Adaptive Variation in Rheotactic and Agonistic Behavior in Newly Emerged Fry of Chinook Salmon, Oncorhynchus tshawytscha, from Ocean- and Stream-Type Populations

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Agonistic and rheotactic behavior and body morphology were compared in recently emerged, laboratory-reared chinook salmon (*Oncorhynchus tshawytscha*) from two "stream-type" and two "ocean-type" populations. Newly emerged chinook fry from the stream-type populations (Slim Creek and the Eagle River) were more aggressive than fry from the ocean-type populations (the Nanaimo and Harrison rivers). Slim Creek fry were consistently the most aggressive. There was no clear distinction in rheotactic behavior between stream- and ocean-type chinook; Harrison River, ocean-type chinook fry had the strongest downstream movement in "dark" current response tests, but fry from the other three populations had similar movement scores in both light and dark tests. Fry from the four populations were morphologically distinct; however, there was no clear separation in body morphology or coloration based on life history type. These differences exhibited in laboratory-reared fry indicate that they are, at least in part, inherited. I conclude that a fundamental genetic difference in agonistic behavior exists between stream- and ocean-type chinook juveniles. A genetic dichotomy between stream- and ocean-type chinook in rheotactic behavior and morphology, however, may be overidden by population-specific local adaptations, independent of life history type.

On a comparé le comportement agonistique et rhéotaxique et la morphologie du corps d'alevins à vésicule résorbée de saumon quinnat (*Oncorhynchus tshawytscha*) appartenant à deux populations « dulçaquicoles » et deux populations « marines » élevées en laboratoire. Les alevins à vésicule résorbée provenant des populations dulçaquicoles (ruisseau Slim et rivière Eagle) étaient plus agressifs que les alevins de populations marines (rivières Nanaimo et Harrison). Ceux venant du ruisseau Slim étaient uniformément plus agressifs. Il n'y avait toutefois pas de différence évidente du comportement rhéotaxique chez les quinnats dulçaquicoles et marins; c'est chez les quinnats marins de la rivière Harrison que l'on a observé les plus grands déplacements vers l'aval au cours d'expériences de réaction au courant à la noirceur mais on a observé des résultats semblables chez les alevins des trois autres populations soumis à la lumière et à la noirceur. Les alevins des quatre populations étaient différents au niveau morphologique; toutefois, il n'y avait pas de différence évidente de la morphologie ou de la coloration du corps découlant du cycle vital. Les différences révélées chez des alevins élevés en laboratoire révèlent qu'elles sont au moins en partie héritées. L'auteur formule la conclusion qu'il existe une différence génétique fondamentale du comportement agonistique entre les juvéniles dulçaquicoles et marins. Des adaptations locales particulières à chaque population, indépendantes du type de cycle vital, peuvent toutefois l'emporter sur la dichotomie génétique du comportement rhéotaxique et de la morphologie chez les quinnats dulçaquicoles et marins.

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The chinook salmon (*Oncorhynchus tshawytscha*) exhibits a wide range in the length of time juveniles spend rearing in freshwater before migrating seaward as smolts (Reimers 1973; Healey 1983; Carl and Healey 1984). Juveniles that migrate to sea as newly emerged fry or after a few months in freshwater are called "ocean-type" whereas those that rear in freshwater for extended periods and migrate to sea as age 1+ smolts are called "stream-type."

Apart from differences in scale growth pattern (Gilbert 1913; Reimers 1973), studies by Healey (1983) and Carl and Healey (1984) have documented distributional, electrophoretic, and morphological differences between stream- and ocean-type chinook within and among populations. Taylor and Larkin (1986) reported differences in morphology and rheotactic and agonistic behaviors between stream-type and ocean-type wild chinook fry from two tributaries of the Fraser River (Slim Creek and the Harrison River). Newly emerged, stream-type fry from Slim Creek were less likely to move downstream in a current channel, were more aggressive, had more parr markings, and had larger body parts and larger and more brightly colored median fins than fry from the Harrison River, an ocean-type population. These behavioral and morphological differences are similar to those among juveniles of *Oncorhynchus* (e.g. pink (*O. gorbuscha*) and coho (*O. kisutch*) salmon) which exhibit a similar range of freshwater life history patterns to that present among chinook life history types. Coho salmon rear in freshwater for a year or more are territorial, have relatively deep bodies with distinct parr markings, and have large, brightly colored median fins. In contrast, pink salmon migrate seaward as newly emerged fry, are schooling, nonterritorial, relatively slim-bodied, lack parr marks, and have smaller, transparent median fins (Hoar 1951, 1976; Chapman 1962).

If natural selection is responsible for the divergent life history patterns of chinook salmon fry, then this variability must have a genetic basis. The goal of the present study was to test whether the behavioral and morphological differences between stream-type and ocean-type chinook fry are inherited. Environmental variation between the populations was eliminated by studying chinook fry which had been incubated and reared in the laboratory under identical conditions.

Materials and Methods

Study Populations

Two of the chinook populations studied were Slim Creek (stream-type) and the Harrison River (ocean-type), two tributaries of the Fraser River as described by Taylor and Larkin (1986). An additional stream-type population came from the Eagle River, another tributary of the Fraser River which enters Shuswap Lake near Sicamous, B.C. From scale analysis of adults, Eagle River chinook are largely (>95%) stream-type and juveniles overwinter in freshwater (Shepherd et al. 1986b). An additional ocean-type population came from the Nanaimo River, on southeastern Vancouver Island near Nanaimo, B.C. I studied the "fall run" subpopulation which spawns in the lower Nanaimo River (see fig. 1 of Carl and Healey 1984). This lower river subpopulation produces fry which are predominantly (>98%) ocean-type, moving downstream to the Nanaimo estuary soon after emergence (Healey 1980; Carl and Healey 1984).

Gamete Collection and Incubation

Eggs and milt were collected from ripe, wild chinook salmon during September (Slim Creek and Eagle River), October (Nanaimo River), and November (Harrison River) of 1985. Slim Creek adults were collected on the spawning grounds by electroshocking, while adults from the Eagle, Harrison, and Nanaimo rivers were collected at fences or by seining in conjunction with enhancement operations on these rivers. Eggs were fertilized in the field by mixing eggs and milt from a small number of females and males (Slim Cr., 4 females × 7 males; Eagle R., 6 females × 4 males; Nanaimo R., 3 females × 4 males; Harrison R., 3 females × 2 males). Water-hardened zygotes were transported to the laboratory in 4-L glass jars filled with water. During transport, water temperature was maintained as close as possible to 5°C by placing the glass jars in coolers filled with crushed ice. Elasped time from fertilization to placement in the incubator ranged from 2 h (Harrison River) to 24 h (Slim Creek).

The incubation apparatus consisted of a large (1.8 × 0.6 × 0.9 m) cooling unit supplied with dechlorinated water at about 2 L·min^{-1}. Within the cooling unit, zygotes were incubated in "corner-type" aquarium filters with about 3–4 cm of pea gravel provided as substrate. Each filter had its own air supply which generated a flow of water over the incubating zygotes and larvae. The incubation temperature was set at 5°C; actual incubation temperature over the 7-mo incubation period was 4.5 ± 0.86°C.

TABLE 1. Mean (± SE standard lengths (SL, mm) and weights (Wt, g) of laboratory-reared chinook fry from the four study populations before and at the end of the aquaria tests. $N = 25$ for each population.

	Slim Cr.		Eagle R.		Nanaimo R.		Harrison R.	
	SL	Wt	SL	Wt	SL	Wt	SL	Wt
Start	31.9	0.39	30.3	0.31	34.9	0.46	34.1	0.44
	(0.16)	(0.01)	(0.36)	(0.01)	(0.46)	(0.02)	(0.25)	(0.01)
Finish	32.6	0.42	31.9	0.38	36.5	0.48	35.6	0.49
	(0.12)	(0.01)	(0.23)	(0.02)	(0.29)	(0.01)	(0.24)	(0.02)

Upon emergence, fry were placed in 94-L fiberglass rearing troughs where they were left for 24 h. The water flow through the troughs was maintained at 4 L·min^{-1} and fry were fed Oregon Moist Pellet (OMP) food thrice daily. Daily light schedule followed the natural photoperiod and was provided by a single 40-W fluorescent bulb per trough. A single 25-W light bulb controlled by a rheostat-timer was suspended over each trough to provide a "dawn–dusk" period each day.

Chinook Fry Behavior

I studied rheotactic behavior in the newly emerged fry during current response tests run in two artificial, oval-shaped stream channels (3.8-m stretched length). The current channels and test protocol were as described by Taylor and Larkin (1986). Both current channels were subdivided into 22 compartments ranked from −10 (most downstream) through 0 (central compartment) to +10 (most upstream). Each trial consisted of assessing the movements of 20 chinook fry through the channel compartments during successive "light" and "dark" tests. Each test was 2.5 h in duration with 0.5 h between successive tests. For each test a movement score was calculated by summing the products of the number of fish in a compartment multiplied by the rank of that compartment and dividing by 20, the number of fish in each test. To provide a net movement score the downstream score was subtracted from the upstream score; a constant of 10 was added to eliminate negative scores. Twenty trials, each consisting of 20 "dark" and 20 "light" tests, were run for each population. Water temperature was maintained between 10 and 10.5°C for all tests and water velocity through the channel compartment openings averaged about 10 cm·s^{-1}. During the period of spring fry migration, 10°C is within the range of temperatures in the four study streams and was the temperature best controlled in the current channels. Data were analysed by two-factor analysis of variance with illumination (light, dark) and population as the main effects.

To study agonistic behavior in fry from the four populations, I recorded the number and duration of agonistic behaviors observed during individual-fry, aquaria tests (10°C) and during multiple-fry, stream tank tests (11°C). In all cases, methods and test conditions were identical to those described by Taylor and Larkin (1986). In the single-fry, aquaria tests, fry were observed for 3-min periods for their reactions to their mirror images (mirror-image-stimulation (MIS, Gallup 1968)). Tests continued for seven consecutive days on 25 fry per population. I used an OS-3 event recorder to score "null," "swim-against-mirror," "lateral display," and "wigwag" behaviors (see Taylor and Larkin (1986) for definitions. Fry were weighed and meas-

TABLE 2. Mean (± SE) standard lengths (mm) of newly emerged chinook and coho salmon fry used in the interspecific stream tank tests. $N = 8$ all cases.

	Stream tank section	
	Section 1	Section 2
Slim Creek chinook fry	32.4 (0.21)	32.5 (0.16)
Coho fry	32.4 (0.26)	32.2 (0.35)
Eagle River chinook fry	33.0 (0.35)	32.5 (0.33)
Coho fry	31.3 (0.46)	31.8 (0.39)
Nanaimo River chinook fry	35.8 (0.31)	35.6 (0.49)
Coho fry	33.8 (0.36)	33.7 (0.31)
Harrison River chinook fry	36.2 (0.38)	35.8 (0.21)
Coho fry	34.4 (0.44)	34.6 (0.41)

ured (standard length) before and after each 7-d test (Table 1). A power failure prevented collection of behavioral data on the seventh day for Eagle River chinook.

In the stream tanks tests, I observed chinook fry during single-species and double-species (with coho salmon) tests. Sixteen newly emerged chinook fry were observed by scan sampling in each of two replicate stream tank sections (see Taylor and Larkin (1986) for description) for 10 min three times per day for five consecutive days. The behaviors recorded were "null," "approach," "lateral display," "wigwag," "charge," and "nip" (see Taylor and Larkin (1986) for definitions). Fry were fed after each observation period and there was at least 2 h between consecutive observations.

Stream tank tests were repeated for each population using eight chinook fry from the test population and eight coho fry (Table 2). Since coho tend to dominate chinook fry in contrived situations (Stein et al. 1972; Taylor and Larkin 1986), these interspecific tests provide another measure of the relative agressiveness of chinook fry from each population. The tests were identical to the single-species tests and lasted for five consecutive days. The coho fry were progeny from crosses of adults spawning in Black Creek, east-central Vancouver Island and were also incubated and reared in the laboratory. Data in the MIS aquaria tests and the stream tank tests were analysed by two-factor repeated measures ANOVA with population and observation day as the main effects.

Chinook Fry Morphology

Morphological analysis on preserved (10% buffered formalin) newly emerged chinook fry consisted of body measurements and counts (left side only). All measurements were as in Taylor and Larkin (1986) and followed Hubbs and Lagler (1967). All measures except standard length were made under a dissecting microscope fitted with a micrometer eyepiece. Standard length was measured with Vernier calipers. A general evaluation of coloration of the body and fins of fry was made on anaesthetised specimens after the stream tank tests. To minimize size-related differences in body shape, body measurements were adjusted to the overall sample mean standard length. The adjustment procedure used was covariance analysis on $\log_{10}$-transformed data, and t-tests assessed differences in the adjusted means among the study populations.

TABLE 3. Mean net movement scores (± SE) of laboratory-reared, newly emerged chinook fry from the four study populations. Underlining indicates those mean scores which are not significantly different ($p > 0.05$). A score of 0 = maximum downstream movement, 10 = no net movement upstream or downstream, and 20 = maximum upstream movement. $N = 20$ in all cases.

	Slim Cr.	Eagle R.	Nanaimo R.	Harrison R.
Light tests	11.74 (0.43)	10.90 (0.47)	12.28 (0.41)	10.44 (0.44)
Dark tests	6.37 (0.44)	6.14 (0.44)	7.48 (0.42)	3.02 (0.43)
Overall	8.99 (0.31)	8.51 (0.35)	9.98 (0.38)	6.64 (0.31)

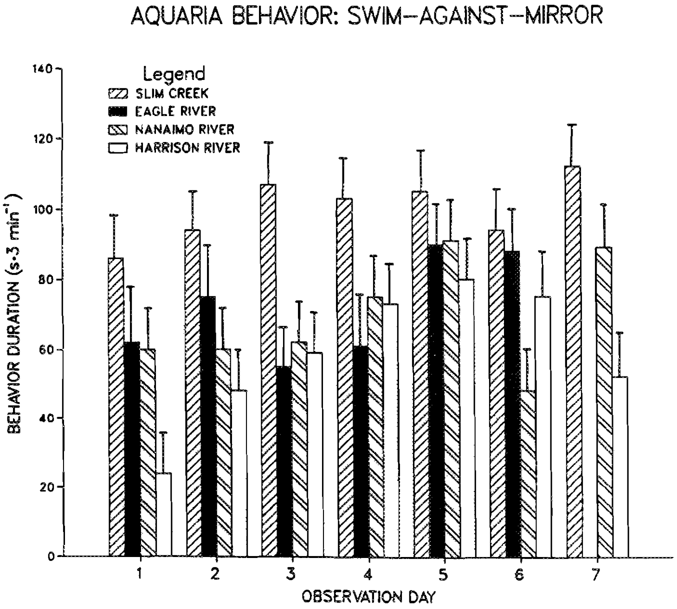
AQUARIA BEHAVIOR: SWIM-AGAINST-MIRROR

FIG. 1. Durations (mean ± SE) of swim-against-mirror behavior for newly emerged chinook salmon fry from Slim Creek, Eagle River (stream-type), Nanaimo River, and Harrison River (ocean-type). $N = 25$ fry per population per day.

Results

Rheotactic Behavior

In the current channels, the laboratory-reared chinook fry from all populations responded by "holding" or swimming slightly upstream during light tests while moving downstream during dark tests (light versus dark factor, $p < 0.0001$). In addition to moving in opposite directions in light and dark tests, fry movement tended to be more pronounced during dark tests, with all populations showing significant downstream movement (t-tests for $\mu = 10$, all $p < 0.001$), while during light tests, all fry except those from the Harrison River showed slight, but significant, upstream movement ($p < 0.05$) (Table 3). Ocean-type fry from the Harrison River had a significantly lower overall mean net movement score ($p < 0.0001$) than fry from the three other populations. This overall difference, however, was largely due to significantly greater downstream movement by Harrison River fry during dark tests, since no significant differences in net movement scores were evident among the four populations during light tests (population × illumination factor, $p < 0.01$). In order of increasing downstream movement in the dark the populations ranked Nanaimo, Slim, Eagle, and Harrison whereas in order of increasing upstream movement in the light the populations ranked Harrison, Eagle, Slim, and Nanaimo.

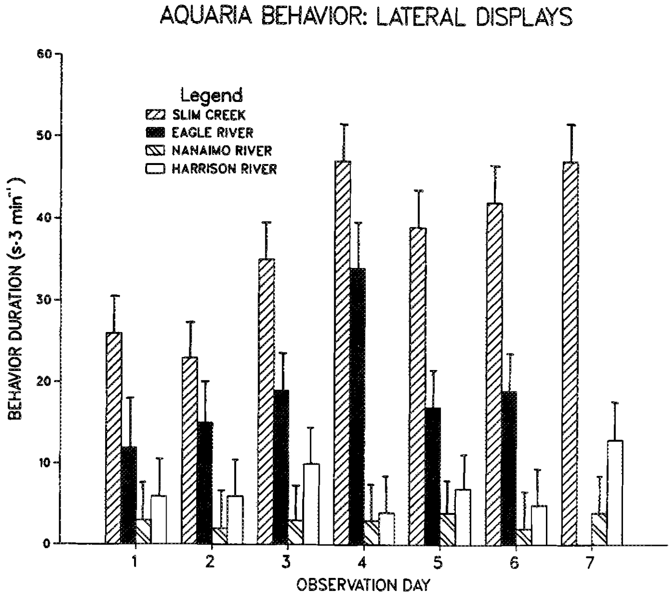

FIG. 2. Durations (mean ± SE) of lateral display behaviors for newly emerged chinook salmon fry from Slim Creek, Eagle River (stream-type), Nanaimo River, and Harrison River (ocean-type). $N = 25$ fry per population per day.

Agonistic Behavior

In the MIS tests, most fry adjusted quickly to the presence of the mirror in their aquaria. Fry typically reacted by orienting towards their mirror image and then generally approaching the mirror followed by bouts of "swim-against-mirror" and "lateral displays." Both the time it took fry to show some overt reaction to their mirror image and to approach it decreased over the 7-d tests. Fry were occasionally observed to "charge" and even "nip" their mirror images, but these behaviors were observed so infrequently that they were not included in the analysis. The laboratory-reared chinook fry from all populations responded similarly by becoming more aggressive over the 7-d test period (Fig. 1, day factor $p < 0.03$, population × day factor $p > 0.5$). The populations ranked Slim > Eagle > Nanaimo > Harrison in terms of mean time spent in "swim-against-mirror" over 7 d; however, there was only one significant difference: Slim Creek fry were more aggressive than the fry from the three other populations ($p < 0.001$).

For "lateral display" behaviors, which included "horizontal," "head-up," and "head-down" wigwags (North 1979), laboratory-reared, stream-type chinook fry from both the Eagle River and Slim Creek spent significantly more time performing lateral displays than ocean-type fry from the Nanaimo and Harrison rivers (Fig. 2, $p < 0.001$). Slim Creek fry, and to a lesser extent Eagle River fry, tended to spend more time performing "lateral display" behaviors as the tests proceeded whereas Nanaimo and Harrison fry had consistently low display durations (day factor $p < 0.02$). The interaction between population and day effects, however, was not significant ($p > 0.1$). Overall, Slim Creek fry were again the most aggressive fry ($p < 0.001$) with greater "lateral display" durations than the fry from the three other populations (Fig. 2).

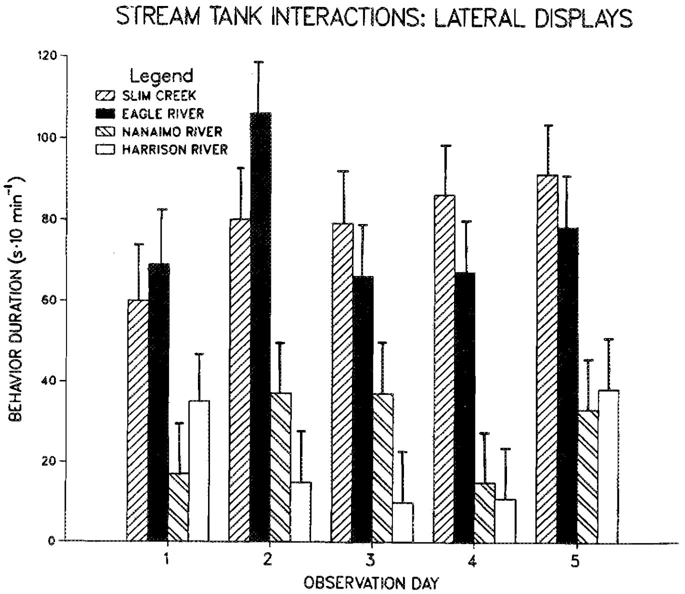

FIG. 3. Durations (mean ± SE) of lateral display behaviors for newly emerged chinook salmon fry from Slim Creek, Eagle River (stream-type), Nanaimo River, and Harrison River (ocean-type) during intraspecific stream tank tests. $N =$ six 10-min observation periods for 16 fry per population per day.

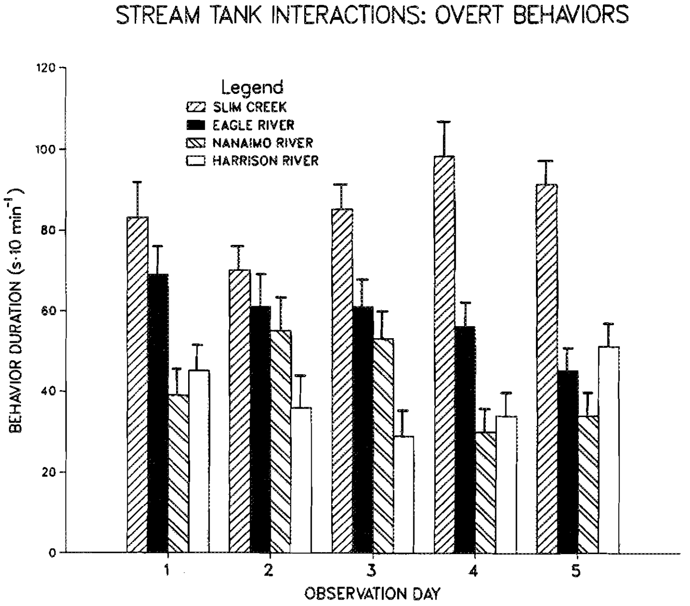

FIG. 4. Durations (mean ± SE) of overt behaviors for newly emerged chinook salmon fry from Slim Creek, Eagle River (stream-type), Nanaimo River, and Harrison River (ocean-type) during intraspecific stream tank tests. $N =$ six 10-min observation periods for 16 fry per population per day.

Stream Tank Tests: Intraspecific Tests

During the stream tank tests the stream-type chinook fry were significantly more aggressive than their ocean-type counterparts (Fig. 3, 4). The laboratory-reared fry from Slim Creek and the Eagle River spent more time performing both overt ("approach," "charge," and "nip") and lateral display behaviors than did the fry from the Nanaimo or Harrison rivers (both $p < 0.001$). Fry from Slim Creek again proved to be the most aggressive fry, since they spent more time performing overt behaviors ($p < 0.001$) than all other fry whereas fry from both ocean-type populations spent similar durations to each other performing agonistic behaviors (both $p > 0.05$). The four populations were most similar in overt behavior durations during observation days 2 and 3; the greatest differences were observed

TABLE 4. Mean (± SE) frequency of agonistic behaviors observed per 10-min observation period for laboratory-reared, newly emerged chinook fry from the four study populations during intraspecific stream tank tests. Underlining indicates means which are not significantly different ($p > 0.05$). $N = 30$ in all cases.

Behavior	Slim Cr.	Eagle R.	Nanaimo R.	Harrison R.
Lateral displays	27.0 (1.9)	12.0 (1.9)	11.6 (1.9)	9.2 (1.9)
Wigwags	21.3 (2.1)	33.0 (2.2)	5.5 (2.2)	4.6 (2.1)
Total displays	48.2 (3.3)	45.1 (3.5)	17.1 (3.3)	13.8 (3.3)
Approach	51.5 (2.5)	44.7 (2.6)	25.8 (2.5)	22.8 (2.5)
Charge	17.1 (1.2)	6.1 (1.1)	11.1 (1.2)	11.2 (1.2)
Nip	26.2 (2.1)	10.1 (2.2)	22.5 (2.1)	19.2 (2.1)
Total overt	95.1 (5.0)	56.1 (5.2)	59.4 (5.0)	53.1 (5.0)

on observation days 1, 4, and 5 (Fig. 4, population × day, $p < 0.05$).

As might be expected from the behavior durations, laboratory-reared, stream-type chinook fry from Slim Creek and the Eagle River performed significantly more lateral display behaviors than ocean-type fry (Table 4), with Slim Creek fry performing the most "lateral displays" and Eagle River fry performing the most "wigwag" displays. Fry from the Nanaimo and Harrison rivers did not differ from each other in frequency of lateral display behaviors (Table 4). For overt behaviors, Slim Creek fry were consistently the most aggressive performing more "approaches" and "nips" than fry from the other populations, while Eagle River fry also performed more "approaches" than ocean-type fry. In contrast, while Nanaimo and Harrison River fry "charged" less frequently than Slim Creek fry, they both "charged" more frequently than stream-type, Eagle River fry. In addition, Nanaimo River fry "nipped" at the same rate as Slim Creek fry, but significantly more frequently than Eagle River chinook fry.

Stream Tank Behavior: Interspecific Tests

In the stream tank tests where coho and chinook fry were studied together, coho tended to dominate chinook (Fig. 5, $p < 0.0001$). A net aggression score was calculated for each observation period by taking the ratio of the sum of all aggressive behavior durations of chinook directed towards coho to the sum of all aggressive behavior durations of coho directed towards chinook. As values of this ratio approach 0, increasing domination of coho is indicated whereas values approaching 1 indicate increasingly equal interaction between the species. Since all mean values are <1, clear domination of chinook by coho is indicated (Fig. 5). The domination by coho was especially evident as the tests proceeded, since mean values tended to decrease over the 5-d tests for all populations except during the Harrison River tests. A few of the trials involving Eagle River chinook and Black Creek coho resulted in net domination by chinook. Slim Creek and Eagle River, stream-type fry, however, tended to be more aggressive towards coho than were the ocean-type chinook fry (Fig. 5, $p < 0.005$).

Morphology and Coloration

Morphological analysis suggested no stream/ocean-type dichotomy with respect to body form or coloration among the laboratory reared chinook fry from the four study populations (Table 5). While chinook from Slim Creek and the Eagle River had the deepest bodies and heads, it was Slim Creek fry and ocean-type, Nanaimo River fry which had the largest median fins. In fact, while Slim Creek fry had consistently the largest fins, in all but one fin measure (af1), Eagle River, stream-type fry had the smallest fins. The populations also differed in the number of parr marks with fry from the Nanaimo and Eagle rivers having the most major and total parr marks (Table 5).

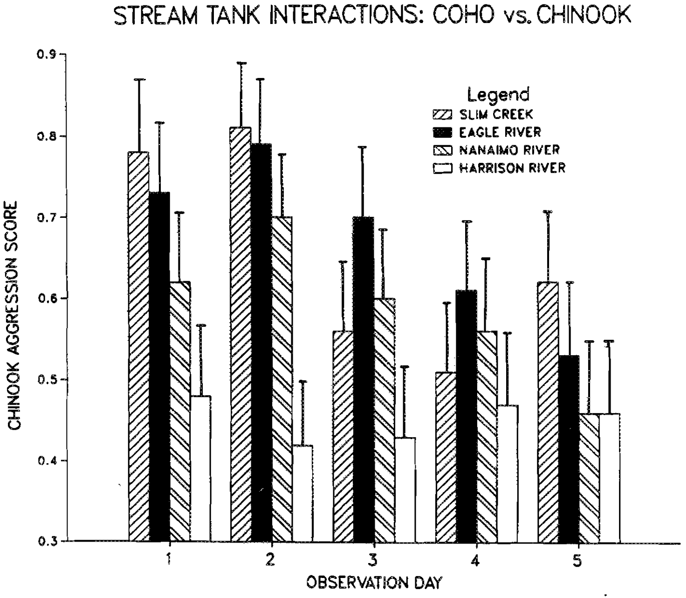

FIG. 5. Aggression scores (mean ± SE) of total agonistic behaviors of newly emerged chinook fry from Slim Creek, Eagle River (stream-type), Nanaimo River, and Harrison River (ocean-type) in stream tank tests with coho salmon fry. See text for explanation of score calculation. N = six 10-min observation periods for eight chinook and eight coho fry per day.

All fry possessed black and white leading edges on the dorsal fin and white tips on their anal fins. The area of greatest distinction with respect to fin coloration among the four populations was in the degree of orange pigment in the median and paired fins. Slim Creek fry were the most elaborately colored fry with prominent orange coloration on all median and paired fins. Nanaimo fry were also well colored, but they lacked the bright orange–black color of the Slim Creek fry caudal fins and orange coloration in the paired fins. Stream-type fry from the Eagle River tended to be lighter in color than fry from either Slim Creek or the Nanaimo River. While Eagle River chinook fry had orange pigment in their median fins, it was not universal, especially in the caudal fin. In addition, many Eagle fry lacked the orange mandible stripe characteristic of the Slim Creek and Nanaimo River fry. The Harrison River, ocean-type fry were the least brightly colored. Harrison fry lacked any trace of orange pigment in their fins, but had some faint yellow color in the caudal fin. While Slim and Nanaimo fry were dark brown with a distinct purple sheen to their sides, Eagle River fry were a lighter grey–brown along their sides. Harrison River fry were greyish–green along their sides and became "silvery" upon preservation in formalin.

Discussion

The behavioral and morphological differences between laboratory-reared, stream-type Slim Creek chinook fry and

TABLE 5. Geometric mean (± SE) standard lengths (mm) and adjusted mean body proportions and parr mark counts of newly emerged, laboratory-reared chinook fry from the four study populations. $N = 30$ in all cases and measurements were adjusted to an overall sample mean standard length of 30.6 mm by covariance analysis. The indicated probability is that all adjusted means are the same.

Character	Slim Cr.	Eagle R.	Nanaimo R.	Harrison R.	*p*
Standard length	30.5 (0.22)	28.6 (0.20)	32.7 (0.29)	31.2 (0.16)	—
Body depth	6.3 (0.06)	6.4 (0.08)	5.7 (0.08)	5.9 (0.06)	<0.001
Head depth[a]	5.8 (0.05)	5.5 (0.06)	5.4 (0.06)	5.4 (0.05)	<0.001
Head length[a]	8.6 (0.05)	8.2 (0.07)	8.5 (0.07)	8.6 (0.05)	<0.001
Dorsal fin height	3.7 (0.07)	2.8 (0.09)	3.1 (0.09)	2.9 (0.07)	<0.001
Dorsal fin length	6.3 (0.07)	5.2 (0.09)	5.7 (0.09)	5.8 (0.07)	<0.001
Anal fin height	3.5 (0.05)	2.8 (0.07)	3.0 (0.07)	2.9 (0.05)	<0.001
Anal fin length	4.8 (0.09)	4.2 (0.12)	4.2 (0.11)	4.4 (0.09)	<0.001
Caudal fin depth[a]	7.7 (0.14)	7.5 (0.18)	7.6 (0.18)	7.5 (0.14)	>0.05
Parr mark length	3.1 (0.11)	2.6 (0.14)	2.5 (0.13)	2.8 (0.10)	<0.005
Parr mark width	1.8 (0.04)	1.4 (0.05)	1.3 (0.05)	1.3 (0.04)	<0.001
No. of major parr marks	9.2 (0.21)	10.6 (0.29)	11.4 (0.28)	10.1 (0.22)	<0.001
No. of total parr marks	16.7 (0.73)	18.4 (0.97)	21.1 (0.93)	15.1 (0.74)	<0.001

[a] Heterogenous standard length – character regression slopes ($p < 0.05$)

ocean-type fry from the Harrison River demonstrated in the present study are similar to the differences between wild-reared fry from these populations (Taylor and Larkin 1986). In both cases, Slim Creek newly emerged fry were more aggressive, less likely to move downstream in the current channels, had larger body parts and median fins, and were more colorful than Harrison River fry. The maintenance of these phenotypic differences in fry reared in the laboratory demonstrates that they are, at least in part, genetic in origin. The inclusion of fry from the Nanaimo and Eagle rivers further demonstrates genetic differentiation in agonistic behavior between stream- and ocean-type chinook fry. Slim Creek fry were, almost without exception, the most aggressive fry whereas Harrison fry tended to be the least aggressive of the four populations. Eagle River and Nanaimo River chinook were intermediate to Slim and Harrison chinook, usually ranking second and third, respectively, in agonistic behavior durations (e.g. Fig. 3). Thus, the stream-type chinook fry (Slim and Eagle) tended to be more aggressive than the ocean-type fry (Nanaimo and Harrison). Unique selective regimes imposed by the different freshwater rearing patterns between stream- and ocean-type chinook juveniles probably account for the higher aggression levels in stream-type chinooks. The elaborate displays often involved in aggressive behavior of juvenile salmonids, and the clear contradictions involved in territorial aggression and seaward migration may have resulted in selection against agonistic behavior in ocean-type populations.

In contrast to the differences in agonistic behavior, no strict stream/ocean-type dichotomy is evident with respect to rheotactic behavior or morphology. The lack of a clear distinction between stream- and ocean-type chinook fry in rheotactic behavior and morphology may result from a tempering of differences between life history types by local conditions unrelated to the length of freshwater residence. For instance, while Slim and Eagle fry moved downstream less readily than Harrison River fry, Nanaimo River, ocean-type fry had the highest net movement scores in both light and dark tests (Table 3). Since Carl and Healey (1984) suggested that the lower Nanaimo River chinook subpopulation is characterized by fry which migrate to the estuary soon after emergence, this result was unexpected. The Nanaimo River estuary is, however, within 5 km of the lower spawning area. In order to reach the estuary soon after emergence, lower Nanaimo chinook fry probably do not require as strong a downstream response as fry from other ocean-type populations such as the Harrison River from which fry must migrate about 100 km to the Fraser River estuary. For Nanaimo River fry a more gradual downstream drift, similar to the behavior of Slim Creek and Eagle River fry, would accomplish this in a short time. Hoar (1976) reported that newly emerged chinook fry require some acclimation time for survival at salinites above 15‰. Since salinities in the Nanaimo River estuary are commonly above 20‰ (Healey 1980), a more gradual movement into the estuary by Nanaimo fry may be necessary to prevent osmoregulatory shock. Healey (1980) also reported that mean weights of chinook fry entering the Nanaimo estuary were about 0.57 g. The fry used in the present study, while completely "buttoned-up," were about 20% lighter (0.30–0.53 g). Perhaps, through a rearing migration, some growth in freshwater must occur before Nanaimo chinook can successfully enter the estuary. Thus, as a consequence of the different migration distances to their respective estuaries, my results suggest that ocean-type chinook from the Nanaimo and Harrison rivers are genetically distinct in their manner of downstream migration as newly emerged fry; Harrison River fry exhibit a more pronounced, directed nocturnal downstream movement.

Furthermore, nocturnal downstream dispersal to freshwater rearing areas is commonly observed in newly emerged fry of various stream-resident salmonids (e.g. Reimers 1973; Randall 1982; Naesje et al. 1986; Shepherd et al. 1986a). Consequently, the current response tests of this study may not be able to readily distinguish between a gradual "drift migration" downstream at night by estuary-bound Nanaimo River chinook fry and a gradual downstream "dispersal" following emergence by stream-type chinooks. In sum, local population factors such as migration distance to nursery areas or estuary size may obscure differences in rheotactic behavior between stream- and ocean-type chinook when testing newly emerged fry. Considerable interpopulation genetic variation in rheotactic behavior exists in newly emerged rainbow trout (*Salmo gairdneri*) and sockeye salmon (*O. nerka*) which maintain residence in freshwater for at least 1 yr (Brannon 1972; Kelso et al. 1981). Alternatively, comparisons of rheotactic behavior over a longer time (e.g. up to 1 yr) may reveal more differences between stream- and ocean-type chinook coinciding with their different ages at seaward migration.

With the exception of major parr mark number, morphological differences between wild chinook fry from the Harrison River and Slim Creek were maintained in the laboratory-reared fry; Slim Creek fry had larger body parts and median fins and were more brightly colored (Table 5). Laboratory-reared chinook fry from Slim Creek had fewer major and total parr marks than did their wild-reared counterparts (1.5 and 7.1 fewer, respectively). Parr mark counts were, however, very similar between laboratory- and wild-reared chinook fry from the Harrison River (0.5 more major and 0.1 fewer total parr marks in the laboratory fry). Consequently, Slim Creek, stream-type chinook fry had only 1.6 more total parr marks than Harrison fry when both were reared in the laboratory compared with a difference of 8.6 for wild fry (Taylor and Larkin 1986). Clearly, a significant environmental component to parr mark number is suggested, since differences between Slim and Harrison fry were minimal when both were incubated and reared in the same laboratory environment. Incubation water temperature regime can alter parr mark counts in chinook fry; lower water temperatures produce higher counts (C. C. Lindsey and E. B. Taylor, unpubl. data). Therefore, water temperature differences in the incubation environments of the Harrison River and Slim Creek (colder) probably account, in large part, for the greater differences in parr mark number in the wild fry.

Despite the clear, inherited differences in morphology between chinook fry from Slim Creek and the Harrison River, these differences could not fully be attributed to a distinction between chinook life history types. While Slim Creek fry had the largest body parts and median fins and were the most colorful fry, fry from both ocean-type populations tended to have larger fins that Eagle River chinook fry (Table 5). Furthermore, Nanaimo River fry were as brightly colored as were fry from the Eagle River. Again, local population factors unrelated to juvenile migration patterns may account for the morphological differences among the four populations. Selection associated with migration distance, water flow levels, and predation have been associated with interpopulation differences in morphology and coloration in stream fishes (Endler 1980; Riddell and Leggett 1981; Taylor and McPhail 1985).

In summary, inherited behavioral and morphological differentiation among populations of juvenile chinook salmon has been demonstrated in this study which supports earlier evidence of genetic divergence among chinook salmon populations (e.g. Ricker 1972; Carl and Healey 1984). At least a portion of this inherited variation may result from a behavioral divergence between stream- and ocean-type life history types. At present it would, however, be premature to describe whole suites of inherited characteristics as either "stream-" or "ocean-type" and to assign them to chinook populations broadly designated as one life history type or the other, particularily if this designation is inferred only from analysis of scales.

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References

BRANNON, E. L. 1972. Mechanisms controlling the migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. 21: 86 p.

CARL, L. M., AND M. C. HEALEY. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (*Oncorhynchus tshawytscha*) in the Nanaimo River, B.C. Can. J. Fish. Aquat. Sci. 41: 1070–1077.

CHAPMAN, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19: 1047–1080.

ENDLER, J. A. 1980. Natural selection on colour patterns in *Poecilia reticulata*. Evolution 34: 76–91.

GALLUP, G. G. 1968. Mirror-image stimulation. Psychol. Bull. 70: 782–793.

GILBERT, C. H. 1913. Age at maturity of Pacific coast salmon of the genus *Oncorhynchus*. Bull. U.S. Bur. Fish. 32: 57–70.

HEALEY, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. Fish. Bull. U.S. 77: 653–668.

1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon (*Oncorhynchus tshawytscha*). Can. Field-Nat. 97: 427–433.

HOAR, W. S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. J. Fish. Res. Board Can. 8: 241–263.

1976. Smolt transformation: evolution, behaviour, and physiology. J. Fish. Res. Board Can. 33: 1234–1252.

HUBBS, C. L., AND K. F. LAGLER. 1967. Fishes of the Great Lakes region. Cranbrook Inst. Sci. Bull. No. 26: 213 p.

KELSO, B. W., T. G. NORTHCOTE, AND C. F. WEHRHAHN. 1981. Genetic and environmental aspects of the response to water current by rainbow trout (*Salmo gairdneri*) originating from inlet and outlet streams of two lakes. Can. J. Zool. 59: 2177–2185.

NAESJE, T. F., B. JOHNSON, AND O. T. SANDLUND. 1986. Drift of cisco and whitefish larvae in a Norwegian river. Trans. Am. Fish. Soc. 115: 89–93.

NORTH, E. 1979. Aggressive behaviour in juvenile brown trout, *Salmo trutta* L.: an analysis of the wigwag display. J. Fish Biol. 15: 571–577.

RANDALL, R. G. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. Can. J. Zool. 60: 2239–2244.

REIMERS, P. E. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Ore. Fish Comm. Res. Rep. 4: 43 p.

RICKER, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations, p. 19–160. *In* R. C. Simon and P. A. Larkin [ed.] The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C. 231 p.

RIDDELL, B. E., AND W. C. LEGGETT. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 38: 308–320.

SHEPHERD, B. G., J. E. HILLABY, AND R. J. HUTTON. 1986a. Studies on Pacific salmon (*Oncorhynchus* spp.) in Phase 1 of the Salmonid Enhancement Program. Volume I: Summary. Can. Tech. Rep. Fish. Aquat. Sci. 1482: 180 p.

1986b. Studies on Pacific salmon (*Oncorhynchus* spp.) in Phase 1 of the Salmonid Enhancement Program. Volume II: Data appendices. Can. Tech. Rep. Fish. Aquat. Sci. 1482: 375 p.

STEIN, R. A., P. E. REIMERS, AND J. D. HALL. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook (*O. tshawytscha*) salmon in Sixes River, Oregon. J. Fish. Res. Board Can. 29: 1737–1748.

TAYLOR, E. B., AND P. A. LARKIN. 1986. Current response and agonistic behavior in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from stream- and ocean-type populations. Can. J. Fish. Aquat. Sci. 43: 565–573.

TAYLOR, E. B., AND J. D. MCPHAIL. 1985. Variation in body morphology among British Columbia populations of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 42: 2020–2028.