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1 **Diel migration pattern of pink salmon fry in small streams**

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15
16 **Ethical Statement**

17 All fish collection was legally conducted in accordance with the permit from the
18 Hokkaido Government. All animal handling in the surveys was conducted according to
19 the guidelines of animal care at Hokkaido University.

20
21 **Abstract**

22 Downstream migration is a critical stage in the anadromous salmonid life cycle; however,
23 previous studies have shown different results between rivers or surveys for the diel
24 downstream migration pattern of the fry of the pink salmon *Oncorhynchus gorbuscha*.

25 We investigated the diel migration pattern of pink salmon fry in three small streams. Our
26 results showed that pink salmon fry migrate mainly within a few hours after sunset; 89.9%
27 of migration occurred between 18:00 and 23:00. Therefore, the results indicated that
28 sunset time influences the diel migration pattern of pink salmon fry in small streams. This
29 pattern could be a predator-avoidance behaviour.

30

31 **Key Words:** Salmonidae, salmonids, movement, behaviour, freshwater, stream.

32 Many animals exhibit “migration” as a behaviour to acquire more favourable feeding
33 grounds, habitats, and spawning sites (Dingle, 2014; Dingle & Drake, 2007).
34 Anadromous salmonids migrate according to the stages of their life cycles (Quinn, 2018):
35 “downstream migration” to rapidly grow using marine environments with better growing
36 conditions than those of most freshwater habitats and “homing migration” to return to
37 natal rivers to spawn. Downstream migration is a critical stage of the anadromous
38 salmonid life cycle because the high mortality of salmon during downstream migration
39 affects adult populations and overall population persistence (Thorstad *et al.*, 2012;
40 Williams *et al.*, 2001).

41 Several salmonids perform downstream migration at night (Hintz & Lonzarich,
42 2012; Johnston, 1997; Pavlov & Mikheev, 2017). In general, except for some large rivers,
43 high turbidity conditions, and polar-day conditions, the fry of the pink salmon
44 *Oncorhynchus gorbuscha* perform downstream migration at night (Ali & Hoar, 1959) and
45 finish their migration overnight (Heard, 1991); however, since the previous studies about
46 diel migration of pink salmon have been conducted in rivers of various sizes (e.g., Kirillov
47 *et al.*, 2018; Neave, 1955; Pavlov *et al.*, 2015), these studies have shown different results
48 between rivers or surveys. Thus, a comprehensive understanding of the diel migration
49 pattern of pink salmon fry has not been achieved. Here, we examined the diel migration
50 pattern of pink salmon fry in three small streams on the Shiretoko Peninsula, Japan. Since
51 small streams have less variation in environmental factors along their course, they are the
52 most suitable model system for examining the diel migration pattern of pink salmon fry.

53 We selected three small streams on the Shiretoko Peninsula as the study streams
54 (44.07°N, 145.12°E; Table 1): Chienbetsu stream, Funbe stream, and Syoji stream.
55 Hatchery programs have never been implemented in these streams, and natural spawning

56 sustains the pink salmon populations (T. Yamada, unpublished data). In each stream, we
57 established a sampling point for salmon fry that was located near the mouth of the stream
58 and was not affected by sea waves.

59 In May 2021, to determine the diel migration pattern of pink salmon, we
60 conducted fish collection over a 24-h period in each stream (Table 1). In Japan, the peak
61 of downstream migration of pink salmon fry occurs in May. We placed two drift nets
62 (Matsui Corp., Tokyo, Japan; 50 cm squared opening, 100 cm long, 3 mm mesh) at a
63 sampling point for 15 minutes at hourly intervals. Since long-term sampling with drift
64 nets would result in the death of many fry, we limited the sampling effort. We used stakes
65 to fix the nets to the streambed so that the net openings ranged from the stream surface to
66 the streambed. Drift nets have often been used to capture the fry of salmonids (Hintz &
67 Lonzarich, 2012; Johnston, 1997). We recorded the number of individuals without using
68 anaesthesia and then immediately released all individuals. All surveys started at 10:00
69 and finished at 09:15 the following day. To evaluate stream discharge at each sampling
70 point, we constructed a transect and measured the wetted width. Then, we measured the
71 depth and current velocity at $0.2 \times \text{depth}$ and $0.8 \times \text{depth}$ at ten points along the transect.
72 We calculated the sectional areas between the measurement points or between the
73 measurement point and the streambank, multiplied each sectional area by the average
74 velocity, and summed them to calculate stream discharge. To evaluate the water filtered
75 by drift nets, we measured the wetted sectional area of the net and current velocity at 0.2
76 $\times \text{depth}$ and $0.8 \times \text{depth}$ at three points (left, right, and centre) on each net. We multiplied
77 the wetted sectional area of each net by the average velocity and summed them to
78 calculate filtered water by drift nets. All measurements were taken between 15:00 and
79 17:00. Finally, we used the ratio of the water filtered by drift nets to stream discharge to

80 estimate the total migrants in each stream at each time point.

81 Then, we analysed the data using a generalized additive mixed model (GAMM)
82 with a binomial distribution and logit link function. We used the migration activity of
83 pink salmon fry as a response variable and the cumulative time from survey start time as
84 a smooth term and stream ID as a random effect. Migration activity represents the
85 proportion of the estimated number of migrants at each time to the estimated total number
86 of migrants obtained through each 24-hour survey. All data analysis was conducted with
87 R v. 4.1.2 (R Core Team, 2021) using “mgcv” v. 1.8.38 (Wood, 2004) for GAMM.

88 From April to June 2021, we conducted a “peak survey” to confirm whether the
89 downstream migration pattern obtained from the 24-hour survey described above is
90 universal. This peak survey was conducted six, six, and three times in the Chienbetsu
91 stream, Funbe stream, and Syoji stream, respectively. The survey was conducted between
92 18:00 and 22:15 based on a previous study conducted in a stream with a runnable reach
93 length close to those in our study streams (Neave, 1955). We used the same method to
94 catch pink salmon fry as that used in the 24-hour survey. Additionally, we estimated the
95 total number of migrants using the same method as that used in the 24-hour survey. We
96 conducted all surveys, including 24-hour surveys, when the water in the streams was
97 transparent and flooding conditions were not observed. In addition to pink salmon, the
98 fry of chum salmon *O. keta* and juveniles of Dolly Varden *Salvelinus malma* were also
99 collected in these surveys.

100 The 24-hour survey showed that pink salmon fry mainly migrated downstream
101 within a few hours after sunset (Figure 1A). The model indicated that time was significant
102 ($P < 0.0001$, adjusted $R^2 = 0.564$), with 89.9% of the migrations occurring between 18:00
103 and 23:00 (Figure 1A). Additionally, all peak surveys indicated that the peak for

104 downstream migration of pink salmon fry was between 19:00 and 22:00 (Figure 1B). The
105 results indicated that sunset time influences the diel migration pattern of pink salmon fry
106 in small streams. Pink salmon fry emerged from the riverbed and moved actively to the
107 current for downstream migration in the first two (maximum three) hours after nightfall
108 (Pavlov *et al.*, 2019). Therefore, our study shows that individuals emerging in small
109 streams quickly migrated to the sea. Other salmonids show nocturnal downstream
110 migration: the brown trout *Salmo trutta*, coho salmon *O. kisutch*, Atlantic salmon *S. salar*,
111 and rainbow trout *O. mykiss* (Hintz & Lonzarich, 2012; Johnston, 1997; Pavlov &
112 Mikheev, 2017). Nocturnal migration may be a strategy to avoid predation (Ibbotson *et*
113 *al.*, 2011; Johnston, 1997; Kennedy *et al.*, 2018). Selection may have favoured the
114 nocturnal migration strategy in pink salmon fry, as observed in other salmonids.

115 There are several reasons why the peak of downstream migration for pink salmon
116 fry occurs within a few hours after sunset. First, early night may be the best time to avoid
117 predation. The Dolly Varden, which occasionally preys on fish (Denton *et al.*, 2009), is
118 dominant in the studied streams (T. Yamada, unpublished data). The foraging activity of
119 the Arctic charr *S. alpinus*, which is closely related to Dolly Varden, declines just after
120 sunset (Björnsson, 2001). If Dolly Varden have the same feeding pattern as that of Arctic
121 charr, then the best time for pink salmon fry to avoid predation is just after sunset. An
122 alternative explanation for the timing of peak migration is the strategy of completing
123 downstream migration during the night in rivers with various channel lengths. If pink
124 salmon spawned far from the mouth of the river, then fry would need a longer time to
125 reach the mouth of the river. Therefore, by starting downstream migration immediately
126 after sunset, pink salmon fry can reach the river mouth at night in small streams when
127 predation pressure is low. Pavlov *et al.* (2019) suggested that pink salmon in a longer

128 river would repeat this behaviour for several nights. Pink salmon, with their higher
129 straying rate among Pacific salmon (Hendry *et al.*, 2004), may have adapted to complete
130 their downstream migration at night even if they were born in rivers different from their
131 natal rivers.

132 This study revealed the diel migration pattern of pink salmon fry; however,
133 previous studies have shown different results between the studied rivers or between
134 surveyed dates (Kirillov *et al.*, 2018; Neave, 1955; Pavlov *et al.*, 2015). Genetic drift
135 between neighbouring river populations of pink salmon often occurs (Hendry *et al.*, 2004)
136 due to their higher straying rate. Therefore, genetic differences between neighbouring
137 river populations in the same year class are small (Aspinwall, 1974; Gharrett *et al.*, 1988;
138 Hendry *et al.*, 2004; Shaklee *et al.*, 1991); thus, the differences in diel patterns between
139 neighbouring rivers should be determined by factors other than genetic factors. By
140 selecting rivers as study sites with different lengths of spawnable reaches between the
141 studied rivers (range 1.6–16.1 km) or longer spawnable reach lengths (maximum distance
142 21 km), these studies may not have identified the diel migration patterns of pink salmon
143 fry. In the case of differing spawnable reach lengths between rivers, even if pink salmon
144 fry start their downstream migration at the same time, the time for the fry to reach the
145 mouth of the river would vary among rivers. Additionally, when rivers have longer
146 spawnable reach lengths, the location of the spawning redds makes a difference in terms
147 of the time it takes to reach the mouth of the river. In this study, by selecting streams that
148 have the same spawnable reach lengths between streams and short spawnable reach
149 lengths, we were able to elucidate the diel migration pattern.

150 This study indicated that pink salmon fry exhibit a diel downstream migration
151 pattern that depends on the time of sunset in the small streams. The diel pattern of

152 organisms is affected by light pollution (Longcore & Rich, 2004). Pink salmon fry avoid
153 light (Hoar *et al.*, 1957); therefore, the diel pattern of pink salmon fry may change
154 dramatically with light pollution, and the survival rate of salmon fry may decline as
155 optimal downstream strategies cannot be selected. Future studies should examine the
156 effect of light pollution on the diel pattern and survival of pink salmon fry.

157

158

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161 the field survey and gave valuable comments. We thank K. Morita and T. Nobetsu for
162 their helpful comments on the sampling method.

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164

165 **Contributions**

166 T. Y. and H. U. conceived the ideas. T. Y. conducted the field survey, performed the
167 analyses, and led the writing. All authors read and commented on the manuscript.

168

169

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246

247

248 **Table captions**

249 Table 1: Physical characteristics and environmental conditions on the dates of the 24-
250 hour survey of the three studied streams.

251 *Note:* RunnableL represents the reach length from the sampling point to the unpassable
252 dam or fall; DistFromSG represents the distance between the upstream edge of the main
253 spawning grounds and the sampling points.

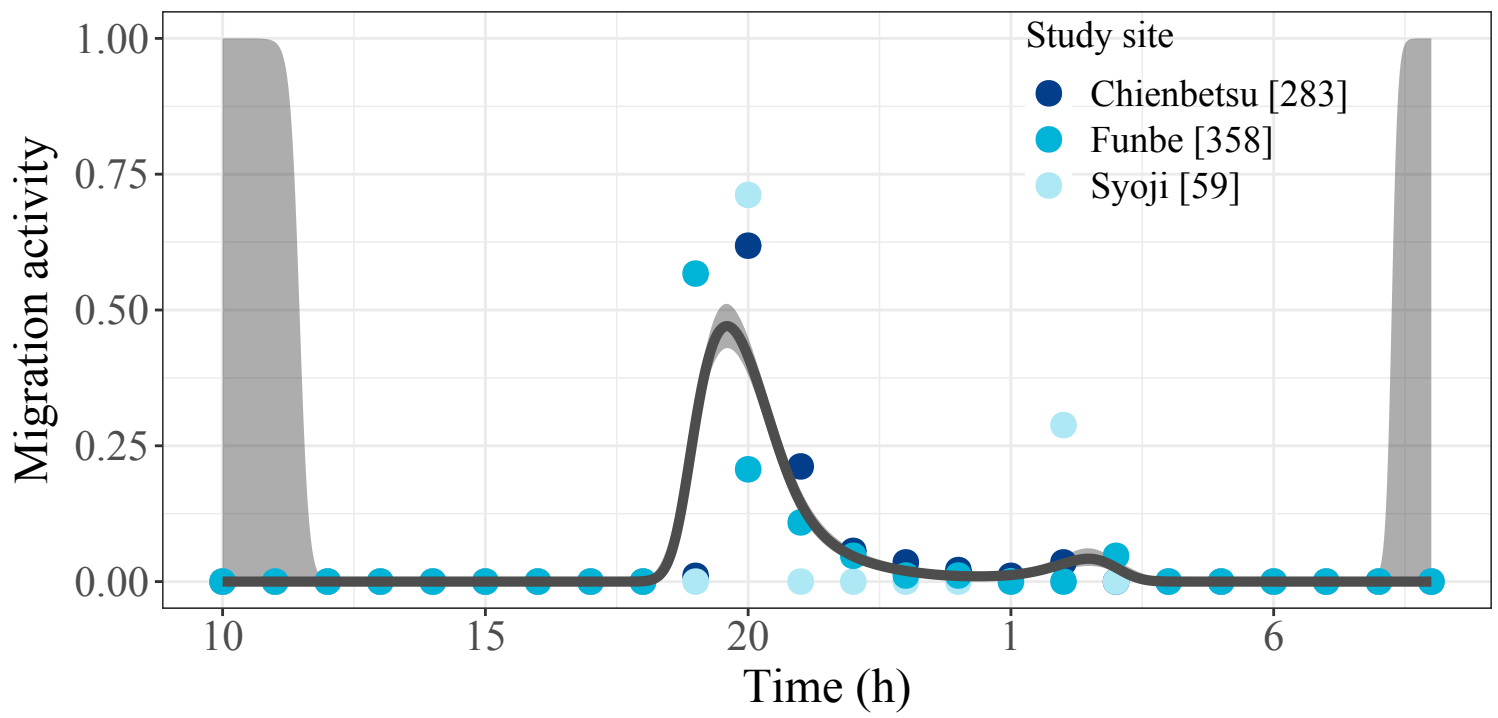
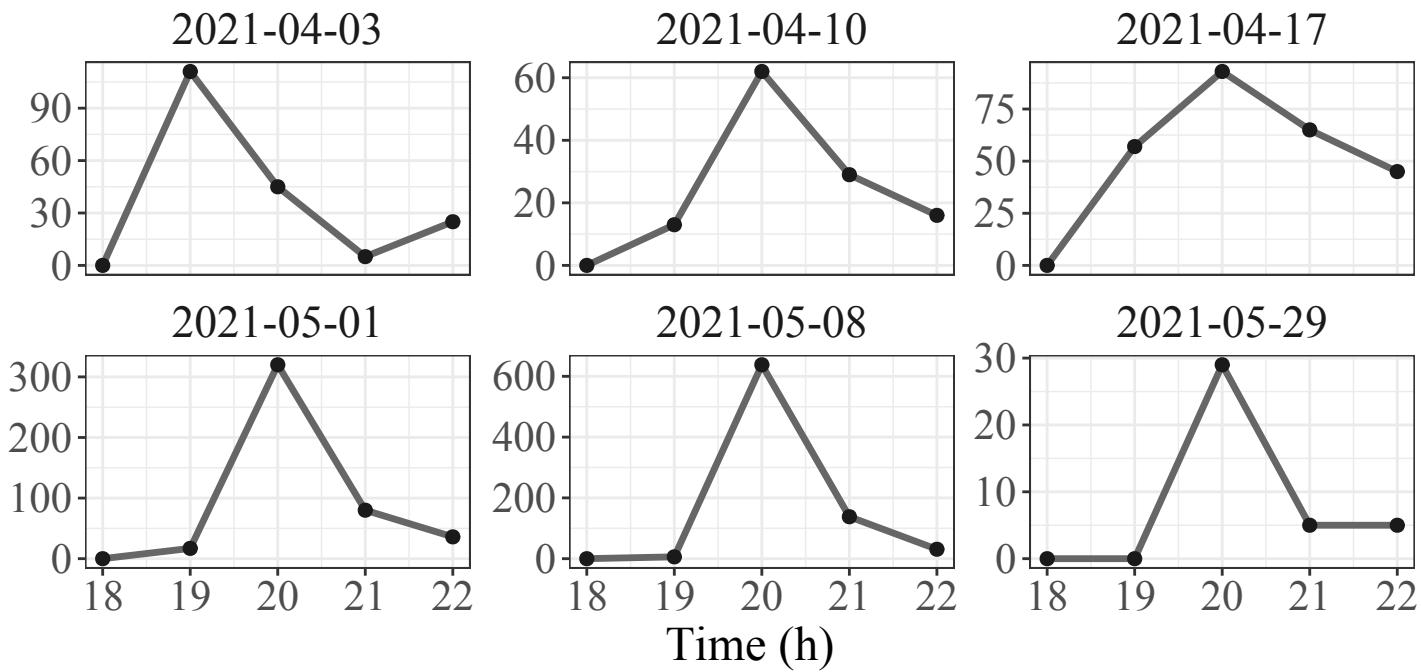
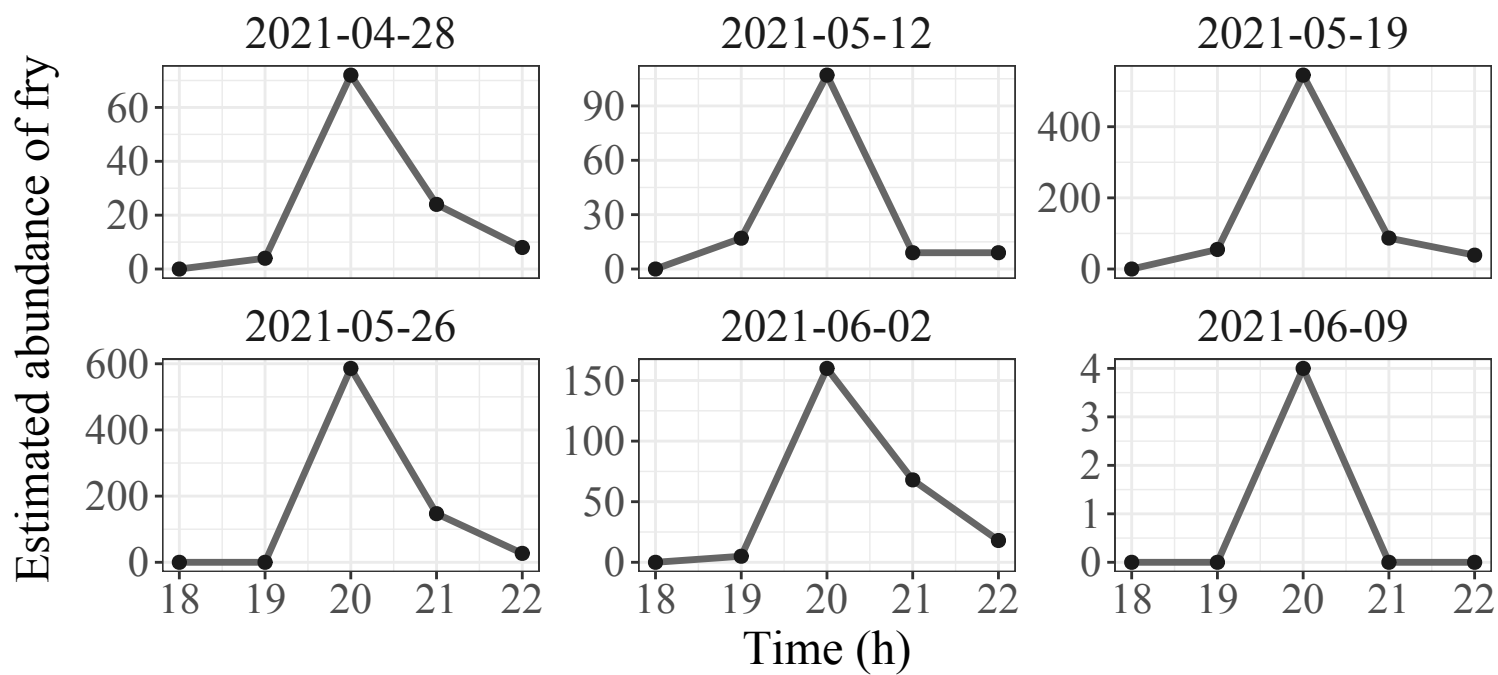
Table 1 Physical characteristics and environmental conditions on the dates of the 24-hour survey of the three studied streams.

Metric	Chienbetsu stream	Funbe stream	Syoji stream
RunnableL (m)	409.1	348.2	211.3
DistFromSG (m)	326.5	348.2	169.2
Start date	2021-05-15	2021-05-05	2021-05-21
Sunset time	18:38:17	18:27:43	18:44:42
Sunrise time	3:51:50	4:04:24	3:46:06
Sunshine duration (min / 24 h)	334	411	0
Weather condition at night	Cloudy	Cloudy then clear	Cloudy
Precipitation (mm / 24 h)	0.0	0.0	0.0
Lunar age	3.3	23.0	9.3
Average water temperature (C°)	8.1	6.3	7.8
Stream discharge (m ³)	65.1	91.6	166.8
Filtered water by drift nets (m ³)	20.5	21.2	19.7

Note : RunnableL represents the reach length from the sampling point to the unpassable dam or fall; DistFromSG represents the distance between the upstream edge of the main spawning grounds and the sampling points.

1 **Figure captions**

2 Figure 1: (A) Estimate of migration activity in relation to time in three streams.
3 Confidence interval (95%) is shown as the shaded area. The numbers in the brackets
4 indicate the estimated total number of pink salmon *Oncorhynchus gorbuscha* fry. (B)
5 Results of the peak survey in the Chienbetsu stream (1), Funbe stream (2), and Syoji
6 stream (3).

A**B-1****B-2****B-3**