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This is the accepted version of a paper published in *Environmental Biology of Fishes*. This paper has been peer-reviewed and includes the final publisher proof-corrections.

Citation for the original published paper (version of record):

Österling, M., Ferm, J., Piccolo, J. (2014)

Parasitic freshwater pearl mussel larvae (*Margaritifera margaritifera* L.) reduce the drift-feeding rate of juvenile brown trout (*Salmo trutta* L.).

Environmental Biology of Fishes, 97: 543-549

<http://dx.doi.org/10.1007/s10641-014-0251-x>

Access to the published version may require subscription.

N.B. When citing this work, cite the original published paper.

The final publication is available at link.springer.com

Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:kau:diva-33943>

30		Revised
31		Accepted 2 March 2014
32	Abstract	<p>In this paper we describe, for the first time, the effects of freshwater pearl mussel (<i>Margaritifera margaritifera</i> L.) encystment on the drift-feeding behavior of juvenile brown trout (<i>Salmo trutta</i> L.). Because both mussel and salmonid populations are often threatened, this study not only adds knowledge to the understanding of host-parasite systems, but it is also of conservation value. Individual trout, mussel-encysted (25.1 ± 5.7 larvae $\cdot$ g⁻¹ body weight, $n=5$) or non-encysted ($n=5$), were fed with chironomid larvae in a flow-through stream aquarium. Feeding trials were filmed and analyzed by counting the numbers of chironomid larvae each individual ate, and by estimating the prey-capture distance. Non-encysted trout had a significantly higher drift-foraging rate than did encysted trout, and they captured significantly more prey further away from their focal point. The reduced foraging success of encysted trout was mainly due to their failure to catch prey relatively further from their focal point. This suggests that reduced foraging success of encysted trout may be due to poorer energetic status, but the physical effects of mussel larvae on prey handling time cannot be ruled out. Encysted trout caught approximately 20 % fewer prey, which would result in a reduction in growth potential during the period of mussel encystment. Reduced energetic status might also result in reduced competitive ability or in increased exposure to predation risk.</p>
33	Keywords separated by ' - '	Host - Parasite - Unionid mussels - <i>Margaritifera</i> - <i>Salmo trutta</i> - Drift-feeding - Foraging - Conservation
34	Foot note information	

Parasitic freshwater pearl mussel larvae (*Margaritifera margaritifera* L.) reduce the drift-feeding rate of juvenile brown trout (*Salmo trutta* L.)

Martin E. Österling · Julia Ferm · John J. Piccolo

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Received: 4 June 2013 / Accepted: 2 March 2014
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Abstract In this paper we describe, for the first time, the effects of freshwater pearl mussel (*Margaritifera margaritifera* L.) encystment on the drift-feeding behavior of juvenile brown trout (*Salmo trutta* L.). Because both mussel and salmonid populations are often threatened, this study not only adds knowledge to the understanding of host-parasite systems, but it is also of conservation value. Individual trout, mussel-encysted (25.1 ± 5.7 larvae $\cdot g^{-1}$ body weight, $n=5$) or non-encysted ($n=5$), were fed with chironomid larvae in a flow-through stream aquarium. Feeding trials were filmed and analyzed by counting the numbers of chironomid larvae each individual ate, and by estimating the prey-capture distance. Non-encysted trout had a significantly higher drift-foraging rate than did encysted trout, and they captured significantly more prey further away from their focal point. The reduced foraging success of encysted trout was mainly due to their failure to catch prey relatively further from their focal point. This suggests that reduced foraging success of encysted trout may be due to poorer energetic status, but the physical effects of mussel larvae on prey handling time cannot be ruled out. Encysted trout caught approximately 20 % fewer prey, which would result in a reduction in growth potential during the period of mussel encystment. Reduced energetic status might also result in reduced competitive ability or in increased exposure to predation risk.

Keywords Host · Parasite · Unionid mussels · *Margaritifera* · *Salmo trutta* · Drift-feeding · Foraging · Conservation

Introduction

Numerous effects of parasites on fish behavior have been described, including effects of both internal and external parasites on foraging and risk-taking behavior of several fish species (Barber et al. 2000). One aspect of parasitism that is just at an early exploration stage is the effect of gill parasites on the drift foraging behavior of stream fish. Crane et al. (2011) measured behavior of two mussels belonging to the order Unionidae. In this paper we describe, for the first time, the effects of a mussel belonging to the family Margaritiferidae, namely the freshwater pearl mussel (*Margaritifera margaritifera* L.) encystment on the drift-feeding behavior of juvenile brown trout (*Salmo trutta* L.). Mussels of this family, as mussels in the family Unionidae, both belong to the order Unionoida, and are examples of organisms that are parasitic on fish during their larval stage, but free-living for most of their lives. From a conservation standpoint this host-parasite system is somewhat unique, because often both unionid mussel species and their host fish species are considered valuable components of ecosystem biodiversity and are threatened (Strayer et al. 2004; Österling and Högberg 2013). Both species are either sensitive or threatened throughout much of their native range (Klemetsen et al. 2003; Geist 2010; Österling et al. 2010; Arvidsson et al.

M. E. Österling (✉) · J. Ferm · J. J. Piccolo
Department of Biology, Karlstad University,
651 88 Karlstad, Sweden
e-mail: martin.osterling@kau.se

2012), but there are no published accounts of the effects of the mussels on trout foraging behaviour.

The highly threatened unionid mussels live as parasites on the gills of fish during their larval stage, before they drop off the fish to find suitable habitat in the stream substrate (Strayer et al. 2004). The freshwater pearl mussel (classified as endangered in the IUCN classification) is a gill parasite on brown trout or Atlantic salmon (*S. salar*) for a period of about 10 months (Young and Williams 1983; Young and Williams 1984). The larval parasites may potentially impact growth and reproduction of the host fish, especially since the *M. margaritifera* larvae grow on the host fish during their parasitic stage (Österling and Larsen 2013). Very little is known about the specific interactions between trout and mussels, however, in terms of energetic or physiological effects (Gethin et al. 2013). Because both the mussels and many of the trout populations are considered vulnerable, improving the understanding of the interactions in this unique host-parasite system is of high conservation value.

Stream salmonids, including brown trout, obtain significant portions of their energy intake through drift-feeding, wherein they maintain a position in the stream current and capture invertebrate prey as it drifts past their position, commonly called a focal point (Fausch 1984; Hughes and Dill 1990; Hughes et al. 2003). Drift-feeding salmonids are thought to maximize their net energy intake (NEI) by selecting focal points in slower water velocities which lie nearby areas of faster velocities that have been shown to deliver more prey (Everest and Chapman 1972; Hughes and Dill 1990). There is, in fact, a growing body of literature, both theoretical and applied, that supports the hypothesis that fish select, and compete for, positions that offer relatively high NEI (see Piccolo et al. 2014). Of late, NEI foraging models have served as the foundation for stream production and population-process models (Hayes et al. 2007), and it appears that these models are poised to expand into wider use in stream management.

The ability of fish to capture prey while drift feeding is a major determinant of their NEI (Hill and Grossman 1993; Hughes and Dill 1990; Piccolo et al. 2008a, b). Environmental and biotic factors (e.g. turbidity, velocity and competition) have been shown to impact drift-feeding behavior (Sweka and Hartman 2001; Zamor and Grossman 2007; Hazelton and Grossman 2009). To our knowledge, however, there have been no investigations of the effects of parasites on drift-feeding

efficiency, despite the possible energetic consequences of mussel encystment. Here, we report the results of experiments to test the effects of freshwater pearl mussel glochidia encystment on the drift-foraging behavior of juvenile brown trout. We did this at a period when the encysted mussels have approximately one month until they release from the fish, which is a time when the encysted mussels are at their largest size, and therefore probably has a relatively large impact on the host fish. We hypothesized that brown trout that were encysted with mussel larvae would have reduced drift-foraging abilities compared to non-encysted fish.

Methods

In the case of freshwater pearl mussel parasitism on brown trout, glochidia encystments are often greatest on young-of-the-year (YOY) brown trout (Hastie and Young 2001; Österling et al. 2008). Thus, the YOY brown trout we used for our experiments are the age class most likely to be heavily encysted, and therefore negatively influenced by mussel larvae. YOY brown trout originating from the stream Oxsjöå in the Ljungan catchment, Sweden, were collected in September 2010 from a fish farm situated 30 km south of Sundsvall. Gravid mussels were collected in September 2010 in the stream Maljan, a tributary to the Ljungan main stream. The brown trout and the mussels were transported to Karlstad University, and placed in aquaria to acclimatize at a temperature of 16 °C. Inspection for free living, ripe glochidia larvae was performed on a daily basis in the container with mussels, by placing 1 ml of the suspended water under a dissecting microscope.

On 10 September high densities of “snapping” (ripe), glochidia larvae were found suspended in the water. Infestation by mussel larvae on the brown trout gills was performed by placing a concentration of 30 000 larvae·l⁻¹ in containers, whereupon brown trout were put into the containers for 30 min. The larvae in each container were kept in suspension by constant stirring of the water. The infestation was terminated by removing the trout to 100 L aquaria. The water was changed twice a week, and constantly filtered (EHEIM 2215 filter). The light regime was 11 h daylight, 1 h dusk, 11 h darkness and 1 h dawn each day. The fish were fed approximately 2 % of their weight with chironomid larvae 3 times each week. Water temperature was

measured three times a week, and was 18.4 ± 0.67 °C at 10 September, and then slowly decreased to 14.0 ± 0.17 °C when the experiment was started.

The experiment was started at 6 November, when we visually assessed mussel encystment level on trout gills. This was done by sedating the trout (Benzocaine) and gently lifting the gill cover with a probe. We have previously shown this method to accurately describe encystment rate (Österling 2011). Five encysted trout (25.1 ± 5.7 larvae $\cdot$ g⁻¹ body weight) and five non-encysted trout were randomly chosen for the experiment. The mean weight of the trout did not differ between encysted (2.16 ± 0.28 g) and non-encysted (2.62 ± 0.47 g) trout (One-Way ANOVA, $F_{1,8}=0.88$, $n=10$, $p=0.38$). The water temperature was measured every hour using loggers (Onset, Hobo pendant temp logger UA-002-64). The number of day degrees between the glochidial attachment and the start of the experiment (769 ± 9.2 day degrees) was similar to the number of day degrees between the infestation and early June approximately 9 months after infestation (727 ± 26.0 day degrees, own unpublished field data from 19 streams in the Ljungan Catchment).

We investigated the effects of mussel encystment on YOY brown trout on drift-foraging rate in a 0.58 m wide, 1.5 m long and 0.16 m deep flow-through aquarium with a mean water velocity of 0.16 m $\cdot$ s⁻¹. This approximates the velocity at which juvenile brown trout are known to hold a drift feeding station. The bottom was covered with gravel, which was arranged to form a slight incline at the downstream end. A single larger stone was placed in the center to serve as a focal point.

The fish were starved 24 h prior to the start of the experiment, when one trout was carefully netted from the holding tank and placed in the flow-through aquarium. The fish were allowed to acclimate until they were observed to have taken a position at the focal point and begun to feed. Chironomid larvae with a length of < 10 mm were used as food, and were released into the flow-through aquarium through one of three plastic tubes which entered the aquarium at three laterally-equidistant points across the upstream cross-section of the stream (Fig. 1). Twenty-four chironomid larvae per minute, evenly distributed between the three tubes, were released into the flow-through aquarium. This prey density was chosen to ensure that the fish's functional response would be saturated, so that we could measure maximum foraging rate. The experiments were filmed, and analyzed by counting the numbers of chironomid

larvae eaten during the first 3 min (hereafter called “the early feeding event”) and during the last minute (hereafter called “the late feeding event”) of the experiment. The foraging rate was calculated by dividing the numbers of prey eaten with time the fish were eating. The feeding efficiency was calculated by dividing the numbers of food items eaten with the total numbers of food items that were released. The “early feeding event” was considered the experimental test, while the “late feeding event” was used to test if the fish still foraged and was not satiated. If no significant reduction in feeding activity were found, we could argue that the fish was not satiated at “the early feeding event”. A feeding distance of at least 3 fish lengths were defined as a distant feeding distance, while a shorter distance was defined as a close feeding distance. These distances were chosen based on prior results from fine-scale 3-D analysis of prey capture area (Piccolo et al. 2007, 2008a).

Differences in drift-foraging rate between encysted and non-encysted trout at the two periods (early and late) were analyzed with a mixed effects factorial ANOVA, with Encystment as one factor (between subject effects), and Period as the other factor (within subjects effects). Differences in drift-foraging rate between encysted and non-encysted trout at the two distances (close and distant) were analyzed with a mixed effects factorial ANOVA, with Encystment as one factor (between subject effects), and Distance as the other factor (within subjects effects). Post hoc tests were performed with Student-Newman-Keuls test (SNK-test) (Tybout and Sternthal 2001). The data was normally distributed for the encysted and the non-encysted fish at every analysis (Shapiro-Wilks-test, $p > 0.05$). All analyses were performed with the SPSS program (IBM SPSS Statistics, Version 19).

Results

The feeding efficiency of non-encysted and encysted trout was 22 % and 16 %, respectively, for the early period. A mixed model analysis for drift-foraging rate showed that there was a significant effect of Encystment (Mixed Effects Factorial Repeated ANOVA, $F_{1,8}=9.1$, $n=10$, $p=0.017$), but not of Period (Mixed Effects Factorial Repeated ANOVA, $F_{1,8}=1.6$, $n=10$, $p=0.24$) or the interaction of Encystment and Period (Mixed Effects Factorial Repeated ANOVA, $F_{1,8}=1.6$, $n=10$, $p=0.24$). Therefore, fish at the early feeding event were not

Fig. 1 Experimental set-up in the artificial stream tank aquaria with flow-through water from the right to the left. The prey (chironomid larvae) were distributed evenly into the three food

tubes and introduced to the water. The fish behavior was filmed and videotaped by the use of a camera placed behind a curtain

considered to be satiated during the early event. The non-encysted trout had a higher foraging rate then did the encysted trout at the early feeding event (SNK-test, $n=10$, $p<0.05$; Fig. 2). This was also true for the late period event (SNK-test, $n=10$, $p<0.05$).

Non-encysted trout caught 65 % of their prey at the close feeding distance and 35 % of their prey at the distant feeding distance during the early feeding event, whereas encysted trout caught 75 % of their prey at the close distance and 25 % of their prey at the distant feeding distance at the early feeding event. A mixed model analysis for drift-foraging rate showed that there was a significant effect of Encystment (Mixed Effects Factorial ANOVA, $F_{1,8}=7.6$, $p=0.025$; see the analyses above and Fig. 2), and of Distance (Mixed Effects Factorial ANOVA, $F_{1,8}=9.8$, $p=0.014$), but not of the interaction between Distance and Encystment (Mixed Model Analysis, $F_{1,8}=0.31$, $p=0.60$). The feeding rate

was higher at the close than at the distant distance (SNK-test, $p<0.05$). However, the feeding rates between the non-encysted and the encysted trout differed among the two distances. There was no significant difference in the drift-foraging rate between the encysted and non-encysted trout at the close feeding distance (SNK-test, $n=10$, $p>0.05$). At the distant feeding distance, there was a significantly higher drift-foraging rate for the non-encysted trout than for the encysted trout (SNK-test, $n=10$, $p>0.05$; Fig. 3).

Discussion

This is the first study to document the effects of unionid mussel encystment on drift-feeding fish. Our study showed that non-encysted fish had a higher drift foraging rate than did encysted fish, primarily due to a

Fig. 2 Feeding rate of juvenile brown trout that were not encysted with glochidia larvae (black bar) or were encysted with glochidia larvae (white bar). Measures of variation are given as ± 1 SE

Fig. 3 Feeding rate of juvenile brown trout that were not encysted with glochidia larvae (black bar) or were encysted with glochidia larvae (white bar) at a close and at a distant feeding distance. Measures of variation are given as ± 1 SE

- 293 reduced foraging distance of encysted fish. Ongoing
294 experiments have confirmed that both hatchery and wild
295 trout may have lower foraging rates at different water
296 velocities when encysted by mussel larvae (Österling
297 unpubl. data). Although our study is restricted to a small
298 sample size and a limited portion of the complex host-
299 parasite relationship between brown trout and freshwa-
300 ter pearl mussels, it demonstrates one possible negative
301 effect of the parasite on the host's energetic status, the
302 trout's net energy intake (NEI). These findings may
303 have energetic consequences for drift-feeding brown
304 trout during the important growth period in the late
305 spring to the early summer period, even if the impact
306 from the mussel parasite does not reduce the trout fitness
307 to a large extent, given the dependence of the mussel on
308 its host.
- 309 Potential energetic consequences of mussel encystment
- 310 For drift-feeding fish, the net energy intake (NEI) is
311 considered to be the result of a tradeoff between the
312 costs of swimming to hold position and catch prey,
313 versus the benefits of encountering more prey at faster
314 water velocities (Fausch 1984; Hughes and Dill 1990).
315 Because mussel encystment appears to reduce a fish's
316 maximum foraging rate, a parasitized fish would expe-
317 rience a reduced NEI, at least at high prey densities.
318 Encysted fish caught approximately 20 % fewer prey,
319 which would result in a reduction in growth potential
320 during the period of mussel encystment. Individual-
321 based models of fish distribution and growth based on
322 NEI (Hayes et al. 2007; Railsback and Harvey 2013)
323 have yet to include a parasite effect, but this might be a
324 worthwhile consideration if the models were applied to
325 mussel-trout ecosystems.
- 326 The fact that the reduction of foraging rate of
327 encysted fish was largely due to reduced prey capture
328 distance suggests that reduced energetic status, and
329 hence reduced swimming ability (Crane et al. 2011;
330 Taeubert and Geist 2013), may be the underlying mech-
331 anism. Fish with encysted larvae have higher respiration
332 rates than do trout without encysted larvae (Crane et al.
333 2011; Gethin et al. 2013), which may further reduce the
334 energetic status and reduce the prey capture distance.
335 Reduced energetic status due to mussel encystment
336 might also result in reduced competitive ability for
337 encysted fish (Crane et al. 2011), potentially further
338 reducing their NEI or exposing them to increased pre-
339 dation risk. These hypotheses remain to be generally
340 tested, however. Because we did not measure prey han-
341 dling times, we also cannot rule out the possibility that
342 mussel encystment physically impairs foraging ability
343 by reducing the efficiency of gill raker functioning.
- 344 We chose a water velocity, depth, and temperature to
345 simulate approximate conditions that drift-feeding YOY
346 brown trout might encounter around the early summer
347 period in boreal streams (Klemetsen et al. 2003; Eros
348 et al. 2012). Thus our foraging rates ought to approxi-
349 mate natural stream conditions when YOY trout are
350 infected by mussel larvae. We saturated prey density to
351 determine maximum foraging rate – our mean rates for
352 both encysted and non-encysted fish fall roughly within
353 those described for juvenile stream salmonids in the
354 wild under comparable conditions (Hayes et al. 2007).
355 This suggests that during daytime feeding activity pe-
356 riods juvenile salmonids forage at or near their maxi-
357 mum rate. One additional result of our study, therefore,
358 is that we now have a range of maximum foraging rates
359 for this life stage under these conditions, which should
360 be of value in the further development of foraging-based
361 habitat selection models.
- 362 Trout-mussel host-parasite interactions
- 363 Currently, the mechanisms that allow continued coexis-
364 tence of the trout-mussel relationship at the
365 physiological-, behavioral-, and population-level, are
366 largely unknown (Strayer et al. 2004). These include
367 trout physical and immune responses to larvae, encyst-
368 ment mechanisms, and growth and survival of encysted
369 trout. In other fish-mussel systems, for example, mus-
370 sels have evolved elaborate physical and behavioral
371 mechanisms such as “lures” to entice fish to ingest
372 larvae (Haag and Warren 2000). The freshwater pearl
373 mussel does not seem to have evolved such mecha-
374 nisms; how it ensures adequate infection rates is un-
375 known. Encystment rates are known to vary within and
376 among streams, and they appear to be higher on both
377 younger trout and on trout strains with a history of
378 within-drainage sympatry with mussels (Taeubert et al.
379 2012; Österling and Larsen 2013). Thus, trout popula-
380 tion structure and migratory behavior probably play an
381 important role for mussel populations. The answers to
382 these broader-perspective questions will need to be
383 based in part on a better understanding on the physi-
384 ology and behavior of trout and mussels. This should
385 contribute to conservation and restoration of both trout
386 and mussel populations.

Trout have not been observed to benefit in any way from mussels, but we are not aware of any studies that have investigated this. At the ecosystem level, however, other species of freshwater mussels have been shown to both influence organic matter processing and to increase benthic fauna production (Vaughn and Hakenkamp 2001; Vaughn et al. 2004; Vaughn and Spooner 2006; Limm and Power 2011) which could increase invertebrate drift densities. The historic abundances of freshwater pearl mussels and brown trout in streams where they historically co-existed can only be guessed at. In Sweden, mussels were harvested commercially to obtain pearls, and records suggest they could reach great biomass. It is interesting to speculate on the food web effects of extensive mussel beds in trout streams; how might these ecosystems function and how might they influence trout production? Hopefully, efforts to restore mussel populations will allow us the opportunity to find out.

Conclusions

Our experiments were of limited scope in terms of time and space, and were further limited to a narrow set of physical and biological conditions (e.g. temperature, light, prey, fish size, mussel encystment rate, water velocity). Thus, the inferences that we can draw are restricted. These limitations notwithstanding, there is a clear measurable effect of mussel encystment on trout foraging behaviour. The extent to which this effect influences the relationship between trout and mussel populations is unknown, but given the conservation concerns of both species, it offers a fruitful area for further exploration.

Acknowledgments We thank Fortums nordiska miljöfond, the Knowledge Foundation and Karlstad University for financing this study, and the land owners, fishing organizations and the County Administration Board in Västernorrland for permissions. The study was approved by the Board of Agriculture (Dnr A 54-10).

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