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ORIGINAL PAPER

# Sexual size dimorphism in a landlocked Pacific salmon in relation to breeding habitat features

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**Abstract** Many animal species exhibit size dimorphism between sexes. Sexual selection, whereby male–male competition favors larger body sizes, has been considered a likely cause of sexual size dimorphism. Habitat features in breeding areas could affect the outcome of male–male competition, yet few attempts have been made to relate breeding habitat features with interpopulation variation in sexual size dimorphism. In this study, we examined interpopulation variation in sexual size dimorphism by studying the landlocked amago salmon (*Oncorhynchus masou ishikawae*) at a microgeographic scale. We found that female body size was independent of stream size but that male body size decreased with smaller stream sizes. A likely explanation is that the relationship between reproductive success and the size of males is influenced by the availability of refuges that are only available to small-bodied males. Sexual differences in body size increased with decreasing stream sizes, supporting the hypothesis that the reproductive success of larger males is reduced in smaller streams. In contrast, the maturation-length threshold increased with stream size for both sexes. The stream-size-based interpopulation variation in sexual size dimorphism and size at maturity in landlocked amago salmon may therefore have arisen through a combination of sexual and natural selection.

**Keywords** Amago salmon · Competition · Local adaptation · Rensch's rule · Sexual selection

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## Introduction

Many animal species show sexual size dimorphism (SSD). Males typically evolve larger body sizes than females in polygynous species, whereas females tend to evolve larger body sizes than males in promiscuous mating systems and situations where there is strong dependence of fecundity on body size (Stearns 1992; Cox et al. 2003; Pyron et al. 2013). Among species or populations, male body sizes usually vary more than female body sizes, a macroecological pattern known as Rensch's rule (Székely et al. 2004; Young 2005; Dale et al. 2007). Rensch's rule can be evaluated by regressing average female body sizes against average male body sizes: a slope less than 1 supports the rule (Fairbairn and Preziosi 1994; Young 2005). Sexual selection via male–male competition that favors larger male body sizes has been considered a cause of SSD and Rensch's rule. For example, domesticated animals often showed reduced SSD or defy Rensch's rule compared with their wild relatives (Petersson and Järvi 1993; Polák and Frynta 2009; Remeš and Székely 2010; but see Polák and Frynta 2010). The patterns of SSD could also vary within a species among populations because habitat features at different breeding sites could affect the outcome of male–male competition. However, few attempts have been made to relate breeding habitat features with interpopulation variation in SSD (Holtby and Healey 1990; Jonsson and Jonsson 2015).

Salmonid fishes show strong homing instincts, wherein 95–99% of fish that survive to adulthood return to their natal breeding site, leading to populations with a variety of local adaptations to features of their breeding ground (Taylor 1991; Quinn 2005). If the breeding ground is structurally clear and imposes no environmental constraints preventing behavioral performance, larger males are expected to have higher reproductive success than smaller males (Fleming 1996; Quinn 2005). However, structurally complex or shallow-water breeding habitats could make females more accessible to smaller males via increased availability of refuges (Holtby and Healey 1990; Gross 1991; but see Koseki et al. 2002). Recently, Jonsson and Jonsson (2015) showed that SSD in anadromous brown trout (*Salmo trutta* L.) decreased with stream discharge ($m^3/s$, an index of stream size), suggesting that narrow streams may limit the competitive success of large males. Other studies on anadromous salmonids have shown that size at maturity of precocious males tends to decrease in the upstream direction, which is an indicator of migration cost (Baum et al. 2004; Aubin-Horth et al. 2006; Sahashi and Morita 2013). These studies suggested that individuals should mature at a smaller size without migration (i.e. adoption of resident tactics) in a high-migration-cost situation. Moreover, several studies have found latitudinal variation in SSD in relation to macrogeographic environmental gradients (Blanckenhorn et al. 2006; Tamate and Maekawa 2006; Estlander et al. 2016). As such, it may be difficult to examine the effects of habitat features on SSD at macrogeographic scales, especially for migratory species.

In the present study, these potentially confounding factors were ameliorated by the use of a landlocked Pacific salmon (amago salmon *Oncorhynchus masou ishikawae* Jordan and McGregor) that is non-migratory. Amago salmon remain in the vicinity of the breeding area throughout their lifespan (Nakano et al. 1990). It is therefore expected that local adaptation should be common, even at the microgeographic scale. We hypothesized that the patterns of SSD vary among populations in relation to breeding habitat features that affect the outcome of male–male competition. More specifically, we hypothesized that female body size is independent of stream size but that male body size decreases in narrow streams where the reproductive success of small males is elevated owing to increased shallow areas, which constitute refuges from larger, dominant males.

## Materials and methods

Amago salmon is a subspecies of the more widespread masu salmon *Oncorhynchus masou* (Brevoort) that is endemic to the northwestern Pacific. Although a few populations show anadromy, most amago salmon are landlocked, including in streams of western Japan (Kato 1991). Native landlocked amago salmon inhabit colder headwaters isolated by waterfalls, dams, or high-temperature thermal barriers. In this study, amago salmon were collected using a backpack electrofisher (Model 12B, Smith-Root, Inc., Vancouver, Washington) and a dip net at eight isolated streams during the breeding season (October) in 2010 and 2011. All samples were from small, mountainous streams of the Fuji River basin of central Japan (N35°07′–35°57′, E138°21′–138°51′, altitude 690–1210 m, stream width 1.7–4.6 m; Table 1). The populations studied were genetically pure, native populations that are registered as locally endangered in Yamanashi Prefecture (Tsuboi et al. 2013).

In total, 844 salmon were caught during the study. The captured fish were anesthetized with phenoxyethanol (ca. 0.5 mL/L water), measured (fork length), categorized (immature, mature male, or mature female), and then returned alive to the capture site after recovering consciousness. Mature females were distinguished by a swollen urogenital opening and by the rounded impressions of eggs on the ventral side of the body. Mature males were distinguished by milt release when subjected to abdominal pressure.

To quantify the stream size, stream width was measured at 51 transects per stream, spaced approximately 2 m apart, within the sample reach. Stream depth was measured at three evenly spaced points (1/4, 1/2, 3/4) along the 51 transects. Maximum depth was also registered at each transect. The first principal component (PC1) of stream width, depth, and maximum depth was used as a metric of stream size. This axis accounted for 90.4% of the variation in these three variables, and all three of the variables had loading factors between 0.895 and 0.982. In addition, the proportion of a stream with <5 cm

**Table 1** Stream characteristics and body sizes (fork lengths, mean ± SD) of mature landlocked amago salmon across eight populations in the Fuji River system, central Japan

| River | Stream characteristics | | | Fork length at maturity (mm) | |
|---|---|---|---|---|---|
| | Depth (cm) | Width (m) | Altitude (m) | Males | Females |
| Sabu-sawa | 16.5 | 4.6 | 1110 | 139.1 ± 36.2 (19) | 167.1 ± 27.5 (24) |
| T2 (Kuroberaonsen) | 7.5 | 1.7 | 1140 | 124.8 ± 37.9 (30) | 173.1 ± 33.8 (15) |
| Tsubame-sawa | 8.6 | 2.7 | 970 | 121.3 ± 33.1 (23) | 175.4 ± 36.2 (11) |
| Itajiki-sawa | 7.9 | 2.1 | 1200 | 115.9 ± 31.8 (32) | 156.5 ± 17.3 (11) |
| Takanari-sawa | 21.0 | 3.7 | 690 | 192.4 ± 33.4 (11) | 172.2 ± 26.5 (10) |
| Toiwa-sawa | 10.0 | 3.1 | 940 | 160.0 ± 54.6 (10) | 169.4 ± 22.2 (10) |
| Kage-sawa | 10.2 | 3.5 | 1210 | 169.5 ± 38.1 (13) | 170.2 ± 17.2 (9) |
| Kadoi-sawa | 6.7 | 1.9 | 770 | 134.3 ± 40.4 (31) | 203.4 ± 18.9 (10) |

The number of specimens measured is given in parentheses depth was calculated to quantify the availability of shallow area. Because amago salmon with a length of approximately 20 cm fork length have a body depth of about 5 cm, stream depths of <5 cm were deemed to constitute refuge for small fish from competition with large fish.

The traditional method for analyzing SSD was followed here by simply comparing the mean length of adults (i.e. sexually mature individuals) between males and females. In addition, the maturation-length threshold relative to immature fish was calculated using parameters obtained by multinomial logistic regression analyses, as $-\beta/\alpha$, where $\alpha$ and $\beta$ are the regression slope and intercept, respectively (cf. Sahashi and Morita 2013). For each population, two measures of SSD were calculated: SSD-mean = mean length of mature males/mean length of mature females, and SSD-threshold = maturation-length threshold of males/maturation-length threshold of females. As a test of Rensch's rule, the logarithm of female length was regressed against the logarithm of male length. Because all lengths were subject to measurement error, model II (reduced major axis) regression was used to fit and estimate the parameters (McArdle 1988; Fairbairn 1997). Bias-corrected percentile bootstrap confidence intervals were calculated for each parameter from 10,000 re-samplings (cf. Manly 2007). Model II analysis of variance (ANOVA) was used to quantify the magnitude of variation in length of sexually mature individuals both within and between populations (Sokal and Rohlf 2012). Covariance among populations for the measures of SSD, mean length of adults, maturation-length threshold, proportion of stream with <5 cm depth, and stream size was tested using Spearman's rank correlation coefficient.

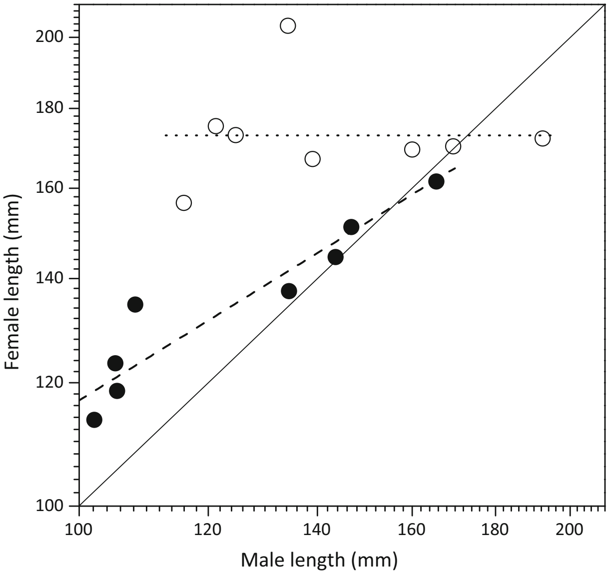
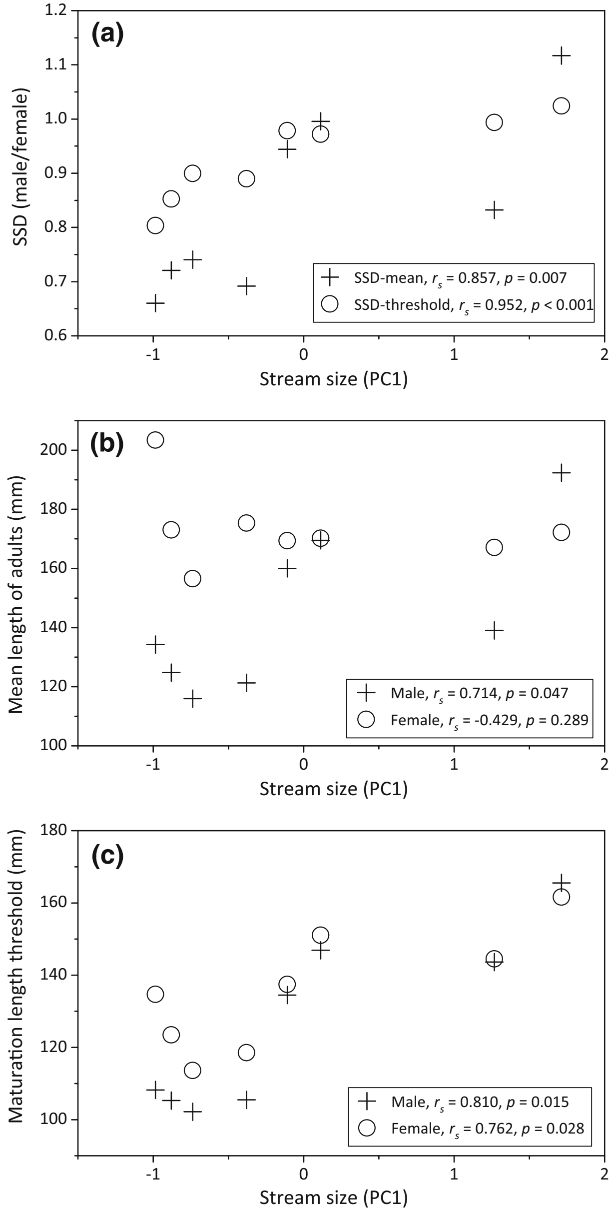


**Fig. 1** Relationship between male and female lengths among eight landlocked populations of amago salmon. *Open circles* mean length of adults, $r_s = -0.024$, $p = 0.955$. *Solid circles* maturation-length threshold, $r_s = 0.976$, $p < 0.001$. The *dashed line* is the model II regression fit: $\log_{10}Y = 0.648 \times \log_{10} X + 0.772$. The *dotted line* indicates the mean female length independent of male lengths. The *solid line* represents 1:1

## Results

The mean lengths of sexually mature individuals differed significantly among populations for both males and females (ANOVA, males: $F_{7,161} = 7.89$, $p < 0.001$; females: $F_{7,92} = 2.65$, $p = 0.015$). Substantially greater interpopulation variation occurred for

**Fig. 2** Relationship between stream size and **a** sexual size dimorphism (SSD), **b** mean length of adults, and **c** maturation-length thresholds for eight landlocked populations of amago salmon



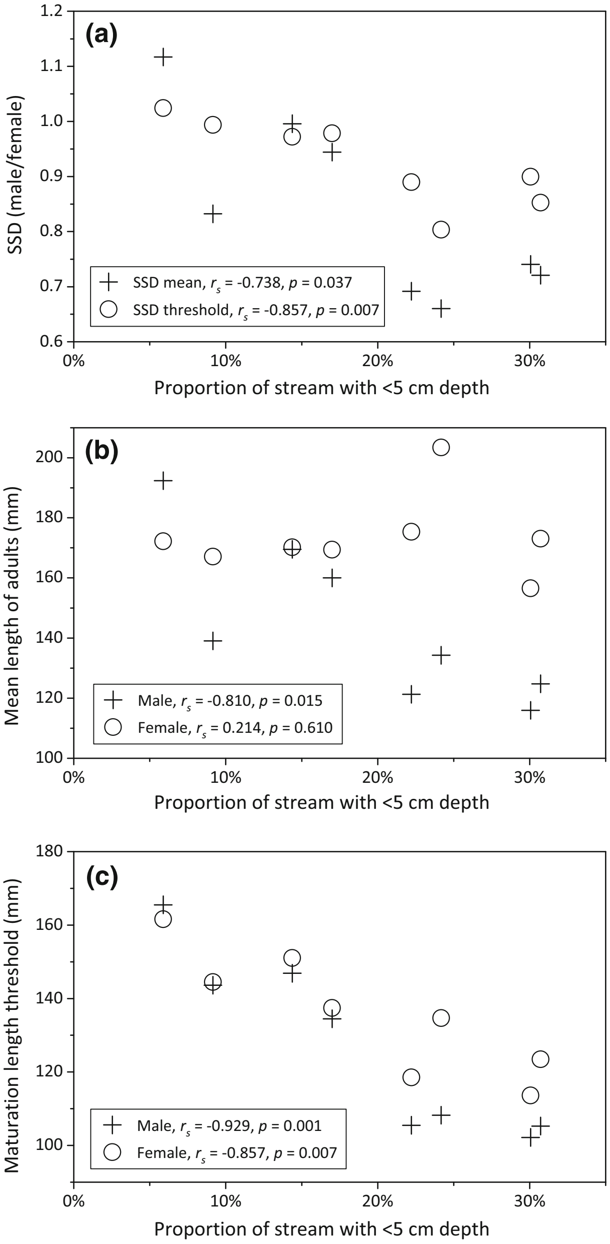


**Fig. 3** Relationship between the proportion of stream with <5 cm depth and **a** sexual size dimorphism (SSD), **b** mean length of adults, and **c** maturation-length thresholds for eight landlocked populations of amago salmon

males (25.0%) than for females (11.9%). The mean length of sexually mature females was independent of the lengths of males (Fig. 1). The maturation-length threshold of females increased with the maturation-length threshold of males: the regression line slope was less than 1, consistent with Rensch's rule (Fig. 1; 95% CI slope, 0.46–0.76). SSD-means and SSD-thresholds increased with stream size (Fig. 2a) and decreased with proportion of the stream with <5 cm depth (Fig. 3a). The mean length of sexually mature males increased with stream size and decreased with proportion of the stream with <5 cm depth, but the mean length of sexually mature females was independent of both metrics (Figs. 2b, 3b). Finally, for both sexes, the maturation-length threshold increased with stream size and decreased with proportion of the stream with <5 cm depth (Figs. 2c, 3c).

## Discussion

Our finding that greater interpopulation variation exists in amago salmon body size for males than for females is consistent with Rensch's rule and with observations of other anadromous salmonids (e.g. Young 2005; Jonsson and Jonsson 2015). Because female body size was less variable between populations, differential sexual selection toward male body size likely operates between populations of landlocked amago salmon. In this study, interpopulation variation in SSD was significantly correlated to stream size, supporting the hypothesis that male–male competition of salmonids is reduced in narrower streams (Jonsson and Jonsson 2015).

In our study area, the mean water depth was less than 10 cm and the stream proportion of <5 cm depth was 30% for small streams, yet the body length of sexually mature males ranged from 10–20 cm, equivalent to 2–5 cm body depth. Therefore, we can surmise that shallow areas constitute refugia for small males, though large males would be able to monopolize females through male–male competition in deeper areas. Indeed, precocious males were often observed using very shallow shoreline areas to escape larger attacking males during a spawning act. In addition, external fertilization in salmon enables small adult males to fertilize eggs by so-called sneaking tactics (Watanabe et al. 2008). Thus, the reproductive success of small males could eventually increase with the availability of refugia. In contrast, the reproductive success of females would be largely limited by fecundity, which is constrained by body size. Although recent advances in genetic parentage analysis have revealed the effects of adult body size on the number of offspring produced (Garant et al. 2001; Dickerson et al. 2005; Serbezov et al. 2010), few studies have examined the interaction of body size and breeding environment on reproductive success. Such a study would contribute to comprehensive understanding of the evolution of interpopulation variation in SSD.

In our study, the maturation-length threshold of both males and females increased with stream size. A positive relationship between maturation-length threshold and stream size might result from natural selection that acts on both sexes. Xu et al. (2010) showed that, in brook trout, extremely low summer water flows reduced survival of large fish only in small streams and had no significant effects on small fish. Therefore, natural selection would favor early maturation in small streams, resulting in smaller maturation-length thresholds for both sexes, thereby decreasing mortality risk before maturation. Similar positive relationships between maturation length and stream size were reported previously in salmonids (Jonsson et al. 1991, 2001; Kikko et al. 2011). The interpopulation variation in SSD and size at maturity (and specifically the relationships to stream size) in the landlocked amago salmon likely arose via a combination of sexual and natural selection.

The observed patterns in SSD and maturation size could result from genetic changes (Piché et al. 2008), phenotypic plasticity (Morita et al. 2009), or a combination of both. Irrespective of mechanism, however, the pattern can be viewed as a local adaptation in each stream. Accordingly, each local population, rather than the amago salmon subspecies as a whole, would be an evolutionary significant unit. Local populations of landlocked amago salmon are highly threatened by habitat deterioration and hybridization with stocked hatchery fish (Kawamura et al. 2012; Miyahara et al. 2012; Tsuboi et al. 2013), and therefore the conservation of each local population is urgent.

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