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PRIMARY RESEARCH PAPER

Impacts of invasive crayfish (*Pacifastacus leniusculus*) on endangered freshwater pearl mussels (*Margaritifera laevis* and *M. togakushiensis*) in Japan

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Abstract The invasive alien crayfish *Pacifastacus leniusculus* is considered harmful to freshwater pearl mussels *Margaritifera laevis* and *M. togakushiensis*. It also often colonises mussel habitats in Japan. In order to test the negative effects of alien crayfish on mussels, we evaluated the predation impact of signal crayfish on freshwater pearl mussels in vitro. We tested the relationship between the survival/injury rates of mussels and crayfish predation with respect to different sizes of mussels (four classes based on shell length: 10, 30, 50 and 70 mm). Crayfish selectively fed on the flesh of the 10-mm size class mussels after breaking their shells. The shell margins of mussels in all size classes were injured by crayfish. Results also showed that crayfish particularly injured the 50-mm size class of mussels. This observation could be attributed to this mussel size being the most suitable shell size (29.56–37.73 mm in carapace length) that the crayfish can effectively hold. This study shows that the presence of invasive crayfish reduces freshwater pearl mussel populations by damaging the shell margins and/or killing the mussels. This negative impact of invasive crayfish not only decreases the mussel population but could also limit mussel recruitment, growth and reproduction.

Keywords Injured shells · Margaritiferidae · Mussel predation · Signal crayfish

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Introduction

Freshwater pearl mussels (Margaritiferidae) are highly threatened, long-lived bivalves that occur in cold running water in the Northern Hemisphere (Strayer, 2008; Geist, 2010), and two margaritiferid species from Japan, *Margaritifera laevis* and *M. togakushiensis*, are known (Kondo & Kobayashi, 2005; Kurihara et al., 2005). The habitats and abundance of these species have declined in Japan, and species have already disappeared from several local habitats (Ministry of the Environment, 2012).

The signal crayfish *Pacifastacus leniusculus* was originally introduced into Japan from the Columbia River in North America between 1926 and 1930. In July 2007, signal crayfish were distributed in eastern, northern and central Hokkaido and three prefectures in Honshu (Usio et al., 2007). Given its detrimental impacts on native biodiversity and ecosystem functions, the signal crayfish was designated as an Invasive Alien Species (IAS) by the Ministry of the Environment of Japan on 1

February, 2006. The signal crayfish has a negative impact on the endangered native crayfish *Cambaroides japonicus* (Nisikawa et al., 2001; Nakata & Goshima, 2003). Crayfish dramatically affect the structure and function of ecosystems by predating macrophytes and aquatic invertebrates (Nishikawa et al., 2009).

In a recent study, the signal crayfish was found in the habitat of freshwater pearl mussels (Machida et al., 2012). The study suggested that crayfish might negatively affect the mussels by breaking the posterior margins of mussel shells. Some cases of predation by signal crayfish have been reported for the zebra mussel *Dreissena polymorpha* (zu Ermgassen & Aldridge, 2011) and for the pond snail *Lymnaea stagnalis* (Nyström & Perez, 1998; Nyström et al., 2001). The predation of *M. margaritifera* by crayfish has been suggested in previous studies (Strayer, 2008; Geist, 2010); however, few studies have examined their predation threat to freshwater pearl mussels in Europe. The habitats of native Japanese crayfish (*C. japonicus*) include shallow bottom at upper reaches of a river and a crater lake on a mountain (Kawai & Takahata, 2010). The Japanese crayfish and freshwater pearl mussel show allopatric occurrence in a river system. *C. japonicus* mainly feed on fallen leaves and branches (Kawai et al., 1995) and predation of *C. japonicus* on freshwater mussel is not present, indicating that *C. japonicus* is harmless to freshwater pearl mussel. This study aims to analyse the predation of margaritiferid mussels found in Japan by signal crayfish and to evaluate the effects of predation on the basis of the survival/damage rates in the mussels.

Materials and methods

Freshwater pearl mussels (*M. laevis* and *M. togakushiensis*) were sampled from the Abashiri River system between 13 August and 2 October, 2012. The mussels used in the following experiment were treated as margaritiferid mussels because species identification was difficult for the smallest individuals. In the preliminary survey, the collection locality was found to be devoid of crayfish, and had a high density of mussels (83 individuals m^{-2}) with various sizes of mussels, including juveniles [14.7–114.5 mm in shell length (SL)]. This survey suggested that the mussel population was stable and free from the threat of predation by crayfish. SLs of the collected mussels were measured to an accuracy of 0.01 mm, and they were divided into four different size classes (10 mm = median 15.74; range 10.09–19.37 mm, 30 mm = median 32.61; range 30.29–37.54 mm, 50 mm = median 56.45; range 50.51–58.41 mm, 70 mm = median 73.70; range 70.65–76.39 mm). Mussels were kept in a 20-l tank (W38 cm × D22 cm × H24 cm), and 20 individuals per class were randomly selected for the experiments.

Signal crayfish (*P. leniusculus*) were collected using dip nets in the Uguisu River between 25 August and 12 October, 2012. The carapace lengths (CLs) of the collected crayfish were measured to an accuracy of 0.01 mm, and crayfish with CL of 29.56–37.73 mm were selected for the experiments. The crayfish were kept in a 972-l tank (W270 cm × D60 cm × H60 cm). Before the experiments, the crayfish were sufficiently provided with food. The experiment was conducted after obtaining permission from the Ministry of the Environment for the use and maintenance of signal crayfish. Each mussel and crayfish was used only once to maintain the independence of the data for statistical analysis. Mussels and crayfish were separately maintained in the laboratory. The predation impact of signal crayfish on freshwater pearl mussels was tested in a plastic case (W30.0 cm × D19.5 cm × H20.5 cm) where pebbles (5 mm in diameter) were laid to a depth of 8 cm. A cylindrical shelter (18 cm in length and 6 cm in diameter) for crayfish, proposed by Nakata et al. (2003), was positioned before placing fallen leaves (*Betula platyphylla* and *Cerasus sargentii*) on the pebbles. The fallen leaves were mainly food for the crayfish; however, they also provided shelter for the mussels. Twelve cases were prepared and placed in a 972-l tank filled with water, which was maintained at 15°C (±1°C) with an 8 h dark:16 h light cycle. One mussel was added per case in the Control experiment. In the Crayfish experiment, one crayfish was added per case after the mussel had successfully burrowed into the pebbles within a day of adding the mussel. Eight experimental sections were established, i.e., each of the experimental and control groups comprising of four size classes of mussels and one trial for each section was replicated 10 times. The plastic cases used in the experiments were reused after washing with water before subsequent tests. With smaller mussels (10- and 30-mm size classes), the whole body was buried in pebbles, whereas with larger mussels (50- and 70-mm size classes), the posterior part of the body was often exposed from the surface of the pebbles. Crayfish were allowed to feed on the chironomid larvae. The trial was run for seven nights. Photographs of all mussels were taken before and after the trials to check the mussel status. The mussels were categorised as follows: The mussels that were preyed on by crayfish were recorded as 'killed mussels', and the mussels that were preyed on and injured by crayfish were recorded as 'injured mussels'. The mussel status was recorded for each individual. The mussels and crayfish used in the experiments were not returned to the sampling site to prevent the spread of the fungal disease caused by crayfish plague, *Aphanomyces astaci* (Ackefors, 1999). These organisms were preserved as specimens at the Bihoro Museum (BIHM).

The mussel predation or injury rates in the Control and Crayfish trials were compared using two-tailed Fisher's exact tests for each size class. The crayfish mussel size preference was tested by comparing the damage rates among the four different size classes using a Kruskal–Wallis rank sum test, followed by a two-tailed Fisher's exact test. The *p* values obtained from the latter test were corrected using Holm's procedure for multiple testing (Legendre & Legendre, 1998). Statistical analyses were performed using R-2.15.2 (R Core Team, 2012). A P value <0.05 was considered to be statistically significant.

Results

Freshwater pearl mussel predation by crayfish

Signal crayfishes preyed on a few juvenile mussels and damaged many mussel shells. Three individual freshwater pearl mussels (SL: 10.09, 12.59 and 18.07 mm), belonging to the smallest size class (SL: 10.09–19.37 mm), were preyed on by signal crayfish (CL: 32.98, 34.21 and 33.66 mm). Their shells were chipped into powder-like fragments or occasionally crushed outright (Fig. 1). All the mussels in the smallest size class survived in the Control experiments, and the survival rates of the smallest mussels in the Control and Crayfish trials were not significantly different (two-tailed Fisher's exact test, $P = 0.21$; Table 1). All the mussels in the other size classes (SL: 30.29–37.54, 50.51–58.41 and 70.65–76.39 mm) survived in the Crayfish and Control trials indicating that the survival rate was not significantly different in the Crayfish and Control trials for these size classes (two-tailed Fisher's exact test, $P = 1$; Table 1). The crayfish selectively preyed on the small mussels, although results show mussels with SL > 50 mm were fed on seemingly without the need for excavating them since the posterior of the mussel body was exposed above the surface of the pebbles. The predation rate was significantly different among the mussel size classes (Kruskal–Wallis rank sum test, $\chi^2 = 9.49$, degrees of freedom $= 3$, $P = 0.023$), although using Fisher's exact test, $P > 0.05$ after correction using Holm's procedure, the predation rate in the smallest mussel size class was not significantly different from that in the other mussel size classes.

Freshwater pearl mussels injured by crayfish

Mussels injured by crayfish accounted for 50–100% of individuals in each size class (Fig. 1; Table 1). The number of 'injured mussels' differed significantly in the Control and Crayfish trials for all size classes (Fisher's exact test, 10- and 30-mm size classes: $P = 0.033$; 50-mm size class: $P = 1.1 \times 10^{-5}$; 70-mm size class: $P = 0.011$; Table 1). In particular, 100% of mussels were injured in the 50-mm size class, showing severe damage. The injury rate for mussels in all size classes was significantly different from that in the Control experiments (Kruskal–Wallis rank sum test, $\chi^2 = 8.94$, degrees of freedom $= 3$, $P = 0.030$), whereas the injury rate did not differ significantly among size classes (Fisher's exact test, $P > 0.05$ after correction using Holm's procedure).

Some mussels were unhurt and alive in all size classes. The number of 'unharmed mussels' in the Control and Crayfish trials differed significantly for all size classes (two-tailed Fisher's exact test, 10- and 30-mm size classes: $P = 0.033$; 50-mm size class: $P = 1.1 \times 10^{-5}$; 70-mm size class: $P = 0.011$). The rate of remaining unharmed was significantly different among all size classes of mussels (Kruskal–Wallis rank sum test, $\chi^2 = 8.94$, degrees of freedom $= 3$, $P = 0.030$). However, this rate did not differ significantly among size classes when Fisher's exact test, $P > 0.05$ after correction using Holm's procedure was used.

Discussion

The signal crayfish has opportunistic polytrophic feeding habits, e.g., periphyton, macrophytes, aquatic

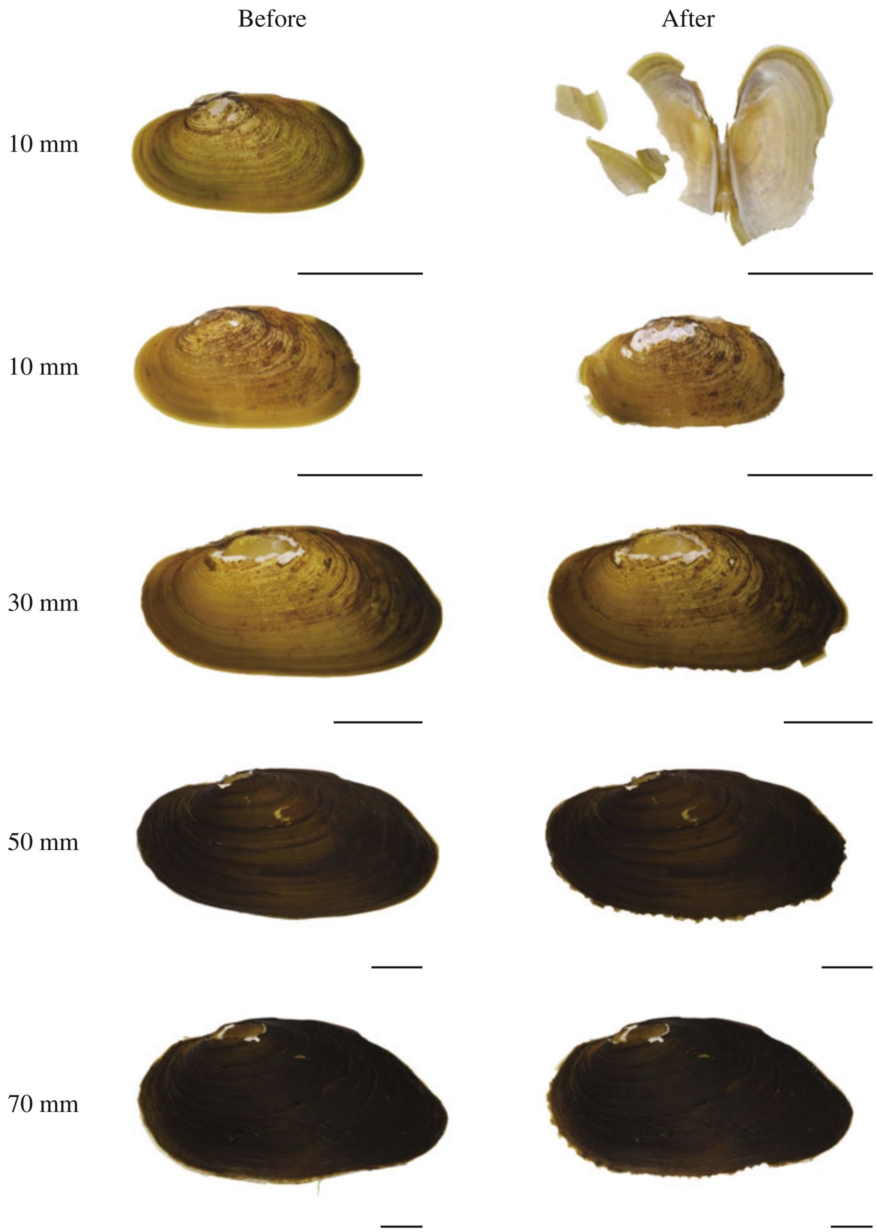

Fig. 1 Shells of freshwater pearl mussels in four size classes before (*left column*) and after (*right column*) the Crayfish experiment. Scale bars indicate 1 cm

insects, detritus, gastropods and bivalves (Lewis, 2002). The feeding behaviour of the signal crayfish on bivalves was described by zu Ermgassen & Aldridge (2011), who stated that when a crayfish forages to eat mussels, chelipeds are used to excavate sediment, following which the second and third pairs of pereopods are used to forage the benthos at random until a prey item is encountered. If the crayfish finds a mussel, the mussel is efficiently picked up by the pereopods and brought to the mouth where it is held by the maxillipeds, occasionally with the support of a second pair of pereopods. Finally, the mussels are chipped from their margins using the mandibles until the flesh is reached. Our study indicated that the smallest class of mussels was chipped and predated by signal crayfish. This indicates that signal crayfish are a direct threat to freshwater pearl mussels by limiting recruitment.

Mussels in the <30-mm class were not predated by crayfish in our study, although the shell margins of

Table 1 Comparison of the predation rate, injury rate and rate of remaining unharmed of freshwater pearl mussels (*M. laevis* and *M. togakushiensis*) between Control and Crayfish for four size classes

	Size classes							
	10 mm		30 mm		50 mm		70 mm	
	Control	Crayfish	Control	Crayfish	Control	Crayfish	Control	Crayfish
Predation	$0/10^{NS}$	$3/10^{NS}$	$0/10^{NS}$	$0/10^{NS}$	$0/10^{NS}$	$0/10^{NS}$	$0/10^{NS}$	$0/10^{NS}$
Injury	0/10*	5/10*	0/10*	5/10*	0/10***	10/10***	0/10*	6/10*

Each numeric character means number of event occurrence/number of trials

NS no significance

* $P < 0.05$; *** $P < 0.001$

many mussels were injured. In particular, crayfish preferred larger mussels that measured >50 mm, which is the mature size according to Kondo (2008). Shell repair has a high energetic cost, e.g., the ribbed mussel *Aulacomya ater* invests up to 26% of its total body energy in this process (Griffiths & King, 1979). This result suggests that crayfish will affect mussel reproduction and the mussel population size.

However, the damage rate in smaller mussels (SL: 10.09–19.37, 30.29–37.54 mm) was lower than that in larger mussels. The entire body of a freshwater pearl mussel measuring <50 mm was buried beneath the riverbed pebbles (Terui et al., 2011). In the present study, most small individuals (10- and 30-mm size classes) disappeared from the surface of the pebbles. Therefore, some individual mussels present in the pebbles could not be found by the crayfish. Bivalves sometimes close their valves as a protective response to predators (Wilson et al., 2011). One margaritiferid species, *M. margaritifera*, has longer valve closures when exposed to the odour of a crayfish (Wilson et al., 2012). However, this behaviour leads to a detrimental situation, i.e., increased energy expenditure (Ruppert et al., 2004), loss of feeding time, reduced oxygen absorption and a reduced ability to eliminate waste products (Wilson et al., 2011, 2012). Thus, some mussels may be adversely affected by crayfish even if they manage to avoid predation.

The rapid spread and population outbreaks of invasive crayfish, such as *Orconectes rusticus* in eastern North America, *Procambarus clarkii* in Africa and *O. limosus* in Europe, may threaten unionoid populations, although there is no data regarding crayfish feeding rates on unionoids in nature (Strayer, 2008; Geist, 2010). At present, the signal crayfish, *P. leniusculus*, has a broad distribution throughout Europe, western Russia and Japan (Lewis, 2002; Usio et al., 2007). In Europe, high population densities and rapid dispersal of signal crayfish have been observed (Wutz & Geist, 2013), and they are potential threats to native crayfish populations and freshwater mussels (Ackefors, 1999; Strayer, 2008; Geist, 2010). In the present study, signal crayfish intensively predated the smallest freshwater pearl mussels and also injured mussels of various sizes. We conclude that signal crayfish have direct negative impacts on freshwater pearl mussels, particularly on reproduction, because of juvenile mussel predation by crayfish. Further studies in natural systems are necessary to elucidate the impacts of invasive alien crayfish on endangered freshwater pearl mussels. Evidence of natural predation on *M. margaritifera* has been previously reported (Zahner-Meike & Hanson, 2001; Cosgrove et al., 2007). Cosgrove et al. (2007) reported *M. margaritifera* predation by the oystercatcher, *Haematopus ostralegus*, which selectively catches small- to medium-sized mussels inhabiting a shallow bottom. A muskrat, *Ondatra zibethicus*, selectively feeds on *M. margaritifera* juveniles and adults <75 mm in length (Zahner-Meike & Hanson, 2001). The signal crayfish habitat ranges from small streams to large rivers in Japan (Usio et al., 2007), where freshwater pearl mussels are distributed at the river bottom, particularly with a 0.2–0.6 m water depth (Terui et al., 2011). Signal crayfish and freshwater pearl mussels sympatrically occur in a river system in the eastern part of Hokkaido (Machida et al., 2012). The crayfish may selectively predate small-sized juveniles and injure large-sized adults in natural environments. Thus, the characteristic damage sustained in a *Margaritifera* population differs among predator species, so it may be necessary to vary the countermeasures implemented depending on the predator species to conserve endangered freshwater pearl mussels in an effective manner. For example, oystercatchers break the shells of *M. margaritifera* using their bills when the mussel shells are shut (Cosgrove et al., 2007). The conditions of shells damaged by oystercatchers are noticeably different from those damaged by signal crayfish. Thus, the potential impacts of crayfish on a freshwater pearl mussel population can be determined by assessing the characteristics of the broken mussel shells.

Margaritifera laevis and *M. togakushiensis* are highly threatened, and *M. togakushiensis* is one of the most endangered freshwater bivalves in Japan (Ministry of the Environment, 2012). Several studies have shown that artificial alterations of river fringes, water pollution and reductions in host fish stocks can have adverse effects on freshwater pearl mussels (Awakura, 1969; Matsuoka, 1979; Naito, 1989; Akiyama, 2007; Terui et al., 2011). A lack of juveniles has been observed in several local habitats (Akiyama, 2007; Akiyama, unpublished manuscript). In the present study, we treated *M. laevis* and *M. togakushiensis* as *Margaritifera* spp. because species identification was difficult for the smallest individuals. However, we will have to compare the effects of differential predation rates between the two mussel species in the future.

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