Migration costs drive convergence of threshold traits for migratory tactics

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Partial migration of some, but not all, members of a population is a common form of migration. We evaluated how migration costs influence which members migrate in 10 populations of two salmonid species. The migratory patterns of both species were evaluated based on the size at maturity for resident males, which is the threshold trait that determines the migratory tactics used within a population. In both species, this size was smaller in males located further from the sea, where migration costs are presumably higher. Moreover, the threshold sizes at maturity in males were correlated between both species. Our results suggest that migration costs are a significant convergent selective force on migratory tactics and life-history traits in nature.

1. Introduction

Convergent evolution is the process by which similar features evolve independently in different evolutionary lineages [1]. This evolutionary phenomenon provides an ideal means for evaluating adaptation, because the same phenotype evolves repeatedly and independently under similar circumstances [2]. Migratory animals often exhibit similarities in behavioural, physiological, morphological and life-history traits, such as the migratory syndromes shared by insects, fish and birds [3]. These similarities are thought to have arisen through natural selection, which favours convergent solutions to common problems facing migratory animals [4]. To better understand migration, its evolution and its ecology, there is a need for the development of hypotheses that advance general migratory theory and have cross-species applicability [3].

Partial migration is one of the common forms of migration in which a population contains both migratory and resident individuals [5,6]. Whether alternative migratory tactics are adopted is dependent on life-history traits called ‘threshold traits’ [7]. These traits exhibit two properties: a threshold value that divides the phenotypic distribution (e.g. migrants and residents), and an underlying ‘liability’ trait that differs in a continuous variable [8]. If the value of the liability trait exceeds the threshold, an individual will choose a different migratory tactic than if the value of the trait is below the threshold [9]. The threshold value often varies among populations because genetic variability and environmental differences can affect the trait [10]. Threshold traits have been used to describe the inheritance and evolution of partial migration. A number of studies have examined ecological factors underlying the diversity of specific threshold traits in partially migratory animals, but there have been few cross-species investigations in nature.

The trade-off between benefits and costs is a fundamental mechanism driving life-history divergence. Thus, the threshold traits of partially migratory animals will coevolve to maximize fitness under a given set of migratory conditions. Costs of migration include increased metabolic and energetic requirements during migration [11], decreased reproductive output [12] and higher predation risk [13]. These effects will presumably increase as the migration distance increases. For partially migratory animals, migration costs affect only the migratory individuals, so migration cost is expected to be a general factor that results in the diversity of threshold traits in partially migratory animals.
Partial migration is evident in many species of salmonid fish, such as the white-spotted char, Salvelinus leucomaenis and masu salmon, Oncorhynchus masou. All females and most males in both species live for several years in rivers, then descend to the sea to feed [14,15]. After this feeding migration, these anadromous fish become sexually mature and return to the natal river to spawn [14,15]. By contrast, some males in both species become sexually mature at the parr stage (the darkly pigmented, stream-dwelling juvenile stage of the salmonid life cycle) [14,15]. As with other salmonids, the alternative migratory tactics in both species are associated with alternative reproductive phenotypes during spawning. Anadromous males have high fertilization success by competing for females using their large body size, whereas smaller precocious mature parr achieve fertilizations by adopting a sneaking behaviour [16]. In salmonid males, life-history divergence is thought to depend on whether the current size or growth rate at the time of the life-history decision will result in the male exceeding a threshold size [17,18], such as the size at maturity for parr. Males that exceed this size become precocious mature parr, whereas those below this size become anadromous (see electronic supplementary material, figure S1a). As the threshold size at maturity in males decreases in a population, the proportion of mature male parr increases within the population (see electronic supplementary material, figure S1a,b). Thus, in salmonid populations with high migration costs, the threshold size at maturity in males will be small, resulting in more resident individuals within a population.

However, quantifying the effects of migration costs on threshold size at maturity in males is difficult because other environmental factors can covary with migration costs. Namely, the threshold size at maturity in males may be shaped by other evolutionary and plastic responses to environmental gradients that correlate with migration distance. Recent studies on the partially migratory Atlantic salmon, Salmo salar, have shown that threshold size at maturity in males varies among populations, and the variation is influenced by migration costs such as altitude or migration distance [19,20]. However, these studies did not measure the effects of migration costs on threshold size at maturity in males independently, because they did not examine correlations between migration costs and other environmental factors. For example, water temperature often decreases with increasing altitude, so it can also affect the diversity of threshold size at maturity in males (e.g. [21,22]). Thus, to test the hypothesis that migration cost is a general factor in shaping the diversity of threshold traits, the effects of migration costs on the threshold traits must be quantified under a sampling design that considers multicollinearity among environmental factors.

In this study, we collected data from 10 tributaries in a single river system to investigate the hypothesis that increased migration cost (i.e. distance of migration) causes a decrease in the threshold size at maturity in males (i.e. promotes residency) in two sympatric salmonids: white-spotted char and masu salmon. The study was designed to independently quantify the effects of migration costs on the threshold sizes (see Material and methods). Our objective was to identify the evolutionary factors that promote diversity in threshold size at maturity in males of the two species. We would expect to find the following three schematic scenarios (see electronic supplementary material, figure S1c).

(i) The threshold size at maturity in males decreases with increasing distance from the sea as an indicator of migration cost.
(ii) The proportion of male individuals that mature without migrating to the sea increases with increasing distance from the sea.
(iii) The divergence of threshold size at maturity in males covaries between the two species among tributaries.

2. Material and methods

(a) Study area

This study was conducted in the Kushiro river system in eastern Hokkaido, Japan. We chose one reach in each of 25 tributaries based on the presence of typical biotopes for salmonid parr and spawning. We measured a number of environmental factors in each reach (see below for details). We then chose 10 of the tributaries (figure 1) in which distance from the sea was not correlated with other environmental factors at the site (see electronic supplementary material, table S1). In these 10 tributaries, the mean length of the study reach was 81 m (range: 55–90 m; see electronic supplementary material, table S2). In the Kushiro river system, records of hatchery releases of white-spotted char and masu salmon exist only for Lake Kussharo.

(b) Fish collection and measurement

Sampling was conducted between 13 and 16 September 2010, during the spawning season of salmon and about one month before the spawning season of char. Parr were collected using an electrofisher (200–300 V DC, model 12B, Smith-Root, Vancouver, WA) and a dip net (30 cm width, 3 mm mesh). All parr were immediately frozen for subsequent laboratory measurements. Anadromous adults were collected in some tributaries, but were not analysed. Tributary 9 was re-sampled on 9 November 2010 as no mature parr were collected during the first sampling. Because age 1+ parr cease to grow from September to November [23], age greater than or equal to 1+ parr were included in the analyses without any size transformation.

The following variables were determined for each individual after defrosting: fork length, sex, reproductive state (mature or immature, by visual inspection of gonads) and age (determined using otoliths).

(c) Measurement of environmental factors

As a surrogate for migration cost, the distance from the sea was measured for each tributary using a portable GPS receiver (GPSMAP60CSx, Garmin, Olathe, KS) and 1:25,000 scale topographic maps (http://www.gsi.go.jp/). Previous studies have used altitude as a surrogate for migration cost, but altitude itself can be an indicator of other environmental factors such as water temperature (e.g. [24]). To avoid multicollinearity, altitude was not used as a model parameter. In addition to distance from the sea, eight environmental factors were measured in each tributary: water temperature, tributary width, tributary depth, velocity, substrate, slope, riverine fish growth and fish density (see electronic supplementary material, tables S2 and S3). The environmental factor values in the study reaches represent those of each tributary (see electronic supplementary material, appendix A). Water temperature was measured at hourly intervals in each tributary study reach using fixed data loggers (Stow-Away TidbiT, Onset Computer Corp., Bourne, MA) deployed on the stream beds from June to August 2010 and November 2010 to May 2011. Mean temperature (averaged for the whole study period) and monthly temperature (averaged for each month) were used as indices of water temperature. Tributary width was measured at 5 m intervals in each study reach using otoliths).
reach. Tributary depth, velocity and substrate were measured at 5 m intervals with three evenly spaced transects (1/4, 1/2, 3/4). Substrate composition was sorted into six classes: sand-silt (less than 2 mm), category 1 (as categorized in electronic supplementary material, table S2); gravel (2–16 mm), category 2; pebble (17–64 mm), category 3; cobble (65–256 mm), category 4; boulder (greater than 256 mm), category 5; irregular bedrock, category 6. The mean and standard deviation of the categorical values were used as indices of substrate composition [25]. Velocity was measured at 60% of the depth from the surface to the bed using a propeller-type meter (VR-301; Kenek Co., Tokyo, Japan). Riverine fish growth was quantified using the average fork length in age 0+ parr. Fish densities were estimated in a reach of each tributary during fish collection using the two-pass removal method (model M_all program CAPTURE; available at http://www.mbrwrc.usgs.gov/software/index.html). The density of each species and the combined density of the two salmonids were used as indices of fish density.

(d) Data analyses

To assess threshold sizes at maturity in males, we first calculated the probability of being mature at a particular combination of variables (i.e. maturity ogive) using logistic regression. The logistic regression model was described as logit \( p = a + b_{FL} + b_{Age} + b_{tributary} \) where \( p \) is the probability of maturation, \( a \) is the regression constant, \( b_{FL} \), \( b_{Age} \) and \( b_{tributary} \) are regression coefficients, \( b_{tributary} \) is a tributary-specific constant, FL is the fork length and Age is age in years. The model parameters were estimated using the maximum-likelihood method with a binomial distribution of errors. The significance of model parameters was evaluated using the likelihood-ratio test and the Akaike information criterion (AIC).

The threshold size at maturity in males \( L_{50, \text{first}} \) was defined as the fork length at which the probability of maturing at the first age at maturity is 50%. The ages at first maturity are age 1+ in charr [15] and age 0+ in salmon [22]. At the age of first maturity, the fork length at 50% probability of maturing \( L_{50, \text{first}} \) is the same as the fork length at which the probability of becoming mature is 50%, a feature of the probabilistic maturation reaction norm (PMRN) [26]. We calculated \( L_{50, \text{first}} \) using regression coefficients of the logistic regression described as \(- \left( a + b_{Age} + b_{tributary} \right) / b_{FL} \), where \( Age = 0 \) and 1 for salmon and charr, respectively. We used \( L_{50, \text{first}} \) to test for interspecific covariation and to examine intraspecific variation along environmental gradients. The proportion of male individuals that matured without migrating to the sea was quantified using the maturity rate for all fish exceeding the minimum age at maturity (i.e. charr \( > 1+ \); salmon \( > 0+ \)). The coefficient of variation (CV) was used as a measure of variation in \( L_{50, \text{first}} \) among tributaries within species. Interspecific differences in CV of \( L_{50, \text{first}} \) were tested using the Z-test [27]. All statistical analyses were performed using R v. 2.14.0 for Windows (http://www.r-project.org/).

3. Results

A total of 1106 charr and 890 salmon were caught during the study. Mature male parr were captured in all tributaries, but no mature female parr were collected (see electronic supplementary material, table S3). The maturity rate for all fish exceeding the minimum age at maturity varied considerably among tributaries (range: 17–100% for charr \( > 1+ \) and 3–93% for salmon \( > 0+ \)).

The logistic regression analyses identified significant effects of the tributary, fork length and age on the probability of maturing for both charr and salmon males (table 1). The probability of maturing increased with increasing fork length and age, but these relationships differed among tributaries, resulting in substantial variation in \( L_{50, \text{first}} \) values among tributaries (see electronic supplementary material, table S3 and figure S2). Although the effect of age was insignificant for charr, the model incorporating all three variables \( (b_{tributary}, \text{Age and FL}) \) had the smallest AIC value for both species (\( \Delta \text{AIC} > 1.5 \)).

There was a positive correlation between the \( L_{50, \text{first}} \) values of charr and salmon (figure 2), suggesting there was spatial covariation of threshold size at maturity in males between the species. Among the nine environmental variables we measured, only distance from the sea was negatively correlated with \( L_{50, \text{first}} \) values in both species (table 2). None of the monthly temperatures were significantly correlated with \( L_{50, \text{first}} \) values in both species (see electronic supplementary material, table S4). Moreover, more complex models did not perform better at explaining the probability of maturing for either species (see electronic supplementary material, appendix B). Distance from the sea was not significantly correlated with the other eight environmental variables (see electronic supplementary material, table S1). This indicates that threshold size at maturity in males \( (L_{50, \text{first}}) \) decreased with increasing distance from the sea, an indicator of migration cost (figure 3). The decrease in the threshold size at maturity in males \( (L_{50, \text{first}}) \) was associated with a significant increase in the maturity rate for all fish exceeding the minimum age at maturity in both charr \( (r = -0.802, p = 0.005) \) and salmon \( (r = -0.861, p = 0.001) \). The maturity rate for all fish exceeding the minimum age at maturity increased as the distance from the sea increased, although the correlation with charr was insignificant (charr, \( r = 0.265, p = 0.460 \); salmon, \( r = 0.663, p = 0.037 \)).

The CV of \( L_{50, \text{first}} \) differed significantly between charr and salmon \( (Z_{1,18} = 2.07, p = 0.038) \); it was more than twice as large in salmon (23%) as in charr (11%).
Table 1. Results of a logistic regression of fork length, age and tributary on the probability of maturing for age 1+ male charr and 0+ male salmon. In L, log likelihood for the full model; \( G^2 \), statistic of the likelihood-ratio test.

<table>
<thead>
<tr>
<th>variable</th>
<th>ln L</th>
<th>( G^2 )</th>
<th>d.f.</th>
<th>coefficient</th>
<th>( p )-value</th>
</tr>
</thead>
<tbody>
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<td>(a) white-spotted char</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>fork length</td>
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<td>0.084</td>
<td>&lt;0.001</td>
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<tr>
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<td></td>
<td></td>
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<td>1.172</td>
<td>0.062</td>
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<td></td>
<td>9</td>
<td>−2 470 to 2 017</td>
<td>0.111</td>
</tr>
<tr>
<td>constant</td>
<td></td>
<td>−13 34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) masu salmon</td>
<td>−98.0</td>
<td>57.9</td>
<td>1</td>
<td>0.133</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>fork length</td>
<td></td>
<td></td>
<td>1</td>
<td>2 852</td>
<td>0.001</td>
</tr>
<tr>
<td>age</td>
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<td></td>
<td>1</td>
<td></td>
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<tr>
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<tr>
<td>constant</td>
<td></td>
<td>−13 443</td>
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</table>

![Figure 2](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/on June 30, 2017)

Figure 2. Relationship between white-spotted char \( L_{50, \text{first}} \) and masu salmon \( L_{50, \text{first}} \) in 10 tributaries. \( r \): Pearson’s correlation.

4. Discussion

The threshold sizes at maturity (\( L_{50, \text{first}} \)) in male charr and salmon in a given tributary were correlated. In both species, the size decreased with increasing distance from the sea. This supports our hypothesis that increased migration costs result in a decreased threshold size at maturity in males of both species, thereby promoting residency (see electronic supplementary material, figure S1c).

Distance from the sea to the spawning ground is an indicator of migration cost (energy expenditure and mortality) in anadromous fishes [28]. For example, increased migration costs are associated with a decrease in female ovarian investment and male gonadal mass (e.g. females [12]; males [29]). Male energy reserves and secondary sexual characters decrease with increasing migration cost [30]. The median natural mortality during downriver migration in Atlantic salmon is 2.3% km$^{-1}$ ([31] and references therein). Therefore, the fitness of anadromous individuals decreases with an increase in the distance between the spawning grounds and the sea. By contrast, the fitness of resident individuals is expected to be unrelated to distance from the sea, because they remain their entire life in their natal stream. Bohlin et al. [32] showed that the fitness of resident brown trout, Salmo trutta, did not change with altitude, whereas the fitness of anadromous brown trout tended to decline with altitude, an indicator of migration cost in that study. Therefore, the threshold size at maturity in male salmonid parr is expected to decrease with distance from the sea, an indicator of migration cost, to promote residency.

Genetic factors and plasticity can affect the diversity of life-history traits. The threshold size at maturity of fishes is thought to be influenced by both genetic [33] and environmental (i.e. plastic) [34] factors, but their relative contributions to the PMRN remain unclear [17]. With respect to plasticity, Jonsson et al. [35,36] noted that the threshold size at maturity in Atlantic salmon was affected by both water temperature and food quality. In addition, Morita et al. [21] showed in a transplant experiment that the threshold size at maturity in male charr varies with river width and temperature. However, it is difficult to explain why the plasticity affected the divergence of threshold size at maturity in males, which is related to migration cost. In general, some proportion of salmonids in a population mature as precocious males and they stay in their natal stream without going to the sea. For plasticity to be able to affect the threshold size at maturity in males, male parr would have to be able to estimate their distance from the sea without going to sea. On the other hand, in salmonid fishes, anadromous adults can exhibit very precise natal homing [37], and most phenotypic traits are heritable [38]. In Atlantic salmon, the threshold sizes at maturity of male parr differ genetically among geographically distinct populations [39]. Taken together with our results, this suggests that genetic factors that correspond to the variation in migration cost drive the diversity of threshold size at maturity in males.

Convergent evolution of similar phenotypes in similar environments may be a general evolutionary phenomenon given its prevalence at a variety of taxonomic scales [1]. A number of recent specific studies have tested factors underlying the evolution of partial migration (e.g. table 1 of Chapman et al. [6]). Our results imply that migration costs drive convergence of the threshold traits for partial migration in two sympatric salmonid fishes. Migration costs such as energy expenditure, mortality and predation during migration are expected to be critical factors affecting the fitness of...
migratory animals, thus animals determine their migratory tactics to reduce the migration costs (birds [13]; mammals [40]). In addition, populations that migrate long distances optimize their life-history traits to adapt to the increased migration costs (fish [12,30]; birds [41]; invertebrates [42]). Therefore, migration costs might be one general selective factor that produces convergence in migratory tactics and life-history traits.

Understanding how continuous phenotypic variation across environmental gradients is generated and maintained is critical to our understanding of adaptive evolution [43]. However, most previous studies of adaptive evolution have considered dichotomous environments [44]. This approach is useful for identifying the causes of phenotypic variation, but is problematic for understanding the incidences of underlying patterns of phenotypic variation [44]. Our results suggest that variation in $L_{50}$ differed between charr and salmon, whereby the CV for $L_{50}$ in salmon was nearly twice as large as in charr. The difference in the CV of $L_{50}$ might reflect the homing accuracy of the two species, with salmon homing more accurately (and so showing more local adaptation) than charr.

We demonstrated an independent effect of migration cost on threshold size after accounting for correlations among possible environmental factors. Nonetheless, the possibility of unaccounted factors affecting plastic effects on the threshold size at maturity in males cannot be ruled out. Further study is needed to evaluate this possibility by conducting common garden experiments to better understand how migration costs can affect threshold size.

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Data accessibility. Fish and environmental data are uploaded as electronic supplementary material.

**References**
