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Fish yawn: the state-change hypothesis in juvenile white-spotted char *Salvelinus leucomaenis*

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Abstract

Yawning is a ubiquitous stereotyped action in vertebrates. Yawning may induce behavioral state changes in animals through its arousal function, but no studies have explicitly examined this state-change hypothesis in fish. This study examined the state-change hypothesis in juvenile white-spotted char, *Salvelinus leucomaenis*. We observed 48 yawns in 23 out of 41 juveniles during 600 s of observation in the laboratory. Thirty-two of these yawns occurred while juveniles were stationary on the substrate, and they were concentrated immediately before the behavioral transition from stationary to active. These results support the state-change hypothesis. Sixteen yawns were observed after the behavioral transition, and their durations were longer than those before the transition. Although we suspected that this prolonged yawning after the transition would be associated with feeding and thermoregulation in the juveniles, we could not determine the cause of this difference. Further studies are needed to understand fish yawning and the origin of animal yawning.

Key words: Yawning, Ectotherm, Mouth-gaping, State-change hypothesis, Salmonid

Introduction

Yawning is a stereotyped action characterized by three phases: an involuntary and powerful mouth gaping with inhalation, a temporary period of peak muscular contraction, and a passive closure of the jaw with exhalation (Barbizet 1958; Provine 1986; Gallup 2022).

Yawning has been studied for several decades across vertebrates (Barbizet 1958; Provine 1986; Baenninger 1997; Guggisberg et al. 2010, 2011; Gallup 2011, 2022; Gallup and Eldakar 2013). Several studies have suggested that yawning evolved as a thermoregulatory cooling mechanism in endotherms such as terrestrial mammals and birds (Gallup et al. 2016; Massen et al. 2021). However, its function has yet to be examined in ectotherms.

Recent behavioral studies have distinguished between social yawning and spontaneous yawning (Guggisberg et al. 2010; Gallup 2011, 2022; Gallup and Eldakar 2013). Social yawning is also known as contagious yawning, triggered socially by sensing the yawns of others (Gallup 2022). For example, wild lions infected by the yawning of another individual exhibit behavioral convergence in which their subsequent motor actions are aligned with those of the earlier yawner (Casetta et al. 2021). On the other hand, spontaneous yawning, which occurs in nonsocial contexts, has been widely demonstrated to promote physiological arousal (Provine 1986, 2005; Baenninger 1997; Gallup 2022). This

would be due to the acceleration of heart rate and intracranial circulation by deep inhalation or jaw stretching, or both, during yawning (Gallup 2022). The brain-cooling function of yawning also promotes physiological arousal in individuals (Shoup-Knox et al. 2010; Gallup et al. 2016; Massen et al. 2021). Spontaneous yawning occurs widely across species, and thus its functions are considered to be more primitive than those of social yawning (Gallup 2011, 2022).

Spontaneous yawning often occurs before a behavioral state change. For example, primates such as chimpanzees and lemurs exhibit increased locomotion or behavioral transitions, or both, after yawning (Vick and Paunker 2010; Zannella et al. 2015). Similar results have been reported in lions (Casetta et al. 2021) and bottlenose dolphins (Enokizu et al. 2021). Although it has been pointed out that yawning in ectotherms would not be homologous to that in endotherms (Guggisberg et al. 2010; Gallup 2011), there are several descriptions of the state changes following spontaneous yawning in amphibians (Bakkegard 2017; Hartzell et al. 2017) and fish species (Myrberg 1972; Baenninger 1997). For instance, Bakkegard (2017) observed the yawning of Red Hills salamanders and found that they yawn most frequently when they begin their evening activity. In most of these cases, behavioral activity increases after yawning; therefore, the state-change hypothesis has been

proposed, suggesting that the physiological arousal function of yawning induces the behavioral shift from inactive to active (Zannella et al. 2015; Gallup 2022).

Spontaneous yawning is observed in many fishes (Myrberg 1972; Baenninger 1997; Ritter 2002, 2008; Campbell et al. 2015; Oka et al. 2020). However, to the best of our knowledge, no studies have explicitly examined the state-change hypothesis in fish. Given that fish were probably the first yawners on Earth (Baenninger 1997; Gallup 2011, 2022), studying fish yawning is important for understanding its origin.

Juvenile salmonids exhibit station-holding (SH) behavior, remaining stationary on the river bottom during periods of inactivity (see Arnold et al. 1991; Yamada et al. 2019; Hasegawa et al. 2020). As SH behavior and swimming are contrasting behaviors, they are useful to test the state-change hypothesis. Young-of-the-year juvenile *S. leucomaenis* also exhibit frequent SH behavior (Yamada et al. 2019; Hasegawa et al. 2020). Therefore, this study aimed to describe the yawning of young-of-the-year juveniles and to test the state-change hypothesis in *S. leucomaenis*.

Materials and methods

We used a hand net to sample 46 young-of-the-year juvenile *S. leucomaenis* from the

population in the Kurohajiri River, southern Hokkaido, Japan (lat. 41°58'46"N, long. 140°52'17"E), on 18 May 2019. We could distinguish the young-of-the-year juveniles by their body size and color pattern: They were clearly smaller than the other cohorts in this season and they lacked white spots. We did not identify sex, because in this species there is no sexual dimorphism in the juvenile morphology. The juveniles were transported to a temperature-controlled room (5 °C) in our laboratory at the Hakodate campus of Hokkaido University (lat. 41°48'33"N, long. 140°43'06"E). We had observed frequent SH behavior of juveniles at this temperature in our previous studies (Yamada et al. 2019; Hasegawa et al. 2020). Juveniles were kept in a holding tank (30 × 18 × 24 cm) until subsequent procedures.

One or two days after the sampling, each juvenile was individually placed in an observation tank (60 × 20 × 25 cm; Fig. 1) in the temperature-controlled room in order to observe behavior in a nonsocial context. The side of the tank used for observations was covered with an opaque sheet to ensure that the juveniles would not be disturbed by the actions of the researcher. The water in the observation tank was circulated by a submersible pump (e~ROKA PF701, GEX Co. Ltd., Osaka, Japan) at a flow rate of 0.16 L/s (Fig. 1). Juveniles were gently scooped from the holding tank with a water net that was able to scoop fish along with water (Kyorin Underwater Net, size SS; Kamihata Fish Industries Ltd.,

Hyogo, Japan), and they were introduced to the observation tank along with approximately 90 mL of water. The same volume of water was removed with the individuals after the behavioral observations. Behaviors were recorded by a digital camera (TG-4, Olympus Co. Ltd., Tokyo, Japan) fixed to the inside of the opaque sheet. Both the holding tank and the observation tank were filled with river water from the sampling site. The inside of the observation tank was illuminated by an LED with sufficient intensity for video recording, with an illuminance of approximately 400 lx at the bottom of the tank and 1000 lx at the water surface. As environmental enrichments, the observation tank was designed to prevent fish from directly experiencing unnatural water flow created by the pump, and natural substrate from the riverbanks at the sampling site was placed on the bottom of the tank (Fig. 1).

We defined yawning as the mouth-opening action with three phases described in the Introduction (Fig. 2), and SH behavior as the benthic behavior in which juveniles settle to the substrate and keep their position (see Arnold et al. 1991). Station-holding behavior is usual for wild young-of-the-year juveniles of the genus *Salvelinus* because they normally show a sit-and-wait feeding tactic on the bottom of a river (e.g., Wilson and McLaughlin 2007). Yawning, swimming, and SH behavior were observed for each individual at 1-s

intervals from zero to 600 s. The period of erratic swimming immediately after the introduction was not included in the 600 s. The video data for juveniles whose rostral parts could not be clearly observed were excluded from the following analysis.

After the observations, we counted the number of yawns from the recordings and then determined the time interval between each yawn and the most recent behavioral transition event. This value was calculated to be negative for yawning before the most recent transition event (i.e., yawning during SH) and positive for yawning after the event (i.e., yawning during swimming). If yawns do indeed induce behavioral transitions, then we expected that the time interval would be closer to zero for yawns before the transition event than for those after. We therefore compared the absolute values of this time interval before and after a behavioral transition. In addition, we expected that the intensity of yawning before the behavioral transition might be stronger than that after the transition, given that the shift from the inactive to the active behavioral state would likely require stronger arousal. We therefore chose yawn duration as an index of yawn intensity and compared yawn durations before and after the transition from SH behavior to swimming. The duration was calculated from the number of video frames in the recordings (29.97 frames/s) by using Quick Time Player (version 7.7.9).

We constructed generalized linear mixed models (GLMMs) with a Gamma error distribution and a log link function for the absolute value of the time interval between a yawn and the most recent behavioral transition, and for the duration of yawning. In both models, the type of yawning (yawning before behavioral transition = 0, yawning after behavioral transition = 1) was set as the explanatory variable, using the *glmmTMB* function of the “glmmTMB” package (Brooks et al. 2017) in R version 4.1.0 (R Core Team 2021). The random factor of each GLMM was modeled so that each individual could have a separate intercept for each type of yawning (i.e., [1 | ID: type of yawning]). Note that the data for these GLMMs do not include the six yawns without behavioral transitions (i.e., $n = 42$ yawns).

After the behavioral observations, the left sides of the juveniles were photographed by using a digital camera (TG-4, Olympus Co. Ltd.) fixed on a photographing platform. We used these photographs to measure fork length as an index of body size by using image analysis software (ImageJ, National Institutes of Health, Bethesda, MD, USA). These measurements were conducted on 20 and 21 May 2019. After the experiment, all juveniles were released back to their sampling site.

Results

Behavioral observations were taken for 41 of 46 sampled juveniles (fork length, $36.04 \pm$

3.70 mm, mean $\pm$ SD) for which the rostral parts were clearly observed. Forty-eight yawning events occurred in 23 out of the 41 juveniles (Figs. 3, 4). Station-holding behavior was observed in all 41 juveniles, and transitions from SH behavior to swimming were observed for 42 yawns made by 20 juveniles (Figs. 3, 4). Yawning occurred significantly more frequently during SH behavior than after the transition (binomial test, $H_0: n = 48, P = 0.5; p = 0.03$), with a frequency of 66.7%. The occurrence of yawning peaked immediately before the transition (Fig. 4). Sixteen yawns were observed after the transition. Eleven of these were made by eight juveniles that did not yawn before the transition (Figs. 3, 4), and the remaining five were made by three juveniles that yawned before the transition (Fig. 3).

The GLMM for the absolute value of the time interval between a yawn and a behavioral transition revealed that the interval was shorter for yawns before the transition event than for yawns after the event (type of yawning: $z = 2.57, p = 0.010$). The GLMM estimated the absolute value of the intervals before and after a transition to be 24.552 and 127.154 seconds, respectively (Fig. 5). The GLMM for yawning duration showed that the duration after the behavioral transition was significantly longer than that before the transition (type of yawning: $z = 3.042, p = 0.002$). The GLMM estimated the durations of yawning during SH behavior and after the transition to be 0.880 and 1.238 s, respectively

(Fig. 6).

Discussion

Yawning of juvenile *S. leucomaenis* occurred frequently during SH behavior (Fig. 4), and it was especially concentrated just before the behavioral transition to increased activity (Figs. 4, 5). These results support the state-change hypothesis. There are several studies that suggest that spontaneous yawning of fish may be linked to activeness. For instance, largemouth bass frequently yawn in low-oxygen water (below 1.99 mg/L) and increase their vertical movement in the experimental tank (Hasler et al. 2009). Campbell et al. (2015) observed several behavioral traits of rainbow trout and showed that yawning count was positively correlated with aggressive behavior (display duration) and negatively correlated with “freezing behavior” duration (freezing behavior is similar to SH behavior in that the individuals remain immobile on the substrate). However, to our knowledge, no studies had focused on the behavioral sequence in fish. This study is therefore the first to explicitly show that spontaneous yawning occurs before behavioral transitions in fish.

Our results suggest that the function of fish yawning is partially shared with that in terrestrial vertebrates. Although previous studies had shown that fish yawning is not

homologous to that of endotherms in terms of the respiratory components (see Guggisberg et al. 2011), recent studies have suggested that the mouth-opening action of yawning, regardless of respiration, increases arousal levels (Gallup 2022) and changes the state of inactivity (Enokizu et al. 2021). Our results support this notion in juveniles of the salmonid species *S. leucomaenis*.

Yawning was also observed after the transition from SH behavior to swimming (Figs. 4, 5). Contrary to our expectation, its duration was longer than before the transition (Fig. 6). It is possible that yawning during swimming has a different function than yawning during SH behavior. In fish, yawning is often associated with feeding. The Caribbean reef shark performs yawn-like mouth gaping frequently around feeding scenarios (Ritter 2008). Oka et al. (2020) observed yawning presumably related to feeding in juvenile oarfish *Regalecus russelii*. Yawning in the feeding context is considered to be a maintenance behavior of the jaw elements such as muscles and bones (Ritter 2008; see also Graves and Duvall 1983; Bakkegard 2017; Hartzell et al. 2017). Therefore, the prolonged yawning of *S. leucomaenis* juveniles after the behavioral transition from SH behavior to swimming may reflect a rearrangement of the jaw elements for feeding. If this is the case, there could be differences in yawning morphology. However, the resolution of the video recordings obtained in this

study made it difficult to make detailed comparisons between yawns.

Although we did not examine juvenile body temperature in this study, the observed yawn durations were consistent with the brain-cooling hypothesis (Massen et al. 2021). The observed yawn durations were mostly less than 1 s (Fig. 6). In terrestrial endotherms, yawn durations increase with the size of the brain that needs to be cooled (Gallup et al. 2016; Massen et al. 2021). The yawn duration of our juveniles was shorter than those of most terrestrial mammals and birds (see Gallup et al. 2016; Massen et al. 2021). The small size of the juvenile *S. leucomaenis* may have shortened the yawn duration required for brain cooling. The longer yawn duration after the behavioral transition may have also been related to thermoregulation during swimming. The body temperature of fish is regulated exclusively by behavior (reviewed in Haesemeyer 2020), and it increases when they move into warmer environments (e.g., Rakus et al. 2017). In our observation tank, juveniles swimming in the water column were in a more illuminated position, closer to the LED light source, than those showing SH behavior (see Materials and methods). Direct sunlight raises the body temperature of fish in nature (Nordahl et al. 2018), and thus light intensity may be a reliable cue for juveniles to increase their brain temperature. The prolonged yawning during swimming might therefore be a thermoregulatory behavior induced by the stronger

illumination. Future studies that include parameters relating to body temperature are needed to better test the brain-cooling hypothesis in fish.

Overall, this study provides the first evidence supporting the state-change hypothesis in fish. We also provide a behavioral description of yawn duration, and the results suggest that there are links between fish yawning and feeding ecology, thermoregulation, or both, although the results are still speculative. Further studies are needed for a better understanding of fish yawning and the origin of animal yawning.

Conflict of interest

The authors declare that they have no conflict of interest.

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Data availability statement

The datasets for this study are available from the corresponding author on reasonable

request.

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Figure legends

Figure 1

Schematic of the observation tank. For simplicity, the opaque sheet has been omitted from the illustration.

Figure 2

Sequence of yawning (i.e., a mouth-opening action with three phases) in juvenile white-spotted char *Salvelinus leucomaenis*.

Figure 3

Stacked frequency distribution of the number of yawns made by individuals during 600 s of behavioral observation.

Figure 4

Temporal relationship between yawning and behavioral transitions. Note that yawns before and after the transition from station-holding (SH) behavior to swimming are plotted with negative and positive values, respectively. Data for individuals that yawned during SH but

did not show a behavioral transition during the observations are shown with negative values and shaded lines. Yawning data for all individuals were pooled.

Figure 5

Comparison of the absolute values of the time interval between yawning before or after a behavioral transition and the transition. 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 points indicate the raw data and the two open circles are the time intervals estimated from the generalized linear mixed models with a Gamma error distribution and a log link function.

Figure 6

Comparison of yawn duration before and after a behavioral transition. 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 points indicate the raw data and the two open circles are the yawn durations estimated from the generalized linear mixed models with a Gamma error distribution and a

log link function.

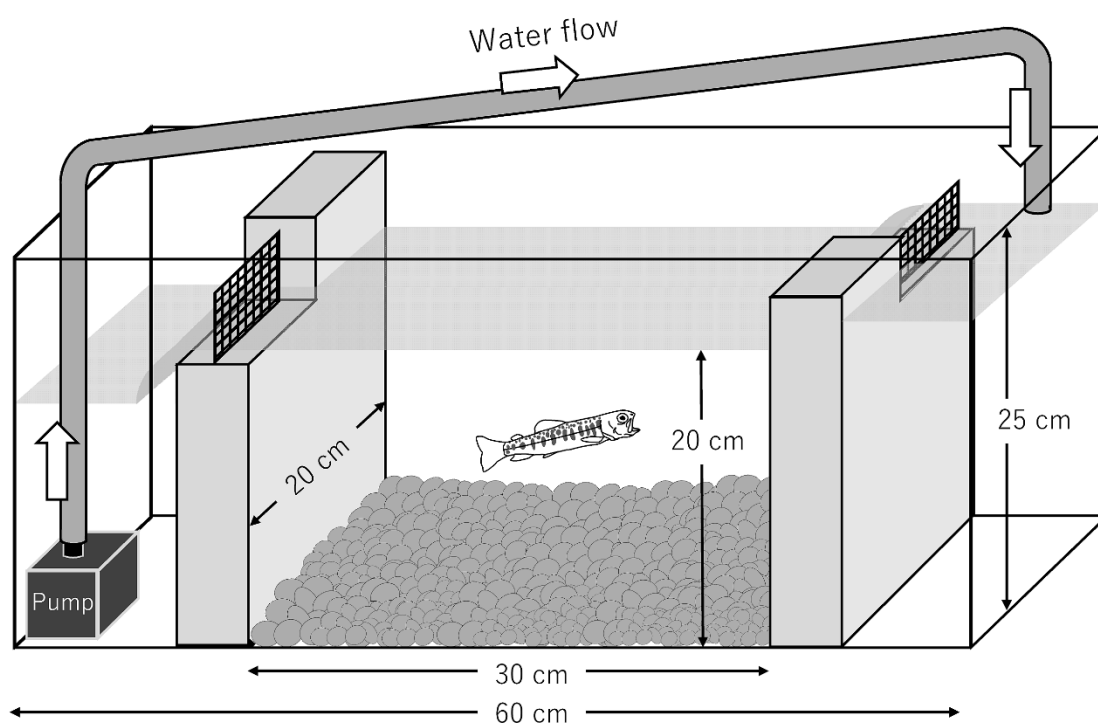


Figure 1

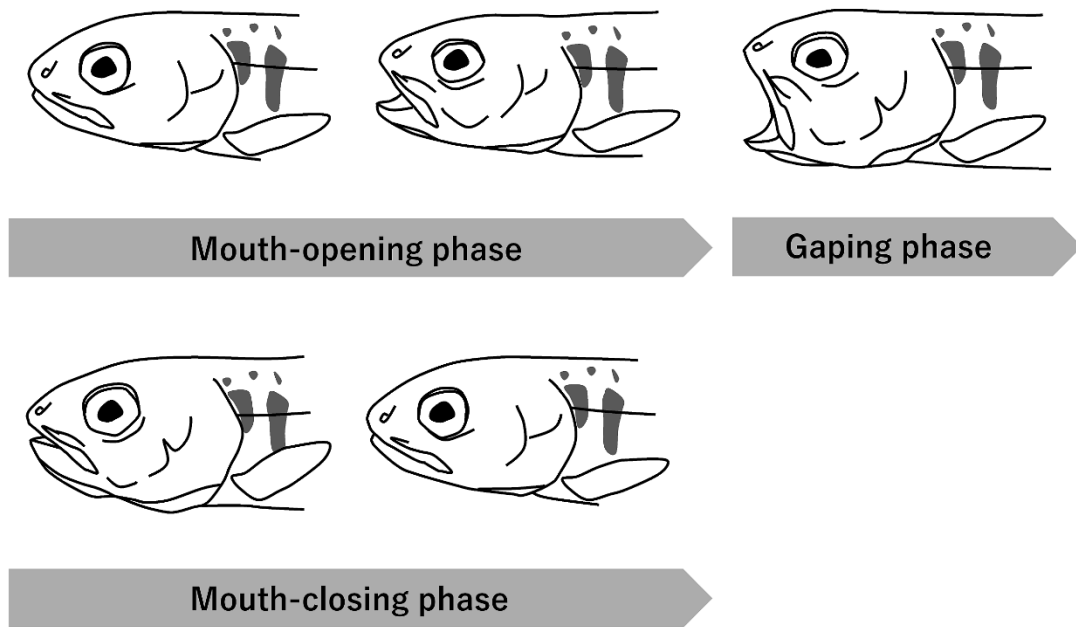


Figure 2

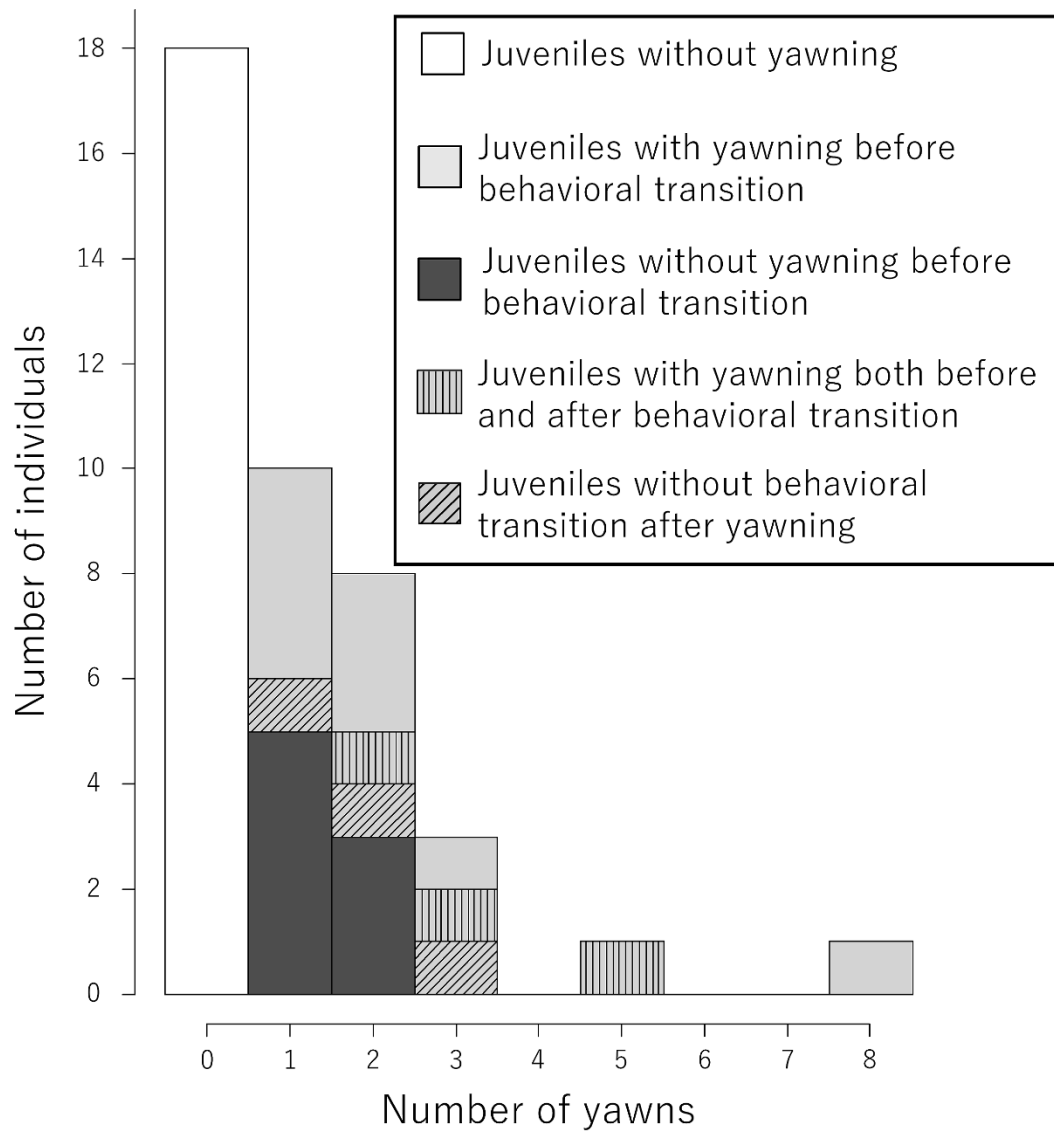


Figure 3

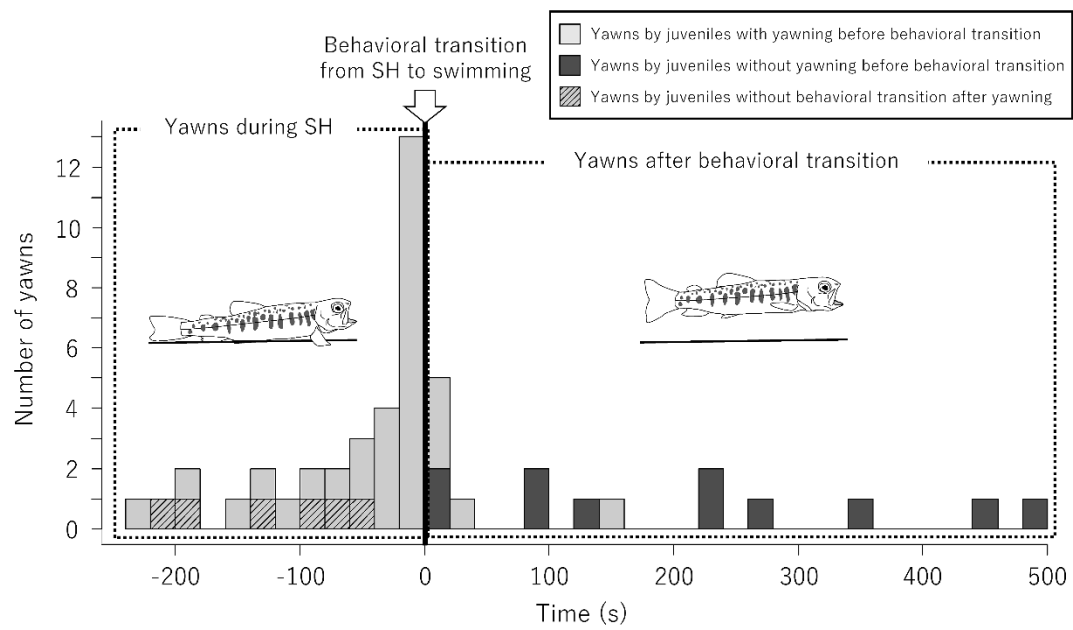


Figure 4

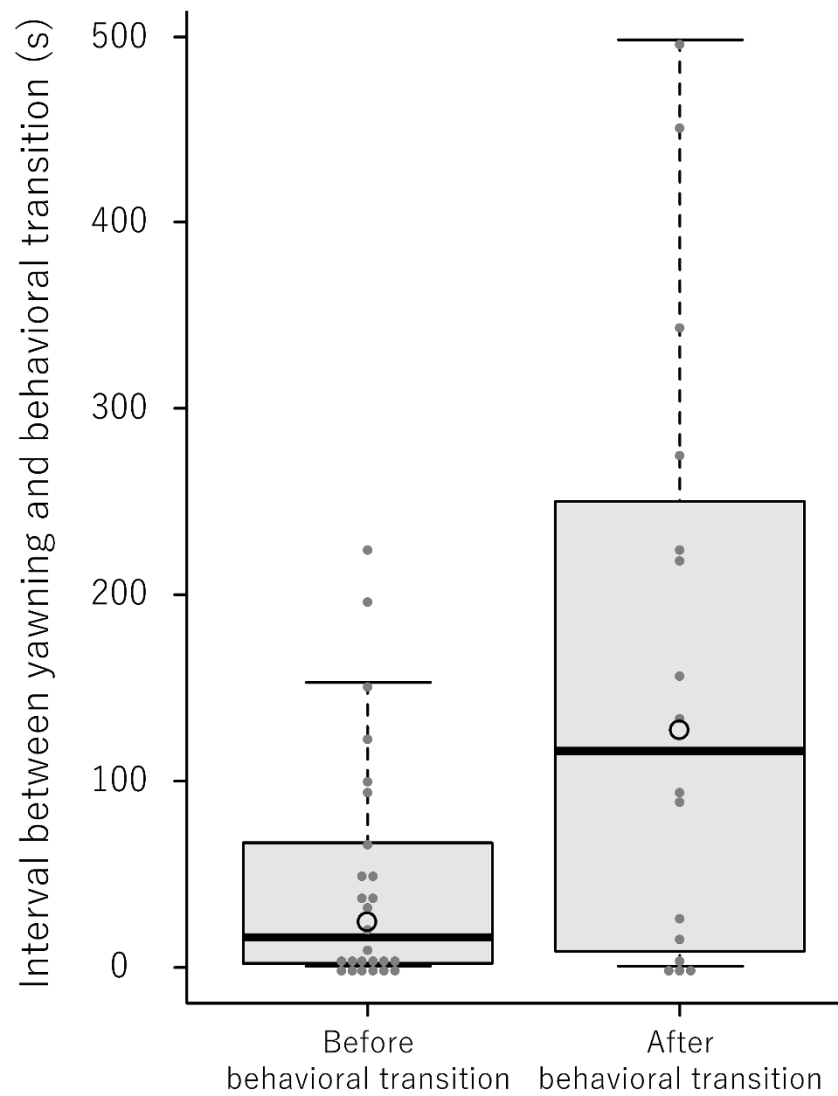


Figure 5

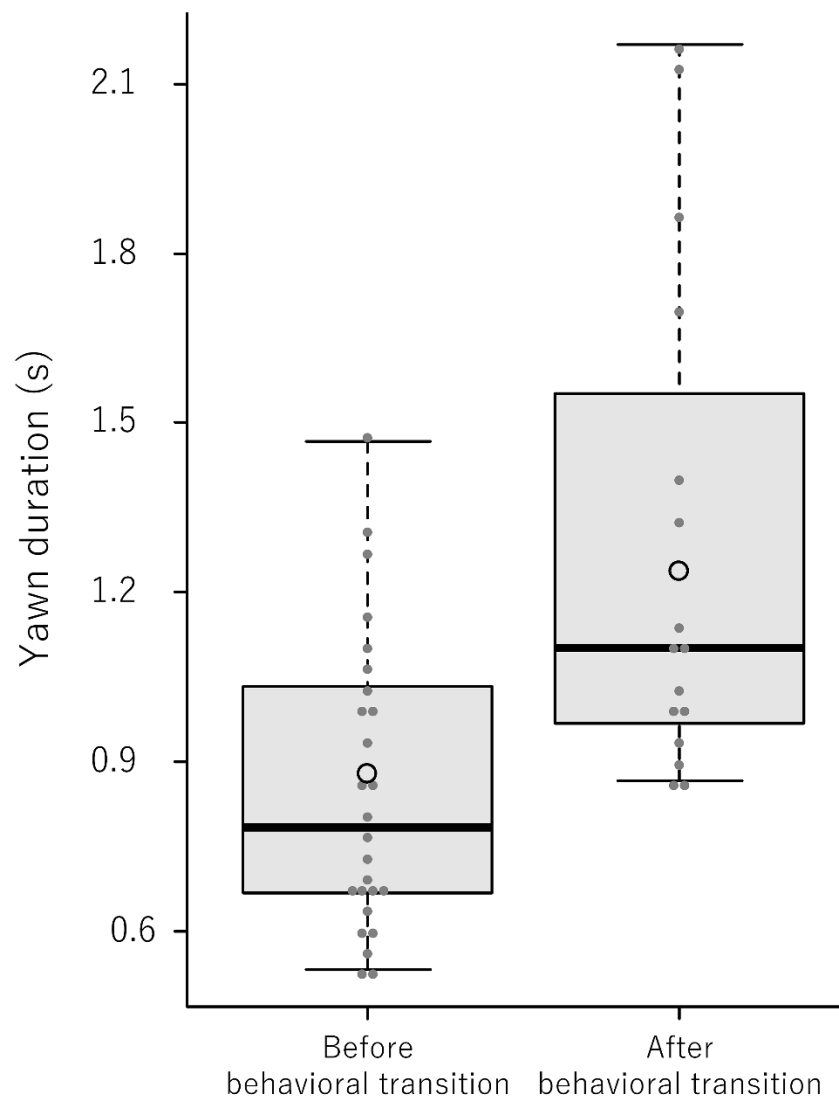


Figure 6