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Title

**Fish yawn: interpopulation variation in yawning characteristics of juvenile white-spotted
char *Salvelinus leucomaenis***

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20 **Number of tables: 1; number of figures: 3**

21

22 **Running head:** Interpopulation variation in juvenile char yawning

23

24 **Abstract**

25 Yawning is a stereotyped behavior and is prevalent across vertebrates, including fish. Although
26 intraspecific variation of yawning behavior in a population has been observed in several taxa, no
27 studies have demonstrated differences in yawning behavior among populations. This study
28 compared yawning behavior among four local populations of juvenile white-spotted char
29 *Salvelinus leucomaenis*. Although there were no differences in the frequency of yawning among
30 the populations, the duration of yawns differed significantly among the four local populations,
31 and between two behavioral states of juveniles, i.e., during swimming and during station-
32 holding behavior, in which juveniles are sedentary on the substrate. Juveniles from Station 1
33 showed yawns with shorter duration than those from Stations 2 and 3 during station-holding
34 behavior. Juveniles from Station 2 showed yawns with longer duration than those from Station 4
35 during swimming. Although we could not determine any ecological or evolutionary factors
36 behind the variations in yawn duration, yawning behavior could be affected by local
37 environmental factors, such as predation pressure. This is the first study demonstrating
38 interpopulation variation of yawning behavior in animals.

39

40 **Key words:** Yawning, Ectotherm, Mouth-gaping, Interpopulation variation, Salmonid

41

42 **Introduction**

43 Yawning is a common and conspicuous stereotyped behavior in vertebrates (Myrberg 1972;
44 Graves and Duvall 1983; Miller et al. 2010; Zannella et al. 2015; Bakkegard 2017). It is defined
45 as a sequence of actions consisting of three phases: an involuntary and powerful mouth gaping,
46 a temporary period of peak muscular contraction, and a passive closure of the jaw (Barbizet
47 1958; Gallup 2022). Yawning has been studied from both physiological and behavioral
48 perspectives. For example, yawning has been shown to promote brain cooling and cranial
49 circulation (Gallup and Eldakar 2013), and consequently increase physiological arousal
50 (Matikainen and Elo 2008; Gallup 2022) and behavioral activity (Sauer and Sauer 1967;
51 Zannella et al. 2015; Bakkegard 2017; Yamada and Wada 2023a). The pervasiveness of
52 yawning behavior and the several hypotheses regarding its function suggest that it may be
53 subject to evolutionary forces and/or exhibit plastic changes in response to the local
54 environment.

55 Microevolution through evolutionary forces, such as natural selection and spatial
56 sorting, results in functional traits that enhance survival (Grant and Grant 2002; Donihue et al.
57 2020), reproductive success (Emlen 2008; Oufiero et al. 2014), and local persistence (Phillips et
58 al. 2006; Bolnick et al. 2009; Shine et al. 2011; Yamada and Wada 2021; Comerford and Egan
59 2022). Microevolution often causes genetic variations in these traits among local populations

(Kawecki and Ebert 2004; Edelaar and Bolnick 2012). For example, small anoles have variations in toe-pad size among populations, perhaps because of geographic variations in the intensity of hurricane-induced natural selection (Donihue et al. 2018, 2020). Juveniles of stream fishes isolated by migration barriers have been shown to have more effective behavior against downstream dispersal compared to those from local populations less affected by habitat fragmentation (Yamada and Wada 2023b; Yamada in press). These behaviors have been suggested to be partly the product of the spatial sorting caused by non-random downstream dispersal (Yamada and Wada 2024; Yamada in press).

Organisms also exhibit phenotypic plasticity in many traits in response to environmental conditions (Marchinko 2003; Kishida et al. 2007; Domenici et al. 2008), and the environmental conditions can differ among local populations. For example, interpopulation variation of jaw morphology in pumpkinseed sunfish is attributed to phenotypic plasticity induced by the shelled snails on which they feed rather than a response to evolutionary pressures (Mittelbach et al. 1999). Interpopulation variation in the anti-predator behavior of tiger snakes is suggested to reflect plastic responses to different predation threats among habitats (Bonnet et al. 2005).

Many behavioral studies of yawning implicitly assume that yawning is highly stereotyped within a species and lacks variation. However, the frequency and duration of

yawning behavior is known to exhibit interspecific variation (Zannella et al. 2015; Gallup et al. 2016; Massen et al. 2021). The frequency of yawning has been experimentally increased by inbreeding in the Sprague-Dawley rat (Urbá-Holmgren et al. 1990), suggesting that yawning behavior has evolutionary potential. The frequency and duration of yawning has also been shown to have plasticity in response to handling stress in budgerigars (Miller et al. 2010) and temperature in the leopard gecko (Kotake et al. 2024). These studies lead us to expect that interpopulation variation in yawning behavior may be promoted by microevolution and/or phenotypic plasticity. However, no studies have investigated interpopulation variation of yawning behavior. This study aims to examine interpopulation variation in the yawning behavior of juvenile white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan.

Materials and methods

Study species and populations

The white-spotted char *S. leucomaenis* is a common riverine salmonid fish in northern Japan. This species has two life history forms: (1) the anadromous form that lives in rivers for several years, descends to the ocean to grow, and then returns to rivers in the breeding season, and (2) the resident form that spends its entire life in a river (Yamamoto et al. 1999; Morita 2001; Morita and Morita 2007). There are many local populations of *S. leucomaenis* in the rivers of

southern Hokkaido, northern Japan. They often persist in areas upstream of dams, where all individuals reproduce as the resident form (Morita et al. 2000; Morita and Morita 2007). Several studies have reported interpopulation variation in the morphology and behavior of this species (Yamada et al. 2019; Hasegawa et al. 2020; Yamada and Wada 2023b). For instance, juveniles in the populations located above a tall dam spent more time in station-holding behavior, in which juveniles are sedentary on the substrate, than those in the remaining populations without the dam (Yamada and Wada 2023b). Yamada and Wada (2023a) described the yawning behavior of juveniles of this species, and reported longer yawn durations during swimming than during station-holding behavior.

In this study, we used yawning data obtained from four local populations of *S. leucomaenis* in southern Hokkaido, Japan. These data were collected from video recordings previously obtained by Yamada and Wada (2023b) for the purpose of comparing the duration of station-holding behavior among the local populations. Juveniles were sampled in 2019 with hand nets on 23 May for Station (Stn.) 1, 26 May for Stn. 2, 28 May for Stn. 3, and 2 June for Stn. 4 (see Fig. 1 in Yamada and Wada [2023b] for a map of the study area). Juveniles were transported to a temperature-controlled room (5 °C) at the Hakodate campus of Hokkaido University and kept in a holding tank (30 × 18 × 24 cm; water depth, 10 cm) until subsequent behavioral observations. The temperature-controlled room was maintained on a 12-h:12-h

light:dark cycle and illuminated from 8:00 AM to 8:00 PM local time. Video data for juveniles whose rostral parts could not be observed were excluded from our analysis. The numbers of observed juveniles from Stns. 1–4 were 33, 34, 31, and 36, respectively.

Behavioral observations

Behavioral observations were conducted one or two days after juveniles were collected in 2019 (i.e., Stn. 1, 24 May; Stn. 2, 27 May; Stn. 3, 29 May; Stn. 4, 3 and 4 June). The juveniles were individually introduced into an observation tank ($60 \times 20 \times 25$ cm) in the temperature-controlled room. The water in the observation tank was circulated by a submersible pump (e~ROKA PF701, GEX Co., Ltd., Osaka, Japan; 0.16 L/s). Details of the observation tanks are given by Yamada and Wada (2023b). The behaviors of the juveniles were recorded by a digital camera (TG-4; Olympus Co., Ltd., Tokyo, Japan) for 540 seconds after an acclimation period of 60 seconds following introduction into the tank. Subsequently, the juveniles were photographed, and their fork length (FL; an index of body size) in millimeters was measured using image analysis software (ImageJ; National Institutes of Health, Bethesda, MD, USA). All juveniles were returned to their original habitat after the above procedures.

The duration of station-holding behavior was determined for each individual following the methods of Yamada and Wada (2023a). Data for the time that juveniles spent in station-

holding behavior (i.e., station-holding time) had already been obtained by Yamada and Wada (2023b), so we used those data in this study. After the behavioral observations, the number of yawns was counted. Juveniles normally breathe rhythmically, slightly opening and closing their mouths. We recorded large mouth-opening behaviors that deviated from the periodic rhythm of breathing as yawning behaviors. Because Yamada and Wada (2023a) found that *S. leucomaenis* juveniles show different types of yawns during station-holding behavior and swimming, we investigated the duration of each yawn of each type. The duration was calculated from the number of video frames in the video recordings (29.97 frames per second) using Windows Media Player version 12.0 (Microsoft Corporation). We also determined the time interval between each yawn and the most recent or subsequent behavioral transition from station-holding behavior to swimming behavior. These values were calculated as negative for yawns during station-holding behavior (pre-transition) and positive for yawns during swimming (post-transition). Juveniles not showing station-holding behavior or swimming were excluded from the analysis.

Statistical analyses

To compare yawn frequencies among the four populations, we constructed generalized linear models (GLMs) with a negative binomial error distribution and a log link function using the

glm.nb function of the package ‘MASS’ (version 7.3.60.2, Venables and Ripley 2002). In the GLMs, population (i.e., Stn. 1–4) was set as an explanatory variable. These models also included the total time spent in station-holding behavior as an offset term (i.e., the number of yawns per second was analyzed for the total time spent in station-holding behavior). Yawn frequency during swimming was also compared with the GLMs, including population as an explanatory variable and total time spent swimming as an offset term.

We also constructed gamma GLMs with a log link function to compare yawn duration among the four populations. These GLMs included population as an explanatory variable. Ten and eight juveniles showed more than two yawns during station-holding behavior and/or swimming, respectively. To avoid pseudo-replication, we calculated the mean duration of each type of yawn (swimming or station-holding) for these juveniles. Populations with a small number of yawns were excluded from comparisons of yawn duration.

We used the *F*-values provided by the function *Anova* in the package ‘car’ (version 3.1.2, Fox and Weisberg 2019) to test the significance of the explanatory variables in all GLMs. Post-hoc comparisons among the four populations were performed using the Tukey method with the *glht* function in the package ‘multcomp’ (version 1.4.25, Hothorn et al. 2008). R version 4.3.1 was used in all statistical analyses (R Core Team 2023).

Results

Yawning was observed in 8 out of 33 total individuals from Stn. 1, 15 of 34 from Stn. 2, 8 of 31 from Stn. 3, and 13 of 36 from Stn. 4. The total occurrence of yawning did not differ among the local populations (Fisher's exact test, $P = 0.282$). At Stn. 2, yawning in juveniles during station-holding behavior peaked just before the behavioral transition to swimming (Fig. 1b), a finding similar to that by Yamada and Wada (2023a). Although there was no clear peak in the occurrence of yawning during station-holding behavior in the juveniles from the remaining populations, 13 out of 15 yawns during station-holding behavior occurred within the 60 seconds before the behavioral transition (Fig. 1a, c, d). These results suggest that yawning during station-holding behavior would be concentrated just before the behavioral transition in all populations. In contrast, the timing between the behavioral change to swimming and the occurrence of yawning during swimming was not consistent among the four populations. At Stn. 4 in particular, four juveniles yawned 200 seconds after the onset of swimming (Fig. 1d).

There were no significant differences in yawn frequency among the local populations (GLM, yawning during station-holding behavior: $F_{3,114} = 1.48$, $P = 0.224$; yawning during swimming: $F_{3,106} = 1.09$, $P = 0.357$). On the other hand, there were significant interpopulation differences in yawn duration (GLM, during station-holding behavior: $F_{2,18} = 11.1$, $P < 0.01$; during swimming: $F_{1,17} = 7.99$, $P = 0.012$). The duration of yawns during station-holding

behavior in juveniles from Stn. 1 was shorter than in those from Stns. 2 and 3 during station-holding behavior (Table 1; Fig. 2). The duration of yawns while swimming was longer in juveniles from Stn. 2 than in those from Stn. 4 (Fig. 3).

Discussion

This is the first study to compare yawning behavior among wild populations of any species. We found significant interpopulation variation in yawn duration of the white-spotted char *S. leucomaenis*. Yawn duration is an important behavioral measurement because it is directly linked to physiological function (Gallup et al. 2016, 2020; Massen et al. 2021; Zannella et al. 2021). Some recent studies have reported interspecific variation in yawn duration (e.g., Gallup et al. 2016, 2020; Massen et al. 2021). For example, Massen et al. (2021) found in birds and mammals that yawn duration was longer in taxa with larger brain mass and neuron number. This behavioral pattern might be a product of adaptive evolution, as taxa with large and complex brains require longer yawn durations for brain cooling (see also Gallup et al. 2016). Evolutionary forces creating variation in yawn duration have therefore been considered to operate at the species level. This study suggests that such evolutionary forces might cause differences in yawn duration even among local populations of the same species.

203 Although we could not identify any factors causing the variation in yawn duration in
204 this study, several candidates can be considered. For instance, yawn duration during station-
205 holding behavior may be affected by predation pressure. Yawning is a conspicuous behavior in
206 nature (Guggisberg et al. 2007; Gallup 2022), and thus potentially carries a risk of attracting
207 predator attention, especially when an animal is resting and immobile (Miller et al. 2010).
208 Yawning during station-holding behavior might disrupt the gravel mimicry function of the color
209 pattern of juvenile salmonids (Donnelly and Dill 1984). Juveniles under high predation pressure
210 might thus evolutionarily and/or plastically shorten the yawn duration during station-holding
211 behavior to avoid predation. Yawn duration could also be affected by olfactory information
212 (Kotake et al. 2024), because the mouth-opening motion of fish is associated with the detection
213 of olfactory cues, as the motion has the effect of inhaling water and any associated chemicals
214 and inflating the olfactory bulb (Nevitt 1991). Therefore, variations in the importance of
215 olfactory information among habitats might also contribute to the observed interpopulation
216 variation in yawn duration via evolutionary and/or plastic mechanisms.

217 We observed no significant interpopulation variation in yawn frequency in this study.
218 However, it should be noted that the observation period was brief (9 minutes). In contrast,
219 Kotake et al. (2024) used an observation period of three days to examine yawn frequency and
220 identified a 24-hour periodicity in yawning. The existence of periodic rhythms and seasonal

changes in behaviors such as foraging, and predation risk, have been documented in many animals (Zoufal and Taborsky 1991; Varpe and Fiksen 2010; Mappes et al. 2014). The frequency and duration of yawns might be associated with these rhythms and changes. Long-term observations are needed to accurately examine yawn frequency, duration, and periodicity.

Yamada and Wada (2023a) demonstrated that yawning by juvenile *S. leucomaenis* occurred with high frequency during station-holding behavior, and was concentrated just before the behavioral transition to increased activity, thereby supporting the state-change hypothesis. This study confirmed a consistent pattern of yawn occurrence preceding behavioral state-change in four additional local populations of *S. leucomaenis*. This robust support for the state-change hypothesis suggests that the physiological function of yawning would not be influenced by differences in local environments.

While this study successfully identified interpopulation variation in the duration of yawning behavior in juvenile white-spotted char, other species may exhibit different interpopulation variations. The biological mechanisms and environmental conditions that generate and maintain interpopulation variation in yawning behavior, as well as the adaptive significance of yawning behavior, remain a subject of speculation. Further research is needed to examine the proximate and ultimate mechanisms that produce interpopulation variation in yawns, and the diversity of animal yawning behavior.

239

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243 sampling and experiments.

244

245 **Author contributions**

246 All authors contributed to the study conception and design. Material preparation and data
247 collection and analysis were performed by Hiroyuki Yamada and Reo Nagasaka. The first draft
248 of the manuscript was written by Reo Nagasaka, and all authors commented on previous
249 versions of the manuscript. All authors read and approved the final manuscript.

250

251 **Ethics statement**

252 Fish were collected in a manner that did not violate the fisheries regulations of Hokkaido
253 Prefecture, therefore no permission was required from the local government. The Hokkaido
254 University Animal Experiment Committee, to which the authors belong, does not require
255 approval for research plans using fish. Therefore, this study did not receive an approval number
256 from the committee. However, we took care to minimize contact with fish and avoid unnatural

257 experimental treatments, and devised ways to reduce stress on the experimental fish. All

258 juveniles were returned to their original habitat after behavioral observations.

259

260 **Conflict of interest**

261 The authors declare that they have no conflict of interest.

262

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266

267 **Data availability statement**

268 The datasets for this study are available from the corresponding authors on reasonable request.

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Table 1. Summary of post-hoc comparisons among the three populations of juvenile white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan (i.e., Stations 1–3) used to analyze interpopulation variations in yawn duration during station-holding behavior. Significant *P* values based on Tukey post-hoc comparisons are shown in bold.

Comparison	Estimate	S.E.	<i>z</i>	<i>P</i>
Stn. 2 vs. Stn. 1	0.390	0.085	4.584	<0.01
Stn. 3 vs. Stn. 1	0.335	0.088	3.820	<0.01
Stn. 3 vs. Stn. 2	-0.055	0.082	-0.676	0.777

Figure legends

Fig. 1.

Temporal relationship between yawning and behavioral transitions among four local populations of juvenile white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan. The time of behavioral transition from station-holding behavior to swimming is defined as time zero. Yawns during station-holding behavior before the transition are plotted as negative values and white bars, and those during swimming as positive values and black bars. Yawning data for all individuals were pooled, although data for juveniles that did not show station-holding behavior or swimming were excluded.

Fig. 2.

Comparison of mean yawn duration during station-holding behavior among four local populations of juvenile white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan. The whiskers indicate the maximum and minimum values of non-outlier data. The bottom and top edges of each box indicate the first and third quartiles, respectively. Thick horizontal lines indicate the medians. Gray filled circles indicate the raw data and open circles are the yawn durations estimated from generalized linear model with gamma error distribution and a log link

function. Letters indicate homogenous subsets at the $P < 0.05$ level based on Tukey post-hoc comparisons. Station 4 was excluded from the comparison because of the small sample size.

Fig. 3.

Comparison of mean yawn duration during swimming among four local populations of juvenile white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan. The whiskers indicate the maximum and minimum values of non-outlier data. The bottom and top edges of each box indicate the first and third quartiles, respectively. Thick horizontal lines indicate the medians.

Gray filled circles indicate the raw data and open circles are the yawn durations estimated from generalized linear model with gamma error distribution and a log link function. Letters indicate homogenous subsets at the $P < 0.05$ level based on generalized linear model with a gamma error distribution. Stations 1 and 3 were excluded from the comparison because of the small sample size.

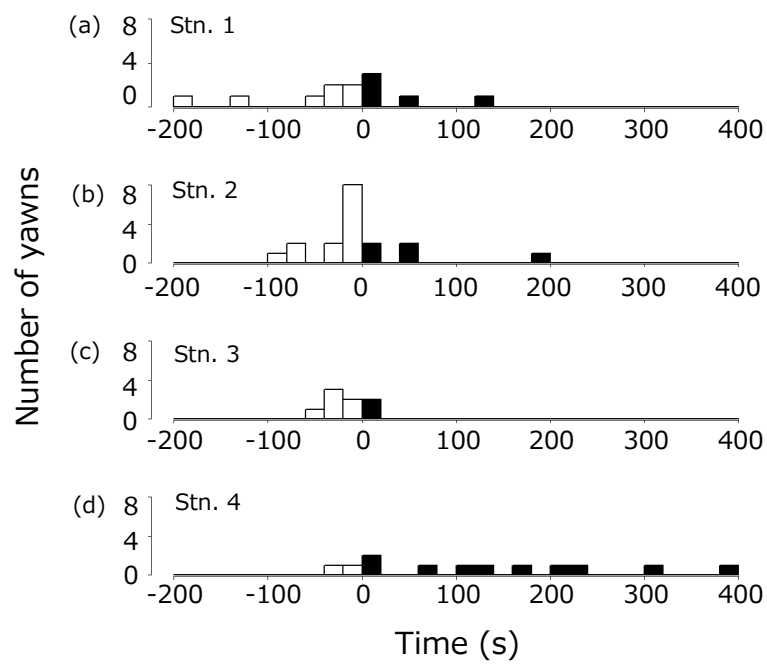


Fig. 1

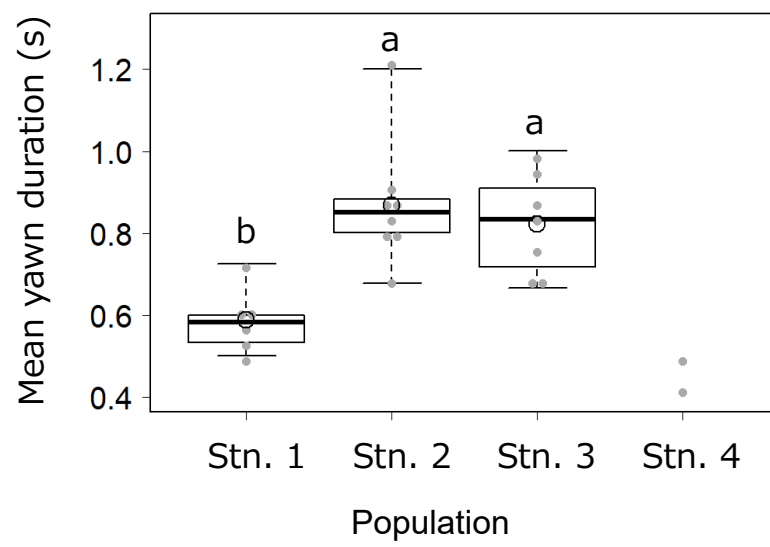


Fig. 2

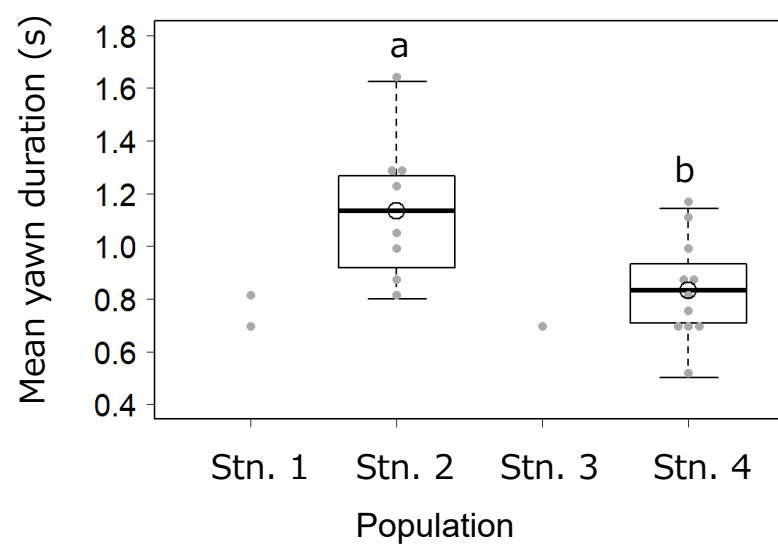


Fig. 3

Comparison	Estimate	S.E.	<i>z</i>	<i>P</i>
Stn. 2 vs. Stn. 1	0.390	0.085	4.584	<0.01
Stn. 3 vs. Stn. 1	0.335	0.088	3.820	<0.01
Stn. 3 vs. Stn. 2	-0.055	0.082	-0.676	0.777