Reproduction success of the invasive *Sinanodonta woodiana* (Lea 1834) in relation to native mussel species

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Abstract Invasions of non-native species are major threats for freshwater ecosystems. One of the most invasive freshwater mussels in Europe is the Asian *Sinanodonta woodiana* (Chinese pond mussel). It occurs in the same waterbodies as the endangered native species *Anodonta cygnea* and *Anodonta anatina* with unknown consequences for them. Thus, the analysis about the host–parasite relationship between the larvae of *S. woodiana* and host fish species in Europe is important to assess impacts on the native mussels regarding their competition for hosts. In this study, host suitability of ten different fish species (native and non-native to Europe) for the glochidia of *S. woodiana* was analyzed by simultaneous infestation of the fish. All fish species were identified as suitable hosts but differed significantly in initial infestation rate as well as duration and rate of juvenile mussel excystment. Surprisingly, the glochidia developed successfully on *Rhodeus amarus* (bitterling), which cannot use *S. woodiana* for its own reproduction, and which is an unsuitable host for native anodontines. Compared to both native *Anodonta*, *S. woodiana* glochidia developed more successfully resulting in a higher number of excysted juvenile mussels at similar larval exposure. Metamorphosis was also faster on all tested fish species. These factors, together with the faster growth and higher number of offspring in *S. woodiana* likely contribute to a competitive advantage over native anodontines. The great likelihood of spreading this mussel on a large number of different possible host fish species deserves attention in fisheries management and stocking programs.

Introduction

Invasive species represent one of the most important global threats to biodiversity (Carlton and Geller 1993; Sousa et al. 2014), with freshwater ecosystems being particularly strongly affected (Geist 2011; Strayer 2006). The introduction of non-native aquatic biota is mostly related to human activities like trade or aquaculture (Cohen and Carlton 1998; Sousa et al. 2014). *Corbicula fluminea* (Müller 1774) or *Dreissena polymorpha* (Pallas 1771) provide examples of widely distributed and extremely successful aquatic invaders (Sousa et al. 2014). For instance, the invasion of

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Dreissena polymorpha, originally native to the Ponto-Caspian region (Strayer et al. 2011), changed the physical, chemical and biological characteristics of many lakes and rivers in North America (Strayer et al. 1999; Strayer 2006), resulting in the extirpation of many populations of native unionid mussels (Ricciardi et al. 1998; Strayer 1999). Invasive freshwater mussels can harm native ones by competition for food and space or by attaching to their shells which hampers their filter feeding (Ferreira-Rodríguez et al. 2018, 2019). The high dispersal ability of the most invasive bivalve species depends not only on their short generation times, rapid growth and early sexual maturity (Sousa et al. 2008), but also on their reproduction strategy itself. They typically have simple life cycles and often produce free-living larvae (Douda et al. 2012; Karatayev et al. 2007; Stoeckel et al. 1997). However, there are also invasive freshwater mussels with a more complex life cycle including an obligatory parasitic stage like *Sinanodonta woodiana* (Lea 1834) in which the factors governing invasion success are less well understood.

S. woodiana is native to tropical eastern Asia, primarily the Amur and Yangtze basins (Cummings 2011; Kraszewski and Zdanowski 2007; Soroka 2005). It has been introduced around the world, for example to the USA, Costa Rica and many Asian and European countries (Bogan et al. 2011; Cummings 2011; Konečný et al. 2018). Microsatellite data indicated a single colonization event and an early establishment of two invasive centers serving as sources for further expansion across Europe (Konečný et al. 2018). A commercial import of Asian carps like silver carp, *Hypophthalmichthys molitrix* (Valenciennes 1844) and grass carp, *Ctenopharyngodon idella* (Valenciennes 1844) from the River Yangtze basin to hatcheries in Romania in the early 1960s was the most likely source of further *S. woodiana* expansion in Europe (Kondakov et al. 2018; Konečný et al. 2018). These fish species were introduced outside their native ranges for food, control of aquatic vegetation or hatchery water quality maintenance (Watters 1997). *S. woodiana* normally prefers relatively warm and either stagnant or slow flowing waters (Soroka 2005; Zettler and Jueg 2006). In Germany, many self-recruiting populations of *S. woodiana* nowadays exist in all parts of the country and in different kinds of waterbodies (Bahr and Wiese 2018; Duempelmann 2012; Pfeifer 2002; Reichling 1999). The increased spreading of *S. woodiana* in Germany in the last decades is especially due to the selling of this non-native species in pet shops and garden centers, where it is often erroneously labelled as native *Anodonta* species (Bahr and Wiese 2018; Schoolmann et al. 2006). The most important factor for the fast spreading of *S. woodiana* is believed to be its ability to use novel host fish species, native to the invading region (Douda et al. 2012). However, relatively little is known about invasive freshwater mussels with host–parasite interactions like *S. woodiana* and their invasion and threat for native species (Sousa et al. 2014). This holds especially true for invasive freshwater mussels with a life cycle which is similar to native Unionida with possible host competition (Donrovich et al. 2017).

Thus, the major aim of this study was to analyze the host–parasite relationship between the glochidial larvae of a self-recruiting German population of *S. woodiana* and ten different host fish species (native and invasive to Germany) in a controlled infestation experiment. The findings were then compared with the results of two other infestation experiments with the larvae of the native *Anodonta anatina* (Huber and Geist 2019) and *Anodonta cygnea* (Huber and Geist 2017) to assess possible impacts of the invasive freshwater mussel on the native ones regarding their competition for hosts. In detail, the following hypotheses were tested: (1) Invasion success of the non-native freshwater mussel species *S. woodiana* in Europe is independent from its original hosts within its native range and instead depends on its capability to use co-invasive non-native fish species as well as indigenous ones as hosts for its glochidia larvae (Douda et al. 2012; Dudgeon and Morton 1984; Watters 1997). Therefore, glochidia of *S. woodiana* attach to and metamorphose on all tested fish species successfully. (2) Although the larvae of *S. woodiana* are host fish generalists, metamorphosis success and success of juvenile mussel excystment are higher on the both co-invasive fish species *Ctenopharyngodon idella* (confirmed host in the native range of *S. woodiana*, Beran 2008; Watters 1997) and *Pseudorasbora parva* (common Asian origin, Britton et al. 2010) than on the native European fish species tested. (3) All three mussel species are host fish generalists and compete for hosts. The invasive *S. woodiana* and the two native *Anodonta* species *Anodonta anatina* and *Anodonta cygnea* have the same habitat preferences and often co-occur in the same water bodies (Beran 2008;

Bössneck and Klingelhöfer 2011; Wojton et al. 2012). Because *S. woodiana* is a broad generalist in host use (Douda et al. 2012), has a high competitive potential and produces a higher number of glochidia than native anodontines (Wächtler et al. 2001), *S. woodiana* shows a higher initial infestation of the tested fish species and a higher juvenile mussel excystment compared to *A. anatina* and *A. cygnea*.

Materials and methods

The host use experiment started on the 24th of May 2016 with the simultaneous infestation of 481 fish of ten different fish species with the glochidia larvae of the freshwater mussel *S. woodiana* following the experimental standards given in Taeubert et al. (2012a). The infestation procedure as well as the whole implementation of the experiment followed the descriptions of Huber and Geist (2017, 2019) to ensure comparability of the results between the two native species *A. cygnea* and *A. anatina* with the invasive *S. woodiana*. All three experiments were performed separately at different times but at the same place, with the same methodology and the same ten fish species.

Adult *S. woodiana* were sampled on the 18th of May 2016 from the wildlife reserve Öberauer Donauschleife (backwater of the Danube near Straubing, Bavaria, Germany), one of the self-recruiting populations in Germany. The sampling of ten adult mussels of the local population was approved by license of the responsible nature conservation authority (license number: 55.1-8642.10 U 12). The mussels were transferred to the laboratory of the Aquatic Systems Biology Unit at Technical University of Munich and the species was genetically confirmed according to the molecular identification key by Zieritz et al. (2012). Mature glochidia were flushed out of the marsupia of five adult mussels with a squirt bottle on the 23rd of May 2016 and stored at 4.0 °C overnight. In total, approximately 500,000 glochidia larvae with a viability of more than 95% were used for the infestation. Larval viability was checked by observing an active valve clamping mechanism after the addition of a NaCl stimulus.

The fish species were chosen according to their co-occurrence with the freshwater mussels *A. cygnea*, *A. anatina* and *S. woodiana* in central Europe. The three

mussel species inhabit especially lakes and slow flowing streams, but populations of *A. anatina* also occur in fast flowing streams with colder temperature regimes (Lopes-Lima et al. 2017; Niemeyer 1993; Soroka 2005). Therefore, limnophilic fish species as well as rheophilic ones with different habitat requirements representing four different fish families were used for the experiment: Salmonidae, *Salmo trutta* (Linnaeus 1758); Cyprinidae, *Leuciscus idus* (Linnaeus 1758), *Gobio gobio* (Linnaeus 1758), *Rhodeus amarus* (Bloch 1782), *Rutilus rutilus* (Linnaeus 1758), *Leucaspius delineatus* (Heckel 1843); Percidae, *Perca fluviatilis* (Linnaeus 1758); and Gasterosteidae, *Gasterosteus aculeatus* (Linnaeus 1758). Due to the origin of *S. woodiana*, two non-native Asian fish species, both cyprinids, which also spread throughout Europe, were included: *C. idella* and *Pseudorasbora parva* (Temminck and Schlegel 1846). Date and place of origin of the different fish species and the number of individuals per species used for the experiment are listed in Table 1. Juvenile fish only were used for the experiment. All fish had no previous contact with unionid mussels to exclude possible pre-immunisation.

All 481 individual fish were infested for 30–45 min in one common infestation bath with a glochidial concentration of around 8500–9000 larvae per liter (glochidia of the five adult mussels were pooled for the infestation). The infestation bath was filled with water (bank filtrate, river Moosach) with a temperature of 12 °C. After the infestation, fish were separated in three replicates per species. Each replicate was then kept in one special funnel-shaped holding unit with a maximum volume of 45 L until the end of the experiment. The number of specimens per replicate and holding unit was adjusted according to the respective weights and sizes of the fish as well as on the different requirements of the fish species to ensure optimal holding conditions during the experiment (Huber and Geist 2017, 2019). For example, from smaller fish species like *L. delineatus* more individuals per holding unit were included than from the bigger ones like *S. trutta*. Due to their high oxygen need, tanks containing *S. trutta* were set up with constant water flow. This water flow also resulted in slightly lower temperatures in holding units with *S. trutta* during the experiment (average water temperature: 12.5 ± 0.4 °C). The average water temperature in all other tanks was 15.8 ± 0.3 °C. Temperatures were

Table 1 Tested fish species (order from fish species with the highest number of excysted juvenile mussels after weight-normalization to species with the lowest number of excysted juveniles after weight-normalization), their status, place and date of origin: RO = Aquaculture M. Rösch, Bärnau, 04.11.2014 (*G. aculeatus*, *L. idus*, *G. gobio*, *R. rutilus*, *P. fluviatilis*) and 12.04.2016 (*R. amarus*), AS = Aquatic Systems Biology Unit, 27.11.2012, LU = Bavarian State Office for Environment, Wielenbach, 12.11.2014, RH = Aquaculture near Rheine, 20.05.2016, PR = Private fish pond, Roth, 17.04.2016; mean size (total length) and weight of applied fish, number of fish in the infestation bath per species, number of control fish per species; average number of excysted juvenile mussels per gram fish weight and species; $\bar{X}$ = arithmetic mean

Fish species	Status	Source	Size $\bar{X} \pm 1$ mm	Weight $\bar{X} \pm 0.1$ g	Nb. of fish infestation bath	Nb. of control fish	Mussels per g fish weight
C. idella (grass carp)	Introduced	LU	90	8.3	32	11	26.2
G. aculeatus (stickleback)	Native	RO	76	4.1	48	16	18.2
L. idus (ide)	Native	RO	112	9.6	22	7	15.6
G. gobio (gudgeon)	Native	RO	121	13.2	21	7	14.7
S. trutta (brown trout)	Native	AS	191	58.2	6	2	8.0
L. delineatus (moderlieschen/sunbleak)	Native	RH	44	0.7	177	59	6.2
R. rutilus (roach)	Native	RO	96	6.8	28	9	2.9
P. fluviatilis (perch)	Native	RO	121	16.4	18	6	2.4
P. parva (topmouth gudgeon)	Introduced	PR	58	2.0	78	26	1.0
R. amarus (bitterling)	Native	RO	64	2.9	51	17	0.3

measured with temperature loggers (Lascar Electronics Limited, Salisbury, UK) every 30 min. Additional to the three replicates of infested fish per species, one separate group of non-infested control fish per species (not-exposed to glochidia) was included (Table 1). This group was treated in the same way as the infested ones to analyze if influences like handling or holding conditions are responsible for the mortality of the fish during the experiment (Huber and Geist 2019).

To calculate the infestation success, glochidia attachment rate on gills, fins and skins of the fish had to be determined for every fish species at different time points. Therefore, some individuals per fish species were sacrificed after 2 days (2 days post infestation, pi), 12 days and at the end of the excystment of juvenile mussels. The number of specimens per fish species sacrificed to calculate the glochidial attachment rate depended on the amount of living fish per species and holding unit at each of the three time points. In total, 20 infested specimens (one specimen of *S. trutta*, *P. fluviatilis*, *L. idus* and *G. gobio*, two specimens of *C. idella*, *R. rutilus* and *G. aculeatus*, three specimens of *R. amarus* and *P. parva*, four specimens of *L. delineatus*) were analyzed 2 days pi and glochidial attachment rate per fish species was calculated. Again, on the 5th of June 2016 (12 days pi, time point of the first detected juvenile mussels), in total 15 infested fish were sacrificed. This additional time point was used as backup only, in case no fish would have survived until the end of the experiment (Huber and Geist 2017, 2019). At the end of the excystment of juvenile mussels, a number of 24 infested individuals (one specimen of *S. trutta*, two specimens of *P. fluviatilis*, *R. rutilus*, *G. aculeatus* and *G. gobio*, and three specimens of *L. idus*, *C. idella*, *R. amarus*, *L. delineatus* and *P. parva*) was analyzed. The number of sacrificed fish per species at each sampling point depended on the number of fish applied in the experiment and the number of fish that were still alive at the respective time point.

The success of metamorphosis was determined by detecting the number of completely developed, living juvenile mussels per fish species. Five liters of water of every holding unit containing infested fish were checked for the presence of excysted juveniles during daily water change (12.5% daily renewal of water) (Huber and Geist 2017, 2019). The first excysted mussels dropped off after 12 days simultaneously from *P. fluviatilis*, *L. idus*, *C. idella*, *R. rutilus*, *L. delineatus* and *G. gobio*. All dropped-off juvenile *S.*

woodiana were then transferred to special holding systems. The last excysted juvenile mussel was counted in the holding unit of *S. trutta*. The whole experiment was terminated on the 27th of July 2016 (64 days pi), 3 days after the last mussel had dropped off.

To account for differences in weight between different fish species and single specimens and to ensure comparability, number of attached glochidia as well as number of excysted juveniles were calculated per gram fish weight. To compare the duration of the metamorphosis phase and the duration of the juvenile mussel excystment on different fish species and at different temperatures, the concept of degree-days (dd, sum of daily water temperatures) was applied (Hruska 1992; Taeubert et al. 2014). Statistical analyses were performed in R version 3.4.3 (R Core Team 2017). To calculate differences between all tested fish species regarding their initial weight-normalized glochidial infestation 2 days pi as well as their rate of weight-normalized juvenile mussel excystment, non-parametric Kruskal–Wallis sum of rank tests and post hoc pairwise Wilcoxon rank sum tests were used since ANOVA assumptions were not fulfilled. Bonferroni correction was applied to correct for multiple testings. Differences between the two groups of good and poor hosts as well as the two groups of native and invasive fish species regarding the initial infestation rate, rate of juvenile mussel excystment and duration of juvenile excystment respectively were also tested with pairwise Wilcoxon rank sum tests including Bonferroni correction. Non-parametric Kruskal–Wallis sum of rank tests were used to identify differences in the duration of juvenile mussel excystment and the duration of the metamorphosis phase between single fish species. Statistical analysis of differences between the three mussel species (*S. woodiana*, *A. anatina* and *A. cygnea*) were performed using Kruskal–Wallis sum of rank tests and post hoc pairwise Wilcoxon rank sum tests with Bonferroni correction. Here, differences in initial infestation, rate of juvenile mussel excystment, duration of excystment and fish mortality rate of all tested fish per mussel species were calculated. Spearman's rank correlation was used to explore the link between the total weight of applied fish (infestation bath) and the initial infestation rate (glochidia per gram fish weight) 2 days pi as well as the correlation between the mortality rate of the fish during juvenile mussel

excystment and the number of juvenile mussels per gram fish weight.

Results

In total, 15,495 living juvenile *Sinanodonta woodiana* were detected following the parasitic phase. Number of attached glochidia and dropped-off juvenile mussels strongly varied between the single host fish species. Similarly, duration of juvenile mussel excystment also differed between the host fishes.

Success of infestation and juvenile mussel excystment

The highest initial infestation rate 2 days pi was measured on *G. aculeatus*, native to Europe, with an average number of 70.5 glochidia of *S. woodiana* per gram fish weight (Table 2). *Rhodeus amarus* had the lowest infestation after 2 days with only 4.8 glochidia g^{-1} (Table 2). There was a statistically significant difference between all fish species in terms of initial infestation per gram fish weight (non-parametric Kruskal–Wallis sum of rank test, $p < 0.01$). The number of excysted juvenile mussels per gram fish weight also differed significantly between all fish species (non-parametric Kruskal–Wallis sum of rank test, $p < 0.001$). In particular, the highest number of juvenile *S. woodiana* per gram fish weight was found on *C. idella*, which is also of Asian origin, with an average of 26.2 juveniles g^{-1} (Table 2). In line with the low initial infestation, the lowest number of juvenile mussels excysted on *R. amarus* (only 0.3 juvenile mussels per gram fish weight, Table 2). Regarding the weight-normalized glochidial loss during the metamorphosis phase, in total 74% of initial attached glochidia were lost until the start of excystment on all fish species. *Perca fluviatilis* and *R. amarus* showed the highest larval loss of 94%. In contrast, *C. idella* only lost 34% of its initially attached glochidia during the metamorphosis (Table 2).

Although all tested fish species were found to be possible hosts for the larvae of *S. woodiana*, they could be divided in two groups: good and poor hosts. Four fish species *C. idella*, *G. aculeatus*, *L. idus* and *G. gobio* formed the group of good hosts due to their high number of excysted juveniles (more than 14 mussels

Table 2 Results of the host fish infestation with larvae of *S. woodiana*: fish species, their determined host status, mean number of glochidia per gram fish weight 2 days post infestation (pi) as well as excystment rate of juvenile mussels per gram fish weight and fish species and percentage of weight-normalized glochidial loss between initial infestation and excystment, start and end of excystment per species in degree-days (dd), average water temperature, host fish mortality (fish that died naturally) during the time span of mussel excystment (mortality is given in percentage and total number of dead fish in brackets); species order: from fish species with the highest number of excysted mussels after weight-normalization to fish species with the lowest number of excysted mussels; * = introduced, non-native fish species; $\bar{X}$ = arithmetic mean

Fish species	Host status	2 days pi	Excystment				
		Glochidia per g fish weight	Mussels per g fish weight	Weight-normalized gloch. loss (%)	Start–end of excystment (dd)	Temperature $\bar{X} \pm SD$ (°C)	Fish mortality (% and total values)
C. idella*	Good	39.8	26.2	34	195–814	16.3 ± 1.1	47 (15)
G. aculeatus	Good	70.5	18.2	74	211–812	16.2 ± 1.1	46 (22)
L. idus	Good	35.1	15.6	56	192–814	16.0 ± 0.9	14 (3)
G. gobio	Good	27.0	14.7	45	193–708	16.1 ± 0.9	14 (3)
S. trutta	Poor	35.5	8.0	77	188–790	12.5 ± 0.4	0 (0)
L. delineatus	Poor	36.7	6.2	83	184–415	15.4 ± 0.6	50 (89)
R. rutilus	Poor	34.9	2.9	92	188–392	15.7 ± 0.7	0 (0)
P. fluviatilis	Poor	43.4	2.4	94	187–406	15.6 ± 0.7	0 (0)
P. parva*	Poor	13.6	1.0	93	201–417	15.4 ± 0.6	9 (7)
R. amarus	Poor	4.8	0.3	94	206–396	15.8 ± 0.7	4 (2)

per gram fish weight). The other six fish species (*S. trutta*, *L. delineatus*, *R. rutilus*, *P. fluviatilis*, *P. parva* and *R. amarus*) formed the group of poor hosts with numbers of excysted juveniles between 8.0 and 0.3 mussels g^{-1} (Table 2). This classification was not evident 2 days pi because some species with a very high initial glochidial infestation also had a high glochidial loss during the metamorphosis phase. For example, *P. fluviatilis* was the second highest infested fish 2 days pi with 43.4 larvae per gram fish weight. In the end, only an average number of 2.4 juvenile mussels per gram fish weight fully developed on this species. There was a statistically significant difference between the group of good hosts and the group of poor hosts in regard to the initial infestation 2 days pi (pairwise Wilcoxon rank sum test with Boferroni correction, $p < 0.05$) and also in regard to the juvenile mussel excystment (pairwise Wilcoxon rank sum test with Boferroni correction, $p < 0.001$). The group of good hosts had higher rates of initial infestation as well as a higher juvenile mussel excystment (good hosts: average glochidial infestation 43.1 larvae g^{-1}, average number of excysted mussels 18.7 juveniles g^{-1}; poor hosts: average glochidial infestation 28.2 larvae g^{-1}, average number of excysted mussels 3.5 juveniles g^{-1}).

Duration of metamorphosis and juvenile mussel excystment

The difference between the two groups of host fish species was also evident from the differences in duration of juvenile mussel excystment which was significantly longer in the group of good hosts than in the other six species (pairwise Wilcoxon rank sum test with Boferroni correction, $p < 0.001$). The average duration of juvenile mussel excystment on the four best hosts was 589 degree-days (dd), the average duration of excystment on the poor host species was 277 dd only. Regarding single fish species, all hosts also differed significantly among each other regarding the duration of juvenile mussel excystment (non-parametric Kruskal–Wallis sum of rank test, $p < 0.001$). The longest duration of excystment could be detected on *L. idus* and *C. idella* (622 dd and 619 dd), the shortest excystment phase was found on *R.*

amarus and *R. rutilus* (190 dd and 204 dd). Duration of juvenile *S. woodiana* excystment on the best four host fish species and number of excysted juveniles per gram fish weight per species over the time in degree-days as well as the cumulative percentage of excysted juveniles over the time in degree-days on the four best hosts is given in Fig. 1a, b. In contrast, there was no significant difference between the host fish species regarding the duration of metamorphosis (time span from the start of the experiment until the beginning of the juvenile mussel excystment, non-parametric

Kruskal–Wallis sum of rank test, $p > 0.05$) (average of 172 dd until the first juvenile mussel drop-off).

Glochidial development on co-invasive fish species

Whilst *C. idella* was the best host fish for *S. woodiana*, the second non-native fish species *P. parva* was one of the least suitable host fish species with an average of 1.0 juvenile mussels g^{-1} only. The glochidia of *S. woodiana* developed more successful on most tested fish species native to Europe (i.e. from outside the

Fig. 1 Duration of juvenile mussel excystment of *S. woodiana* on the four best host fish species: **a** Number of excysted juvenile mussels per gram fish weight and day over the time in degree-days. **b** Cumulative percentage of excysted juvenile mussels over the time in degree-days
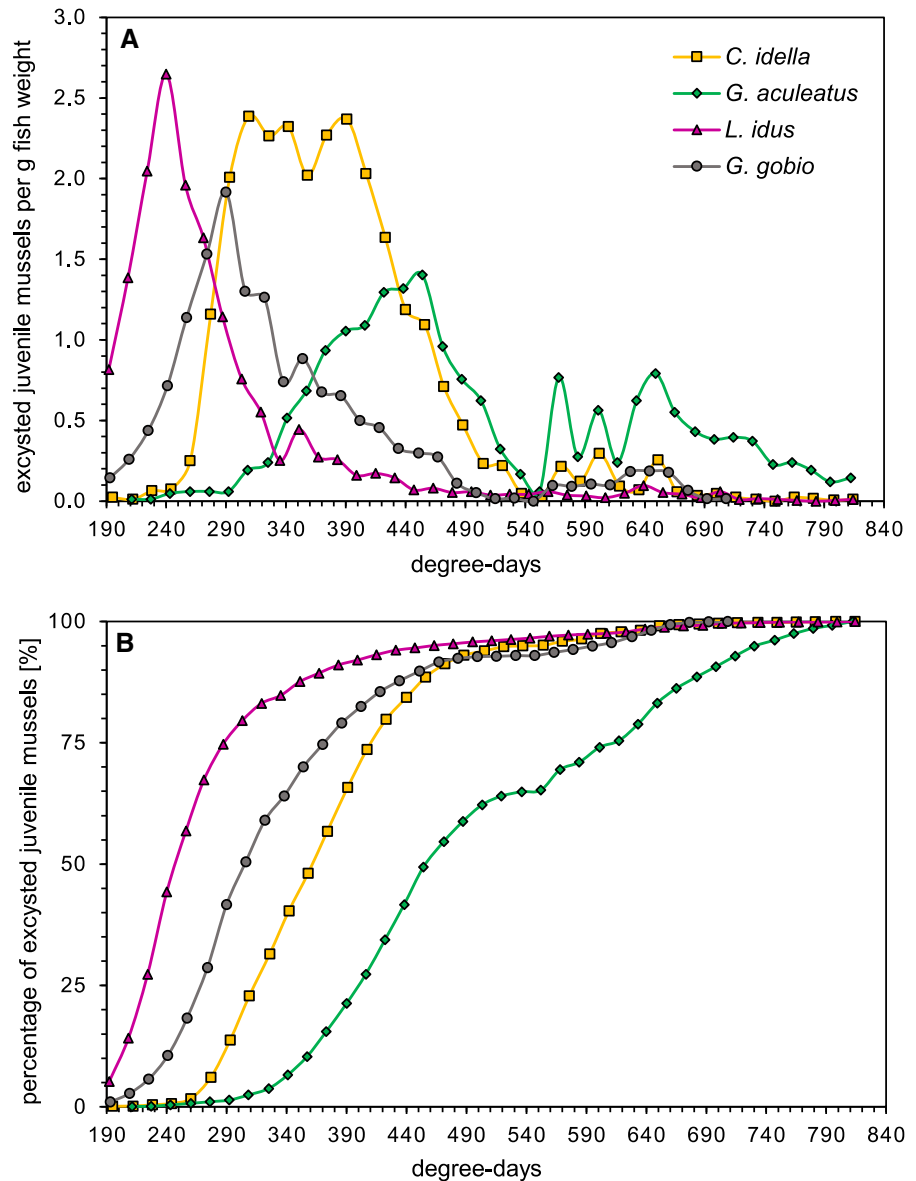
original *S. woodiana* distribution range) than on *P. parva*. There were also no significant differences between native and invasive fish species in regard to initial infestation rate 2 days pi, rate of juvenile mussel excystment and duration of juvenile mussel excystment (pairwise Wilcoxon rank sum test with Boferroni correction, $p > 0.05$ in all cases). Both invasive fish showed a mortality rate of average 28% during juvenile mussel excystment, the native fish species had an average mortality rate of 16%. *Leucaspius delineatus* had the highest mortality rate during juvenile mussel excystment with 50%, followed by *C. idella* (47%). The lowest mortality rates were found in *S. trutta*, *R. rutilus* and *P. fluviatilis* (0% for all three species) (Table 2). In total, the mortality rate calculated for all fish species during juvenile mussel excystment added up to 18%.

Comparison between *S. woodiana* and native *Anodonta* species

The three mussel species differed significantly regarding the initial infestation rate of all fish species (non-parametric Kruskal–Wallis sum of rank test, $p < 0.001$) (Fig. 2a) and the rate of juvenile mussel excystment on all hosts (non-parametric Kruskal–Wallis sum of rank test, $p < 0.001$) (Fig. 2b). *Sinanodonta woodiana* had the highest infestation rates

2 days pi with an average number of 34.1 larvae per gram fish weight calculated for all tested fish species as well as the highest numbers of excysted juvenile mussels per gram fish weight with an average of 9.6 juveniles g^{-1}. Combining the initial infestation rates of both native *Anodonta* species (average values of the initial attachment rate of *A. anatina* and *A. cygnea*), *S. woodiana* showed the highest initial infestation rates on all tested fish species (Fig. 2a). The experiment with *S. woodiana* also revealed significant differences in the duration of juvenile mussel excystment compared to the native *A. anatina* (pairwise Wilcoxon rank sum test with Boferroni correction, $p < 0.001$) and *A. cygnea* (pairwise Wilcoxon rank sum test with Boferroni correction, $p < 0.05$). Regarding the duration of excystment on all tested fish species, *A. cygnea* had in total the shortest duration of juvenile mussel drop-off with an average of 358 dd, followed by *S. woodiana* with an average of 402 dd. The longest duration of juvenile mussel excystment was observed in *A. anatina* (average duration of 600 dd, calculated for all tested fish species). Although all three mussel species differed significantly in initial infestation rate, success of juvenile mussel excystment and duration of excystment, there was no significant difference between the mussel species in regard to the fish mortality rate calculated for all fish species (non-
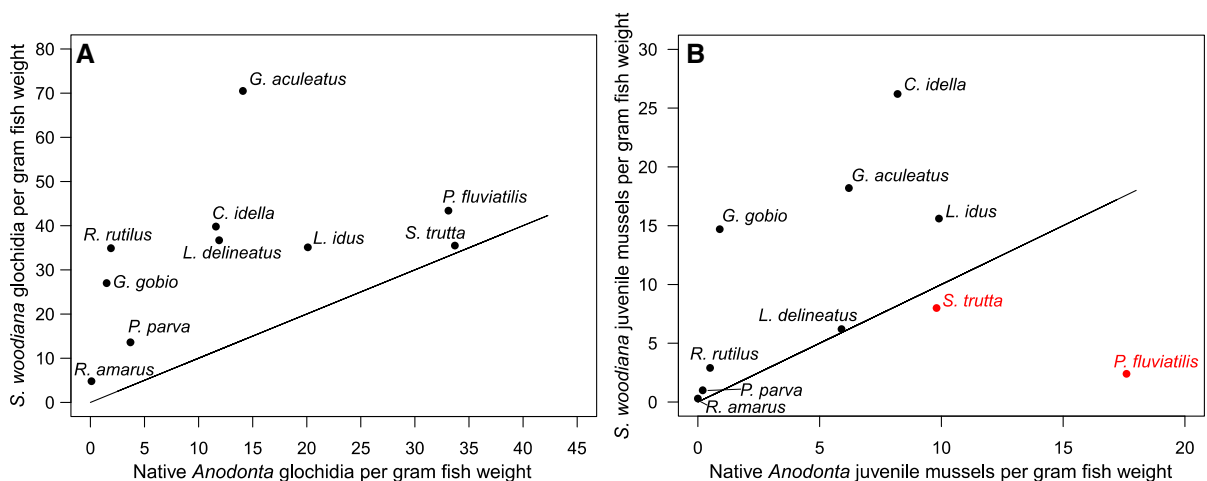

Fig. 2 Comparison of host fish suitability for the mussel species *S. woodiana* with both native *Anodonta* species (*A. anatina* and *A. cygnea*): **a** Average initial infestation of ten different fish species with glochidia of the mussel species (glochidia per gram fish weight); **b** average excystment of juvenile mussels on ten different fish species (juvenile mussels per gram fish weight); points above the line represent fish species with a higher infestation of *S. woodiana* compared to both native *Anodonta*. Marked in red: fish species with a higher rate of native juvenile mussel excystment only

parametric Kruskal–Wallis sum of rank test, $p > 0.05$).

Discussion

Ten different fish species (eight native and two invasive) were simultaneously infested in this study with the larvae from an established German population of the invasive *S. woodiana* (Chinese pond mussel). In line with our hypothesis, all ten different fish species were identified as suitable hosts for the larvae of *S. woodiana* including both native and invasive fishes. Due to the fact that the same experiment was also performed previously with the native *A. anatina* and *A. cygnea* (Huber and Geist 2017, 2019), the results of the infestation success of the three freshwater mussel species allow direct comparisons and conclusions about the impact of the invasive mussel on host competition with native anodontines. Native *Anodonta* populations are already in decline due to diverse reasons and the host competition will increase their decline in light of the ongoing spread of *S. woodiana* in Germany and Europe. The glochidia of *S. woodiana* successfully infested all tested fish species, native and invasive ones, but with marked preferences. This result confirms the findings of Douda et al. (2012) in the Czech Republic, where the larvae of *S. woodiana* also infested invasive as well as native fish. As broad host generalist that has the ability to infest also fish species that do not have evolutionary contact, *S. woodiana* has a high invasion potential as host community structure generally influences the establishment and prevalence of parasites (Holt et al. 2003). Together with the fact that *S. woodiana* can tolerate a variety of different environmental conditions (Douda et al. 2012) and has a higher stress tolerance (Bielen et al. 2016), its fast spreading throughout Europe will likely continue, especially if mussels or infested fish are spread by human activities in fisheries management.

Reproductive success of *S. woodiana*

Whilst the glochidia of *S. woodiana* infested all tested fish species, metamorphosis success as well as success of juvenile mussel excystment and duration of juvenile mussel excystment differed between the hosts, as previously also described for the fish hosts in its

natural Asian range (Dudgeon and Morton 1984). This was also observed for the native *A. anatina* (Huber and Geist 2019) and *A. cygnea* (Huber and Geist 2017) as well as for the native *Unio crassus* (Philipsson 1788) (Taeubert et al. 2012b) and thus seems to be a general characteristic in host use of generalist freshwater mussel species. The different developmental progress of glochidia encysted on different host fish reveals that host suitability itself has substantial influence on glochidial development (Taeubert et al. 2012b). *S. woodiana* is a fast-growing freshwater mussel with a relatively short lifespan (Dudgeon and Morton 1983). Especially, different excystment times on different hosts enhance the possibility for the juvenile mussels to spread continuously by migrating fish and to generate new populations (Huber and Geist 2019; Taeubert et al. 2012b, 2014; Watters and O'Dee 1999).

In total, all tested fish can be separated into a group of good and a group of poor hosts. But in contrast to other host fish generalists (like *A. anatina* or *A. cygnea*), this differentiation of the fish in the two groups of hosts according to their suitability was not already evident after the initial infestation 2 days pi. The glochidia of *S. woodiana* showed high infestation rates on most of the tested fish, but also high larval losses during metamorphosis (for example on *P. fluviatilis*). This is in contrast to results from Douda et al. (2012) where all tested fish species had high rates of transformation and interspecific differences in transformation success among hosts were low. However, Douda et al. (2012) only used a few individuals per species and single specimens were infested separately whereas differences among fish species in juvenile mussel excystment may only be apparent in a simultaneous infestation. The successful invasion of *S. woodiana* into new regions of the world perhaps also depends on this infestation strategy: the glochidia unspecifically attach to all fish, including species from outside the mussels´ original distribution area. Despite of co-infestation of poor hosts with low transformation success of the mussels, chances of colonization of new habitats are increased.

The assumption that the success of larval metamorphosis as well as the success of juvenile mussel excystment of *S. woodiana* would be higher on both co-invasive fish species *C. idella* and *P. parva* was not confirmed. The best host fish species for the glochidia of *S. woodiana* was the co-invasive *C. idella*. This is not surprising, since co-adaptation in mussel-host

relationships has been previously described (Taeubert et al. 2010) and since *C. idella* is also one of the major hosts in the mussels' natural Asian home range (Watters 1997). In contrast, the second non-native fish *P. parva* was one of the worst hosts for *S. woodiana*. *P. parva* often naturally co-occurs in the same Asian regions and basins like *S. woodiana*, for example the River Amur basin (Pinder et al. 2005). Thus, a differentiation in host fish suitability also appears under hosts that naturally co-occur with *S. woodiana* in its native Asian range and even in mussel species using a broad spectrum of hosts. In any case, the further introduction and spreading of *C. idella* and *P. parva* in European water bodies will increase the spreading of *S. woodiana* and should be prevented. Interestingly, larval attachment and juvenile mussel excystment was also detected on the *R. amarus*. It usually parasitizes European freshwater mussels like *A. anatina* or *A. cygnea* for its own larval development (Reichard et al. 2007; van Damme et al. 2007). Reichard et al. (2012) also revealed that *S. woodiana* successfully developed on *R. amarus* whereas the fish was unable to use *S. woodiana* for its own reproduction. Therefore, invasive bivalves may temporarily benefit from a coevolutionary lag by exploiting evolutionary naïve hosts (Sousa et al. 2014). Although *R. amarus* is listed as "Least concern" in Europe (Freyhof 2010), it is recognized as endangered or vulnerable in many European Countries (Kozhara et al. 2007). For example, *R. amarus* is listed as "Vulnerable" in the Austrian Red List (Wolfram and Mikschi 2007) and it is listed as "Endangered" in the German Red List of threatened species (Haupt et al. 2009). Thus, an increasing spreading of *S. woodiana* in Germany could also increase the threat of *R. amarus* if *S. woodiana* reaches extremely high population densities, dislodging native mussels, in waterbodies with *R. amarus* populations, as demonstrated for areas in the Czech Republic (Douda et al. 2012).

Extreme differences in the duration of juvenile *S. woodiana* excystment on different hosts, but no differences in the duration of the metamorphosis were observed. The excystment of juvenile mussels started almost simultaneously on all tested fish, even if the temperatures of the water within the holding units differed from each other. Normally, the developmental time and the growth rates of invertebrates are dependent on water temperatures (Manoj Nair and Appukuttan 2003; Taeubert et al. 2014) and increasing

water temperatures lead to shorter developmental durations and vice versa (until species-specific temperature limits) (Taeubert et al. 2014). Nevertheless, metamorphosis phase of the glochidia of *S. woodiana* on *S. trutta* was shorter than on other fish species maintained at higher average water temperature (comparing the calculations in degree-days) and no prolongation of metamorphosis at lower water temperatures was observed in this species. Instead, duration of excystment was longer in the group of good hosts, irrespective of warmer water temperatures. Thus, the suitability of the host itself seems to be of crucial importance in determining duration of the development and the excystment as for example also true for the excystment of *Margaritifera margaritifera* (Taeubert et al. 2010, 2013). This warrants special caution in fisheries management measures if transferring fish from waters with populations of *S. woodiana* to water bodies where it does not yet occur. The variable time span for reproduction and larval development on the fish requires inspection of fish for larval infestation before translocating them into other water bodies.

Comparison to the reproduction of native *Anodonta*

The most important objective in comparatively analyzing the reproductive success of *S. woodiana* on native and invasive fish species is to get information about possible consequences of the increasing invasion of this Asian mussel for the native freshwater mussel species. Thus, the results of this experiment were compared with the results of two methodologically identical experiments with the native anodontines (*A. cygnea* and *A. anatina*). The comparability of the results of all three experiments could be guaranteed due to the same methodology, for example the same parameters of the infestation bath (temperature and glochidial concentration), the use of the same fish species and the same holding conditions of the fish as well as the same evaluation of the results. Moreover, it was ensured that parameters that differed between the experiments had no influence on the procedure and the results (no correlation between the total fish weight in the infestation bath and glochidial infestation rates 2 days pi (Spearman's rank correlation, p value > 0.05), no correlation between the mortality rate of the fish during juvenile mussel excystment and

the number of juveniles per gram fish weight (Spearman's rank correlation, *p* value > 0.05), colder temperatures within the holding units of the fish did not influence the duration of the metamorphosis phase). Especially different water temperatures in the tanks of the fish could affect the duration of metamorphosis phase and the success of juvenile mussel excystment. Lower temperatures might allow unionids to use some species of hosts that reject infestations at higher temperatures (Roberts and Barnhart 1999) and can also be the reason for an extended duration of metamorphosis and juvenile mussel excystment and the reason for higher survival rates of juvenile mussels due to a longer parasitic phase on the fish (Marwaha et al. 2017). However, duration of the metamorphosis phase was not prolonged at colder temperatures for *S. woodiana*. In general, the different water temperatures may influence the duration of the excystment (as shown for the experiment with *A. anatina*) but cannot be the explanation for the differences in the number of excysted juveniles (Huber and Geist 2019). For example, *S. woodiana* had a higher rate of juvenile mussel excystment on seven out of ten tested fish species only (*C. idella*, *G. aculeatus*, *L. idus*, *G. gobio*, *R. rutilus*, *P. parva* and *R. amarus*) compared to the native anodontines. Moreover, *A. cygnea* had a higher excystment rate on *G. aculeatus* compared to *A. anatina* and *A. anatina* had higher excystment rates on *S. trutta*, *L. delineatus* and *P. fluviatilis* compared to both other mussel species. These differences cannot be explained by differences in water temperatures during the experiments.

Thus, differences in initial infestation and success of juvenile mussel excystment can be driven by differences between the three mussel species. One possible reason for the higher average initial infestation rate of the larvae of *S. woodiana* is the higher attachment capability of the glochidia due to their bigger size (Wächtler et al. 2001). Interestingly, not all fish species had the highest infestation rates with the glochidia of *S. woodiana* ruling out that glochidial attachment capabilities are not the only reason for a higher juvenile mussel excystment. Instead, fish species themselves have a high influence on glochidial development. For example, larval infestation on *S. trutta* was higher with *A. anatina* than with *S. woodiana*. Therefore, *S. trutta*, a fish species which is a very important host for some native freshwater mussels (in fact the exclusive host for *M. margaritifera* in many central European populations) (Geist et al. 2006; Taeubert and Geist 2017), is an unsuitable host for the invasive *S. woodiana*. Due to the unsuitability of *S. trutta* as host and due to the preference of *S. woodiana* for standing and slow flowing waters, we assume that the expansion and competition of *S. woodiana* with native mussels should be low in rivers where *S. trutta* predominates. In the native range of *S. woodiana*, salmonids like *S. trutta* as well as percids like *P. fluviatilis* usually do not co-occur with the mussel. The best host fish in the native Asian range of *S. woodiana* are species from the family of cyprinids (Dudgeon and Morton 1984; Watters 1997). Thus, co-evolutionary mechanisms of host compatibility between mussels and fish species may play a role for *S. woodiana*, as previously described for *U. crassus* (Taeubert et al. 2012b) and *M. margaritifera* (Taeubert et al. 2010). In contrast, one of the best host fish species for the native mussel *A. anatina* was the non-native *C. idella* (Huber and Geist 2019). Suitability of hosts for mussel larvae may therefore not only be determined by co-evolutionary adaptations, but also by the individual fish specimens, their genetic constitution and immune defense.

Invasion of *S. woodiana*: consequences for native mussel species

Regarding the possible consequences for native mussel species due to the increasing invasion of *S. woodiana*, host fish suitability will play a crucial role in the future. It has been shown in this experiment that the glochidia of *S. woodiana* highly infested most of the tested fish species without differentiation between native and non-native fish. Although the success of excystment of *S. woodiana* differed between the tested host fish species, it was on average higher than the excystment success of the native anodontines. Moreover, *S. woodiana* grows faster than the native *Anodonta* and has the ability to produce glochidia two or three times per year (Sarkany-Kiss et al. 2000) in very high numbers (Wächtler et al. 2001). In contrast, native *Anodonta* species produce glochidia only one time per year, between winter and spring (Lopes-Lima et al. 2017; Niemeyer 1993), and in smaller numbers than *S. woodiana* (Wächtler et al. 2001). In addition, our current experiment also suggests that *S. woodiana* uses more host fish species (for example also *R. amarus*, which had no successful

larval development with the glochidia of native anodontines) than the native mussels and has the shortest metamorphosis phase of all three tested mussel species which was also independent from the temperature within the holding units of the fish. Although the experiment with *A. cygnea* also started in May and had the same average water temperatures in the holding units, metamorphosis phase was longer on all tested fish species. Due to a faster metamorphosis and mussel excystment juvenile *S. woodiana* will start their sessile life earlier and have higher chances to survive during the winter months because of better condition. Moreover, Donrovich et al. (2017) found that the transformation success rate of *A. anatina* was significantly reduced on host fish that were infested before with the larvae of *S. woodiana* compared to naïve hosts. Even if the juvenile mussel excystment of *S. woodiana* is lower on some hosts, the high infestation of the fish with its larvae will likely lead to a decreased second infestation with other native mussel larvae that co-occur in the same waterbody.

The increasing number of self-recruiting populations of *S. woodiana* in Europe suggests that their host-larvae relationship is very effective, and their spreading is not limited by missing hosts. For example, the best host fish for *S. woodiana* (the non-native *C. idella*) does not occur in the Öberauer Donauschleife (origin of the mussel specimens used for this experiment) (Barnerßoi 2012), but the population of *S. woodiana* in this habitat is increasing and has persisted for a long time (Barnerßoi 2012; Fischereifachberatung Niederbayern, personal comment). A number of 18 native and four non-native species were described for the Öberauer Donauschleife, including *Perca fluviatilis*, *Rutilus rutilus*, *Rhodeus amarus* and *Pseudorasbora parva* which were also included in this study (Barnerßoi 2012; Bezirksfischereiverein Straubing e.V., personal comment). However, these four species were found to be unsuitable hosts for *S. woodiana*. Matching the results of this study, the population of the Öberauer Donauschleife must be adapted to other host fish species, maybe especially native ones. Many of the self-recruiting populations of *S. woodiana* also occur in fish ponds (for example carp ponds). Use of such fish, infested with *S. woodiana* glochidia, in stocking programs will increase the spread of this invasive mussel. Additionally, direct selling of adult *S. woodiana* in pet shops and garden centers will also increase the risk of further spreading

in to natural lakes and ponds, particularly if staff are not trained and if mussels are declared as native *Anodonta* (Duempelmann 2012). Unfortunately, the selling of this invasive mussel is not yet forbidden by law, but the spreading of the species into natural habitats, where it does not occur naturally, is forbidden for example by German law (Bundesnaturschutzgesetz §40 (1), Bundesministerium der Justiz und Verbraucherschutz 2009).

Factors like a low water temperature are unlikely to constrain the ongoing invasion of *S. woodiana* as visible from the population in the Öberauer Donauschleife (with the area sometimes being completely frozen during winter), or populations in Sweden (von Proschwitz 2008). Due to the same habitat preferences in standing or slow flowing waterbodies, the invasion of *S. woodiana* will especially be an ongoing threat for the native *A. cygnea*, which exclusively occurs in these kinds of water bodies (in contrast to *A. anatina* that also lives in faster flowing rivers) (Niemeyer 1993). *A. cygnea* is endangered in many European countries invaded by *S. woodiana*. For example, *A. cygnea* is listed in Poland as "Endangered" on the Polish Red List (Zając Zajac 2002), it is also listed as "Vulnerable" on the Red List of Threatened Species of the Czech Republic (Farkač et al. 2005) or listed as "Near Threatened" on the Austrian Red List of Molluscs (Reischütz and Reischütz 2007). In Germany, *A. cygnea* is also endangered (Jungbluth and von Knorre 2009), and it has to be monitored how the invasion of *S. woodiana* will affect co-occurring populations of *A. cygnea* (and also all other co-occurring native mussel species) in the wild. The experiment conducted herein only gives first insights into host–parasite relationship of the invasive *S. woodiana* by simultaneous host infestation, showing the higher reproductive success of *S. woodiana* compared to native *Anodonta* species. Further experiments have to follow, where self-recruiting populations of *S. woodiana* and their competition for hosts with native freshwater mussels must be considered and analyzed separately, because host fish suitability can potentially differ among different water bodies and mussel populations.

Compliance with ethical standards

Conflict of interest The authors have no competing interests to declare.

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