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INVESTIGATING THE COST OF MIGRATION IN A FRESHWATER FISH

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Abstract

Migration is a widespread phenomenon in nature, observed in many different taxa. Migration is often caused by changes in food availability, physical conditions and predation risks. Moving is energetically costly, and hence migration is likely to be a trade-off between increased survival and an energetic cost for migrating, the cost could take shape in decreased fecundity and lower body condition. Here, I investigate the reproductive cost of migrant and resident roach (*Rutilus rutilus*) by comparing body condition and reproductive investments. There were no significant reproductive costs to migration for either mature males or females, however a larger proportion of the migrating fish were immature suggesting that migration might delay the maturation age for migrants. Migrants also had larger eggs at the end of the sampling period which could potentially have fitness consequences for offspring. Future research should aim to investigate if the patterns observed in this paper are consistent and also investigate life-histories of migrants and residents by catching tagged fish with a known migratory history.

Introduction

Migration is a widespread phenomenon in nature and has been observed in many different animal taxa such as birds, fish and insects (Dingle and Drake, 2007, Holdo et al. 2009, Sykes et al. 2011). Migration is often coupled with seasonal variation of resources in habitats and the energetic cost of migration is often compensated with several benefits such as increased food availability, increased physical conditions and lower predator abundance (Dingle and Drake, 2007). There is a great variety of migration patterns where some species, like zooplankton, migrates a few meters once a day on a daily basis (Hansson and Hylander, 2009, Reichwaldt and Stibor, 2005) while animals like the artic tern (*Sterna paradisaea*) migrates thousands of kilometers once a year (Lundberg, 1988).

Partial migration occurs when only a part of a population migrates while the rest stay in the resident habitat (Chapman et al. 2011, Lundberg 1988). Partial migration is a common phenomenon in many different species and plays an important role on the ecosystem level (Brodersen et al. 2011, Brodersen et al. 2008a). It has been shown that the timing of partial migration of the cyprinid fish, the roach (*Rutilus rutilus*), can have determinant effects on lake ecosystems (Brodersen et al. 2008b). The partial migrating roach can (to some extent) explain why some shallow eutrophic lakes shifts from a clear water state to a turbid water state (Brönmark et al. 2010, Hargeby et al. 2007). The shifts can be induced by the magnitude and timing of partial cyprinid migration. There is a critical period in late spring were the lake macrophyte germination and growth is started due to increasing water temperatures, it is thus important for the macrophytes that the water is clear during this period to be able to photosynthesize and establish (Brodersen et al. 2008a). However, the partial migration of roach is also taking place during spring and the magnitude and timing of cyprinid migration can result in high predation on zooplankton which leads to reduced grazing on phytoplankton (Brodersen et al. 2008a). This could eventually result in difficulties, due to reduced light penetration, for macrophytes to establish and the water will become more turbid (Brodersen et al. 2008a). Since the turbid water state in lakes has poorer water quality, less biodiversity and lower recreational values is it crucial to know the underlying factors of the partial migration in roach (Brönmark et al. 2010).

It has been suggested that the partial migration in roach is driven by the ratio between predation (P) and growth (G), where the predation risk in the lake is high in the summer and low during the winter due to the temperature dependent metabolism of the most important roach predator, the pike (*Esox lucius*) (Brönmark et al. 2010). Since the pike does not follow the roach into the streams (Skov et al. 2008) the predation risk in the streams are likely to be very low during the whole year. The growth of roach in the lake is high during the summer due to high abundance of zooplankton and almost zero in the winter, in the streams the growth is constant low during the whole year (Brönmark 2010) since the streams is a poor feeding habitat for roach (Skov et al. 2008). Hence, in the winter the G for both lake and streams are basically equal, so why do not all roach migrates into the streams to avoid predation, i.e. why is the migration only partial? It might be because there is an energetic cost of migration in terms of swimming a certain distance to and up the migratory stream (Leonard and McCormick, 1999, Jonsson and Jonsson, 2006), maintain position in the stream (Hinch and Rand, 2000) and reduced feeding due to the poor food quality in the stream (Skov et al. 2008). Since the roach does not migrate vast distances one can predict that the largest cost will probably be due to the reduced feeding in the stream. For the roach, the P/G ratio in the lake should be high in the winter and low in the summer which means that individuals that are in a bad condition should stay in the lake during the winter due to the energetic cost of migration, while fish in good condition can afford to migrate into the connected streams in the fall to avoid predation (Brönmark et al. 2010). Feeding experiments supports the fact that fish in good condition migrates to a higher extent than fish in poor condition (Brodersen et al. 2008b) and telemetry tracking, PIT-tagging, of the fish (Skov et al. 2005) supports the seasonal migration suggested by the model (Brönmark et al. 2008).

The energetic cost of migration is a well-studied area and occurs in many migratory animals such as fishes, birds and insects (Leonard and McCormick, 1999; Barta et al. 2008; Inglesfield and Begon, 1983). The costs can result in the depletion of fat reserves, muscles, skin or gonads which potentially can reduce the migrant's condition and fecundity (Leonard and McCormick, 1999, Rand and Hinch, 1998). Earlier studies have shown trade-offs in growth and fecundity vs. predation risk between migrants and residents for zooplankton (Loose and Dawidowicz, 1994). For the roach, the migrants might suffer from reduced condition and fecundity while the residents will have a higher predation risk which may lead to the same individual fitness between migrants and residents over a life-time, where the migrants lives longer but reproduce more slowly and the residents suffers from predation but can reproduce faster. Alternatively, migrants might allocate the same energy into their gonads as resident, but instead deplete other tissues which results in a reduction in somatic growth (Leonard and McCormick, 1999). If the fitness for migrants and residents are equal, this may explain the maintenance of partial migration in roach (Lundberg, 1987, Kaitala, 1993).

I aim to investigate whether there is a reproductive cost of partial migration for roach, I hypothesize that the condition and the reproductive investment will be lower for migrants than residents, for both males and females due to the energetic cost of moving up the streams, maintain position in the stream and to the lower quality of food found in the streams compared to the lake (Skov et al. 2008). I predict that the migration will not only have a negative effect on the quantity of gonadal investment but also the quality, and therefore I hypothesize that female migrants will have smaller eggs than residents.

Study area

Lake Krankesjön is situated in southern Sweden and is a shallow eutrophic lake (Hargeby et al. 2007). It has three connected streams, the inflowing streams Silvåkrabäcken and Länsmansbäcken and the outflowing stream Ålabäcken. The lake has shifted between clear-water state and turbid state several times during the last century (Hargeby et al. 2007). The planktivorous fish community is dominated by roach whereas the piscivorous fish community is dominated by perch (*Perca fluviatilis*) and pike (Brodersen et al. 2008).

Materials and Methods

Roach were caught just before spawning during ten sampling occasions from 22 of March to 26 of April 2012. The fish were caught by electrofishing in Lake Krankesjön and in Silvåkrabäcken. Fish caught in Silvåkrabäcken were determined as migrants while fish caught in Krankesjön were residents. Only fish over 120 mm were caught to avoid catching immature fish (Vøllestad and L'Abée-Lund, 1987). Fish was chemically killed in the field with an overdose of anaestethic benzocain and then brought back to the lab. In the lab the fish length was measured to the nearest 0,1 cm and weighed to the nearest 0,01 g. The fish was also sexed by opening the abdomen of the fish. The female eggs were taken out of the fish and weighed to the nearest 0,001 g, the eggs were then dried in an owen with 65 ^{0}C for 72 hours to determine the dry weight. The male gonads were treated in the same way as the female eggs.

Female roach from each sampling date were randomly selected for determination of egg size. A subsample of the eggs was put on a microscope and the diameters of 10 eggs from each fish were measured to calculate the mean diameter of the eggs.

Data Analysis

The weight of the gonads was used to calculate the gonado somatic index, GSI:

$$\text{GSI} = \frac{\text{GW}}{(\text{BW-GW})} \cdot 100 \qquad (1)$$

Were GW is the gonad wet weight in grams and BW is the body weight in grams, according to Jobling, 2002. There was a significant and positive relationship between GSI and the size of the fish for both males (r=0,31, p<0,001) and females (r=0,528, p<0,001), thus the residuals from the length-GSI relation was used in the further analysis. There were also a positive significant relation between egg size and fish length (r=0,561, p<0,001), thus the residuals from the linear regression were used in the analysis.

To investigate the relation between gonadal investment and condition of the fish, the Fulton condition factor (F) was calculated:

$$F = (100 \cdot M) \cdot L^{-3} \qquad (2)$$

Were M is the weight in grams and L is the length in centimeters. Since F is an increasing function of body length in natural roach populations (Brodersen et al. 2008a), the residuals from the linear regression between length and F were used to estimate the length-specific condition.

Time was calculated as the number of days with the first sampling date as day 1 and the last as day 36.

General linear models (GLMs) were used to test whether there were differences in condition and reproductive investments between migrants and residents. Linear regression and GLMs were also used to see if reproductive investments correlate with fish condition and time. Chi-square test was performed to see if the sex ratio differed amongst migrants and residents and if there were more immature fish in the stream than expected. All statistics was performed with the software Microsoft Excel© and SPSS©.

Results

A total of 446 fish were caught and analyzed, 220 of these were migrants, and 226 were residents. 266 females, 128 males and 52 immature fish were totally caught. For all the females, 59,4 % (n=158) were residents and the remaining (40,6 %, n=108) migrants, for the males 57 % (n=73) were migrants and the remaining (43 %, n=55) were resident. There were significantly more males in the streams than in the lake and significantly more females in the lake than in the stream (X^2=9,39, df=1, p<0,001). For the immature fish 73 % (n=38) were migrants and the rest (27 %, n=14) residents. There were significantly more immature fish (length>120 mm) amongst migrants than residents (X^2=15,80, df=1, p<0,001).

There was no difference in GSI between migrants and residents for females (GLM, F=0,72, p=0,39) and for males (GLM, F=2,24, p=0,13). The overall GSI significantly increased over time for females (r=0,36, p<0,001) but decreased for males (r=0,41, p<0,001) (fig. 1). There was a significant positive correlation between condition (F) and GSI for females (r=0,38, p<0,001) but not for males (r=0,061, p=0,49) (fig. 2).

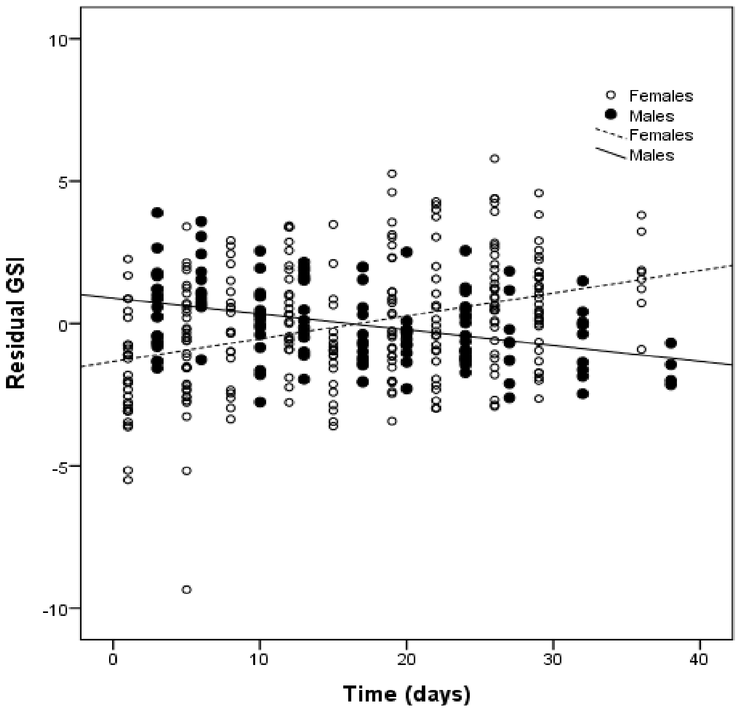

Figure 1. Residuals from the GSI-length relation plotted against time. The reproductive investment increases over time for females but decreases for males. The males and females are separated by 1-2 days for better illustration.

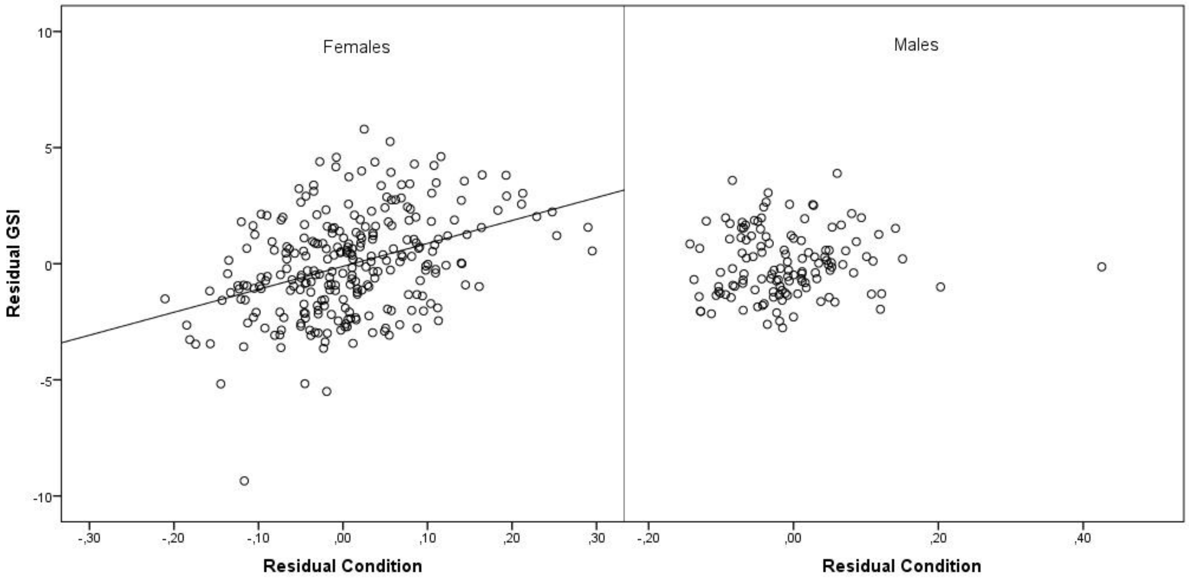

Figure 2. The relationship between body condition (F) and reproductive investment (GSI). As females improve their condition they increase their reproductive investment, this pattern were not seen in males.

There was no difference in egg size between migrants and residents (t-test, t=-0,84, p=0,40), but there was a significant interaction between migratory status and time (GLM, F=4,86, p=0,03) where the migrants have small eggs in the beginning of the sampling period but increases over time and gets larger than the resident eggs in the end of the period (fig. 3). There was also a positive relation between GSI and egg size (r=0,36, p<0,001), which means that females with greater relative reproductive investment produced larger eggs.

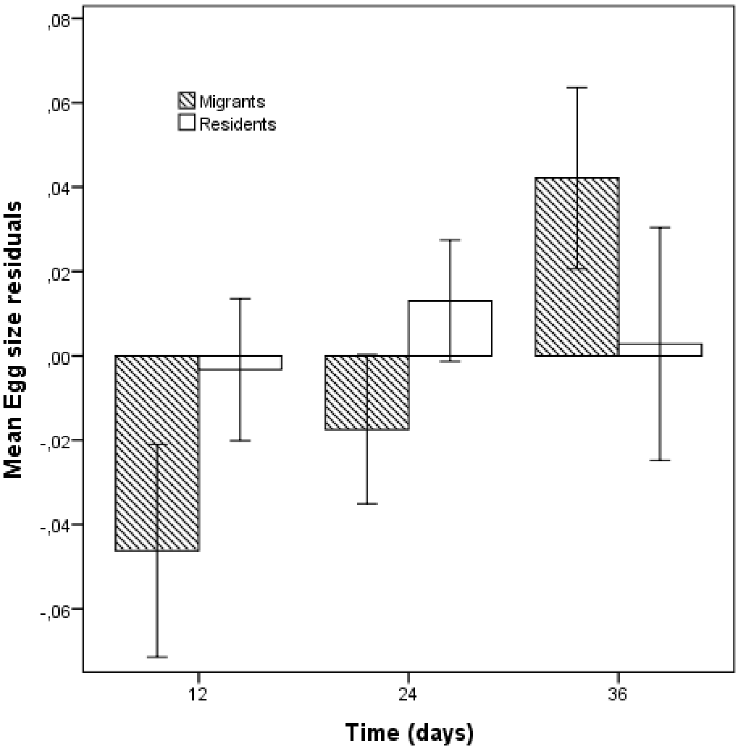

Figure 3. Residuals from the egg size-length relation plotted against time. There is an interaction between migratory status and time; were the migrants have smaller eggs in the beginning but is increasing with time while the resident egg size remains constant during the period. Error bars shows 1 +/- standard error.

There was a significant interaction effect of condition (F) between migratory status and sex (GLM, F=7,54, p=0,006), which means that the difference in condition between migrants and residents is sex dependent (fig. 4), with males being in better condition amongst migrants and females amongst residents.

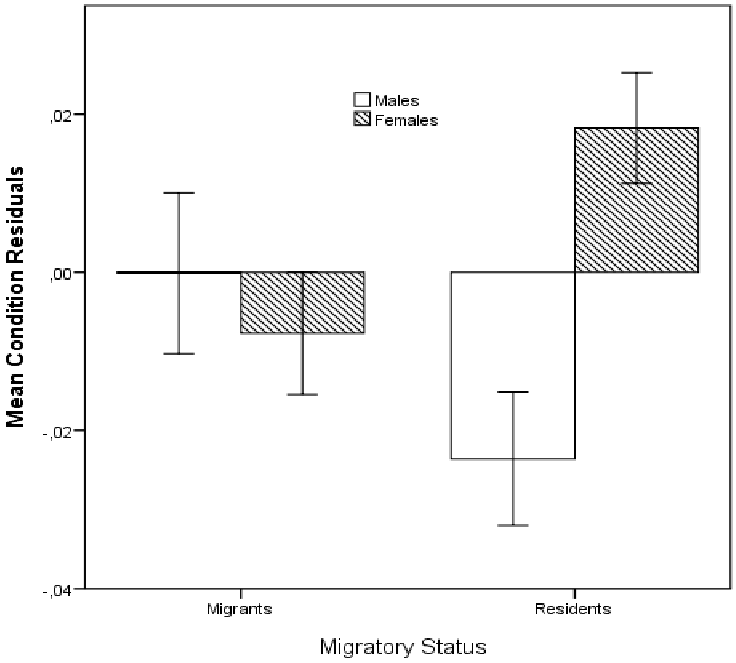

Figure 4. The mean residuals from the condition-length relation for migrants and residents. Error bars shows +/- 1 standard error.

Discussion

This study found no evidence of reproductive cost of migration for mature roach, either in the quantity of the gonads nor the quality. Further, there is no evidence that the condition decreases for migrating roach. The reproductive investment increased for females but not for males during the sampling period. The reproductive investment was condition dependent for females but this pattern was not seen in males. Migrating females had larger eggs than residents in the end of the sampling period.

Reproductive Investment and Conditon

There is no difference in GSI between migrants and residents for both males and females which indicates that there might not be a reproductive cost of partial migration for roach. There was neither a difference in egg size between migrants and residents which also supports the fact that there might not be a cost. Leonard and McCormick (1999) showed that the largest depletion of tissues (63 % depletion) in the migrating American shad (*Alosa sapidissima*) took place in the skin and its subdermal fat layer, possibly to maintain tissues crucial for reproduction i.e. gonads. If the roach use the same strategy as the American shad, this could explain why we don’t see a decline in gonadal investment for migratory roach. This hypothesis is supported by the result that the females in the lake are in better condition than females in the stream (fig. 4), but there is no difference in GSI.

The overall female GSI increases with time which seems natural to allocate energy into the gonads just before spawning (fig. 1), however there is a difference in the quality investment between migrants and residents over time. During the sampling period, the migrants eggs grew larger than average while the resident eggs had the same size during the period (fig. 3). Earlier studies have shown that fry hatched from larger eggs have better survival than fry hatched from small eggs (Bagenal, 1969). There is a possibility that the migrants invest more energy into egg size than egg number and vice versa for residents which lead to no difference in GSI between the groups but increases the survival of the migrant offspring to a cost of decreased number of offspring. Since the resident fish have shorter distance to the best spawning grounds, i.e. the lake, the benefit for migrants, by having larger eggs might be crucial to counter intraspecific competition of spawning grounds and thereby reach equal fitness as the residents (Lundberg, 1987, Kaitala 1993). This theory might explain why the partial migration in roach is maintained, however further research are needed to determine if this is a valid hypothesis.

There was a positive significant relation between GSI and condition for females but not for males (fig. 2). One explanation for this pattern might be that the reproductive investment of males is independent of condition and this might be because males don’t allocate as much energy into their gonads as females. In the Atlantic salmon (*Salmo salar*), females invest about six times as much of their weight into gonads compared to males (Flemming, 1996).

It is remarkable that there is a significant negative relationship with GSI and time for males, the reproductive investment decreases over time just before spawning (fig. 1). One explanation could be that the males have already spawned and then emptied their gonads to some extent, but this suggestion seems unlikely since we have the opposite pattern in females, they do not seem to spawn during this period since they are increasing their gonadal investment.

There was more immature fish in the stream than in the lake, this result might suggest that the sexual maturity is delayed in migrants, possibly due to the energetic costs of migration. Same pattern can be seen in salmonid fishes where the mean size at sexual maturation increases with migratory distance (Jonsson and Jonsson, 2006).

Future studies

A major drawback in this study has been the lack of information about the history of migratory status of the caught fish i.e. some fish migrates to the streams in September while others can migrate as late as March, this means that fishes caught in the stream can have spent different amount of time in the stream. And if there is a cost to migration this will be strongly expressed in early migrants but may be undetectable in late migrant which could obscure evidence of a cost. To be able to perform a more solid study PIT-tagged fish, which has a known migratory history, should be caught and examined in the way that I did in this paper. This would lead to better accuracy in terms of determination of migratory status. Investigating and comparison of the life-history patterns of resident and migratory roach would also be valuable in terms of evaluation of the migratory status effect on fitness, although probably hard to perform.

Even though the reproductive investment is higher for females than males (Flemming, 1996) and the female fecundity have a larger ecological impact (since it limits the number of offspring) than the male it would be interesting to do a qualitative measure of the male reproductive investments compared by migratory status i.e. compare different sperm traits such as swimming velocity, flagella frequency, size and density.

Conclusion

The reproductive cost of a partially migrating freshwater fish, the roach, has been studied. I found no reproductive cost to migration, however this could be explained by a trade-off in somatic growth to be able to maintain reproductive investment. This hypothesis is strengthened by the fact that the migrating females were in worse condition than the resident but showed no difference in GSI. The female migrants had larger eggs than the residents in the end of the sampling period which could indicate that the migratory roach are compensating for their worse access to spawning grounds by producing large eggs that will give larger fry with higher survival than residents, however further research is needed.

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