Biol Invasions (2012) 14:127–137
DOI 10.1007/s10530-011-9989-7

ORIGINAL PAPER

The role of host specificity in explaining the invasion success of the freshwater mussel *Anodonta woodiana* in Europe

K. Douda · M. Vrtílek · O. Slavík · M. Reichard

Received: 4 February 2011 / Accepted: 27 March 2011 / Published online: 9 April 2011

Abstract Several freshwater mussel species represent some of the most problematic invasive species and have considerably altered ecosystems worldwide. Their invasion potential has been partially attributed to their free-living larvae, which have a high dispersal capability. We investigated the invasion potential of *Anodonta* (*Sinanodonta*) *woodiana*, a species of East Asian unionid mussel established worldwide despite having an obligatory parasitic stage (glochidium), which must encyst on host fish. The invasion success of *A. woodiana* has been attributed to the success of worldwide introductions of its sympatric fish hosts. We experimentally found, however, that *A. woodiana* is a broad host generalist, which can complete its development on all eight fish species tested, both coinvasive and native. Subsequently, we used a data on the occurrence and relative abundance of potential hosts in river habitats in the Czech Republic to project scenarios of the effect of host availability on *A. woodiana* invasion. We found that host availability does not constitute a major limit for *A. woodiana* to colonise most aquatic habitats in Central Europe. In addition, we investigated seasonal dynamics of *A. woodiana* reproduction and did not detect any limitations of its reproduction by ambient water temperatures typical of a Central European lowland river. Consequently, we predict that *A. woodiana* may further increase the speed and range of its invasion and we discuss possible consequences to native habitats and communities, especially to the endangered species of unionid mussels.

Keywords Aquatic habitat · Bivalvia · Host-parasite relationship · Host specificity · Mollusca · Unionidae

K. Douda (✉) · O. Slavík
Water Research Institute T.G.M., Podbabská 30,
Prague 160 00, Czech Republic
e-mail: douda@vuv.cz

K. Douda
Faculty of Environmental Sciences, Czech University
of Life Sciences Prague, Kamýcká 1176,
Prague 165 21, Czech Republic

M. Vrtílek · M. Reichard
Institute of Vertebrate Biology, Academy of Sciences
of the Czech Republic, Květná 8, Brno 603 65,
Czech Republic

Introduction

Several freshwater bivalve species are some of the world's most problematic biological invaders (Higgins and Vander Zanden 2010). For example, recent invasions of *Dreissena polymorpha*, *Corbicula fluminea* and *Limnoperna fortunei* have been particularly problematic. These species have altered entire aquatic environments by their filtration and burrowing activities (Higgins and Vander Zanden 2010; Karatayev et al. 2007b; Sousa et al. 2009; Strayer

2009), and they have severely affected native communities by altering habitats and competing for resources (Karatayev et al. 1997; Sousa et al. 2008b; Ward and Ricciardi 2007). Bivalve invasions in freshwater are becoming increasingly common, but our understanding of their biology, including factors that affect their invasion, is still largely incomplete (Keller et al. 2007; Leung et al. 2004; Stoeckel et al. 1997; Strayer 2009).

The most invasive bivalve species have simple life cycles; they either directly release juveniles (Sousa et al. 2008a), or they produce free living dispersal larvae (Karatayev et al. 2007a; Stoeckel et al. 1997). Life histories among bivalves, however, are diverse and may include an obligatory parasitic stage. Freshwater mussels from the superfamily Unionoidea are sedentary benthic invertebrates, which feed primarily through water filtration. Their life cycle includes a larval stage, termed the glochidium, which attaches generally to freshwater fishes for several days to months, depending on the water temperature. Several thousands glochidia are incubated in a female's modified gill chambers. To complete their development into a juvenile mussel, ripe glochidia are released into the water, where they attach to a host tissue and encyst (Wachtler et al. 2001). This relationship of unionids and fishes is more phoretic than nutritive (Barnhart et al. 2008), although glochidia obtain nourishment from their host (Wachtler et al. 2001). This parasitic stage is the key period for unionid mussel dispersal and invasion.

The host-parasite relationship is one of the most challenging issues in invasion biology (Taraschewski 2006). The geographic range extensions of parasites expose them to novel hosts, which has a direct consequences for establishment success of new parasite populations, their population dynamics and potential for invasiveness (e.g., Lee and Klasing 2004; Prenter et al. 2004). Parasites' levels of host specificity are highly variable (Poulin 1992), which affects their dispersal and their reproduction success within their novel range (Taraschewski 2006). Parasites are not always successful in infecting and exploiting their new hosts (Bakke et al. 2002), but they may capitalise on the 'evolutionary naivety' of novel hosts and exploit them more effectively than hosts that they have co-evolved with (e.g., Reichard et al. 2007, 2010). The degree of host specificity is directly related to the parasite's invasion potential, as the availability of suitable hosts species determine the parasite's ability to reproduce and invade (Shea and Chesson 2002).

We investigated how host specificity affects the invasion success of the Chinese pond mussel, *Anodonta* (*Sinanodonta*) *woodiana* (Lea), a unionid mussel species that has recently been reported as being invasive worldwide. *Anodonta woodiana* is native to south eastern Asia, specifically Indochina and southern China to Korea, Japan, Taiwan, Primorye and the Amur Basin in eastern Russia (Graf 2007; Watters 1997). In their native range, glochidia are released in the summer, attach to fins and gills of host fish and are encysted by the host's tissue. Metamorphosis is complete within several days, and juvenile mussels then release from their host (Dudgeon and Morton 1984). The expansion of *A. woodiana's* range began in the second half of the twentieth century; today, *A. woodiana* can be found in the Indonesian islands (Djajasasmita 1982), Central America (Watters 1997), Europe (Kraszewski 2007; Sárkány-Kiss et al. 2000), the Asian part of Turkey (Reichard, unpublished data) and North America (Benson 2011). *Anodonta woodiana* range expansion has been attributed to its parasitic stage and the notion that infected host fishes serve as a vector for spreading. Exports of fish for commercial purposes (mainly carp species from East Asia) are thought to be the main means of human-mediated dispersal (Watters 1997). The establishment of East Asian cyprinid fish populations, such as *Carassius auratus*, *Carrasius gibelio*, *Ctenopharyngodon idella* and *Hypophthalmichthys molitrix*, in non-native areas is believed to enable the persistence of *A. woodiana* populations (Watters 1997). However, direct data concerning host specificity and transformation success of *A. woodiana* glochidia on different host fish species are lacking and it has also been hypothesised that *A. woodiana* may use fish species native to the invaded areas as hosts (Kiss 1995; Sárkány-Kiss et al. 2000; Watters 1997).

The compatibility of a host-parasite combination depends mainly upon the ability of glochidia to survive the host's defensive immune response (Jansen et al. 2001). Most unionid mussel species have a high degree of host specificity and are able to use only one, or a few, host species, though some generalists are reported to use over 30 species (Strayer 2008; Trdan and Hoeh 1982). The parasitic period is critical to unionid mussel population dynamics (Vaughn and

Taylor 2000; Watters 1992; McNichols et al. 2011) because host fish directly affect mussel reproductive success (by contact probability and immunological compatibility) and dispersal (by the host movements).

Information on host specificity of *A. woodiana* glochidia will also help in understanding the spatial pattern of *A. woodiana* invasions. Two alternative hypotheses exist to explain *A. woodiana* invasions. First, *A. woodiana* is spread via the intercontinental introductions of its hosts, and *A. woodiana's* high host specificity limits its distribution to the limits of its co-invasive hosts. High local densities of *A. woodiana* may be explained either by the establishment or repeated import of fish species that serve as hosts to *A. woodiana* in its native range. Second, *A. woodiana* initially co-invades with its native hosts, but its low host specificity enables subsequent colonisation of novel host species populations within the novel range. This scenario also includes the possibility that co-invasive hosts are involved in an initial phase of the invasion, and it predicts that there is a more rapid increase in population density and dispersal due to the multiplying effect on the number of potential sites with exploitable hosts and the overall higher density of hosts at each site. The distinction between these two hypotheses is crucial for the proper management of native communities affected by *A. woodiana* invasion, including measures of prevention, control and potential eradication, as well as restoration plans.

The fact that *A. woodiana* is widespread suggests that both juvenile and adult *A. woodiana* can cope with a wide range of environmental conditions. Corsi et al. (2007) showed that *A. woodiana* has particular physiological predispositions (cholinesterase enzymes activity) that probably enable it to tolerate a variety of unsuitable conditions. On the other hand, Kraszewski (2007) suggested that water temperature may play a pivotal role in the variation of *A. woodiana* abundance and biomass and may limit its distribution. The role of water temperature is most likely to be manifested by the failure of gametes to mature (Galbraith and Vaughn 2009). However, details concerning *A. woodiana* environmental tolerance and the role of temperature and other habitat factors on *A. woodiana* survival and reproduction remain unclear.

Potential ecological and economical consequences of an *A. woodiana* invasion likely come from the adult mussels. Despite the existence of the obligatory parasitic stage, host fish are typically not negatively affected (e.g., Treasurer et al. 2006) and rather serve as a vector. In contrast, adult mussels are known to reach a population biomass of up to 25 kg m^{-2} (Kraszewski and Zdanowski 2007), which may have serious consequences for the surrounding ecosystem due to their filtrating capacity (Vaughn and Hakenkamp 2001) and their competition with native mussel species for space and food. Further, native unionid mussels may be threatened by competition for hosts, as the infected hosts often develop cross-specific immunity after the first glochidia infection (Rogers and Dimock 2003). Indeed, unionid mussels are one of the most threatened animal groups globally (Lydeard et al. 2004) because of their complex life cycles, host specificity and strict environmental condition requirements, which makes them highly vulnerable to the human alteration of freshwater habitats (Bogan 1993; Douda 2010; Vaughn and Taylor 1999).

We investigated potential causes of the recent *A. woodiana* invasion in Central Europe. First, we experimentally tested the host-parasite compatibility of *A. woodiana* with their co-invasive host fish species (sympatric with *A. woodiana* in their natural range) and with several common native European fish species. We compared the dynamics of initial glochidia attachment, the length of the parasitic period and the transformation success of *A. woodiana* glochidia among particular host species. Second, we investigated the potential role of water temperature on *A. woodiana* reproductive success by describing the seasonal dynamics of their reproduction in a Central European lowland river. We discuss our outcomes with an emphasis on the global patterns and consequences of *A. woodiana* invasion.

Materials and methods

Experimental test of host specificity

Gravid females of *A. woodiana* were collected in September 2010 from the Kyjovka River, Czech Republic (N 48°46′45″; E 17°00′60″). Females were transported to the laboratory and held separately in 10-l containers with aerated river water until glochidia clumps were spontaneously released. Eight potential host species (family Cyprinidae) were used for experimental infection by glochidia. Two species were co-invasive (*Pseudorasbora parva* and *Carassius gibelio*, both sympatric with *A. woodiana* in their native range), and five species were of European origin (*Leuciscus cephalus, Rutilus rutilus, Gobio gobio, Barbus barbus* and *Rhodeus amarus*). The origin of *Cyprinus carpio* in Europe is unclear; it is native to Eastern Asia (sympatric with *A. woodiana* populations) and has been hypothesised to be either native to Europe (Kohlmann et al. 2003) or introduced throughout Europe approximately 2000 years ago (Froufe et al. 2002). All species were obtained from a commercial hatchery, except for *R. amarus*, which was collected from a field with a hand net at Štítarský Stream (N 50°16′13″; E 15°11′15″; not populated by *A. woodiana*). Six to ten individual fish per species were used for infections, for a total of 56 individually monitored fish. Ages of experimental fish were either 0 + (*R. amarus*) or 1 + (*B. barbus, C. carpio, C. gibelio, G. gobio, L. cephalus, P. parva* and *R. rutilus*). Two fish (one *R. rutilus* and one *C. gibelio*) died before the end of juvenile detachment (mortality was not related to experimental infection) and subsequently were not included in the analysis.

Spontaneously released glochidia were removed from boxes containing *A. woodiana* using a pipette and were immediately used for laboratory infections. A random subsample of 30 glochidia from each female was tested for viability with sodium chloride (Wang et al. 2007) to confirm their infection potential. Glochidia from six gravid *A. woodiana* females (mean ± SD of shell length 184 ± 14 mm) with a glochidia viability of over 90% were pooled and used for inoculations. Fish were infected by being placed into a dechlorinated tap water bath containing 4,570 ± 1,279 viable glochidia l^{-1}. The glochidia were kept in homogeneous suspension through aeration (volume of the suspension was 0.5 l per fish). After 15 min of inoculation, fish were transferred into a bath that did not contain glochidia for 30 min to rinse off non-attached glochidia. Fish were then individually placed into 56 continuously aerated 5-l plastic tanks with dechlorinated tap water that had 3-mm nets on the bottom. Fish remained in these tanks until the end of the experiment. Fish were fed daily with commercial flake fish food. The temperature in the tanks was recorded automatically every 10 min and was 23.3 ± 0.7°C during the experiment; this agrees with the ambient temperature recorded in the source population during glochidia release (Konečná and Reichard 2011).

Water in individual boxes was partially exchanged (80% of water volume) by siphoning the bottom of the tanks for 26 days, beginning the day after infections and continuing every second day thereafter. Untransformed glochidia and juvenile mussels were isolated from debris in the siphoned water with nylon screens (mesh size 139 and 507 micro m; UHELON). A stereomicroscope with 10–40× magnification was used to count the number of glochidia and transformed juveniles. All individuals that were collected were inspected; if foot activity or valve movement were observed, individuals were classified as live juveniles.

Glochidia infection rate (the number of initially attached glochidia per fish), mean attachment duration of successfully developed glochidia and transformation success were compared between host species with generalised linear models (GLM); host species identity and individual host body weight were used as predictive factors, and the interaction between species and weight was included. Minimal adequate models were constructed using Akaike information criterion. Analysis of deviance tables were computed for fitted model objects. Data for the transformation success of glochidia, expressed as a share between the total number of initially attached glochidia per fish and the total number of living juveniles recovered from the fish, were arcsine-transformed before analyses. Tukey's HSD post-hoc tests were used to examine the pairwise differences between host species. Analyses were done using the R 2.12.0 software package (R Development Core Team 2010).

Host availability under different levels of host specificity

Data from the national fish community monitoring program, established according to the European Water Framework Directive (Czech Hydrometeorological Institute 2010), were used to project scenarios of host availability for *A. woodiana* at two different levels of its specificity (only co-invasive host species, all confirmed host species). A standardised electrofishing method was used to obtain fish data (Jurajda et al. 2010) during 2006 and 2007. Sampling sites were lotic habitats, including upland streams and large lowland rivers, and were evenly distributed throughout the Czech Republic (approximately 78,000 km^2). Lakes were not included as sampling sites because natural lakes only rarely occur outside the active floodplain in Czech Republic (Corine land-cover data, CLC 2000, European Environment Agency). The analysis is based on 49,871 individuals of 40 fish species from 247 sampling sites. First, we calculated the potential availability of the host fish species that are co-invasive with *A. woodiana* in the territory of the Czech Republic as a proportion of sample sites with the presence of at least one of the introduced East Asian species. Second, we calculated the proportion of sample sites that had at least one of the suitable host species for *A. woodiana* experimentally determined by this study. In both scenarios, we also determined the relative abundance of the supposed host species.

Reproduction timing of *A. woodiana* in a Central European lowland river

Anodonta woodiana were sampled monthly between November 2008 and October 2009 in the Kyjovka River to determine the seasonal dynamics of their reproductive cycle. This river sustains a large population of *A. woodiana* that was discovered in 2007 (Reichard, personal observation) but was likely established between 2002 and 2006. At each sampling, 30 individuals were collected by hand, and water temperature was measured. Sampling was conducted at two sites, positioned 7 km apart from each other, because sampling at the first site (48°43′24″N, 16°58′18″E) led to a decrease in local population density. To mitigate the effort needed to collect sufficient number of individuals for analysis, the second sampling site (48°46′44″N, 17°01′00″E), upstream of the first site, was used from June onward. Three hundred sixty-one individual *A. woodiana* were collected over 12 sampling occasions. Adult mussels were targeted.

Mussels were transported alive to the Institute of Vertebrate Biology in Brno, Czech Republic. Mussels were dissected to determine their sex and the developmental phase of their glochidia, which were incubated in marsupia. Individuals were sexed by the appearance of their demibranchs, which is a reliable method for sex determination in mature *Anodonta* mussels (Mackie 1984). Females had swollen outer gills, whereas the outer gills of males did not differ from their inner gills. A sample of the swollen outer gill tissue was dissected from each female, the state of glochidia development was identified under a microscope and glochidia were assigned to three groups: eggs (indiscernible shell structure), immature glochidia and ripe glochidia (amber shells with hook). If glochidia were absent in swollen demibranchs, they were assumed to be recently released.

Results

Host specificity and its effect on host availability

Anodonta woodiana glochidia successfully developed on all host species tested (Fig. 1). Mean (±SD) transformation success of glochidia ranged from $17.6 \pm 12.4\%$ in *G. gobio* to $52.4 \pm 8.4\%$ in *B. barbus*. Mean duration time of successful glochidia development ranged from 6.3 to 7.2 days (Table 1).

The infection rate varied among host species ($F_{7,46} = 123.6$; $P < 0.001$) and was positively affected by fish body mass ($F_{7,45} = 96.8$; $P < 0.001$). The relationship between host body mass and infection rate varied across species ($F_{7,46} = 2.5$; $P < 0.05$). Mean duration of successful development ($F_{7,45} = 4.4$; $P < 0.001$) and transformation success ($F_{7,46} = 5.0$; $P < 0.001$) also differed among species but were not related to host body mass ($P > 0.05$). The transformation success for two co-invasive host species (*P. parva* and *C. gibelio*) was not higher than those for novel hosts (Table 1). One of the East Asian host species, *P. parva*, had lower transformation success than one of the host species indigenous to Central Europe, *B. barbus* (Table 1, Tukey's HSD tests: $P < 0.05$).

At least one of the two co-invasive species (*P. parva* and *C. gibelio*) occurred at 19.4% of the sample sites but had a relative abundance of only 1.4%. In contrast, all host species confirmed as suitable hosts in the host specificity experiment were found in 75.3% of sample sites, with a relative abundance of 39.5%.

Seasonal dynamics of *A. woodiana* reproduction in Central Europe

Mature glochidia were detected from April to September, with maximum numbers detected in July, when 69% of females had ripe glochidia in their outer demibranchs. Fertilised eggs and non-mature glochidia were observed in demibranchs from December to August (Fig. 2). Glochidia maturation was positively associated with increased water temperature;

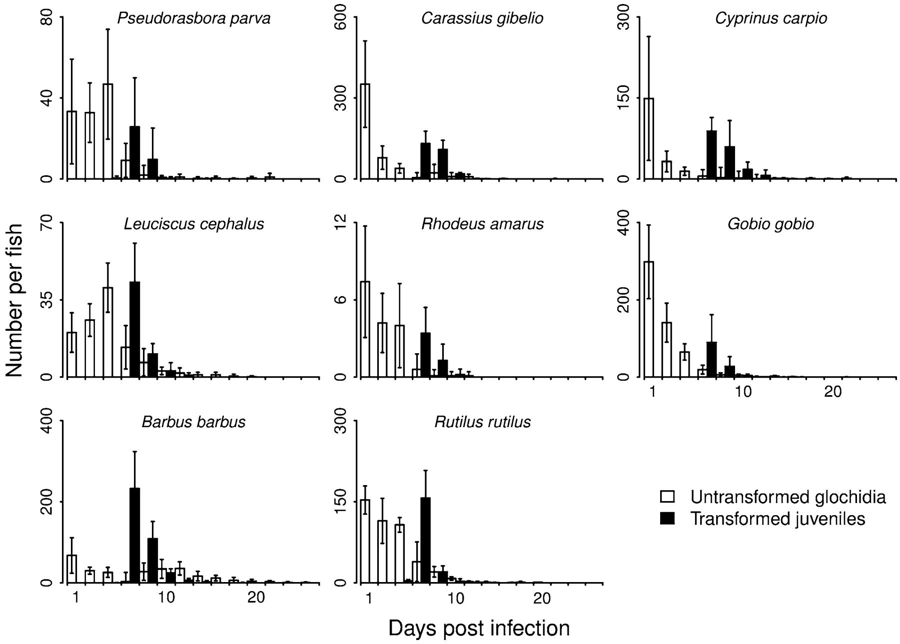

Fig. 1 Developmental dynamics of *A. woodiana* glochidia on different host species. *Bars* indicate the mean ± SD of the number of untransformed glochidia (*white bars*) or live juveniles (*black bars*) recovered per host species in the respective day after attachment

Table 1 Results of host compatibility test (mean ± SD)

Species	Number of fish (n)	Fish length (mm)	Attached glochidia (n)	Transformation success (%)	Duration of successful parasitism (days)
Pseudorasbora parva	10	66.7 ± 4.5	170 ± 55^{a}	20.8 ± 20.4^{b}	6.3 ± 0.4^{a}
Carassius gibelio	5	82.7 ± 9.7	828 ± 250^{c}	33.8 ± 14.2^{a,b}	7.2 ± 0.1^{c}
Cyprinus carpio	6	68.8 ± 7.4	428 ± 268^{b}	40.7 ± 6.7^{a,b}	7.0 ± 0.5^{c,b}
Leuciscus cephalus	6	49.0 ± 0.9	179 ± 36^{a}	31.8 ± 10.1^{a,b}	6.6 ± 0.4^{a,c}
Rhodeus amarus	10	28.7 ± 1.8	22 ± 8^{a}	21.7 ± 13.1^{b}	6.7 ± 0.6^{a,c}
Gobio gobio	6	75.7 ± 3.4	697 ± 113^{c}	17.6 ± 12.4^{b}	6.7 ± 0.2^{a,c}
Barbus barbus	6	97.8 ± 8.2	705 ± 123^{c}	52.4 ± 8.4^{a}	7.0 ± 0.4^{c,b}
Rutilus rutilus	5	97.6 ± 5.5	654 ± 73^{b,c}	28.1 ± 8.7^{a,b}	6.3 ± 0.2^{a,b}

Attached glochidia represent the sum of glochidia and juveniles recovered from fish; transformation success indicates % of attached glochidia that were recovered as live juveniles; the duration of successful parasitism indicates the mean number of days from attachment to excystment of live juveniles. Means denoted by the same superscript letter are not significantly different (Tukey's HSD test at $P < 0.05$)

production of the first ripe glochidia coincided with a temperature of 15.6°C. The sex ratio did not differ from parity at any sampling date or across samples (binomial tests, all $P > 0.05$).

Discussion

We have demonstrated that *A. woodiana*, an invasive unionid species with an obligatory parasitic stage, is a broad generalist; it successfully developed on all eight freshwater fish host species we tested, regardless of whether they were co-invasive or native species. Projection of the invasive potential of *A. woodiana* onto a detailed fish distribution dataset demonstrated that, should dispersal limitation come from host availability, *A. woodiana* has the capability to colonise the majority of river habitats in the Czech Republic. There was also no apparent limitation on *A. woodiana* reproduction due to the ambient temperature range typically found in a Central European lowland river.

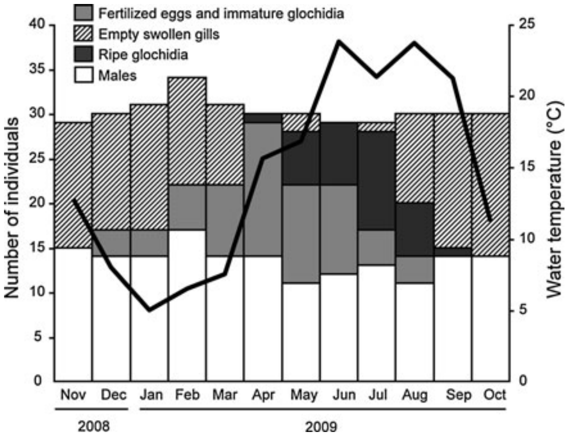

Fig. 2 Seasonal dynamics in sex ratio and glochidia maturation in *A. woodiana* population from the Kyjovka River in 2008–2009, with total numbers of mussels in particular categories. Water temperature recorded at time of mussel collection is indicated by a *solid line*

Invasion potential of *A. woodiana*

Invasions of several freshwater bivalve species (such as *Dreissena polymorpha* or *Limnoperna fortunei*) have caused considerable alterations to ecosystems worldwide (e.g., Sousa et al. 2009), and their invasion potential has been attributed particularly to the existence of their free-living larvae that have high dispersal capabilities (Johnson and Padilla 2010; Stoeckel et al. 1997). We have shown that other species of freshwater mussels may be similarly able to invade rapidly, despite having more complex life cycles. *Anodonta woodiana* has an obligatory parasitic stage, in which the larva must attach and encyst to a freshwater fish host. We found that host specificity in *A. woodiana* was low, allowing for successful glochidia transformation on a variety of host fish, including a species (*R. amarus*) that has been shown to resist glochidia infection of native unionids (Reichard et al. 2006, 2010).

Interspecific differences in transformation success of *A. woodiana* among host species were low; even the least suitable species had a transformation success over 17% and may be considered a functional host. Natural mortality of glochidia often reaches more than 50% of the initially attached glochidia, even in their most compatible mussel-fish relationships (e.g., Jansen et al. 2001; Strayer 2008). In their native range, a Hong Kong population of *A. woodiana* successfully attached to all four host species examined (*Gambusia affinis*—Poecilidae and *Puntius semifasciolatus*, *Metzia takakii* and *Rhodeus sinensis*—Cyprinidae), with the highest abundance observed on the non-native *G. affinis* (Dudgeon and Morton 1984). In Japan, Fukuhara et al. (1986) recorded attached glochidia of *A. woodiana* on five host species (*Rhodeus ocellatus*, *Pseudorasbora parva*—Cyprinidae; *Oryzias latipes*—Adrianichthyidae; *Rhinogobius brunneus*—Gobiidae and non-native *Lepomis macrochirus*—Centrarchidae), with the highest density found on *R. brunneus*. In addition, Kiss (1995) successfully bred juveniles of *A. woodiana* on several cyprinid fishes, most of which were native to East Asia. Although it is the crucial measure of host suitability, transformation success was not unfortunately measured in those studies. Nevertheless, collectively, those data document that *A. woodiana* is able to exploit a wide range of host species.

The generalist behaviour observed in *A. woodiana* plays a critical role in its invasive potential, as host community structure fundamentally influences the establishment and prevalence of parasites (Holt et al. 2003). A generalist parasite strategy is advantageous during changes in host availability during an invasion, and generalist parasites may quickly become independent of their native hosts. For example, a fish-parasitising cestode from East Asia, *Bothriocephalus acheilognathi*, was introduced globally by the intercontinental export of carp species and now has exploited many native fish species in its novel range, causing significant economic losses in fisheries worldwide (e.g., Bean and Bonner 2010; Brouder and Hoffnagle 1997). We predict that *A. woodiana* has the potential to invade areas outside the range of their co-invasive native hosts, even if their initial invasion was likely facilitated by the presence of their native hosts. Hence, the present commercial transportation of many fish species used in aquaculture will likely contribute to the further spread of *A. woodiana* and the establishment of new *A. woodiana* populations.

Our host availability projection quantified the potential of *A. woodiana* to encounter suitable host species at over 75% of lotic habitats in the Czech Republic. This number is the most conservative estimate, as all eight experimentally infected species were suitable hosts. Many host species migrate within the rivers and across the floodplain (Lucas and Baras 2001), further facilitating the spatial dynamics of an *A. woodiana* invasion. Suitability of environmental conditions for adult mussels and glochidia maturation, however, may substantially decrease the proportion of habitats accessible to *A. woodiana*. Data on the water temperature regime for the sites used in the projection were not available and thus could not be incorporated in the analysis.

Water temperature governs the timing of reproduction and gamete maturation in freshwater mussels (Galbraith and Vaughn 2009; Hruška 1992; Watters and O'Dee 2000), and the first reports of *A. woodiana* occurrence in Europe were restricted to the south, or to the thermally-polluted water systems (Kraszewski 2007). Our data from the Kyjovka River indicate that *A. woodiana* reproduction was not constrained by the temperature regime as strongly as previously believed, and its seasonal dynamics are similar to those observed in south-eastern Asia (Dudgeon and Morton 1983). We demonstrated that ripe glochidia were present for 6 months, when ambient temperature ranged from 15 to 27°C (Fig. 2). During that period, the proportion of females with ripe glochidia was high (Fig. 2). *Anodonta woodiana* has recently been reported in colder areas within Europe, such as southern Sweden (von Proschwitz 2008) and the subalpine lake, La Garda, in Northern Italy (Cappelletti et al. 2009). Hence, low water temperature is likely a smaller constraint to *A. woodiana* invasion than previously believed and might be even further relaxed with increasing thermal pollution, global change and evolutionary response of invasive populations to novel conditions.

Potential consequences of *A. woodiana* invasion

Given that neither host availability nor ambient temperatures appear to impede basically *A. woodiana* invasions, we predict that *A. woodiana* may rapidly spread throughout European water bodies. As far as we are aware, no one has examined the foraging ecology of *A. woodiana*, and it is possible that *A. woodiana* may be limited by food availability in nutrient-poor habitats. Freshwater mussel communities are often structured by their metabolic rate (Bauer et al. 1991; Bauer 2001), and *A. woodiana* seems to be more abundant in nutrient-rich habitats, such as in lowland floodplains and in aquaculture ponds (e.g., Paunovic et al. 2006), although a report from a subalpine Lake, La Garda (Cappelletti et al. 2009) imply that *A. woodiana* may be able to exploit a wider range of habitats.

An invasion by *A. woodiana* has three potential negative consequences for the native unionid mussel species. First, *A. woodiana* may directly compete with native mussels for food. High population densities of this species suggest that it may have a capacity to reduce food resources in some habitats. This is supposed to be the primary mechanism of exploitative competition between bivalves, which depends on the minimum food level at which each bivalve can thrive (Strayer 1999). Indeed, competition for food is considered to be the main factor threatening the native populations of North American unionids in areas that have been invaded by *D. polymorpha* (Haag et al. 1993). Second, *A. woodiana* is expected to compete with native unionids for hosts. Direct competition by glochidia for space on hosts or via the activation of innate host tissue responses, such as hyperplasic reaction, may be expected between *A. woodiana* and native species of genus *Unio* because European *Unio* spp. also release their glochidia in the European summer (Blazek and Gelnar 2006; Mackie 1984). Third, glochidia infections can trigger an adaptive immune response by hosts, making them immunised against repeated infections after contact with glochidia (Rogers and Dimock 2003). Such cross-resistance is expected to significantly decrease the proportion of hosts available to native mussels.

Anodonta woodiana abundance increased dramatically within the first two generations it was observed in the Czech Republic. The first report of *A. woodiana* in the Czech Republic comes from 1996 (Beran 1997); however, *A. woodiana* had become a dominant bivalve species in some locations by 2008, with several population outbreaks documented in the southern (warmer) part of the Czech Republic (Beran 2008). This is similar to dynamics documented in other European countries (Cianfanelli et al. 2007; Kraszewski 2007; Paunovic et al. 2006; Popa et al. 2007; Pou-Rovira et al. 2009). Despite an increasing number of invaded regions, there are no comprehensive data documenting effects on native communities by *A. woodiana* invasion, though the first signs of native unionids impairment by *A. woodiana* have been observed in Italy (summarised in Cianfanelli et al. 2007).

The invasion of *A. woodiana* may directly affect an environment by means of physical habitat alternation. In particularly suitable habitats, *A. woodiana* may reach extremely high population densities; a population biomass of up to 25 kg m^{-2} (Kraszewski and Zdanowski 2007), and a density of over 30 individuals m^{-2} was observed in parts of the Kyjovka River (M. Reichard, M. Vrtílek, personal observation). Other invasive freshwater bivalves can seriously affect physical habitat properties (Darrigran 2002; Higgins and Vander Zanden 2010; Sousa et al. 2009; Strayer 2009), and filtration and burrowing activities of unionid mussels may affect organic matter pathways within the sediment and the water column (Vaughn and Hakenkamp 2001).

In conclusion, we have demonstrated that *A. woodiana* has predispositions to be a successful invader in Europe and also probably in other continents. These predispositions include employing a generalist strategy in using its hosts during the parasitic stage and being able to successfully reproduce in environmental conditions previously rendered as suboptimal. We have shown that the spread of *A. woodiana* is not limited by the availability of its hosts and that the temperature conditions in a typical Central European lowland river are suitable for completion of its life cycle. We have also identified potential threats to native habitats and communities, mainly the endangered species of unionid mussels. Given that genetic constraints limiting invasion may be gradually relaxed during the initial establishment (due to adaptive evolution; Sakai et al. 2001), it is possible that tolerance of lower water temperatures will be selected in invasive *A. woodiana* populations, further increasing their ability to colonise new areas.

Acknowledgments The authors thank to Matej Polačik, David Strayer and an anonymous reviewer for their helpful comments on the manuscript. The research was funded by grants awarded by the Ministry of Environment of the Czech Republic (MZP 0002071101), Czech University of Life Sciences Prague (CIGA 42110/1313/3104), and the Grant Agency of the Czech Academy of Sciences (KJB600930802). KD and MR conceived the study, analysed the data and drafted the manuscript; KD designed and performed the experimental work; OS analyzed host availability and MV analysed histological data.

References

Bakke TA, Harris PD, Cable J (2002) Host specificity dynamics: observations on gyrodactylid monogeneans. Int J Parasitol 32:281–308

Barnhart MC, Haag WR, Roston WN (2008) Adaptations to host infection and larval parasitism in Unionoida. J N Am Benthol Soc 27:370–394

Bauer G (2001) Framework and driving forces for the evolution of naiad life histories. In: Bauer G, Wachtler K (eds) Ecology and evolution of the freshwater mussels Unionoida. Springer, Berlin, pp 233–255

Bauer G, Hochwald S, Silkenat W (1991) Spatial distribution of freshwater mussels: the role of host fish and metabolic rate. Freshw Biol 26:377–386

Bean MG, Bonner TH (2010) Spatial and temporal distribution of the Asian fish tapeworm *Bothriocephalus acheilognathi* (Cestoda: Bothriocephalidea) in the Rio Grande (Rio Bravo del Norte). J Aquat Anim Health 22:182–189

Benson AJ (2011) *Sinanodonta woodiana*. USGS nonindigenous aquatic species database. http://nas.er.usgs.gov/queries/FactSheetaspx?speciesID=2824. Accessed 18 Jan 2011

Beran L (1997) First record of *Sinanodonta woodiana* (Mollusca: Bivalvia) in the Czech Republic. Acta Soc Zool Bohem 61:1–2

Beran L (2008) Expansion of *Sinanodonta woodiana* (Lea, 1834) (Bivalvia: Unionidae) in the Czech Republic. Aquat Invasions 3:91–94

Blazek R, Gelnar M (2006) Temporal and spatial distribution of glochidial larval stages of European unionid mussels (Mollusca: Unionidae) on host fishes. Folia Parasit 53: 98–106

Bogan AE (1993) Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. Am Zool 33:599–609

Brouder MJ, Hoffnagle TL (1997) Distribution and prevalence of the Asian fish tapeworm, *Bothriocephalus acheilognathi*, in the Colorado River and tributaries, Grand Canyon, Arizona, including two new host records. J Helminth Soc Wash 64:219–226

Cappelletti C, Cianfanelli S, Beltrami ME, Ciutti F (2009) *Sinanodonta woodiana* (Lea, 1834) (Bivalvia: Unionidae): a new non-indigenous species in Lake Garda (Italy). Aquat Invasions 4:685–688

Cianfanelli S, Lori E, Bodon M (2007) Non-indigenous freshwater molluscs and their distribution in Italy. In: Gherardi F (ed) Biological invaders in inland waters: profiles, distribution and threats. Springer, Dordrecht, pp 103–121

Corsi I, Pastore AM, Lodde A, Palmerini E, Castagnolo L, Focardi S (2007) Potential role of cholinesterases in the invasive capacity of the freshwater bivalve, *Anodonta woodiana* (Bivalvia: Unionacea): a comparative study with the indigenous species of the genus, *Anodonta* sp. Comp Biochem Phys C 145:413–419

Darrigran G (2002) Potential impact of filter-feeding invaders on temperate inland freshwater environments. Biol Invasions 4:145–156

Djajasasmita M (1982) The occurrence of *Anodonta woodiana* Lea, 1837 in Indonesia (Pelecypoda, Unionidae). Veliger 25:175

Douda K (2010) Effects of nitrate nitrogen pollution on Central European unionid bivalves revealed by distributional data and acute toxicity testing. Aquat Conserv 20:189–197

Dudgeon D, Morton B (1983) The population dynamics and sexual strategy of *Anodonta woodiana* (Bivalvia, Unionacea) in Plover Cove Reservoir, Hong-Kong. J Zool 201:161–183

Dudgeon D, Morton B (1984) Site selection and attachment duration of *Anodonta woodiana* (Bivalvia, Unionacea) glochidia on fish hosts. J Zool 204:355–362

Froufe E, Magyary I, Lehoczky I, Weiss S (2002) mtDNA sequence data supports an Asian ancestry and single introduction of the common carp into the Danube Basin. J Fish Biol 61:301–304

Fukuhara S, Nagata Y, Yamada T (1986) Glochidium parasitic period, host-fish and parasitic site of *Anodonta woodiana* in small pond. Venus 45:43–52

Galbraith HS, Vaughn CC (2009) Temperature and food interact to influence gamete development in freshwater mussels. Hydrobiologia 636:35–47

Graf DL (2007) Palearctic freshwater mussel (Mollusca: Bivalvia: Unionoida) diversity and the comparatory method as a species concept. P Acad Nat Sci Phila 156: 71–88

Haag WR, Berg DJ, Garton DW, Farris JL (1993) Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Can J Fish Aquat Sci 50:13–19

Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol Monogr 80: 179–196

Holt RD, Dobson AP, Begon M, Bowers RG, Schauber EM (2003) Parasite establishment in host communities. Ecol Lett 6:837–842

Hruška J (1992) The freshwater pearl mussel in south Bohemia: evaluation of the effect of temperature on reproduction, growth and age structure of the population. Arch Hydrobiol 126:181–197

Jansen W, Bauer G, Zahner-Meike E (2001) Glochidial mortality in freshwater mussels. In: Bauer G, Wachtler K (eds) Ecology and evolution of the freshwater mussels Unionoida. Springer, Berlin, pp 185–211

Johnson LE, Padilla DK (2010) Geographic spread of exotic species: ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. Biol Conserv 78:23–33

Jurajda P, Slavik O, White S, Adamek Z (2010) Young-of-the-year fish assemblages as an alternative to adult fish monitoring for ecological quality evaluation of running waters. Hydrobiologia 644:89–101

Karatayev AY, Burlakova LE, Padilla DK (1997) The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. J Shellfish Res 16: 187–203

Karatayev AY, Boltovskoy D, Padilla DK, Burlakova LE (2007a) The invasive bivalves *Dreissena polymorpha* and *Limnoperna fortunei*: parallels, contrasts, potential spread and invasion impacts. J Shellfish Res 26:205–213

Karatayev AY, Padilla DK, Minchin D, Boltovskoy D, Burlakova LE (2007b) Changes in global economies and trade: the potential spread of exotic freshwater bivalves. Biol Invasions 9:161–180

Keller RP, Drake JM, Lodge DM (2007) Fecundity as a basis for risk assessment of nonindigenous freshwater Molluscs. Conserv Biol 21:191–200

Kiss A (1995) The propagation, growth and biomass of the Chinese huge mussel (*Anodonta woodiana woodiana* Lea, 1834) in Hungary. Dissertation, University of Agricultural Sciences of Gödöllo

Kohlmann K, Gross R, Murakaeva A, Kersten P (2003) Genetic variability and structure of common carp (*Cyprinus carpio*) populations throughout the distribution range inferred from allozyme, microsatellite and mitochondrial DNA markers. Aquat Living Resour 16: 421–431

Konečná M, Reichard M (2011) Seasonal dynamics in population characteristics of European bitterling *Rhodeus amarus* in a small lowland river. J Fish Biol 78:227–239

Kraszewski A (2007) The continuing expansion of *Sinanodonta woodiana* (Lea, 1834) (Bivalvia: Unionidae) in Poland and Europe. Folia Malac 15:65–69

Kraszewski A, Zdanowski B (2007) *Sinanodonta woodiana* (Lea, 1834) (Mollusca)—a new mussel species in Poland: occurrence and habitat preferences in a heated lake system. Pol J Ecol 55:337–356

Lee KA, Klasing KC (2004) A role for immunology in invasion biology. Trends Ecol Evol 19:523–529

Leung B, Drake JM, Lodge DM (2004) Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85:1651–1660

Lucas MC, Baras E (2001) Migration of freshwater fishes. Blackwell Science, Malden

Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of nonmarine mollusks. Bioscience 54:321–330

Mackie GL (1984) Bivalves. In: Tompa AS, Verdonk NH, van den Biggelaar JAM (eds) The Mollusca vol. 7: reproduction. Academic Press, London, pp 351–418

McNichols KA, Mackie GL, Ackerman JD (2011) Host fish quality may explain the status of endangered *Epioblasma torulosa rangiana* and *Lampsilis fasciola* (Bivalvia: Unionidae) in Canada. J N Am Benthol Soc 30:60–70

Paunovic M, Csányi B, Simic V, Stojanovic BCP (2006) Distribution of *Anodonta* (*Sinanodonta*) *woodiana* (Rea, 1834) in inland waters of Serbia. Aquat Invasions 1:154–160

Popa OP, Kelemen BS, Murariu D, Popa LO (2007) New records of *Sinanodonta woodiana* (Lea, 1834) (Mollusca: Bivalvia: Unionidae) from Eastern Romania. Aquat Invasions 2:265–267

Poulin R (1992) Determinants of host-specificity in parasites of freshwater fishes. Int J Parasitol 22:753–758

Pou-Rovira Q, Araujo R, Boix D, Clavero M, Feo C, Ordeix M, Zamora L (2009) Presence of the alien chinese pond mussel *Anodonta woodiana* (Lea, 1834) (Bivalvia, Unionidae) in the Iberian Peninsula. Graellsia 65:67–70

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reichard M, Ondrackova M, Przybylski M, Liu H, Smith C (2006) The costs and benefits in an unusual symbiosis: experimental evidence that bitterling fish (*Rhodeus sericeus*) are parasites of unionid mussels in Europe. J Evol Biol 19:788–796

Reichard M, Przybylski M, Kaniewska P, Liu H, Smith C (2007) A possible evolutionary lag in the relationship between freshwater mussels and European bitterling. J Fish Biol 70:709–725

Reichard M, Polacik M, Tarkan AS, Spence R, Gaygusuz O, Ercan E, Ondrackova M, Smith C (2010) The bitterling-mussel coevolutionary relationship in areas of recent and ancient sympatry. Evolution 64:3047–3056

Rogers CL, Dimock RV (2003) Acquired resistance of bluegill sunfish *Lepomis macrochirus* to glochidia larvae of the freshwater mussel *Utterbackia imbecillis* (Bivalvia: Unionidae) after multiple infections. J Parasitol 89:51–56

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Sárkány-Kiss A, Sirbu I, Hulea O (2000) Expansion of the adventive species Anodonta woodiana (Lea, 1834) (Mollusca, Bivalvia, Unionoidea) in central and eastern Europe. Acta Oecol Univ Sibiu 7:49–57

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Sousa R, Antunes C, Guilhermino L (2008a) Ecology of the invasive Asian clam *Corbicula fluminea* (Muller, 1774) in aquatic ecosystems: an overview. Ann Limnol-Int J Lim 44:85–94

Sousa R, Nogueira AJA, Gaspar M, Antunes C, Guilhermino L (2008b) Growth and extremely high production of the non-indigenous invasive species *Corbicula fluminea* (Müller, 1774): possible implications for ecosystem functioning. Estuar Coast Shelf S 80:289–295

Sousa R, Gutierrez JL, Aldridge DC (2009) Non-indigenous invasive bivalves as ecosystem engineers. Biol Invasions 11:2367–2385

Stoeckel JA, Schneider DW, Soeken LA, Blodgett KD, Sparks RE (1997) Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large-river system. J N Am Benthol Soc 16: 586–601

Strayer DL (1999) Effects of alien species on freshwater mollusks in North America. J N Am Benthol Soc 18: 74–98

Strayer DL (2008) Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press, Berkley

Strayer DL (2009) Twenty years of zebra mussels: lessons from the mollusk that made headlines. Front Ecol Environ 7:135–141

Taraschewski H (2006) Hosts and parasites as aliens. J Helminthol 80:99–128

Trdan RJ, Hoeh WR (1982) Eurytopic host use by two congeneric species of freshwater mussel (Pelecypoda, Unionidae, Anodonta). Am Midl Nat 108:381–388

Treasurer JW, Hastie LC, Hunter D, Duncan F, Treasurer CM (2006) Effects of (*Margaritifera margaritifera*) glochidial infection on performance of tank-reared Atlantic salmon (*Salmo salar*). Aquaculture 256:74–79

Vaughn CC, Hakenkamp CC (2001) The functional role of burrowing bivalves in freshwater ecosystems. Freshw Biol 46:1431–1446

Vaughn CC, Taylor CM (1999) Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conserv Biol 13:912–920

Vaughn CC, Taylor CM (2000) Macroecology of a host-parasite relationship. Ecography 23:11–20

von Proschwitz T (2008) The Chinese giant mussel *Sinanodonta woodiana* (Lea, 1834) (Bivalvia, Unionidae): an unwelcome addition to the Swedish fauna. Basteria 72:307–311

Wachtler K, Dreher-Mansur MC, Richter T (2001) Larval types and early postlarval biology in naiads (Unionoida). In: Bauer G, Wachtler K (eds) Ecology and evolution of the freshwater mussels Unionoida. Springer, Berlin, pp 93–125

Wang N, Augspurger T, Barnhart MC, Bidwell JR, Cope WG, Dwyer FJ, Geis S, Greer IE, Ingersoll CG, Kane CM, May TW, Neves RJ, Newton TJ, Roberts AD, Whites DW (2007) Intra- and interlaboratory variability in acute toxicity tests with glochidia and juveniles of freshwater mussels (Unionidae). Environ Toxicol Chem 26:2029–2035

Ward JM, Ricciardi A (2007) Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Divers Distrib 13:155–165

Watters GT (1992) Unionids, fishes, and the species-area curve. J Biogeogr 19:481–490

Watters GT (1997) A synthesis and review of the expanding range of the Asian freshwater mussel *Anodonta woodiana* (Lea, 1834) (Bivalvia:Unionidae). Veliger 40:152–156

Watters GT, O'Dee SH (2000) Glochidial release as a function of water temperature: beyond bradyticty and tachyticty. Proceedings of the conservation, captive care, and propagation of freshwater mussels symposium. Ohio Biological Survey, Ohio, pp 135–140