 5.67$ ($R^2 = 0.83$, $P < 0.001$); *U. pictorum* uninfested: $y = 2.22x - 3.31$ ($R^2 = 0.71$, $P < 0.001$); *U. pictorum* lightly infested: $y = 2.16x - 2.83$ ($R^2 = 0.44$, $P < 0.001$) and *U. pictorum* highly infested: $y = 1.18x + 1.70$ ($R^2 = 0.15$, $P < 0.05$).

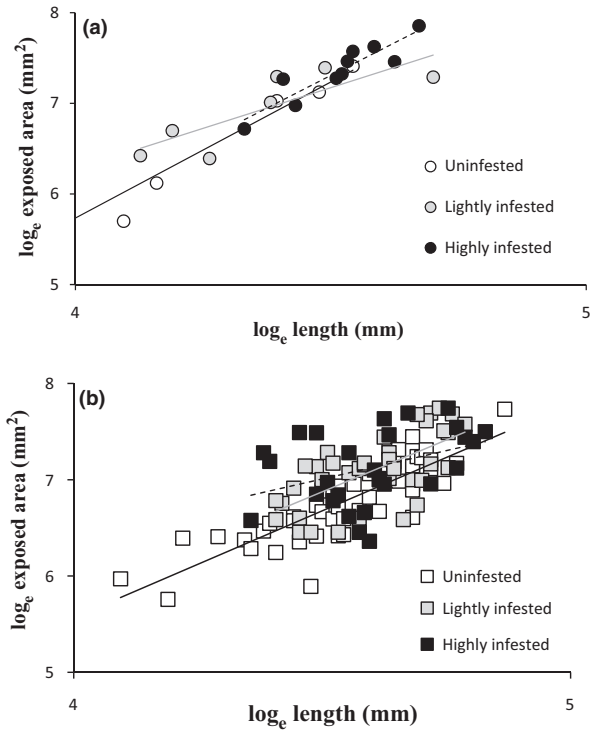infested or uninfested mussels, showed (i) that longer mussels had a lower condition index ($F = 13.64$, $P < 0.001$), (ii) that there was an interaction between the two species, with *U. pictorum* showing a steeper negative gradient ($F = 4.00$, $P = 0.048$), and (iii) that infested mussels had a significantly lower condition than unifested mussels ($F = 5.05$, $P = 0.027$) (Fig. 4a). When a similar analysis was conducted to compare the glycogen content between infested and uninfested individuals of the same species, the length of mussel and all interaction terms were not significant. However, uninfested mussels had a higher glycogen content than infested mussels ($F = 31.24$, $P < 0.001$), and *U. pictorum* had a higher glycogen content than *A. anatina* ($F = 15.42$, $P < 0.001$) (Fig. 4b).

Glycogen content was negatively correlated with wet mass of zebra mussels attached to unionoids (*A. anatina*: $r = -0.462$, $P < 0.05$; *U. pictorum*: $r = -0.714$, $P < 0.001$) (Fig. 5), with *U. pictorum* being more affected by zebra mussels than *A. anatina* as
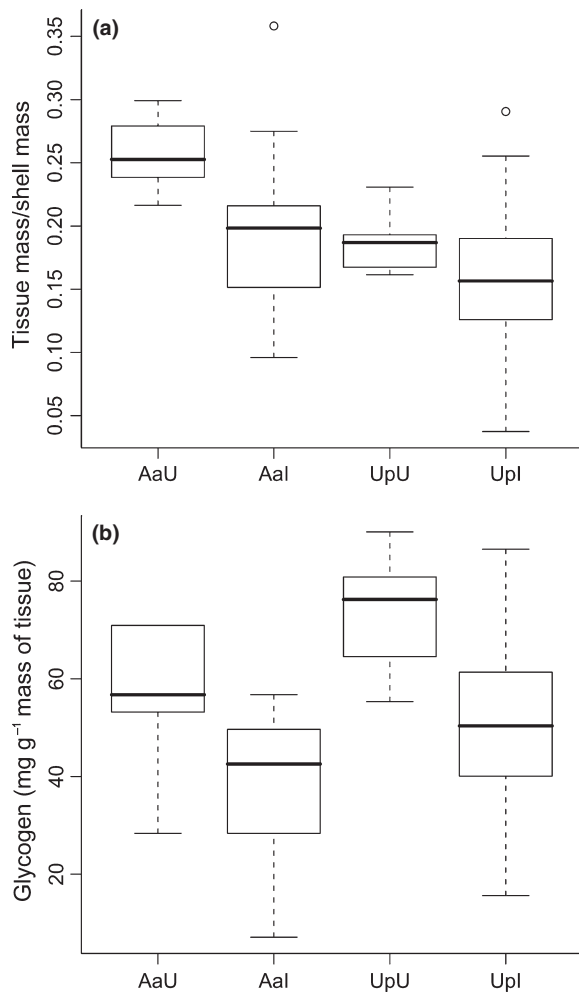
**Fig. 4** The physiological condition of unionoids measured (a) as tissue mass : shell mass ratio and (b) glycogen content for uninfested (U) and infested (I) individuals of *Anodonta anatina* (Aa) and *Unio pictorum* (Up) from the River Stour.

infestation rates increase (ANCOVA with wet weight of attached zebra mussels as covariate, interaction between species: $F = 7.478$, $P = 0.007$).

## Discussion

Our data provide the first evidence that zebra mussels have a deleterious impact on the physiological status of native unionoids in Europe. This was true for both measures used (tissue mass : shell mass ratio and glycogen content), even though infestation rates were not very high (maximum of 34 zebra mussels per unionoid). This contrasts with Lewandowski (1976), who found no differences in the dry mass per shell length relationships between unionoids with (mean of
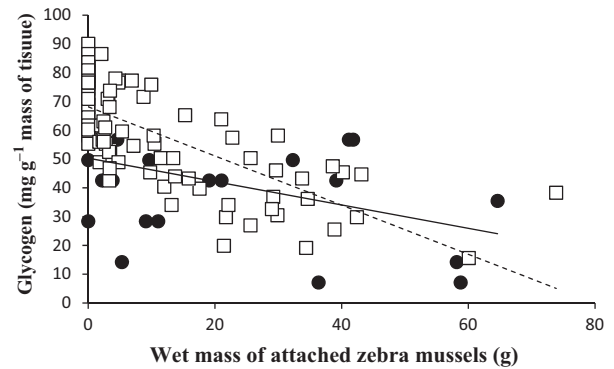


**Fig. 5** Linear regressions of the glycogen content on the wet mass of zebra mussels attached to *Anodonta anatina* (black circles, solid line) and *Unio pictorum* (white squares, dashed line) from the River Stour. *Anodonta anatina*: $y = -0.41x + 50.31$ ($R^2 = 0.21$, $P < 0.05$) and *U. pictorum*: $y = -0.85x + 68.18$ ($R^2 = 0.51$, $P < 0.001$).

20 zebra mussels) and without attached *D. polymorpha* in Lake Mikolajskie (Poland). In addition, despite the fact that both condition indicators gave broadly similar results, the independence of glycogen measurement from the size of the mussel makes this a particularly powerful tool in situations where sample size may be low. While the standard measure of tissue mass : shell mass ratio is very easy to obtain, and can give a general indication of mussel condition in the population under survey, caution must be taken when drawing comparisons between populations or even adjacent habitats because shell morphology can vary considerably over very small distances (Zieritz & Aldridge, 2009) and because shells thicken as they approach the asymptotic length.

Our results are consistent with those obtained by other authors in North America and show that glycogen content in unionoids is very sensitive to fouling by *D. polymorpha*, generally resulting in a reduction in energy stored (Haag *et al.*, 1993; Baker & Hornbach, 2000, 2008). However, not all unionoid species seem equally vulnerable to zebra mussel infestation. For example, in this study *Pseudanodonta complanata* (Rossmässler, 1835), which is the most endangered European unionoid that is sympatric with *D. polymorpha* (Red Data Book 'Near Threatened', IUCN), seems to be the least affected species. It buries deeply with only a tiny proportion of its shell vulnerable to fouling (Killeen, Aldridge & Oliver, 2004), and so *P. complanata* may be relatively protected from *Dreissena*. The reasons that explain these interspecific differences may be related to distinct

ecological traits (e.g. surface area of exposed shell, burrowing activity and substratum preferences) and also shell texture and morphology (Haag *et al.*, 1993). Species that have higher exposed areas and lighter shells (e.g. *A. anatina* and *Anodonta cygnea*) have been described as more susceptible to the impact of *D. polymorpha*, which may include changes in the centre of gravity and increases in energy expenditure to maintain position in the substratum (Nalepa, 1994). Larger exposed surface areas can support more zebra mussels, and this can result in greater competition with the underlying unionoid for suspended food (Hörmann & Maier, 2006). In our study, *A. anatina* had a higher exposed area and a higher rate of infestation by zebra mussels than *U. pictorum* and also had broadly lower glycogen content. However, the decline in glycogen in response to zebra mussel load was more pronounced in *U. pictorum*. Therefore, the simple use of the exposed area as a key ecological trait explaining the fouling intensity and consequent reduction in physiological fitness may be an over-simplification. One possible explanation for the greater sensitivity of *U. pictorum* in our study was that it was conducted in July, shortly after the brooding period of *U. pictorum* (April to June; Aldridge, 1999), but before that of *A. anatina* (August to March; Aldridge, 1999). As such, *A. anatina* may have had relatively large energy reserves in July, which could buffer the deleterious impacts of *D. polymorpha*. Under such a scenario, we might predict that different patterns would emerge if the study had been conducted at a different time of year, and this would be worthy of further investigations.

The scatter in our data shows that there is also considerable intraspecific variation in zebra mussel fouling. Ecological traits, such as exposed area, sex, type of sediment, burrowing activity and the presence of predators may explain some of these differences. For example, is well known that small individuals, principally juveniles, are almost completely burrowed in the sediments, which complicate the possible infestation. Haag *et al.* (1993) also found greater mortality in females fouled with zebra mussels. However, our study did not find differences in the degree of infestation of males and females of *U. pictorum* in the River Stour.

Given our evidence of reduced body condition in fouled unionoids, and the recent, rapid increase in zebra mussels across Europe (Araujo & Alvarez, 2001;

Pollux *et al.*, 2003; Aldridge *et al.*, 2004), it is pertinent to consider whether such fouling could drive widespread decline in European unionoids. The decline of unionoid mussels following the introduction of zebra mussels has been well documented in North America, with near total extinction within a few years after invasion in several lakes (e.g. Lake St. Clair and Lake Erie) and rivers (e.g. St. Lawrence River) with very high fouling intensities (Gillis & Mackie, 1994; Nalepa, 1994; Schloesser & Nalepa, 1994; Ricciardi, Whoriskey & Rasmussen, 1996; Martel *et al.*, 2001). However, Strayer & Malcom (2007) also showed that, after initial declines, unionoid populations in Hudson River have stabilised or even recovered, with the initial declines in population sizes and body condition correlated with the filtration rates of zebra mussels but not with fouling. Rapid declines have been also described in European lakes, such as Lake Balaton in Hungary (Sebestyén, 1938; Ponyi, 1992), Lake Mikolajskie in Poland (Lewandowski, 1991) and Lake Hallwil in Switzerland (Arter, 1989).

Uncertainty exists about possible differences in effects of *D. polymorpha* on unionoids in North America and in Europe, with possibly a greater effect in North America. Our results show clearly that zebra mussels are also having a negative impact on the physiological condition of European unionoids. Although a number of European unionoids show Ponto-Caspian sympatry with *D. polymorpha* resulting in possible ancient coexistence, the majority of European species have been sympatric with *D. polymorpha* for a maximum of 200 years. Therefore, our study seems to support the idea that European unioniods are just as vulnerable to impacts of zebra mussel fouling as are many of the North American species.

While quantitative data are not available on the change in abundance of live unionoids at our study sites, the only locality where there was a noticeable and dramatic decline is Barden Lake (e.g. *A. cygnea* was not found in our latest survey). In contrast, while our results showed that unionoid populations in the Rivers Thames, Great Ouse, Nene and Stour have suffered an increased infestation over time, this situation has not resulted in an apparent unionoid decline (D. Aldridge, pers. obs.). Indeed, the infestation rates described in our study, at least in lotic systems, do not follow the proposed model of Ricciardi, Neves & Rasmussen (1998), which predicted a

local extinction or near extinction (>90% decline in abundance) of unionoids 4–8 years following invasion. This pattern might result from the greater habitat heterogeneity found in rivers than in lakes, which may thus provide refugia from fouling. Indeed, several habitats can serve as refugia, since spatial heterogeneity within a system is an important factor in the creation of niches with different physiological tolerances for native unionoid species and *D. polymorpha*. Places that can easily be colonised by unionoids (e.g. habitats with finer sediments and rich in organic matter) are not suitable for *D. polymorpha*, principally in the summer when temperature increases and dissolved oxygen decreases (MacIsaac, 1996). In addition, the infestation rates detected in our study were much lower than those reported for American ecosystems (Schloesser *et al.*, 1996; but see Strayer & Malcom, 2007 who showed similar rates in Hudson River as described in Europe). Therefore, although we were able to confirm a reduction in the physiological status of infested unionoids, it appears that the infestation rates are not sufficient to lead to massive mortalities. Nevertheless, even small local declines may have broader conservation and ecological effects since unionoid mussels are important taxa in freshwater ecosystems. They are involved in key ecosystems processes (e.g. suspension feeding by mussels can reduce turbidity and modify plankton communities; mussel glochidia larvae are important parasites of fish; mussels shells can provide habitat for other organisms; mussels can bioturbate and oxygenate the top layer of the sediments; mussels are a potential prey for predators; Vaughn & Hakenkamp, 2001; Aldridge *et al.*, 2007) and are among the most endangered groups of animals on the planet (i.e. their abundance and diversity have declined dramatically in the last decades; Lydeard *et al.*, 2004; Strayer *et al.*, 2004a). Although these species have been facing several threats (e.g. habitat destruction, increased siltation, pollution, river modification, loss of fish hosts, commercial exploitation; Bogan, 1993), the impact generated by the introduction of *D. polymorpha* is nonetheless considerable and increasing.

In conclusion, *D. polymorpha* clearly affects the physiological status of European unionoid species although the mechanisms behind this impact may be highly context dependent and species may be affected unequally. Considering the well-known economic and ecological impacts of *D. polymorpha* worldwide, their current spread in Europe requires continued attention and the effects of *D. polymorpha* on unionoids should be a conservation priority.

## References

Aldridge D.C. (1999) The morphology, growth and reproduction of Unionidae (Bivalvia) in a fenland waterway. *The Journal of Molluscan Studies*, **65**, 47–60.

Aldridge D.C., Elliot P. & Moggridge G.D. (2004) The recent and rapid spread of the zebra mussel (*Dreissena polymorpha*) in Great Britain. *Biological Conservation*, **119**, 253–261.

Aldridge D.C., Fayle T. & Jackson N. (2007) Freshwater mussel abundance predicts biodiversity in UK lowland rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **17**, 554–564.

Araujo R. & Alvarez R.M. (2001) El mejillón cebra en el Ebro: un grave caso de riesgo ambiental en Aragón. *Naturaleza Aragonesa*, **8**, 39–46.

Arter H.E. (1989) Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland). *Aquatic Sciences*, **51**, 87–99.

Baker S.M. & Hornbach J. (2000) Physiological status and biochemical composition of a natural population of unionid mussels (*Amblema plicata*) infested by zebra mussels (*Dreissena polymorpha*). *American Midland Naturalist*, **143**, 443–452.

Baker S.M. & Hornbach J. (2008) Zebra mussels (*Dreissena polymorpha*) attached to native mussels (Unionidae) or inanimate substrates: comparison of physiological rates and biochemical composition. *American Midland Naturalist*, **160**, 20–28.

Bogan A.E. (1993) Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. *American Zoologist*, **33**, 599–609.

Burlakova L.E., Karatayev A.Y. & Padilla D.K. (2000) The impact of *Dreissena polymorpha* (Pallas) invasion on

unionid bivalves. *International Review of Hydrobiology*, **85**, 529–541.

Caraco N.F., Cole J.J., Raymond P.A., Strayer D.L., Pace M.L., Findlay S.E.G. & Fischer D.T. (1997) Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology*, **78**, 588–602.

Effler S.W., Brooks C.M., Whitehead K., Wagner B., Doerr S.M., Perkins M.G., Siegfried C.A., Walrath L. & Canale R.P. (1996) Impact of zebra mussel invasion on river water quality. *Water Environmental Research*, **68**, 205–214.

Gillis P.L. & Mackie G.L. (1994) Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. *Canadian Journal of Zoology*, **72**, 1260–1271.

Haag W.R., Berg D.J., Garton D.W. & Farris J.L. (1993) Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 13–19.

Hecky R.E., Smith R.E.H., Barton D.R., Guildford S.J., Taylor W.D., Charlton M.N. & Howell T. (2004) The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1285–1293.

Hörmann L. & Maier G. (2006) Do zebra mussels grow faster on live unionids than on inanimate substrate? A study with field enclosures. *International Review of Hydrobiology*, **91**, 113–121.

IUCN (2010) *IUCN Red List of Threatened Species*. Version 2010.1. Available at: http://www.iucnredlist.org, accessed 5 May 2010.

Jokela A. & Ricciardi A. (2008) Predicting zebra mussel fouling on native mussels from physicochemical variables. *Freshwater Biology*, **53**, 1845–1856.

Karatayev A.Y., Burlakova L.E. & Padilla D.K. (1997) The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *Journal of Shellfish Research*, **16**, 187–203.

Kerney M.P. (1999) *Atlas of the Land and Freshwater Molluscs of Britain and Ireland*. Harley Books, Colchester.

Kerney M.P. & Morton B.S. (1970) The distribution of *Dreissena polymorpha* in Britain. *Journal of Conchology*, **27**, 97–100.

Killeen I.J., Aldridge D.C. & Oliver P.G. (2004) *Freshwater Bivalves of Britain and Ireland*. FSC, AIDGAP Occasional Publication 82, 114pp.

Lewandowski K. (1976) Unionidae as a substratum for *Dreissena polymorpha* Pallas. *Polish Archives of Hydrobiology*, **23**, 409–420.

Lewandowski K. (1991) Long-term changes in the fauna of family Unionidae bivalves in the Mikolajskie lake. *Ekologia Polska*, **39**, 265–272.

Lydeard C., Cowie R.H., Ponder W.F. *et al.* (2004) The global decline of nonmarine mollusks. *BioScience*, **54**, 321–330.

MacIsaac H.J. (1996) Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist*, **36**, 287–299.

MacIsaac H.J., Lonnee C.J. & Leach J.H. (1995) Suppression of microzooplankton by zebra mussels: importance of mussel size. *Freshwater Biology*, **34**, 379–387.

Mackie G.L. (1991) Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, **219**, 251–268.

Martel A.L., Pathy D.A., Madill J.B., Renaud C.B., Dean S.L. & Kerr S.J. (2001) Decline and regional extirpation of freshwater mussels (Unionidae) in a small river system invaded by *Dreissena polymorpha*: the Rideau river, 1993-2000. *Canadian Journal of Zoology*, **79**, 2181–2191.

McIvor A.L. & Aldridge D.C. (2007) The reproductive biology of the depressed river mussel, *Pseudanodonta complanata* (Bivalvia: Unionidae), with implications for its conservation. *The Journal of Molluscan Studies*, **73**, 259–266.

Minchin D., Lucy F. & Sullivan M. (2002) Zebra mussel: impacts and spread. In: *Invasive Aquatic Species of Europe: Distribution, Impact and Management* (Eds E. Leppäkoski, S. Gollasch & S. Olenin), pp. 135–146. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Nalepa T.F. (1994) Decline of native unionid bivalves in Lake St. Clair after infestation by the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2227–2233.

Olenin S., Orlova M. & Minchin D. (1999) *Dreissena polymorpha* (Pallas, 1771). In: *Case Histories on Introduced Species: Their General Biology, Distribution, Range Expansion and Impact* (Eds S. Gollasch, D. Minchin, H. Rosenthal & M. Voigt), pp. 37–42. Logos-Verlag, Berlin, Germany.

Pace M.L., Findlay S.E.G. & Fischer D. (1998) Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology*, **39**, 103–116.

Pollux B., Minchin D., van der Velde G., van Alen T., Moon-van der Staay S.Y. & Hackstein J. (2003) Zebra mussels (*Dreissena polymorpha*) in Ireland, AFLP-fingerprinting and boat traffic both indicate an origin from Britain. *Freshwater Biology*, **48**, 1127–1139.

Ponyi J.E. (1992) The distribution and biomass of Unionidae (Mollusca, Bivalvia), and the production of *Unio tumidus* Retzius in Lake Balaton (Hungary). *Archiv für Hydrobiologie*, **125**, 245–251.

Pyšek P., Richardson D.M., Pergl J., Jarošík V., Sixtová Z. & Weber E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, **23**, 237–244.

Ricciardi A., Whoriskey F.G. & Rasmussen J.B. (1995) Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1449–1461.

Ricciardi A., Whoriskey F.G. & Rasmussen J.B. (1996) Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1434–1444.

Ricciardi A., Neves R.J. & Rasmussen J.B. (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology*, **67**, 613–619.

Schloesser D.W. & Nalepa T.F. (1994) Dramatic decline of unionid bivalves in offshore waters of western lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2234–2242.

Schloesser D.W., Nalepa T.F. & Mackie G.L. (1996) Zebra mussel infestation of unionid bivalves (Unionidae) in North America. *American Zoologist*, **36**, 300–310.

Sebestyén O. (1938) Colonization of two new fauna-elements of Pontus-origin (*Dreissena polymorpha* Pall. and *Corophium curvispinum* G.O. Sars forma devium Wundsch) in Lake Balaton. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **8**, 169–181.

Sousa R., Gutiérrez J.L. & Aldridge D.C. (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions*, **11**, 2367–2385.

Stanczykowska A. (1977) Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Polish Archives of Hydrobiology*, **24**, 461–530.

Strayer D.L. & Malcom H.M. (2006) Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. *Freshwater Biology*, **51**, 117–130.

Strayer D.L. & Malcom H.M. (2007) Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: the beginning of the end or the end of the beginning? *Journal of the North American Benthological Society*, **26**, 111–122.

Strayer D.L., Caraco N.F., Cole J.J., Findlay S. & Pace M.L. (1999) Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. *BioScience*, **49**, 19–27.

Strayer D.L., Downing J.A., Haag W.R., King T.L., Layzer J.B., Newton T.J. & Nichols S.J. (2004a) Changing perspectives on pearly mussels, North America's most imperilled animals. *BioScience*, **54**, 429–439.

Strayer D.L., Hattala K. & Kahnle A. (2004b) Effects of an invasive bivalve (*Dreissena polymorpha*) on fish populations in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 924–941.

Strayer D.L., Pace M.L., Caraco N.F., Cole J.J. & Findlay S.E.G. (2008) Hydrology and grazing jointly control a large-river food web. *Ecology*, **89**, 12–18.

Vaughn C.C. & Hakenkamp C.C. (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*, **46**, 1431–1446.

Zieritz A. & Aldridge D.C. (2009) Identification of ecophenotypic trends within three European freshwater mussel species (Bivalvia: Unionoida) using traditional and modern morphometric techniques. *Biological Journal of the Linnean Society*, **98**, 814–825.