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Influence of host fish age on a mussel parasite differs among rivers: Implications for conservation☆

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ABSTRACT

Unionoid mussels are obligate parasites on one or more fish species. The objective was to compare growth and survival of encysted mussel larvae of the freshwater pearl mussel (*Margaritifera margaritifera*) on young-of-the-year (YOY) versus one-year old brown trout (*Salmo trutta*). YOY and one-year old trout from the Brattefors and Lärje Rivers, Sweden, were infested with mussel larvae from their home river. The mass-normalized encystment abundance was higher on YOY trout than on one-year old trout. The proportional decrease in mass-normalized encystment abundance was larger on YOY brown trout from the Brattefors River than on YOY brown trout from the Lärje River. Encystment per individual fish was higher on YOY trout than on one-year old trout from the Brattefors River, whereas this relationship was reversed for trout from the Lärje River. Larval growth was higher on YOY trout than on one-year old trout. There was a larger difference in larval growth between YOY trout and one-year old trout from the Brattefors River than on the brown trout from the Lärje River. The ability to use both YOY and older fish, such as in the Lärje River, may increase the reproduction potential of mussel populations, compared to a reduced ability to use more than one year class, such as in the Brattefors River. This may also affect the dispersal of mussels, as older brown trout often move and migrate to a higher degree within and between rivers. The dispersal potential of mussels may therefore be relatively high in the Lärje River, but low in the Brattefors River. In rivers where the mussels have to rely on YOY brown trout, it could be worth facilitating passage through migration obstacles for YOY brown trout. Infested YOY brown trout could be artificially re-distributed within rivers, to places with former mussel distributions. It could also be worth testing the suitability of brown trout of different age classes when starting breeding programs.

Introduction

Unionoid mussels are obligate parasites on one or more fish species (Strayer et al., 2004). An individual mussel's contribution to a population increases with the number of larval offspring that metamorphose and drop off the host fish as juvenile mussels. A juvenile mussel's size also has an impact on recruitment, where a large juvenile has a higher chance of survival compared to a smaller sized mussel. One factor that regulates the condition and abundance of hatched juveniles is the host fish species (Arvidsson et al., 2012; Taeubert et al., 2012). Another factor that impacts the number of hatched juveniles may be the age of the host fish. This can be a result of differences in the immune responses of fish of different ages (Greischar and Koskella, 2007; Uribe et al., 2011).

Movement and migration of the host fish is the most important way by which mussels disperse (Strayer et al., 2004; Schwalb et al., 2011). Life history attributes such as movement and migration differ among host fish species and with the age of the fish. Therefore, some fish species or fish of different ages are relatively stationary, while others move and migrate to a higher degree (Bagliniere et al., 2005). Thus, the variation of a mussel's dispersal ability probably increases with the ability to use several host fish species and fish of different age.

The freshwater pearl mussel (*Margaritifera margaritifera*) has an obligate parasitic stage on the gills of brown trout (*Salmo trutta*) or Atlantic salmon (*Salmo salar*) (Young and Williams, 1984). The glochidia larvae, which are released from the gravid mussel in late summer to early autumn, have to attach to, and be encapsulated by the epithelial cells on the gills of the host fish. The mussels grow on the host fish during the parasitic stage, and release from the fish after 10 – 12 months (Bauer, 1986, 1987a; Hastie and Young, 2001, 2003), which is a relatively long period in comparison to other mussel species. The larval growth during the parasitic stage is considered to be important since a large juvenile mussel likely

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have a higher probability of survival compared to a small mussel (Österling and Larsen, 2013). However, the influence of the host fish may be relatively large, given the long period of growth during the parasitic stage. This may induce a response of the host fish to ward off the mussels (Bauer and Vogel, 1987; Treasurer et al., 2006).

Brown trout often migrate long distances, from their tributary to lakes or to the sea (Klemetsen et al., 2003). Brown trout can also be stationary in streams and rivers, but often they move around frequently also within a stream (Crisp, 1993; Gowan et al., 1994). Migration and movement often differ depending on the size and age of the brown trout, and larger fish can move longer distances than smaller sized fish (Ombredane et al., 1998; Bagliniere et al., 2005). The use of fish of different age classes may thus increase the distance from their birthplace to which mussels can recruit to the benthic population.

The objective was to compare the growth and survival of encysted mussel larvae on young-of-the-year (YOY) versus one-year old brown trout in two sympatric mussel-brown trout river systems. It is hypothesized that (1) larval encystment suitability is higher on YOY brown trout than on one-year old brown trout, (2) encystment will decrease more slowly on YOY than on one-year old brown trout, and (3) growth of the parasitic larvae is higher on YOY than on one-year old brown trout. As a consequence, higher numbers of larger juvenile mussels is supposed to excyst as juvenile mussels from YOY brown trout than from one-year old brown trout.

Material and methods

The investigation was performed with mussels and fish from the Brattefors River and the Lärje River. These two rivers flow out into the Skagerrak in the Atlantic Ocean on the Swedish west coast. Ten gravid mussels were collected in each river at 12 August 2010. Gravid mussels were investigated by careful opening using tongs (Hastie and Young, 2003; Österling et al., 2008; Österling, 2014) whereupon they were transported to Karlstad University, and acclimatized at 16 °C in separate containers in the aquaria facility at Karlstad University. Brown trout was collected in the Brattefors River and in the Lärje River by electro-fishing (petrol-driven electro shocker, LUGAB) at 12 and 14 August 2010, respectively. The fish were transported to Karlstad University in separate aerated coolers, and were acclimatized at 16 °C. The fish were visually examined for mussel encystment, but no larvae were found. The mussels from the two rivers were kept in separate containers and were never mixed. Fish from each river were also kept in separate containers and were never mixed over the experiment period. Likewise, YOY and one-year old brown trout from the same river were kept in separate aquaria over the experiment period.

Inspection of released glochidia larvae was performed each day by placing 500 μl of the suspended water under the microscope. On 20 August (Brattefors mussels) and 23 August (Lärje mussels), high densities of snapping larvae were found suspended in the water.

The experiment was initiated on 20 August, by placing nineteen YOY brown trout individuals from the Brattefors River in two separate containers, and 24 one-year old brown trout individuals from the Brattefors River in two separate containers, each with water containing a concentration of 30,000 larvae l^{-1} from the Brattefors River. On the 23 August, the same procedure was performed when 25 YOY brown trout individuals and twenty one-year old brown trout individuals from the Lärje River were mixed with 30,000 larvae l^{-1} from the Lärje River. Thereby, YOY brown trout and one-year old trout from the Brattefors River were mixed separately, only with mussel larvae from the Brattefors River, whereas YOY brown trout and one-year old trout from the Lärje River were mixed separately with mussel larvae from the Lärje River. The encystment was terminated after 30 min by the movement of each of the YOY and one-year old brown trout from the Brattefors River and the Lärje River, respectively, to three 100 l aquaria each (12 aquaria in total). Pumps (EHEIM) were constantly cleaning the water, which was changed once a week. The water temperature was measured every hour using loggers (Onset, Hobo pendant temp logger UA-002-64). Water temperature was 18.4 °C at the start of the experiment, and slowly decreased to 13.1 °C when the experiment was terminated at 14 October.

The light regime was 11 h day, 11 h night, and 1 h dusk and 1 h dawn each day. The fish were fed with chironomid larvae (2% of their wet mass) three times each week. The number of day degrees between the infestation event when the experiment started, and the termination of the aquaria experiment in the lab (716.6 ± 8.5 day degrees) was similar to what has been measured in *M. margaritifera* populations in the field from the glochidial attachment event in late August until before the start of the juvenile mussel release in early June (727.3 ± 26.0 day degrees, $n \equiv 19$, own data).

Between two and five brown trout individuals of the YOY and the one-year old brown trout were collected from each aquarium at one early and one late occasion. The length and weight of the fish were measured before the fish were stored in formaldehyde 31 August (Brattefors River: YOY, 50.3 ± 2.2 mm, 1.19 ± 0.47 g, and one-year old, 99 ± 4.1 mm, 8.2 ± 1.0 g) and 2 September (Lärje River: YOY, 65.8 ± 3.5 mm, 2.60 ± 0.23 g, and one-year old, 121 ± 3.6 mm, 14.9 ± 1.5 g) (hereafter called the early occasion). The experiment was terminated at 12 October (Brattefors River: YOY, 53.8 ± 1.7 mm, 1.34 ± 0.17 g, and one-year old, 98.5 ± 4.1 mm, 7.2 ± 0.5 g) and 14 October (Lärje River: YOY, 67 ± 1.8 mm, 2.48 ± 0.19 g, and one-year old, 118 ± 2.4 mm, 14.1 ± 0.7 g), when the remaining brown trout individuals were collected and put in formaldehyde (hereafter called the late occasion), where they were stored for 4 weeks. The fish were then put in flow through tap water for 3 days. The first (outer) gill arch on the left and the right sides were removed with a razor blade, whereupon the numbers of encapsulated larvae were counted under a microscope (Hastie and Young, 2003). The length between the anterior and the posterior mussel parts was measured as the larval length. The length represents the suitability of the mussels to the brown trout, where a large larva is believed to have a higher probability of survival than a small larva.

The mass-normalized encystment abundance represents the suitability of the mussels to the brown trout, and any bias because of incomplete encystment is very unlikely after 53 days, when the experiment was terminated (Bauer, 1987b; Taeubert et al., 2010). The survival and size of the larvae during the experiment period was considered to be related to the size and abundance of excysted juvenile mussels (Bauer, 1987a; Hastie and Young, 2001; Österling and Larsen, 2013). The mass-normalized encystment abundance of each individual fish was calculated by dividing the mean number of glochidia larvae (at the first gill arch on the left and the right sides) by the mass of brown trout. In both rivers, YOY brown trout had a higher growth than one-year old brown trout. Therefore, the statistical differences between YOY and one-year old brown trout should not be biased, but should be even stronger (see the results). The encystment abundance represents the numbers of encysted larvae per fish individual. The encystment abundance was calculated by the summation of the larvae on both gill arches divided by two. Mean values of the larval length on each brown trout individual were based on measurements from 10 glochidia larvae.

Difference in mass-normalized encystment abundance, encystment abundance and larval size between YOY and one-year old brown trout at the early and the late collections of brown trout were analyzed with 2-Way ANOVA, with Age (YOY and one-year old) and Occasion (early and late) as the factors. All measures of variation are given as ±1 SE. The data were normally distributed