

Yusuke Koseki · Koji Maekawa

Sexual selection on mature male parr of masu salmon (*Oncorhynchus masou*): does sneaking behavior favor small body size and less-developed sexual characters?

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Abstract In many salmonid species, males exhibit morphological dimorphism associated with alternative mating behaviors. “Precocious males” have a small body size with little or no development of sexual characters and adopt sneaking to gain access to females, while “migratory males” of large body size and well-developed secondary sexual characters fight. We quantified selection on precocious male parr of masu salmon (*Oncorhynchus masou*) under simulated natural conditions to examine the contribution of morphology to sneaking success. In contrast to the prediction that sneaking behavior favors small body size, we detected selection favoring relatively large body size for sneaking success. This selection pressure was caused by the dominance hierarchy within parr and may have been facilitated by indifference of dominant migratory males to parr. Unlike the secondary sexual characters exhibited by migratory male salmon, such as the hooked snout and humped back, no morphological characters other than body size contributed to the reproductive success of masu salmon parr. This non-contribution may have been responsible for the lack of development of sexual characters in precocious males.

Key words Alternative mating behavior · Morphological dimorphism · Sexual selection · Mature male parr · *Oncorhynchus masou*

Introduction

Alternative mating behaviors among males are commonly observed in many animal species (reviewed in Tabor-sky 1994; Gross 1996). For example, “sneaking” and

acting as a “satellite” are common non-competitive behaviors which are alternatives to fighting or courting for access to mates (e.g., insect: Crespi 1988; Emlen 1997; anuran: Sullivan 1982; Fukuyama 1991; fish: Kodric-Brown 1986; Reynolds et al. 1993). In many cases, the adoption of alternative behaviors depends on body size and/or morphological characters which are representative of competitive ability or social status (Gross 1984; Hayashi 1985; Hughes 1985). Individuals which adopt non-competitive behavior have a smaller body size and/or less-developed morphological characters than those that compete directly. Moreover, in some species, intrasexual variation in morphology consists of two or more discrete frequency distribution modes, the upper and lower modes being associated with competitive and non-competitive behaviors, respectively (Eberhard 1982; Danforth 1991; Shuster and Wade 1991; Emlen 1997). Such di- and polymorphism may represent morphological specialization corresponding to the alternative behaviors.

Salmonid species show the typical male dimorphism associated with alternative mating behaviors and life histories. Many salmonid species include two forms, precocious males, such as “jacks” and “mature male parr” which are small in body size and young in age at maturity, and migratory males which are large and late-maturing. Precocious and migratory males adopt sneaking and fighting for access to females, respectively (Jones 1959; Hanson and Smith 1967; Maekawa 1983; Gross 1985; Myers and Hutchings 1987). Morphological differences between migratory and precocious males exist in body size and other characters, such as snout length and hump size, which are secondarily developed in migrants at maturity (Maekawa 1978, 1984). As for other dimorphic species, salmonid dimorphism is interpreted as morphological specialization for alternative behaviors. Large body size with well-developed sexual characters and small body size without these characters appear to be suited for fighting and sneaking, respectively (Gross 1985, 1991). Indeed, the large body, hump, and snout sizes of migratory males in Pacific salmon (*Oncor-*

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Y. Koseki (✉) · K. Maekawa
Laboratory of Conservation Biology, University Forests,
Hokkaido University, N9 W9, Sapporo 060-0809, Japan
e-mail: koseki@exfor.agr.hokudai.ac.jp;
Tel. +81-11-706-3655; Fax +81-11-706-3450

rhynchus spp.) are favored by sexual selection through intrasexual competition (Fleming and Gross 1994; Quinn and Foote 1994). However, despite a large number of studies concerning fertilization success (e.g., Maekawa and Onozato 1986; Hutchings and Myers 1988; Jordan and Youngson 1992; Morán et al. 1996; Foote et al. 1997), the contribution of morphology to reproductive success remains unclear for precocious males (but see Thomaz et al. 1997). Gross (1985) showed that smaller jacks can get closer to females in coho salmon (*Oncorhynchus kisutch*). In contrast, Maekawa (1983) and Myers and Hutchings (1987) reported that a dominance hierarchy was established among mature male parr, with the largest gaining closest access to females in Miyabe charr (*Salvelinus malma miyabei*) and Atlantic salmon (*Salmo salar*). Furthermore, Thomaz et al. (1997) found that fertilization success was positively correlated with body size in Atlantic salmon parr. More studies are needed to conclusively explain the morphological specialization of precocious males in salmonids.

In this study, we examined, in mature male parr of masu salmon *O. masou*, (1) what morphology is favored by sexual selection, or which morphological characters contribute to reproductive success, and (2) how the characters contribute to the reproductive success, or what mechanisms operate on the contribution of morphology to reproductive success. Our hypothesis was that, since a less-conspicuous morphology should reduce aggression from dominant migrants (Gross 1985), small body size will contribute to sneaking success but the other morphological characters will not. Under this hypothesis, we predicted that selection favoring small body size intensifies with the dominant's aggression. To test this prediction, we conducted a semi-natural mating experiment in which the density of migrants was manipulated to vary the dominant's aggression against parr. We observed the reproductive behavior and success of parr during the experiment to quantify selection acting on morphology.

Methods

Fish studied

Masu salmon (*O. masou*) are distributed throughout the Far Eastern Asian region of the Pacific Ocean (Tsiger et al. 1994). Almost all females migrate to the sea from the natal stream but males have three life history forms: large, late-maturing migratory males which descend to the sea like females, small mature male parr residing in the natal stream throughout their lives, and intermediate-sized migrants whose life history is similar to that of coho salmon jacks (the frequency of latter form is extremely low; Tsiger et al. 1994). In Hokkaido, northern Japan, migrants and parr usually mature at age 3 or 4 and at age 1 or 2, respectively (Sano 1951; Utoh 1976). All migrants die after breeding while some parr breed in 2 or more years (Tsiger et al. 1994; Y. Koseki and K. Maekawa, unpublished data).

We used landlocked masu salmon in Toya Lake, Hokkaido, Japan. The masu salmon in this lake were introduced in the early 1930s from some river systems in Hokkaido (T. Yamamoto, personal communication). Several inlets of this lake provide spawning grounds for the fish, so that they have similar life histories to anadromous masu salmon (T. Yamamoto, K. Edo, H. Ueda, un-

published data). Mature male parr commonly occur in these inlets (personal observation). In the breeding season, the pairs of migratory fish are present patchily at the spawning ground and each forms a spawning aggregation with several mature male parr (Y. Koseki and K. Maekawa, unpublished data).

Fish collection

Migratory fish were collected from the Sobetsu Stream (42°38' N, 140°51' E) flowing into Toya Lake, in September 1997. From 5 to 14 September, fish were caught with a weir set across the stream, while on 23 September, an Electrofisher (Smith-Root Inc.) was used. The collected fish were stocked in water tanks at the Toya Lake Station (TLST) of Hokkaido University until transportation. Mature male parr artificially bred from wild fish were collected from the TLST tanks. We confirmed that parr were mature by softly pushing their bellies and releasing a very small amount of semen. The fish were transported in a cooled and aerated tank truck on 16 and 24 September to the Tomakomai Experimental Forest (TOEF) of Hokkaido University. The transported fish were kept in holding facilities at the Horonai Stream (42°40' N, 141°36' E) running within the TOEF prior to the experiment.

Experiment

The mating experiment was conducted from 18 to 25 September in a reach of the Horonai Stream. The reach is about 4 m in width, 10–26 cm in depth, with a flow rate of 0.3–0.7 m/s, and a substrate consisting mainly of gravel. Several salmonids including masu salmon have reproduced in this stream (e.g., Kitano et al. 1993; Taniguchi et al. 1996). We constructed six enclosures (4×4 m each) using plastic fences and drew black vinyl curtains along the reach banks to observe fish behavior without disturbance. Small colored ribbon-tags (3 cm long, 2 mm wide) were sewn on the backs of all parr for individual identification after being anesthetized with 2-phenoxyethanol. In the enclosures, fish were allowed to spawn and mating behavior was observed at least once every 2 h from dawn to dusk (0500–1800 hours). Restricting observations to daylight hours did not affect the results – there was no evidence that spawning occurred at night. After a spawning aggregation had formed, we videotaped the attending males to record all aggressive encounters and determine the sneaking success of parr (defined as rushing into the nest at oviposition). We also measured the distance from each parr to the nest (egg pit) when the female crouched for oviposition. The distance from parr to the nest (cm) was estimated relative to fish size or colored markers on the gravel (1×1 m grids).

To test whether the aggression from dominant migrants intensifies selection acting on parr, the mating experiment comprised three migrant-density treatments: one, two, or four migratory males with five parr and one female. We expected that, while the aggression among migrants increases with an increase in the density of migrants (Quinn et al. 1996), this decreases the aggression of dominant migrant against parr. Five new parr were used in each trial, although several migratory fish were re-used; one of nine females was used twice and two were used three times, and 7 of 24 males were used twice, and 1 was used three times. This was done because not enough fish were available to use fresh individuals in each trial. The behavior of the re-used fish did not appear to differ among the successive trials. We minimized the differences of parr body size (postorbital–hypural length) among trials; the variance did not differ among either the trials or the treatments (Bartlett's test for homogeneity of variances: among trials, $\chi^2=7.26$, $df=13$, $P=0.89$; among treatments, $\chi^2=1.36$, $df=2$, $P=0.51$), nor did the mean (ANOVA: among trials, $F_{13,55}=0.76$, $P=0.70$; among treatments, $F_{2,66}=1.20$, $P=0.31$) (see Table 1). To minimize the effects of time-dependent factors, the three treatments (× two replicates) were performed simultaneously in six enclosures. The enclosures were randomized for the treatments. Spawning took place in five, four, and five trials for the treatments including one, two, and four

Table 1 Experimental design and body length and body weight (mean±SD) of the fish used in each trial

Treatment ^a	Enclosure	Trial day in September 1997	Mature male parr		Migratory male		Female	
			Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)
1 (1)	2	19	88.1±15.3	17.4±7.6	396	1,454	397	1,332
	3	25	102.4±11.2	26.9±8.0	369	1,250	423	1,338
	4	21	100.9±7.0	24.0±4.7	399	1,506	374	903
	5	19	97.7±11.3	23.6±5.9	389	1,447	420	1,448
	6	21	93.6±11.6	23.0±9.1	346	1,018	373	1,264
2 (2)	1	21	90.1±7.1	18.8±4.9	384±13	1,353±101	433	1,493
	2	19	88.9±8.5	19.5±5.1	401±2	1,715±64	397	1,332
	4	21	95.6±11.8	23.6±8.8	344±4	1,165±219	374	903
	5	18	97.4±10.4	24.1±6.7	369±23	1,175±227	408	1,524
3 (4)	1	21	102.1±13.1	25.1±5.7	362±19	1,209±174	433	1,493
	2	20	99.8±14.2	25.2±11.0	371±18	1,330±108	397	1,332
	3	18	92.0±18.0	20.3±10.9	366±10	1,250±277	453	1,980
	4	20	96.9±8.3	24.0±6.7	342±25	1,167±208	374	903
	6	25	102.4±9.2	25.6±5.3	366±10	1,250±277	418	1,586

^a In parentheses, the number of migratory males

migratory males, respectively. Table 1 presents details of the experiment and the size of fish used in each trial.

In contrast to our expectation, the density of migrants had no effects on the aggression of dominant migrant against parr or on the mating behavior of parr (see Results). Therefore, we combined the three treatments (14 trials in total) to analyze the data of 69 individuals (one parr was lost) simultaneously.

Morphological characters and their transformation

Parr recaptured after the experiment were weighed (nearest gram) and the following ten morphological characters were measured (nearest 0.1 mm): body (postorbital–hypural) length, body height (the longest distance from the back to the belly, perpendicular to body length), caudal–peduncle depth, snout length, dorsal fin height, anal fin height, pectoral fin length, pelvic fin length, adipose fin length, and caudal fin length (see Fleming and Gross 1994). Dorsal fin height, adipose fin length, and caudal fin length were not measured for some individuals due to damage, and were excluded from the analyses. Multicollinearity – strong correlations among the characters – due to allometric growth was detected (Appendix). Many authors have indicated that multicollinearity confuses the estimation of selection gradients (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Crespi and Bookstein 1989). It was therefore reduced by a size-adjustment procedure (see Fleming and Gross 1994). In this procedure, all characters are ln-transformed and each character except body size is then regressed on body size. The value of each individual character relative to standard size is expressed as residual from this ln-ln regression. Like Fleming and Gross (1994), we chose body weight as a useful measure of body size because its explanatory power during regression analyses was the best. Prior to the regression analyses, body weight (g) was cube root-transformed to reduce its dimensions. After this size-adjustment procedure, only the correlation between pectoral and pelvic fins was still significant at the multiple-comparison level (Appendix). All characters were then standardized (mean=0, variance=1) to compare the strength of selection (i.e., selection gradient) among characters and across components of reproductive success.

Measuring selection

Selection was estimated for each of two components of reproductive success: proximity to nest (ranked in each trial in order of actual distance) and sneaking success (binary: one or zero). The val-

ue of each individual in the components was divided by the mean value based on five individuals in the corresponding trial for transformation to relative success. To detect directional selection, we estimated the standardized linear selection gradients for the set of characters measured for all individuals (Lande and Arnold 1983; Arnold and Wade 1984). Standardized linear selection gradients were calculated as the partial regression coefficients from the multiple regression of relative success on the set of standardized characters. To determine whether selection was non-linear (stabilizing or disruptive), we estimated standardized non-linear selection gradients for the characters (Lande and Arnold 1983). Standardized non-linear selection gradients were calculated from the multiple regression including the linear and quadratic terms of the standardized characters. Each partial regression coefficient of the quadratic term is the non-linear selection gradient for the character.

Statistical analyses

The frequency of aggressive encounters (number of encounters per 10 min) and the percentage of encounters won (number of victories/number of encounters) were ln- and arcsine root-transformed for parametric testing, respectively. Analyses of variance (ANOVAs) were performed for comparison among treatments. Pearson's correlation coefficient was used for examining some correlations. A large number of the correlation coefficients among characters were tested by sequential Bonferroni tests for multiple comparisons (Rice 1989). The significance tests of selection gradients were performed with a randomization test, due to the non-normality of the relative success (Manly 1997). In this test, we constructed 999 pseudo-data matrices by randomizing the relative success of individuals for their character set in each matrix. The expected distribution of each multiple regression coefficient was generated from the 999 coefficients of the matrices, and then used for quantifying the unlikelihood of the coefficient of the original data matrix.

Results

Mating behavior of masu salmon with special reference to parr

In the treatments including two or four migratory males, the dominants completely defeated the other migrants

immediately after the initiation of trials, and the subordinates never participated in the spawning aggregation, except in the case of one migrant in one trial. No aggressive interactions were observed between subordinate migrants and parr, or between females and males, including parr. Although the dominants exhibited “threatening” behavior, quickly shaking their head toward parr swimming close to their heads, this behavior rarely developed into more intense aggression, such as chases and bites. Therefore, the frequency of aggressive behaviors from dominant migrants to parr was low (mean±SD=1.9±1.7 times per 10 min, $n=14$), and did not differ among the treatments ($F_{2,11}=0.37$, $P=0.70$). Neither the number of satellite parr nor the number of parr successful in sneaking was affected by the treatments (number of satellites, $F_{2,11}=1.56$, $P=0.25$; number of successful parr, $F_{2,11}=0.82$, $P=0.47$).

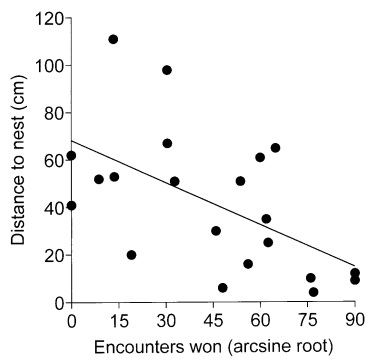


Fig. 1 Relationship between the percentage of aggressive encounters won and the distance to the nest in satellite parr. Regression line: $y=68.2-0.6x$, $R^2=0.32$, $F_{1,19}=8.96$, $P<0.01$

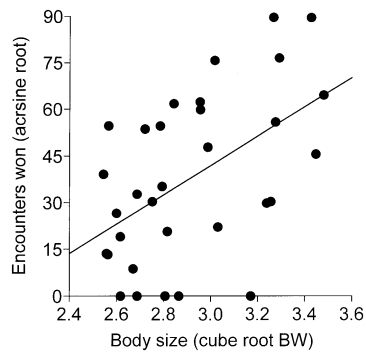


Fig. 2 Relationship between body size and the percentage of aggressive encounters won by parr which participated in aggressive interactions. Regression line: $y=-100.5+47.5x$, $R^2=0.27$, $F_{1,30}=10.84$, $P<0.01$

Aggressive encounters among parr were frequently observed (mean±SD=7.2±6.3 times per 10 min, $n=14$) and resulted in the formation of dominance hierarchies. Twenty-five (36%) parr were present as satellites around females at spawning in 12 (86%) of 14 trials, and 12 (17%) parr succeeded in sneaking in 8 (57%) trials. The distance from each satellite parr to the nest at spawning ranged from 4 to 111 cm (mean±SD=42.3±28.9, $n=25$). The distance to the nest was negatively related with the percentage of aggressive encounters won (linear regression, $R^2=0.32$, $F_{1,19}=8.96$, $P<0.01$; Fig. 1). The percentage of encounters won was positively related with body size (linear regression, $R^2=0.27$, $F_{1,30}=10.84$, $P<0.01$; Fig. 2).

Selection on morphology of parr

A significant standardized linear selection gradient was found for body size, both for proximity to the nest and for sneaking success (proximity: $\beta=0.36\pm0.08$, $P<0.001$; sneaking success: $\beta=0.59\pm0.24$, $P<0.05$; Table 2). The standardized non-linear selection gradients (i.e., multiple regression coefficients for quadratic terms) were not statistically significant ($P>0.05$).

Discussion

We expected selection to favor smaller body size in mature male parr during breeding as small size may be suitable for sneaking (Gross 1985). In contrast to our expectations, we found that selection favors larger body size which allows a position closer to the nest to be gained and consequently increases sneaking success. Behavioral observations showed that selection on body size acted through competition within parr rather than aggression of the dominant migratory male. Like other salmonid species (Maekawa 1983; Myers and Hutchings 1987; Hutchings and Myers 1988), aggressive encounters within parr were observed in masu salmon and this resulted in the formation of a dominance hierarchy according to body size. However, unlike other salmonids (Jones 1959; Maekawa 1983; Maekawa and Onozato 1986; Myers and Hutchings 1987), the migratory males of masu salmon rarely attacked parr although the dominant migrants quickly chased away subordinates from the spawning aggregations. Therefore, we suggest that the size-structured dominance hierarchy within parr is the main cause of selection favoring large body size of parr. The indifference of migrants to parr may also have facilitated the advantage for parr in being larger to gain closer access to the nest.

Table 2 The standardized selection gradients on the morphological characters of parr for the two components of reproductive success (* $P<0.05$, *** $P<0.001$ in randomization tests; Manly 1997)

Component of reproductive success	Body size	Body height	Caudal-peduncle depth	Snout length	Pectoral fin	Pelvic fin	Anal fin
Proximity	0.32***	0.04	-0.03	0.08	0.11	-0.03	-0.10
Sneaking success	0.43*	0.04	-0.05	0.25	0.19	-0.22	-0.02

In this experiment, we studied the reproductive success of parr during only a short portion of the breeding season (i.e., one spawning bout). In natural populations, male salmon (both parr and migrants) become exhausted as the breeding season progresses (Jonsson et al. 1991), and environmental conditions may vary. Moreover, no components of reproductive success other than proximity to nest and sneaking success (e.g., number of females sneaked, and fertilization success based on DNA paternity analysis) were examined. Nevertheless, selection favoring larger parr is probably invariable, because the contribution of body size toward fertilization success in the successive spawnings in Atlantic salmon parr (Thomaz et al. 1997) and toward the reproductive activity and mating success through the entire breeding season in male fluvial Dolly Varden (Kitano 1996) has been documented.

Given this, why do mature male parr not attain even larger body sizes? First, selection pressure may change as parr evolve toward larger body size. This study showed that selection pressure by migrants was absent because migrants were almost indifferent to satellite parr. However, migrant indifference may decrease as parr size increases to a point where they become potential competitors of migrants. In a natural stream running into Toya Lake, dominant migratory masu salmon aggressively chase jack-like males of intermediate size between migrants and parr, along with subordinate migrants (T. Yamamoto, K. Edo, K. Maekawa, unpublished data). The sneaking success of jack-like males appears to be much lower than that of parr. Therefore, the benefit of being larger, or enjoying dominance within parr, may be canceled or exceeded by the cost of increased aggression by migrants (disruptive selection; Gross 1985; Fleming and Gross 1994). The potentially conflicting selection pressures on body size may have driven evolution to an optimal body size for parr. Second, ecological constraints may prevent parr from an evolutionary response to selection. A major constraint for parr may be restricted resource abundance in their habitat. In the fluvial stage of the early life history of salmonids, populations are regulated by density-dependent mechanisms (Elliott 1985, 1990), and resource use is unequal among individuals (Nakano 1995). These phenomena suggest that resources for individual growth are limited in streams.

This study indicates that the selection pressure on the morphology of precocious male parr differs from that on migratory males, partially supporting our expectations. In migratory males, the elongated hooked snout and humped back, which represent dominance in fighting as well as body size, apparently contribute to reproductive success (coho salmon: Fleming and Gross 1994; sockeye salmon: Quinn and Foote 1994). In contrast, snout length and body height did not contribute to reproductive success in masu salmon parr. Therefore, conspicuous sexual characters may not have evolved in mature male parr. The exaggerated sexual characters associated with male-male competition should result in a high energy cost for individuals. In dimorphic brown trout (*Salmo trutta*), the somatic energy content is lower in small resident fish

than in large migrants, probably due to the poor resources in streams (Jonsson and Jonsson 1997). Therefore, mature male parr should invest energy toward improving behavioral and/or physiological characters concerned with reproductive success rather than toward developing morphological characters which make no contribution to sneaking success. The quantitative and qualitative characteristics of gametes of Atlantic salmon parr may be such a strategic energy allocation. Atlantic salmon parr have a larger gonadosomatic index than migratory males (Gage et al. 1995; Fleming 1996; but see Jonsson and Jonsson 1997) and their ejaculated sperm are more motile and survive longer than those of migrants (Gage et al. 1995). Such gamete characteristics have been shown for sneakers in other fish species as well (de Fraipont et al. 1993; Taborsky 1998). The results of our study and the above information suggest that mature male parr increase their reproductive success through sperm competition rather than behavioral competition (Gage et al. 1995; see also Simmons et al. 1999).

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Appendix

Correlations among the characters of masu salmon parr before and after a size-adjustment procedure (see text). Correlation coefficients (sample number in parentheses) before and after size adjust-

ment are represented in the upper and lower triangle, respectively (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ in sequential Bonferroni tests; Rice 1989)

	Body weight	Body length	Body height	Caudal-peduncle depth	Snout length	Pectoral fin	Pelvic fin	Dorsal fin	Anal fin	Adipose fin	Caudal fin
Body weight		0.951*** (69)	0.912*** (69)	0.915*** (69)	0.892*** (69)	0.777*** (69)	0.737*** (69)	0.759*** (68)	0.636*** (69)	0.526*** (53)	0.751*** (65)
Body length	-0.094 (69)		0.869*** (69)	0.892*** (69)	0.900*** (69)	0.821*** (69)	0.750*** (69)	0.768*** (68)	0.674*** (69)	0.562*** (53)	0.744*** (65)
Body height	-0.056 (69)	-0.138 (69)		0.884*** (69)	0.836*** (69)	0.790*** (69)	0.758*** (69)	0.732*** (68)	0.662*** (69)	0.587*** (53)	0.734*** (65)
Caudal-peduncle depth	0.032 (69)	0.049 (69)	0.163 (69)		0.869*** (69)	0.814*** (69)	0.767*** (69)	0.775*** (68)	0.643*** (69)	0.564*** (53)	0.752*** (65)
Snout length	-0.045 (69)	0.240 (69)	0.002 (69)	0.168 (69)		0.737*** (69)	0.679*** (69)	0.710*** (68)	0.586*** (69)	0.471** (53)	0.719*** (65)
Pectoral fin	-0.017 (69)	0.305 (69)	0.255 (69)	0.303 (69)	0.035 (69)		0.791*** (69)	0.727*** (68)	0.706*** (69)	0.478** (53)	0.745*** (65)
Pelvic fin	-0.029 (69)	0.132 (69)	0.219 (69)	0.260 (69)	-0.055 (69)	0.479* (69)		0.669*** (68)	0.670*** (69)	0.592*** (53)	0.718*** (65)
Dorsal fin	-0.023 (68)	0.154 (68)	0.009 (68)	0.199 (68)	0.008 (68)	0.279 (68)	0.224 (68)		0.660*** (68)	0.442** (52)	0.711*** (64)
Anal fin	0.002 (69)	0.166 (69)	0.166 (69)	0.106 (69)	-0.033 (69)	0.388 (69)	0.322 (69)	0.304 (68)		0.524*** (53)	0.593*** (65)
Adipose fin	0.117 (53)	0.116 (53)	0.206 (53)	0.149 (53)	-0.101 (53)	0.050 (53)	0.295 (53)	0.004 (52)	0.220 (53)		0.408** (50)
Caudal fin	-0.001 (65)	0.073 (65)	0.111 (65)	0.148 (65)	0.162 (65)	0.322 (65)	0.319 (65)	0.264 (64)	0.173 (65)	-0.008 (50)	

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