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サケ稚魚における瞬発遊泳能力の発達と体長依存性：飼育個体と野生個体の比較

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Size-dependent development of burst swimming ability in juvenile chum salmon: comparisons between reared and wild juveniles

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In this study, we examined the development of burst swimming ability in juvenile chum salmon *Oncorhynchus keta*, comparing the swimming abilities of laboratory-reared fish, wild-caught fish, and juveniles confirmed as wild. Burst swimming was measured using an escape measurement method with sound stimuli. Across all groups, burst speed (BS) increased significantly with fork length (FL), demonstrating size dependence. However, the rate of increase differed among groups, with significant differences observed in the slopes of the BS–FL relationships. Despite these differences in developmental trajectories, no significant differences in BS were observed between groups within the body size class corresponding to the start of the downstream migration period (FL 30–45 mm). Our results suggest that, with respect to origin, there is no difference in burst swimming ability between hatchery-reared and wild fish, and that effects associated with growth and ecological processes in the wild may be involved.

キーワード：burst speed, juvenile, laboratory reared, *Oncorhynchus keta*, salmonid, swimming performance, wild fish

The chum salmon *Oncorhynchus keta* is the most abundant species of Pacific salmon in Japan, with its primary production region located in Hokkaido. In Hokkaido, artificial hatchery stocking programs have been continuously operated since the 1880s. Currently, approximately one billion juveniles are released annually from about 150 hatcheries (Miyakoshi *et al.*, 2013b; Fig. 1a). Although these hatchery programs play a crucial role in sustaining salmon fisheries resources in Hokkaido, studies on other salmonids have suggested that domestication caused by hatchery rearing over repeated generations can potentially reduce their fitness in the wild (Araki *et al.*, 2008).

Swimming ability is one of the most important functional traits affecting fish survival and fitness. It plays key roles in dispersal, migration, habitat selection, predator avoidance, and reproductive behavior (Tsukamoto *et al.*, 1975; Beamish, 1978; Stobutzki and Bellwood, 1997; Kolok, 1999; Wolter and Arlinghaus, 2003). Among the different components of swimming ability, burst swimming is particularly important as it is strongly associated with escape behavior from predators (Taylor and McPhail, 1985; Jayne and Lauder, 1993). Consequently, burst speed (BS) serves as an important

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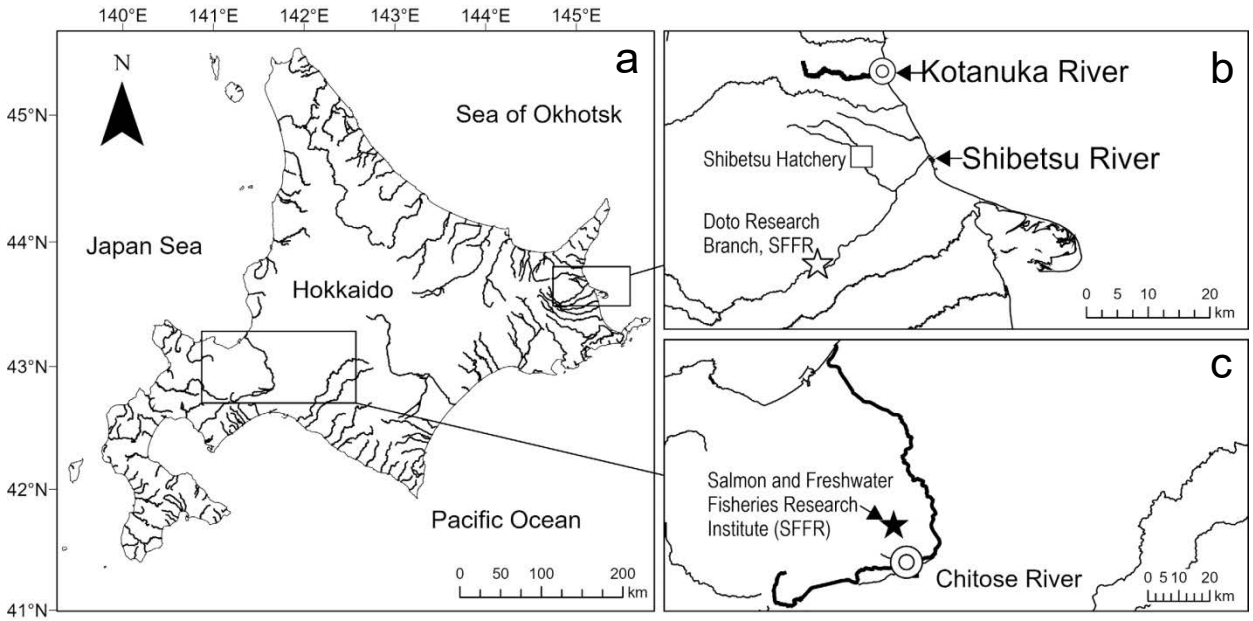

Fig. 1　Locations of recorded chum salmon release rivers in Hokkaido (a), and origins of chum salmon used in this study (b, c). Two figures on the right show origins of salmon used in burst swimming experiments. Upper right panel shows locations of Shibetsu Hatchery (□), origin of salmon used in experiments in 2013 and 2014, and Doto Research Branch of the Salmon and Freshwater Fisheries Research Institute (SFFR), Hokkaido Research Organization (☆), facility where salmon were reared under laboratory conditions. These juveniles were treated as the reared group. Kotanuka River (◎) had no releases, but collected juvenile chum salmons were defined as wild-caught groups, considering the possibility of strays from other rivers. Bottom right panel shows Chitose River, a tributary of the Ishikari River, and collection sites (◎) for wild group juvenile. Fish collected in 2023 and 2024 were confirmed as wild fish based on the absence of otolith thermal markings. Juveniles collected from the Chitose River were used in experiments at the SFFR (★).

indicator of the survival potential of juvenile fish in natural environments. After emergence, juvenile chum salmon begin their downstream migration, experiencing substantial predation pressure in both riverine and coastal environments (Kubo, 1946; Hikita *et al.*, 1959; Fresh and Schroder, 1987; Takami and Nagasawa, 1996; Sturdevant *et al.*, 2009; Miyakoshi *et al.*, 2013a). Therefore, burst swimming ability during the early life stages may be closely related to their overall survival.

Previous studies have suggested that salmonids reared under hatchery conditions for longer periods, such as sockeye salmon, coho salmon, and Atlantic salmon, which are reared under hatchery conditions for more than one year and released as smolts, exhibit lower swimming ability compared to wild fish (Pedersen *et al.*, 2008; Hammenstig *et al.*, 2014). Although the rearing period for chum salmon after emergence is approximately two months—shorter than that of the aforementioned species—research on the ontogenetic development of swimming ability in juvenile chum salmon is limited (Ohkuma *et al.*, 1988). Furthermore, comparisons between hatchery-reared and wild juveniles have been previously reported only by Kobayashi and Ohkuma (1983) and Nobata *et al.* (2022), and furthermore, only within a limited size range. Therefore, whether hatchery rearing affects the development of swimming ability in juvenile chum salmon remains uncertain.

The objective of this study was to investigate the ontogenetic development of burst swimming ability in juvenile chum salmon and to evaluate differences between hatchery-reared and wild fish. Specifically, we investigated: (1) the size-dependent relationship between fork length (FL) and BS; (2) whether the developmental patterns of BS differ among origin groups; and (3) whether differences in BS exist among groups within body sizes corresponding to the early river life stage prior to downstream migration.

MATERIALS AND METHODS

Definition and origin of experimental fish　Definitions of wild and hatchery fish followed criteria proposed by Morita and Ohkuma (2015). 'Wild fish' were defined as individuals originating from natural spawning, regardless of whether their parents were wild or hatchery-origin fish. 'Hatchery fish' were defined as individuals that were produced by artificial fertilization and subsequently released from hatcheries

irrespective of whether the broodstock originated from wild or hatchery returns.

Juvenile chum salmon used in the laboratory rearing experiment originated from the Shibetsu River, a major river supporting salmon enhancement programs in the Nemuro region of eastern Hokkaido (Fig. 1b). Fertilized eggs of the 2012 brood year were obtained on 12 September and 11 December 2012, and those of the 2013 brood year were obtained on 1 October 2013 through artificial insemination conducted as part of hatchery programs in the Shibetsu River. Eyed eggs managed at the Shibetsu hatchery of the Nemuro Salmon Enhancement Association were transported to the Doto Research Branch of the Salmon and Freshwater Fisheries Research Institute, Hokkaido Research Organization, where they were incubated in a vertical incubator until emergence. After emergence, juveniles were placed in a plastic rearing chamber (length × width × height, 3.26 m × 0.33 m × 0.33 m). The initial rearing density was approximately 2000 fish per chamber, and the density was gradually reduced so that approximately 1000 fish remained when average body mass reached 1 g and fewer than 300 fish remained when body mass exceeded 2 g. Aerated groundwater (approximately 9.5 °C water temperature) was supplied continuously to the chamber, and the measured water flow velocity within the chamber was less than 1 cm s^{-1}. Fish were fed a commercial diet (Alpha Crumble EX Masu C 1 and C 2; Nippon Nosan Co., Ltd.). BS measurements were conducted on hatchery-origin juveniles reared in the laboratory. In 2013, measurements were performed on eight occasions between March and May with 8–12 fish per trial (n = 84). In 2014, measurements were conducted on 13 occasions between February and April with 4–10 fish per trial (n = 120). Although these fish originated from the hatchery, they were not released into natural environments. Therefore, this study defines these as laboratory-reared fish.

Juvenile chum salmon were collected from the Kotanuka River in the Nemuro region (Fig. 1b) and the Chitose River in western Hokkaido (Fig. 1c). In the Kotanuka River, sampling was conducted approximately 400 m upstream from the river mouth using a cast net and an electrofisher (Electrofisher Model 12, Smith-Root Inc.). To minimize potential impacts on fish, the electrofisher voltage was set to 200 V. Fish were collected on 25 April and 5 July 2013 (12 and 13 individuals, respectively; total n = 25) and on 18 May 2014 (n = 25). After capture, the fish were transported to the Doto Research Branch and held in a plastic rearing chamber for 24–30 h to allow recovery prior to measuring BS. Although juvenile chum salmon had been released into the Kotanuka River until 1986, no release had occurred for 27 years at the time of this study (https://www.fra.go.jp/shigen/salmon/publications/files/hsh100thyear_stat.pdf, retrieved 16 May 2026). Therefore, juveniles collected from the Kotanuka River were considered to be primarily of wild origin. However, recent surveys have reported that some relatively large juveniles collected in the Kotanuka River were marked fish from the nearby Uebetsu River that chum salmon juveniles were released and subsequently entered the Kotanuka River after a brief marine migration (Kasugai and Saneyoshi, 2015; Miyamoto *et al.*, 2016). Consequently, the possibility that some of the fry collected from this river originated from other rivers cannot be excluded. For this reason, fish collected from the Kotanuka River were classified as wild-caught fish in this study.

The fish were also collected from the Chitose River, one of the major salmon enhancement rivers on the Sea of Japan side of Hokkaido. In the Chitose River, natural spawning by wild chum salmon has been observed even after December, when the catch operations for hatchery programs end (Hasegawa *et al.*, 2014). Since 2001, all hatchery-released juveniles in the Chitose River have been marked through otolith thermal marking by the Fisheries Resources Institute of the Japan Fisheries Research and Education Agency. Therefore, hatchery-origin and wild-origin juveniles can be completely distinguished by examining their otolith marks. Sampling was conducted in a section approximately 80 km upstream from the river mouth, where salmon spawning behavior has been confirmed. Juveniles were collected using an electrofisher after the annual hatchery release had been completed. A total of 54 juveniles were collected in 2023 (18 on 18 May, 27 on 26 May, and 9 on 7 June), and 69 juveniles were collected in 2024 (34 on 21 May, 19 on 27 May, and 16 on 3 June). After capture, fish were transported to the rearing facility of the Salmon and Freshwater Fisheries Research Institute, Eniwa (SFFR), and held in a plastic rearing chamber until BS measurements were conducted. Following the swimming trials, the fish were dissected, and their otoliths were examined to confirm the absence of thermal marks. Because all individuals used in the analysis were confirmed to lack otolith thermal marks, they were classified as wild fish.

Burst swimming experiments BS was measured using an escape measurement method based on sound startle stimulation (Torao *et al.*, 2020). Individual juveniles were placed in a circular plastic tank (56 cm in diameter) filled with

freshwater. The water temperature during the experiment at the Doto Research Branch was 9.5 °C, while it ranged from 9.2–9.6 °C during the experiment in SFFR. Escape responses were induced by striking a weight against the outer wall of the tank to produce a sudden sound stimulus. Two sound stimuli were delivered at 10-s intervals. The escape responses were recorded using a digital video camera. Video frames were analyzed to estimate swimming speed based on the distance measured every three frames (equivalent to 0.1 s). The maximum velocity observed during the escape response was defined as the BS. After the swimming trials, the fish were anesthetized and their body weight (BW) (in g) and fork length (FL) (in mm) were measured. The condition factor (CF) was calculated as:

$$CF = 10^5 \times BW/FL^3$$

Individuals that did not exhibit any escape response to the sound stimulus were excluded from the analysis. In total, BS data were obtained from 204 laboratory-reared fish, 50 wild-caught fish, and 112 wild fish.

Statistical analysis　As the primary objective of this study was to examine differences among origin groups, potential differences between sampling years within each group were not statistically tested. Data from different years were therefore pooled for subsequent analyses. All statistical analyses were conducted using the R version 4.5.0 (R Core Team, 2025). The relationships between FL and BS were evaluated separately for each group using linear regression analysis. Relative burst swimming speed (RBS, expressed in FL/s) was defined as burst swimming speed divided by fork length, and the relationship between FL and RBS was evaluated in the same manner. Pearson's correlation coefficients were calculated, and relationships were considered statistically significant at $P < 0.05$. To compare the slopes of the regression relationships among groups, analysis of covariance (ANCOVA) was conducted. Differences in slopes were tested using the emtrends function in the *emmeans* package (Lenth, 2019). Pairwise comparisons were then performed to evaluate differences in slopes among the groups. Because most wild juveniles collected from the Chitose River were ≤ 45 mm FL, larger individuals were assumed to have already migrated downstream. To compare burst swimming performance at body sizes corresponding to the early riverine stage, fish were grouped into two size classes: 35 mm class (30–39 mm FL) and 40 mm class (40–44 mm FL). Within each size class, differences in BS among the three groups were tested using Welch's *t*-test. Since the objective of this study was to examine differences in BS at a stage where the effects of rearing were minimal, we limited our analysis to comparisons between reared fish and wild-caught or wild fish.

RESULTS

Body size and burst speed of experimental fish

Summary statistics of FL, BW, CF, BS, and RBS for each group are presented in Table 1. FL of the reared fish ranged from 34–71 mm, with BW ranging from 0.27–3.61 g. The mean CF was similar between sampling years (8.56–8.63). Mean BS was 105.2 ± 16.2 cm s^{-1} in 2013 and 105.5 ± 22.4 cm s^{-1} in 2014, and RBS ranged from 13.5–29.2 FL s^{-1}.

Wild-caught fish collected from the Kotanuka River ranged from 36.0–63.2 mm in FL and from 0.29–2.00 g in BW. Mean FL was 47.5 ± 8.64 mm in 2013 and 51.8 ± 6.14 mm in 2014, and mean BW was 0.89 ± 0.57 g and 1.06 ± 0.41 g, respectively. The mean CF values were 7.13 and 7.28, respectively. Mean BS was 97.9 ± 28.8 cm s^{-1} in 2013 and 97.0 ± 18.6 cm s^{-1} in 2014, corresponding to RBS of 18.7–20.3 FL s^{-1}.

Wild fish collected from the Chitose River were generally smaller than those from the other groups. Most individuals were ≤45 mm FL, although a few larger individuals were collected in 2024, with a maximum FL of 74 mm. Mean FL was 38.3 ± 3.67 mm in 2023 and 40.9 ± 8.91 mm in 2024, and mean BW was 0.40 ± 0.18 g and 0.59 ± 0.68 g, respectively. The mean CF ranged from 6.75–6.95. Mean BS ranged from 81.8–82.5 cm s^{-1}, and RBS ranged from 20.5–21.6 FL s^{-1}.

Relationship between BS and body size　BS increased significantly with increasing FL in all three groups (Table 2; Fig. 2). In reared fish, BS showed a significant positive relationship with FL (slope = 1.64, $t = 13.34$, $P < 0.001$; Fig. 2a). Similarly, BS increased significantly with FL in wild-caught fish (slope = 2.47, $t = 9.07$, $P < 0.001$; Fig. 2b). A significant positive relationship was also observed in wild fish (slope = 0.69, $t = 5.60$, $P < 0.001$; Fig. 2c). Considerable variation in BS was observed among individuals of similar body size, particularly in the reared fish.

Relationship between relative burst speed and body size　The relationship between RBS and FL differed among groups (Table 3). In both reared and wild fish, RBS decreased significantly with increasing FL, indicating a negative relationship with body size (reared fish: slope = − 0.072 ± 0.022, $P = 0.002$; wild fish: slope = − 0.226 ± 0.030, $P <$

Table 1 Morphological traits and burst swimming performance of juvenile chum salmon from three origin groups: laboratory-reared (Shibetsu River), wild-caught (Kotanuka River), and wild (Chitose River)

Fish	Location	Year	Sample size	Fork length (FL, mm)	Body weight (W, g)	Condition factor (CF)	Burst speed (cm s^{-1})	Relative burst speed (FL s^{-1})
Laboratory-reared	Doto Research Branch	2013	84	54.90 ± 6.79 (39.45–67.00)	1.51 ± 0.66 (0.53–2.97)	8.56 ± 1.02 (5.46–10.35)	105.15 ± 16.18 (74–146)	19.31 ± 3.01 (13.53–28.46)
		2014	120	51.36 ± 9.01 (34.81–71.27)	1.33 ± 0.71 (0.27–3.61)	8.63 ± 0.96 (5.82–10.16)	105.50 ± 22.42 (63–167)	20.55 ± 2.39 (14.23–29.24)
Wild-caught	Kotanuka River	2013	25	47.51 ± 8.64 (35.98–62.20)	0.89 ± 0.57 (0.29–1.98)	7.13 ± 1.03 (5.26–8.93)	97.92 ± 28.76 (48–161)	20.29 ± 3.31 (12.26–27.08)
		2014	25	51.80 ± 6.14 (41.30–63.20)	1.06 ± 0.41 (0.47–2.00)	7.28 ± 0.50 (6.51–8.37)	97.04 ± 18.59 (65–139)	18.70 ± 2.55 (14.13–23.28)
Wild	Chitose River	2023	55	38.31 ± 3.67 (32.57–56.10)	0.40 ± 0.18 (0.23–1.48)	6.75 ± 0.56 (5.41–8.38)	82.49 ± 10.00 (58–110)	21.58 ± 2.28 (16.31–27.82)
		2024	57	40.85 ± 8.91 (33.20–74.10)	0.59 ± 0.68 (0.24–3.47)	6.95 ± 0.76 (6.01–10.83)	81.79 ± 10.21 (65–105)	20.47 ± 2.92 (11.25–26.25)

Values were expressed by means ± standard deviation.
Condition factor was calculated by the following formula: $CF = 10^5 \times W/(FL)^3$.
The values in parentheses indicate the respective ranges.

Table 2 Results of regression analysis between burst speed (cm s^{-1}) and fork length (FL) in different groups (laboratory-reared, wild-caught, wild) of juvenile chum salmon

Explanatory variables	Group	Coefficient	Estimate	Standard error	t value	Pr(>|t|)	R^2	P value
FL	Laboratory-reared	Intercept	18.737	6.574	2.850	0.005	0.47	< 0.001
		FL	1.640	0.123	13.340	0.000		
	Wild-caught	Intercept	-25.237	13.702	-1.842	0.072	0.63	< 0.001
		FL	2.473	0.273	9.066	0.000		
	Wild	Intercept	54.969	4.930	11.151	0.000	0.22	< 0.001
		FL	0.686	0.123	5.595	0.000		

0.001). In contrast, wild-caught fish showed a significant positive relationship between RBS and FL (slope = 0.110 ± 0.054, P = 0.049).

Comparison of burst speed–fork length relationships among groups Analysis of covariance revealed significant differences among groups in the slopes of the regression lines describing the relationship between BS and FL across the observed size range (Table 4). The slope of the regression line for reared fish was significantly greater than that for wild fish (difference in slope = 0.959 ± 0.212, P < 0.0001). In contrast, the slope for reared fish was significantly smaller than that for wild-caught fish (difference = − 0.823 ± 0.266, P = 0.0060). The slope for wild fish was also significantly smaller than that for wild-caught fish (difference = − 1.782 ± 0.301, P < 0.0001).

Comparison of burst speed among groups within size classes Comparisons of BS among groups within the 35 mm and 40 mm size classes are shown in Table 5. Within the 35 mm size class, mean BS was 78.8 ± 9.09 cm s^{-1} for reared fish and 71.0 ± 17.6 cm s^{-1} for wild-caught fish, with no significant difference between the two groups (Welch's t-test, P = 0.299). The mean BS of wild fish (79.6 ± 8.89 cm s^{-1}) also did not differ significantly from that of the reared fish (P = 0.734). Within the 40 mm size class, mean BS was 87.3 ± 10.1 cm s^{-1} for reared fish and 80.0 ± 11.8 cm s^{-1} for wild-caught fish, and the difference was not significant (P = 0.507). Likewise, no significant difference was detected between reared fish and wild fish (89.6 ± 9.31 cm s^{-1}; P = 0.128).

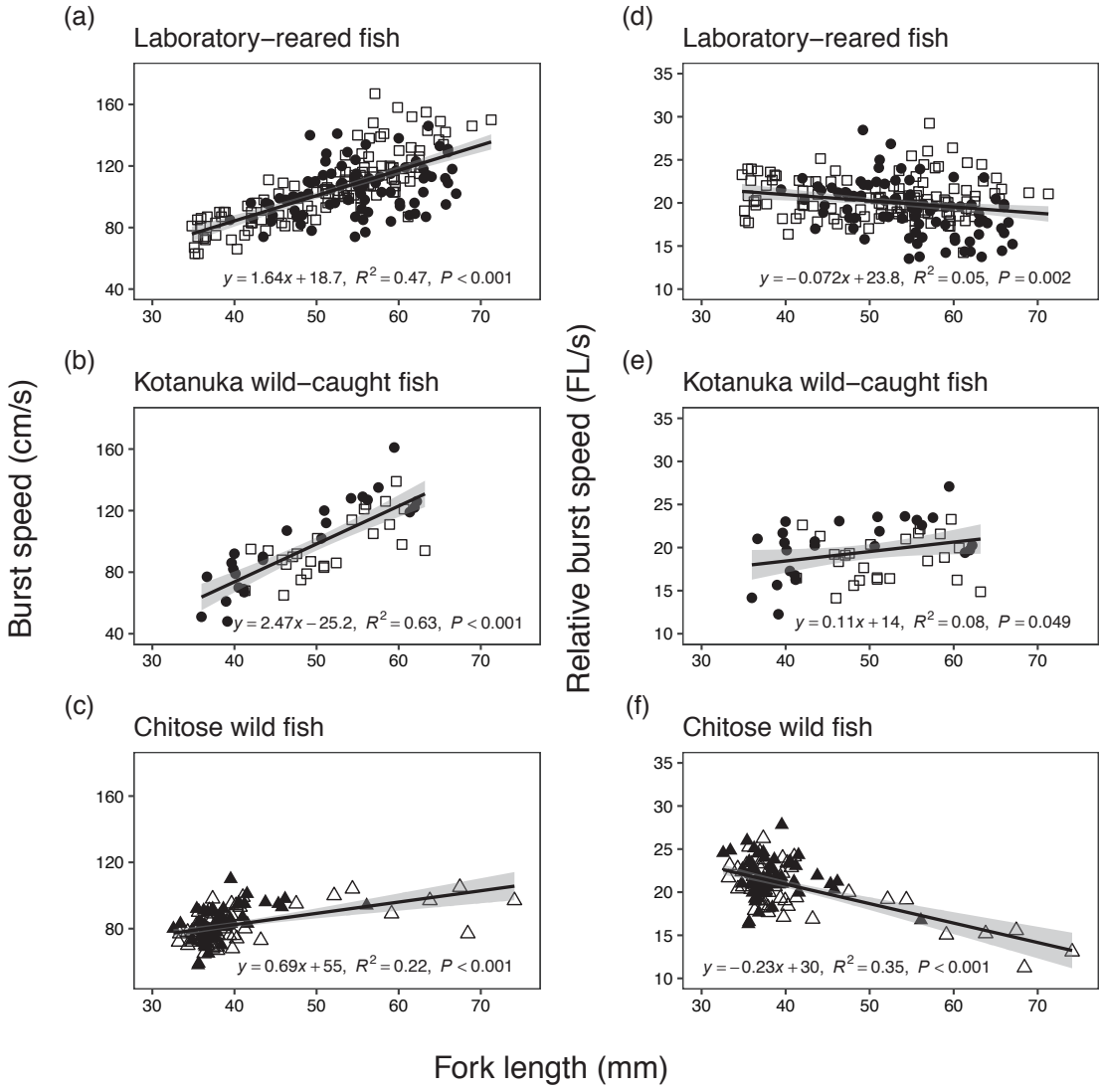

Fig. 2　Relation of burst speed (left column) or relative burst speed (right column) with fork length of (a)(d) laboratory reared (n = 204), (b)(e) wild-caught in Kotanuka River (n = 50), and (c)(f) Chitose River wild juvenile chum salmon (n = 112). Black circles represent laboratory-reared fish or fish collected from Kotanuka River in 2013, while white squares represent those from 2014. Black triangles show wild fish from Chitose River in 2023, and white triangles show those from 2024. Correlations were evaluated using Pearson's correlation coefficient test, and multiple R-squared (R^2) and p-value (P) were calculated. $P<0.05$ were considered significant correlation. Solid lines indicate linear regression relationships, and shaded areas represent 95% confidence intervals.

Table 3　Results of regression analysis between relative burst speed (FL s^{-1}) and fork length (FL) in different groups (laboratory-reared, wild-caught, wild) of juvenile chum salmon

Explanatory variables	Group	Coefficient	Estimate	Standard error	t value	Pr(>|t|)	R^2	P value
RBS	Laboratory-reared	Intercept	23.828	1.199	19.868	0.000	0.05	0.002
		BS/FL	-0.072	0.022	-3.195	0.002		
	Wild-caught	Intercept	14.040	2.734	5.136	0.000	0.08	0.049
		BS/FL	0.110	0.054	2.021	0.049		
	Wild	Intercept	29.955	1.192	25.132	0.000	0.35	< 0.001
		BS/FL	-0.226	0.030	-7.614	0.000		

Table 4 Pairwise comparisons of regression slopes describing the relationship between fork length and burst speed among groups (reared, wild-caught, and wild)

Comparison	Difference in slope	Standard error	df	*t* value	*P* value
Reared – (Wild-caught)	-0.823	0.266	360	-3.094	0.006
Reared – Wild	0.959	0.212	360	4.523	<0.0001
Wild – (Wild-caught)	-1.782	0.301	360	-5.914	<0.0001

Slopes were estimated using ANCOVA with an interaction between fork length and group, and pairwise differences were evaluated using post hoc comparisons of estimated marginal trends.

Table 5 Comparison of burst speed between reared, wild-caught, and wild juvenile salmon within each fork length class

Fork length class (mm)	Group	*n*	Burst speed (cm/s, Mean ± S.D.)	Comparison	*P* value
35	Reared	19	78.79 ± 9.09		
	Wild-caught	7	71.00 ± 17.57	Reared vs Wild-caught	0.299
	Wild	77	79.58 ± 8.89	Reared vs Wild	0.734
40	Reared	21	87.33 ± 10.12		
	Wild-caught	9	80.00 ± 11.83	Reared vs Wild-caught	0.507
	Wild	13	89.62 ± 9.31	Reared vs Wild	0.128

The fork length ranges for the 35 mm and 40 mm size classes were determined as 30–39 mm and 40–44 mm, respectively. *P* values indicate results of Welch's *t*-tests.

Discussion

The present study revealed three main findings. First, burst swimming performance increased significantly with body size in juvenile chum salmon. Second, the rate of increase differed among origin groups. Third, despite these differences in developmental trajectories, BS did not differ significantly between reared and wild fish within body sizes corresponding to the early riverine stage.

The juveniles examined in this study ranged from 32–74 mm FL, encompassing the majority of the typical body size range observed during the riverine life stage of chum salmon. Within this size range, BS increased significantly with increasing body length in all groups, indicative of a significant size-dependent relationship. Size dependence of swimming ability has been widely reported in fishes, as larger individuals generally show higher swimming ability (Beamish, 1978; Plaut, 2001; Wolter and Arlinghaus, 2003; Cano-Barbacil *et al.*, 2020). Ohkuma *et al.* (1998) measured the burst swimming speed of reared chum salmon with 30–50 mm FL and obtained results nearly identical to those of the present study. The present results indicate that the same pattern applies to juvenile chum salmon across the riverine life stage. In some fish species, the relationship between body size and swimming ability can change depending on the ontogenetic stage associated with shifts in their life history (Ducos *et al.*, 2022). However, within the riverine stage examined here, burst swimming performance of juvenile chum salmon appeared to increase in a linear manner with body size. The size-dependent increase in burst swimming ability observed in the present study is consistent with previous findings on the development of other swimming abilities in juvenile chum salmon. Iino *et al.* (2021) reported that the critical swimming speed, reflecting sustained swimming ability, also increases with body size and develops particularly rapidly during early life stages. These findings suggest that both burst swimming ability and sustained swimming ability in juvenile chum salmon develop progressively with growth.

Substantial individual variation in BS was observed within similar body size ranges. Large individual variation in swimming performance has previously been reported in salmonids of a single origin (Ojanguren and Braña, 2003). Such variability may reflect differences in physiological condition, growth history, or behavioral traits among individuals. In hatchery environments, compared to natural environments where selective pressures are stronger, even individuals with relatively poor swimming ability may survive, and differences in ability among individuals may persist for a longer period.

Although BS increased with FL in all groups, the slopes of the regression relationships differed significantly among different origin groups. In particular, wild-caught fish from the Kotanuka River exhibited significant increase in BS with increasing FL compared with the other groups. This difference may reflect variation in growth history or environmental conditions rather than intrinsic differences between hatchery and wild fish. One possibility is that rearing conditions impair the development of swimming ability in hatchery fish. Juveniles reared in hatcheries typically experience relatively stable environments with low water velocities and abundant food resources. Consequently, they may have fewer opportunities to perform sustained or burst swimming behaviors associated with foraging, station holding, or predator avoidance compared with fish in natural rivers (Sundström and Johnsson, 2001; Johnsson *et al.*, 2001). Such environmental differences could influence the developmental trajectory of swimming performance. Another possible explanation for the steeper relationship observed in wild-caught fish is the results of size-selective predation. Juvenile chum salmon experience substantial predation pressure in riverine and coastal environments, and predators often select prey based on body

size and escape ability (Duffy and Beauchamp, 2008; Hasegawa *et al.*, 2021). Therefore, larger individuals may represent survivors with relatively high swimming performance. Reports indicate that the relatively large juveniles collected in the Kotanuka River include individuals from other rivers (Kasugai and Saneyoshi, 2015; Miyamoto *et al.*, 2016). This process could lead to an apparent increase in burst swimming ability with body size among larger individuals captured in wild-caught fish from the Kotanuka River. In addition, fast-growing, large-sized individuals expand their distribution into faster stream velocities (Kaeriyama, 1986). Larger individuals might improve their swimming ability by experiencing faster flow velocities. Generally, relative burst swimming ability decreases with increasing body length (Beamish, 1978). In reared fish and wild fish from the Chitose River, RBS decreased as FL increased; in contrast, wild-caught fish from the Kotanuka River demonstrated that larger individuals possessed relatively higher burst swimming ability. This suggests that large individuals with high burst swimming speeds are present in the Kotanuka River.

In contrast, wild fish from the Chitose River exhibited a significantly smaller slope in the relationship between BS and body size. Many of the individuals collected from this river were relatively small, although a few larger juveniles were also present. Previous studies have reported that most juvenile chum salmon begin downstream migration soon after emergence, whereas some individuals remain in the upper reaches of the river for an extended period and migrate at larger sizes (Neave, 1955; Kobayashi *et al.*, 1965; Mayama *et al.*, 1983; Kaeriyama, 1986). The larger juveniles observed in the present study may be such river-resident individuals. Interestingly, these larger fish exhibited relatively low BS compared with individuals of similar size in other groups, which may have contributed to the lower slope of the regression relationship. The presence of resident individuals may be related to the river environment in the upper reaches of the Chitose River. The site where the juveniles were collected appeared to have a slow current and sufficient cover. Such environments may be conducive for fry to remain in the site, potentially contributing to the presence of individuals that grow to large sizes. Kaeriyama (1986) observed that individuals that emerged early tended to remain near spawning sites for extended periods. That report also noted that the downstream migration might be related to food availability, suggesting that food shortages could trigger the migration. The downstream migration speed of hatchery *S. salar* smolt is inversely correlated with feed intake (Lans *et al.*, 2011). This suggests that when food is readily available, fish tend to remain at that site. Although such a response has not been observed in chum salmon juveniles, it is possible that in environments where sufficient food is available, juveniles may exhibit inhibitory behavior toward downstream migration. Fast currents are less likely to be experienced by individuals in the slow-flowing environments near spawning sites, which might affect the development of their burst swimming abilities. However, the cause of the low burst swimming in large juveniles, or the relationship between low burst swimming and retention in rivers, remains unclear. The ecological significance of this phenomenon remains unclear, and further research is needed to verify the relationship between burst swimming ability and differences in downstream migration behavior.

Despite the differences in developmental trajectories among groups, no significant differences in BS were detected between reared fish and either wild-caught or wild fish within the body size classes corresponding to the early riverine stage. This finding suggests that reared juvenile chum salmon do not necessarily possess inferior burst swimming performance compared with wild fish at body sizes typical of the early downstream migration stage. Previous studies on other salmonids have reported that fish reared to the smolt stage demonstrate lower swimming ability compared to wild fish (McDonald *et al.*, 1998; Pedersen *et al.*, 2008; Van Leeuwen *et al.*, 2011; Hammenstig *et al.*, 2014). In contrast, chum salmon are generally released at much earlier life stages and experience relatively short hatchery rearing periods. The absence of clear differences in BS observed in the present study may therefore reflect the limited duration of rearing. Furthermore, when comparing flow velocities in their habitats, during the early stages of their life in natural rivers, juvenile chum salmon prefer to use locations with a gentle flow velocity of less than 10 cm/s (Hasegawa *et al.*, 2011). The difference in flow velocity experienced by reared and wild fish during these periods is relatively small, so its effect on the development of their swimming ability may be limited.

For hatchery enhancement programs for chum salmon, optimizing release size and release timing remains an important management issue. Future studies should investigate how environmental conditions during rearing, such as water velocity, structural complexity, and exercise opportunities, influence the development of swimming performance. Such information will be valuable for developing rearing methods

that enhance functional traits that are important for survival in the wild.

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