Plasticity in probabilistic reaction norms for maturation in a salmonid fish

Kentaro Morita1,* and Jun-ichi Tsuboi2

1Hokkaido National Fisheries Research Institute, Fisheries Research Agency, Kushiro 085-0802, Japan
2Yamanashi Fisheries Technology Center, Yamanashi 400-0121, Japan
3National Salmon Resources Center, Fisheries Research Agency, Sapporo 062-0922, Japan
*Author for correspondence (moritah@affrc.go.jp).

1. INTRODUCTION

The relationship between body size and the probability of maturing, often referred to as the probabilistic maturation reaction norm (PMRN), has been increasingly used to infer genetic variation in maturation schedule. Despite this trend, few studies have directly evaluated plasticity in the PMRN. A transplant experiment using white-spotted char demonstrated that the PMRN for precocious males exhibited plasticity. A smaller threshold size at maturity occurred in charr inhabiting narrow streams where more refuges are probably available for small charr, which in turn might enhance the reproductive success of sneaker precocious males. Our findings suggested that plastic effects should clearly be included in investigations of variation in PMRNs.

Keywords: mature male parr; phenotypic plasticity; threshold; probabilistic reaction norm

2. MATERIAL AND METHODS

To evaluate the plasticity in PMRNs in a natural environment, a transplant experiment was conducted in the Onbetsu River, eastern Hokkaido, Japan (figure 1). The experimental design was set up in a way to control for any potential genetic effects on PMRN. A total of 1500 fry (age 0+ year) were captured at a donor site using electrofishing and night-time hand netting on 10–11 August 2007. Fry captures were conducted in a river section approximately 1 km long. Captured fry were initially transferred to a single fish cage (60 × 50 × 50 cm), mixed well and then divided into five different cages. Each of the five cages held 300 fry. The donor site was located approximately 40 km upstream of the river mouth, where the main spawning ground of the anadromous white-spotted char is situated (fig. 8 of Morita et al. 2009). Because the number of spawning adults at the donor site exceeded 1000 in the previous year, the collected fry represented a large sample of families. Three hundred fry were released at each of five different transplant sites on 11 August 2007. The fork lengths of 30 fry were measured at each transplant site before release, and no significant differences existed among sites (mean ± s.d., 54.1 ± 9.2 mm; analysis of variance, \( F_{4,17} = 1.77, p > 0.05 \)). All transplant sites were separated by several impassable dams and lacked charr, probably due to local extinctions (Morita & Yamamoto 2002).

We sampled mature and immature age 1+ year charr in late September to early October 2008, during the breeding season of this species (table 1). In total, 178 charr (11.9%) were recaptured at the transplant sites, and 76 age 1+ year charr were captured at the donor site via electrofishing. The following variables were determined for these fish: fork length (millimetres), somatic weight (grams), sex and reproductive state by visual inspection of the gonads, and age confirmation using otolith analysis. Parr densities were estimated in a 100 m reach of each site using the three-pass removal method (model \( M_{by} \), program \( CAPTURE \), available at http://www.mbr-pwrc.usgs.gov/software/index.html). At the same time, four physical characteristics (river width, depth, velocity and substrate code) were measured in each 100 m reach of each site following Morita et al. (2004). Water temperatures were measured at each site at hourly intervals using data loggers (Stow-Away TidbiT, Onset Computer) from August 2007 to September 2008 (figure 1). Because one logger was lost in late April 2008, the mean temperatures from May to August 2008 were used as representative temperatures for each site.

A PMRN method based on logistic regression (Heino et al. 2002) was used to analyse the relationships between body size and the probability of becoming mature for age 1+ year male parr. Because no charr matured at age 0+ year (Morita et al. 2009), maturing charr of age 1+ year were considered to be first-time matures. The logistic regression model for this study was described as

\[
\logit(p) = a + b_1/l + \epsilon_{\text{site}},
\]  
(2.1)

or alternatively, with the site effect replaced by appropriate environmental factors

\[
\logit(p) = a + b_1/l + b_2E_1 + b_3E_2 + \cdots + b_kE_k,
\]  
(2.2)

where \( p \) is the probability of becoming mature, \( a \) is the regression constant, \( b_1 \) are regression coefficients, \( \epsilon_{\text{site}} \) is a site-specific constant, \( l \) is body size (fork length or weight) and \( E_k \) represents potential environmental factors: river width, depth, velocity and substrate code, temperature and density.

The model parameters were estimated using maximum likelihood methods. The significance of the model parameters was evaluated using the likelihood-ratio test and the Akaike information criterion (AIC). Details of the analyses are described in the electronic supplementary material. Because the use of fork length and somatic
weight yielded the same qualitative results and the use of length resulted in lower AIC values, only length-related results are reported below.

3. RESULTS
The logistic regression analysis identified significant effects of body size and site on the probability of maturing for male age 1+ year charr, indicating that the probability of maturing increased with increasing body size; however, these relationships differed across the transplant and donor sites (table 2). By replacing the site factor with various environmental factors, stepwise logistic regression ($p < 0.05$ to add and $p > 0.10$ to remove) identified three variables: fork length, river width and temperature, as the best predictors of the probability of maturing, although the effect of temperature was marginal (table 2). The model including these three variables exhibited the smallest AIC and thus represents the best model considered here. The resulting logistic model predicted 83.6 per cent of the maturation. The regression coefficient for river width was negative, while those for fork length and temperature was positive (table 2). Thus, the probability of maturing for male age 1+ year charr increased with increases in fork length and temperature but decreased with increases in river width (figure 2). In other words, threshold size at maturity increased with increasing river width and decreased with increasing temperature (electronic supplementary material).

4. DISCUSSION
Our transplant experiment using white-spotted charr demonstrated that the PMRN, i.e. the relationship between fish body size and the probability of becoming mature at a given age, exhibited plasticity. Furthermore, two environmental variables, river width and temperature, were related to changes in the threshold size at maturity of precocious males. Although the relative importance of genetic versus plastic effects on changes in PMRNs remains controversial, recent studies have increasingly incorporated both types of effects into a general understanding of changes in the PMRN (Kuparinen & Meri 2007; Marshall & Browman 2007). Our findings support this approach; in particular, plastic effects should clearly be included in investigations of variation in PMRNs.
Male salmonid fishes exhibit two alternative mating tactics: sneaking and fighting (Gross 1991). In general, small males sneak, whereas larger males fight for access to females. In our study system, the breeding population structure includes precocious and larger anadromous charr (mean fork length ± s.d., precocious males: 155 ± 40 mm, n = 148; anadromous males: 440 ± 92 mm, n = 57; anadromous females: 519 ± 96 mm, n = 52). Therefore, precocious male charr require a sneaking tactic. In addition to body size, several other environmental factors could affect the reproductive success of sneakers, e.g. refuge availability, frequency of sneakers and water level (Gross 1991).

The unexpected finding in this study was that the river width was the most important environmental factor affecting the probability of maturing at a given size for precocious males. Increasing river width was associated with lower probabilities of maturing at a given size. This finding was similar to the spatial variation in threshold size at maturity observed in Atlantic salmon: threshold size at maturity decreases in the upstream direction (Baum et al. 2004; Aubin-Horth et al. 2006). We deduced that the greater proportion of edge habitat with overhanging cover in narrow streams (cf. Kozel & Hubert 1989) might be positively associated with refuge availability for sneakers.

The experiments were made possible by sampling permits issued by the Governor of Hokkaido.

We thank Munetaka Shimizu for valuable suggestions on the physiological aspects of maturation. This work was supported by a Grant-in-Aid for Young Scientists B (No. 19780155) from the Japan Society for the Promotion of Science.


