Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia

TERRY D. BEACHAM AND CLYDE B. MURRAY

*Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station,
Nanaimo, B.C., Canada V9R 5K6*

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Embryos and alevins of coastal-spawning and interior-spawning sockeye (*Oncorhynchus nerka*) and chinook (*O. tshawytscha*) salmon stocks in British Columbia were incubated under controlled water temperatures of 2, 4, 8, 12, and 15°C. At low incubation temperatures, interior-spawning stocks of both species had smaller eggs and higher embryo survival rates than did coastal-spawning stocks. Interior-spawning stocks had faster developmental rates to alevin hatching and fry emergence than did coastal-spawning stocks. Interior-spawning stocks had proportionately larger alevins or fry at 2°C (for sockeye salmon) or 4°C (for chinook salmon) relative to their performance at 8°C than did coastal-spawning stocks. Red-fleshed chinook salmon had higher embryo survival rates at 15°C than did white-fleshed chinook salmon, as well as an indication of proportionately larger alevins or fry relative to the performance at lower incubation temperatures. Differences in developmental biology of interior- and coastal-spawning stocks may reflect adaptation to the thermal conditions experienced during development.

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Des embryons et des alevins de Saumons nerka (*Oncorhynchus nerka*) et de Saumons chinook (*O. tshawytscha*) provenant de stocks de Colombie-Britannique frayant sur la côte ou à l'intérieur des terres ont été gardés à 2, 4, 8, 12 ou 15°C. Les stocks des deux espèces à fraye interieure produisent des oeufs plus petits et leurs embryons ont des taux de survie aux températures faibles plus élevés que les embryons des stocks à fraye côtière. Le développement jusqu'à l'éclosion des alevins vésiculés et l'émergence des alevins plus avancés est plus rapide chez les embryons des stocks à fraye intérieure que chez les embryons des stocks frayant sur les côtes. Chez les stocks à fraye intérieure, les alevins des deux stades sont plus gros à 2°C (Saumon nerka) ou à 4°C (Saumon chinook), proportionnellement à leur performance à 8°C, que les alevins des stocks à fraye côtière. Les Saumons chinook à chair rouge ont des taux de survie embryonnaire à 15°C plus élevés que les Saumons chinook à chair blanche et leurs alevins élevés à cette température semblent plus gros que ceux élevés à des températures plus froides. Ces différences entre les stocks qui frayent sur la côte et les stocks qui frayent à l'intérieur sont probablement le reflet d'adaptations aux conditions thermiques qui prévalent au cours du développement.

[Traduit par la revue]

Introduction

In British Columbia, sockeye salmon (*Oncorhynchus nerka*) spawn during August through November (Foerster 1968), migrating relatively short distances up coastal rivers or, in major rivers like the Fraser or Skeena, migrating up to 700 km upstream in areas far removed from coastal climates. Chinook salmon (*O. tshawytscha*) spawn during July through November, and the spawning sites range from being immediately above tidal limits to over 1000 km upstream in the Fraser River drainage (Aro and Shepard 1967). Sockeye and chinook salmon thus have stocks spawning in areas subject to the mild winter coastal climate and the more severe winter climate in the interior of the province.

Unlike other *Oncorhynchus* species, chinook salmon have two distinct flesh colour forms, being red-fleshed or white-fleshed (Milne 1964; Godfrey 1975). The white-fleshed form apparently does not deposit coloured dietary carotenoids in the flesh (Withler 1986). During sexual maturation, the muscle carotenoids are transported from the flesh to the skin of both sexes and to the eggs of females (Crozier 1970; Kitihara 1984). White-fleshed chinook salmon females produce eggs of lower pigment content than red-fleshed ones, and if egg quality is associated with egg pigment content (Craik 1985), developmental differences may occur between red- and white-fleshed chinook salmon.

In the present study, two comparisons of variation in developmental biology are conducted. The first comparison is between coastal- and interior-spawning stocks of both sockeye and chinook salmon. The second comparison is between red- and white-fleshed forms of chinook salmon. In both comparisons, evidence for adaptive variation in developmental characters is examined.

Materials and methods

Sockeye salmon gametes were collected on 29 October 1986 from Weaver Creek, a coastal tributary of the Fraser River, and on 31 October 1986 from Adams River, an interior tributary in the Thompson River (eventually Fraser River) drainage (Fig. 1). Gametes were collected from 10 males and 10 females per stock and were transported to the laboratory, and then sperm from a single male fertilized the eggs of a single female (full-sib family). Chinook salmon gametes were collected on 15 August 1986 from the Kitimat River and on 19 September 1986 from the Bella Coola River, both coastal rivers on the northern coast of British Columbia. Gametes were collected from five males and five females to produce five full-sib families per stock. The flesh colour of the parents from these two stocks was not determined. Chinook salmon gametes were also collected on 26 September 1986 from the Quesnel River, an interior upper Fraser River tributary. Gametes from four red-fleshed males and females and four white-fleshed males and females were collected, and fertilizations were conducted to produce four red-fleshed and four white-fleshed full-sib families. The fertilized eggs of both sockeye and chinook salmon were incubated in vertical stack incubators with target temperatures of 2, 4, 8, 12, and 15°C. Two replicates per family were incubated at each temperature, and water temperatures were recorded daily.

Egg diameter (mm) and egg weight (mg) were determined from 30 water hardened eggs per female, with the eggs preserved at least
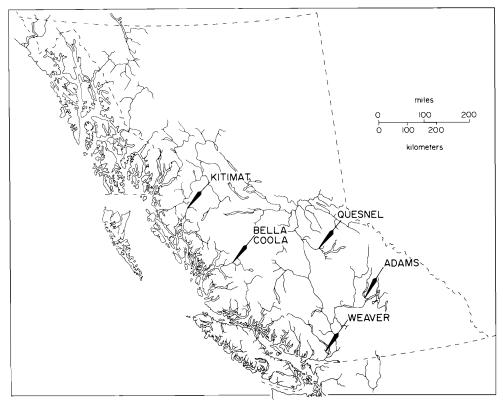
FIG. 1. Locations of salmon stocks examined, with sockeye salmon surveyed at Weaver Creek and Adams River, and with chinook salmon surveyed at Kitimat River, Bella Coola River, and Quesnel River.

3 months in 10% formalin. During incubation, dead eggs were removed, stored in Stockard's solution, and later inspected to remove unfertilized eggs. Embryo survival rates were then calculated based upon the number of fertilized eggs.

During hatching, alevins were counted on a daily basis, and within 1 day of 50% hatching, we anesthetized and then preserved a sample of alevins in 10% formalin for subsequent determination of alevin length and weight. Fork length was recorded to the nearest 0.1 mm, total weight recorded to the nearest milligram, and the yolk was separated from the rest of the body and weighed, with tissue weight determined by subtraction. Dead alevins were also removed and counted to determine alevin survival rates. The timing of fry emergence was determined by placing the alevins in an emergence trap modified from Mason (1976) and Godin (1980), where the alevins were classified as newly emergent fry only when they became neutrally buoyant and positively phototactic. Because it was difficult to maintain 2°C in the emergence traps, timing of fry emergence at 2°C was based upon visual inspection, and when 50% of the alevins had the yolk sacs entirely covered with chromatophores ("buttoned-up") (late stage 36 of Vernier 1969), they were defined to have emerged. At all other temperatures, the time of fry emergence was defined as occurring when 50% of the fry emerged. Length and weight of emergent fry were determined as for alevins.

Variation in sockeye and chinook salmon egg size was examined with a random effect nested analysis of variance model (species separate):

$$Y_{ijk} = \mu + S_i + F_{ij} + e_{ijk}$$

where Y_{ijk} is the egg diameter or weight; μ, the mean; S_i, the effect of stock ($i = 1-3$); F_{ij}, the effect of female ($j = 1-10$) within stock i; and e_{ijk}, the error term of kth egg in subgroup ij. Variation in embryo and alevin survival rates was examined by calculating survival rates for each family as proportions and then transforming them to radians with the arcsine square root transformation. Variation in survival rates was analyzed with the same model as outlined for egg size. Incubation temperatures and species were considered separately in the analysis.

Variation in survival rates of red- and white-fleshed Quesnel River chinook salmon was analyzed with a similar model, the only difference being that the random effect of stock was replaced by the fixed effect of colour.

Variation in alevin and fry size was analyzed with the model

$$Y_{ijkl} = \mu + T_i + S_j + TS_{ij} + F_{jk} + TF_{ijk} + e_{ijkl}$$

where Y_{ijkl} is the size character; μ, the mean; T_i, the effect of incubation temperature ($i = 1-5$); S_j, the effect of stock ($j = 1-3$); TS_{ij}, the temperature × stock interaction; F_{jk}, the effect of female within stock ($k = 1-10$); TF_{ijk}, the temperature × female interaction; and e_{ijkl}, the error term of the lth alevin or fry in subgroup ijk. Temperature was considered fixed with other effects random. Satterthwaite's (1946) approximation was necessary to calculate an approximate mean to test the effect of stock. Species were considered separately in the analysis. Variation in alevin and fry size for red- and white-fleshed Quesnel River chinook salmon was analyzed with a similar model, with the fixed effect of colour replacing the random effect of stock.

Results

Egg size

Substantial differences in egg size were observed between the two sockeye salmon stocks. Eggs from the coastal-spawning Weaver Creek stock had a mean diameter of 6.54 mm (SE = 0.02 mm) and mean weight of 144.1 mg (SE = 0.7 mg), with a mean female postorbital−hypural length of 476 mm. Eggs from the interior-spawning Adams River stock had a mean diameter of 5.77 mm (SE = 0.01 mm) and mean weight of 97.2 mg (SE = 0.7 mg), with a mean female postorbital−hypural length of 483 mm. Although females from the two stocks were of similar size, eggs from the interior-spawning stock were substantially smaller ($F_{1,18} = 92.1$, $P < 0.01$) and lighter ($F_{1,18} = 84.6$) than those from the coastal-spawning stock. Significant differences were also

observed among females within stocks for both egg diameter and weight (both $P < 0.01$). However, differences between stocks accounted for 82% of the total observed variation in egg diameter, whereas differences among females accounted for 9%. Similarly, differences between stocks accounted for 87% of the total observed variation in egg weight, whereas differences among females accounted for 10%.

Chinook salmon in the two coastal-spawning stocks also had larger eggs than in the interior-spawning stock. Eggs from the coastal-spawning Kitimat River stock had a mean diameter of 8.85 mm (SE = 0.03 mm) and mean weight of 356.1 mg (SE = 4.3 mg), with a female postorbital–hypural length of 821 mm. Eggs from the Bella Coola River stock were 9.14 mm (SE = 0.04 mm) in diameter and 396.0 mg (SE = 4.8 mg) in weight, with female length unavailable. Eggs from the interior-spawning Quesnel River stock were 8.47 mm (SE = 0.02 mm) in diameter and 317.4 mg (SE = 1.5 mg) in weight with a female postorbital–hypural length of 803 mm. Egg diameter ($F_{2,15} = 6.10$, $P < 0.05$) and weight ($F_{2,15} = 4.50$, $P < 0.05$) varied among stocks and among females within stocks for both characters (both $P < 0.01$). Differences among stocks accounted for 37% of the total variaton in egg diameter and 36% of the variation in egg weight, with differences among females accounting for 42 and 59% of the total variation for egg diameter and weight, respectively. No significant difference in egg diameter ($F_{1,6} = 1.37$, $P > 0.05$) or egg weight ($F_{1,6} = 1.91$, $P > 0.05$) was observed between red- and white-fleshed female Quesnel River chinook salmon. Mean egg diameter of red-fleshed females was 8.41 mm with a mean weight of 309 mg, whereas that of the white-fleshed females was 8.54 mm and 326 mg, respectively.

Survival rates

Substantial differences in embryo survival rates were observed between the two sockeye salmon stocks incubated at 2°C (Table 1). Embryos from the interior-spawning Adams River stock survived significantly better than embryos from the coastal-spawning Weaver Creek stock ($F_{1,18} = 24.7$, $P < 0.01$). Embryo survival rates at 2°C were less than 40% for 7 of the 10 Weaver Creek families examined but less than 40% for only 1 of 10 Adams River families (Fig. 2). No significant differences in embryo survival rates were observed at any of the other incubation temperatures (all $P > 0.05$).

Sockeye salmon alevin survival rates were different between the two stocks at only 15°C, with alevins from the coastal-spawning Weaver Creek stock surviving better than those from the interior-spawning Adams River stock ($F_{1,18} = 7.5$, $P < 0.05$) (Table 1). All Weaver Creek families had alevin survival rates above 90% at 15°C, whereas only 5 of the 10 Adams River families had alevin survival rates above 90% (Fig. 2). The interior-spawning stock had higher embryo survival rates at a low incubation temperature and lower alevin survival rates at a high incubation temperature than did the coastal-spawning stock. These differences suggest that this variation is adaptive relative to the thermal conditions that these stocks would likely encounter during development.

No chinook salmon embryos survived at 2°C and embryo survival rates were significantly different among stocks at only 4°C ($F_{2,15} = 8.8$, $P < 0.01$). Embryos from the interior-spawning Quesnel River stock had the highest survival rates, and those from the coastal-spawning Kitimat River stock had the lowest rates (Table 1). No substantial difference in embryo survival rates was observed between the Bella Coola River and

Quesnel River stocks. Embryo survival rates at 4°C were less than 60% in four of the five Kitimat River families examined and greater than 97% in seven of eight Quesnel River families examined (Fig. 3).

Chinook salmon alevin survival rates were significantly different among stocks at only 15°C ($F_{2,15} = 23.6$, $P < 0.01$), with Bella Coola alevins surviving less well than did alevins from the other two stocks (Table 1). For both sockeye and chinook salmon embryo and alevin survival rates, significant differences among families within stocks were observed at low (2°C or 4°C) and high (15°C) incubation temperatures (Figs. 2, 3). Although sockeye salmon showed variations in embryo and alevin survival rates suggestive of thermal adaptations to spawning habitats, the results for chinook salmon were less conclusive. The interior-spawning stock had the highest embryo survival rates at 4°C, but a coastal stock had the lowest alevin survival rates at 15°C.

For the Quesnel River chinook salmon stock, embryo and alevin survival rates of red- and white-fleshed fish were compared for the four incubation temperatures at which embryos survived. The only significant difference occurred at 15°C, with red embryos surviving better than white embryos ($F_{1,6} = 6.06$, $P < 0.05$) (Table 2). Three of the four red families had embryo survival rates in excess of 95%, whereas only one white family had embryo survival rates over 95% (Fig. 3). Differences in survival rates of red and white embryos occurred only at high incubation temperatures.

Hatching and emergence time

Sockeye salmon alevins from the Adams River stock hatched earlier than did those from the Weaver Creek stock at all incubation temperatures. Differences between the stocks were accentuated at low incubation temperatures, with Weaver Creek alevins taking approximately 8 days longer to hatch at 2°C than Adams River alevins (Table 1). The same trend was observed in fry emergence timing, with Weaver Creek fry emerging later than those from Adams River. The faster developmental rate of the interior-spawning Adams River stock may reflect an adaptation to colder thermal conditions encountered during development.

Chinook salmon alevins from the interior-spawning Quesnel River stock hatched earlier at all incubation temperatures than did those from the coastal-spawning Kitimat and Bella Coola River stocks (Table 1). This trend was again observed in fry emergence timing. The Kitimat River stock was the earliest spawning of the three stocks examined, and fry from this stock took the longest time to emerge. No difference in development rate was observed between red- and white-fleshed chinook salmon from Quesnel River. The faster development rate of the interior- and later-spawning Quesnel River stock may, as with sockeye salmon, reflect adaptations to a colder thermal regime during development.

Alevin size

Sockeye alevin length differed significantly among incubation temperatures, with the longest alevins observed at either 4 or 8°C and the shortest at 15°C ($F_{4,4} = 21.0$, $P < 0.05$) (Table 3). Alevins were heaviest under at 8°C temperature regime and lightest under either an extreme high (15°C) or low (2°C) temperature regime. The yolk weight of alevins at hatching increased with increasing incubation temperature ($F_{4,4} = 26.4$, $P < 0.05$), but there was no significant effect with respect to incubation temperature on alevin tissue weight at

TABLE 1. Survival rates of embryos and alevins for two stocks of sockeye salmon and three stocks of chinook salmon incubated at controlled temperatures of 2, 4, 8, 12, and 15°C

| | Embryo | | | | Alevin | | | | |
| | | | | | | | Survival rate | | |
Stock	Temperature (°C)	N	Survival rate (fertilization to hatching)	Time to 50% hatching (days)	Temperature (°C)	N	Hatching to emergence	Fertilization to emergence	Time to 50% emergence (days)
				Sockeye salmon					
Weaver	2.0±0.06	2128	0.328	198.2±2.0	2.0±0.10	697	0.954	0.313	283.7±2.2
	3.9±0.32	2058	0.980	134.3±1.8	3.9±0.40	2016	0.989	0.968	197.5±7.5
	7.8±0.36	2125	0.983	79.2±0.8	7.8±0.32	2088	0.983	0.966	122.7±4.3
	11.9±0.32	2149	0.980	51.4±0.6	12.0±0.35	2105	0.986	0.966	79.9±0.2
	14.9±0.27	2172	0.823	43.1±0.7	15.0±0.26	1787	0.968	0.796	66.6±0.1
Adams	2.0±0.06	3876	0.913	189.9±1.9	2.0±0.10	3527	0.983	0.897	275.3±2.0
	3.9±0.32	4745	0.972	130.1±1.3	3.9±0.40	4614	0.994	0.966	196.5±5.2
	7.8±0.36	4761	0.996	76.6±0.8	7.8±0.33	4742	0.992	0.988	117.2±1.4
	11.9±0.32	4782	0.984	50.2±1.4	12.0±0.34	4704	0.983	0.967	80.1±0.5
	14.9±0.27	4456	0.938	42.2±1.1	15.0±0.26	4181	0.815	0.815	66.6±0.8
				Chinook salmon					
Kitimat	2.0±0.06	736	0.000	—	—	0	—	—	—
	3.9±0.86	789	0.697	132.5±2.8	3.9±0.69	550	1.000	0.697	220.0±0.8
	8.0±0.68	756	0.997	70.6±0.8	7.9±0.56	754	0.999	0.996	126.7±3.3
	12.0±0.50	707	0.992	44.1±0.5	12.0±0.54	701	0.993	0.984	78.2±0.6
	15.2±05.0	703	0.913	34.3±0.3	15.1±0.47	642	0.952	0.869	61.9±0.7
Bella Coola	2.0±0.06	1470	0.000	—	—	0	—	—	—
	3.9±0.63	1507	0.959	128.5±2.7	3.9±0.53	1445	0.978	0.938	211.4±1.2
	7.9±0.50	1438	0.996	71.1±1.0	7.9±0.48	1432	0.992	0.987	116.1±0.3
	12.0±0.57	1423	0.978	44.1±0.3	11.9±0.47	1392	0.977	0.956	76.8±0.2
	15.0±0.40	1514	0.931	36.1±1.3	15.0±0.34	1410	0.606	0.564	62.8±0.1
Quesnel	2.0±0.06	1930	0.000	—	—	0	—	—	—
	3.8±0.55	2097	0.979	125.6±1.2	3.9±0.47	2054	0.992	0.972	211.3±1.3
	7.9±0.53	1885	0.989	68.9±0.8	7.9±0.47	1864	1.000	0.989	115.3±0.8
	12.1±0.56	1874	0.994	42.2±0.8	12.0±0.48	1863	0.997	0.997	76.1±0.6
	15.0±0.39	1858	0.957	34.1±0.8	15.0±0.33	1778	0.937	0.897	61.7±0.2

NOTE: Times of 50% hatching of the alevins and 50% emergence of the fry are also indicated. Mean temperature observed at each controlled temperature regime for each stock is also recorded. N is number of fertilized eggs (for embryo survival rates) or alevins hatching (for alevin survival rates). Values are means ± SE.

hatching ($F_{4,4} = 1.2$, $P > 0.05$) (Table 3). Stock differences occurred in all of the alevin size characters ($P < 0.05$), as might be expected given the substantial difference in mean egg size between the two stocks. Significant differences were also observed among families within stocks (Fig. 4), but these differences were probably largely attributable to variation in egg size.

If the two sockeye salmon stocks are adapted to different thermal regimes during development, there should be different trends in the alevin size characters with respect to incubation temperature. This would be illustrated by an interaction between stock and incubation temperature. Significant interactions were observed for alevin length ($F_{4,71} = 6.9$, $P < 0.01$), total weight ($F_{4,71} = 27.8$, $P < 0.01$), and tissue weight ($F = 32.0$, $P < 0.01$). As an example, Adams River alevins were heavier and more efficient at converting yolk to body tissue at 2°C relative to stock performance at 8°C than were Weaver Creek alevins. At 2°C, total body weight of Adams River alevins was 88.9% that observed at 8°C, and tissue weight was 84.4%. Comparable figures for Weaver Creek alevins were 88.0 and 83.3%, respectively. Adams River alevins may be more efficient at converting yolk to body tissue under a very low incubation temperature. Significant interactions were also observed between incubation temperature and family for all alevin size characters (all $P < 0.01$)

(Fig. 4). The response of families to a changing incubation environment was not uniform within stocks, indicating that sufficient variation exists within stocks to respond to a variable thermal regime.

Incubation temperature had a significant effect on chinook salmon alevin length ($F_{3,6} = 16.1$, $P < 0.01$), total weight ($F_{3,6} = 20.3$, $P < 0.01$), yolk weight ($F = 15.4$, $P < 0.01$), and tissue weight ($F = 68.2$, $P < 0.01$). Alevins were generally the longest and had the greatest tissue weight at 4°C. Alevins were the heaviest at 8°C and had the most yolk at 15°C (Table 3). Stock differences also occurred in all alevin size characters, but as with sockeye salmon, these largely reflect differences in initial egg size. For example, eggs were heaviest from the Bella Coola River stock and lightest from the Quesnel River stock, and alevin weights reflect this difference (Table 3). Significant differences in alevin size characters were also observed among families within stocks (Fig. 5), again mostly reflecting differences in initial egg size.

A significant interaction between stock and temperature was observed for chinook salmon alevin length ($F_{6,45} = 7.35$, $P < 0.01$) but not for any of the weight characters (all $P > 0.05$). The interaction occurred because Kitimat River alevins declined in length as temperature increased from 4 to 8°C, whereas alevin length in the other two stocks increased (Table 3, Fig. 5). Significant interactions were also observed between
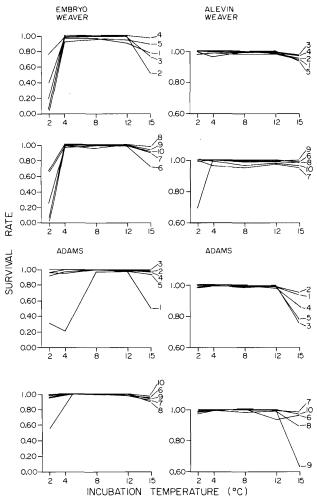
FIG. 2. Survival rates of embryos from fertilization to hatching and of alevins from hatching to emergence for Adams River and Weaver Creek sockeye salmon. Ten full-sib families were examined in each stock.
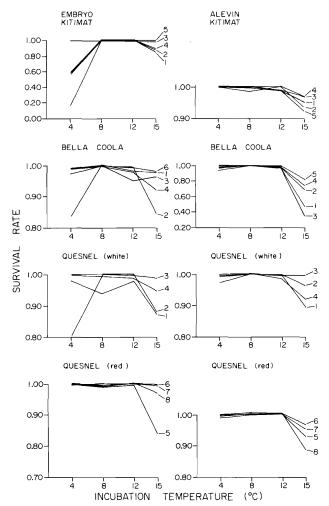

FIG. 3. Survival rates of embryos and alevins for Kitimat River (five families), Bella Coola River (five families), and Quesnel River (four red-fleshed, four white-fleshed families) chinook salmon.

TABLE 2. Survival rates of embryos and alevins for red-fleshed and white-fleshed Quesnel River chinook salmon incubated at controlled temperatures of 4, 8, 12, and 15°C

Temperature (°C)	Colour	Embryos		Alevins	
		Number	Survival rate	Number	Survival rate
4	Red	1196	0.997	1193	0.994
	White	901	0.956	861	0.990
8	Red	1034	0.995	1029	1.000
	White	851	0.981	835	1.000
12	Red	987	0.999	986	1.000
	White	887	0.989	877	0.994
15	Red	1012	0.984	996	0.933
	White	846	0.924	782	0.942

family and incubation temperature for all alevin size characters (Fig. 5), illustrating that substantial variation exists within stocks to respond to variable thermal regimes.

If red- and white-fleshed chinook salmon alevins are adapted to different temperature regimes, an interaction between colour and incubation temperature would be expected. No significant interactions were observed, although the interaction between colour and temperature approached significance for alevin length ($F_{3,18} = 2.10$, $0.10 < P < 0.15$). This occurred because white alevins were longer than red ones at 4°C (white 21.7 mm, red 21.6 mm) and 8°C (white 21.8 mm, red 21.7 mm), a result to be expected based upon the initial egg size differences. However, white alevins were shorter at 12°C (white 19.9 mm, red 20.0 mm) and 15°C (white 19.3 mm, red

TABLE 3. Mean egg weight, egg diameter, and female postorbital−hypural length, fork length, total weight, yolk weight, and tissue weight for sockeye and chinook salmon alevins and fry maintained at 2, 4, 8, 12, and 15°C

Stock	Mean egg weight (mg), diameter (mm), and female length (mm)	Temperature (°C)	Alevin					Fry				
			N	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)	N	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)
						Sockeye salmon						
Weaver	144.1±12.4	2	147	19.3±1.3	128.9±10.2	69.4±6.0	59.5±8.1	156	27.6±0.9	185.9±13.3	13.8±6.4	172.1±16.2
	6.54±0.26	4	288	20.3±0.7	148.2±11.2	71.5±9.0	76.7±9.0	287	28.2±1.2	207.8±18.5	9.7±6.6	198.1±22.0
	476±16	8	293	20.2±0.6	146.4±12.2	75.0±8.8	71.4±8.9	293	27.9±1.0	209.6±12.0	12.7±6.0	196.9±13.7
		12	293	18.8±0.6	143.6±13.0	81.6±9.0	62.0±9.1	293	26.4±0.6	191.8±11.9	22.6±6.1	169.6±10.9
		15	293	17.6±0.6	140.9±12.1	83.9±8.3	57.1±8.4	289	24.2±0.6	168.0±13.0	36.8±8.8	131.2±12.9
Adams	97.2±12.0	2	277	18.0±0.8	98.1±11.2	49.4±7.4	48.8±7.2	287	26.5±0.9	140.4±15.2	7.1±3.5	133.3±15.8
	5.77±0.24	4	272	18.8±0.8	101.1±11.6	49.5±7.2	50.6±6.9	283	26.6±1.0	141.9±14.4	9.2±4.5	132.7±14.8
	483±9	8	296	18.9±0.6	110.6±10.2	52.8±7.8	57.8±6.7	300	25.6±0.9	149.2±16.2	11.8±4.4	137.4±16.6
		12	288	17.6±0.8	109.7±10.1	57.8±8.0	51.9±8.2	289	25.1±0.7	140.8±14.3	15.3±4.0	125.5±13.3
		15	279	17.1±0.5	109.5±10.5	58.2±9.9	51.3±8.5	282	23.2±0.9	124.9±12.6	24.1±5.5	100.8±12.9
						Chinook salmon						
Kitimat	356.1±52.4	4	113	22.3±0.7	345.3±37.9	212.6±30.0	132.7±15.5	117	33.6±0.9	522.7±52.7	69.2±24.7	453.5±41.7
	8.85±0.40	8	148	21.5±0.9	356.6±50.7	234.2±39.2	122.4±19.0	150	34.8±1.2	561.5±67.2	62.8±36.1	498.7±52.9
	821±46	12	134	20.8±0.6	339.8±48.1	232.5±36.2	107.3±19.4	139	33.2±1.1	507.5±72.8	83.1±29.4	424.4±53.7
		15	128	19.7±0.8	328.3±42.1	225.3±30.0	103.1±21.0	122	31.1±1.7	451.0±50.8	106.6±35.6	344.5±45.1
Bella Coola	396.0±59.1	4	148	22.2±0.8	392.9±45.6	254.5±44.6	138.3±15.8	150	35.1±0.9	587.7±59.5	104.0±35.1	483.7±37.4
	9.1±0.51	8	150	22.7±0.9	401.0±55.2	263.8±45.4	137.1±17.8	150	35.4±1.0	456.4±48.7	120.1±30.8	456.4±48.7
		12	148	21.9±0.7	383.4±55.3	262.1±44.2	121.3±18.6	150	34.3±1.3	543.6±69.2	112.9±26.8	430.7±50.5
		15	139	20.1±1.1	379.9±65.1	263.5±45.2	116.5±31.6	119	32.7±1.2	508.7±54.1	136.3±35.2	372.4±41.4
Quesnel	317.4±22.7	4	238	21.7±0.5	318.9±19.3	195.6±14.1	123.3±13.2	240	33.8±0.8	501.7±28.9	55.6±14.3	446.1±29.2
	8.47±0.28	8	238	21.8±0.5	326.4±22.1	212.2±20.4	114.2±15.2	240	33.9±0.7	486.2±31.6	69.2±14.9	417.0±31.5
	803±62	12	240	19.9±0.9	306.4±19.4	208.4±13.6	98.0±13.5	240	32.9±0.8	455.1±31.9	68.8±13.7	386.3±26.9
		15	239	19.6±0.9	306.1±19.7	210.0±13.2	96.1±12.6	240	31.7±1.0	424.7±27.4	89.0±26.3	335.7±38.7

NOTE: N is number of alevins and fry measured for all families in each stock. Thirty eggs were examined for each female. Values are mean ± SE. Female length was not available for the Bella Coola stock.
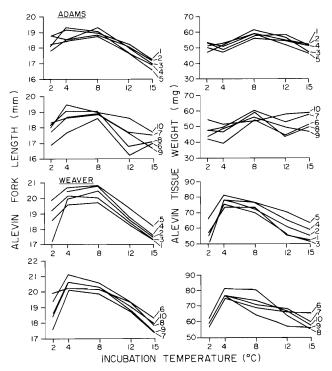
FIG. 4. Fork length and tissue weight of alevins at 50% hatching for Adams River and Weaver Creek sockeye salmon incubated at 2, 4, 8, 12, and 15°C.
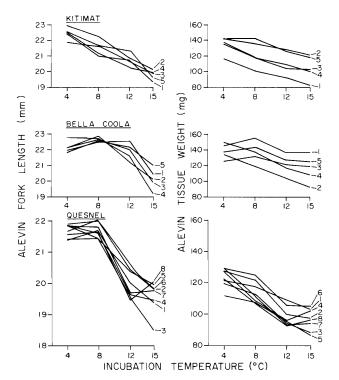

FIG. 5. Fork length and tissue weight of alevins at 50% hatching for Kitimat River, Bella Coola River, and Quesnel River chinook salmon incubated at 4, 8, 12, and 15°C.

19.9 mm) than red ones, indicating a weak differential response to incubation temperature.

Fry size

Significant temperature effects were observed in all sockeye salmon fry size characters (all $P < 0.01$). The longest fry occurred at 4°C, and the lightest fry occurred at 15°C (Table 3). Fry emerging at 15°C had the greatest amount of yolk, as was observed for alevins. Stock differences were also observed in all fry size characters, with larger fry produced in the Weaver Creek stock, which also had larger initial egg size. As with the alevins, significant differences were also observed among families within stocks for all fry size characters (all $P < 0.01$) (Fig. 6), probably largely attributable to variation in egg size.

Significant stock and temperature interactions were observed for all the sockeye salmon fry size characters (all $P < 0.01$). Adams River fry grew better at 2°C than did Weaver Creek fry, relative to their performance at 8°C. For example, tissue weight of Adams River fry at 2°C was 97% of that observed at 8°C, whereas that of Weaver Creek fry at 2°C was only 87% of that observed at 8°C. This illustrates that the interior-spawning Adams River stock appears to be better adapted to a low temperature thermal regime during development than the coastal-spawning Weaver Creek stock. Significant family and temperature interactions were also observed for all fry size characters (all $P < 0.01$) (Fig. 6), illustrating that families within stocks are not all equally adapted to respond to the same thermal regime during development.

Incubation temperature had a significant effect on all chinook salmon fry size characters (all $P < 0.01$). The shortest and lightest fry with the most yolk at emergence occurred at 15°C (Table 3). The heaviest fry occurred at 4°C for the Bella Coola River and Quesnel River stocks and at 8°C in the Kitimat River stock (Table 3). Significant stock and

family differences were observed in all fry size characters (all $P < 0.01$), but these were largely attributable to variation in initial egg size.

Significant stock and temperature interactions were observed for fry length ($F_{6,45} = 2.69$, $P < 0.05$), yolk weight at emergence ($F_{6,45} = 4.95$, $P < 0.01$), and tissue weight ($F = 3.41$, $P < 0.01$) (Fig. 7). For example, Quesnel River fry emerging at 4°C had 7% more tissue weight relative to those emerging at 8°C; Bella Coola River fry had 6% more; and Kitimat River fry had 9% less tissue weight for fry emerging at 4°C compared with 8°C. Trends in fry tissue weight with respect to incubation temperature varied among stocks, resulting in the significant statistical interaction. The marginally higher fry growth rates at a low temperature of the interior-spawning Quesnel River stock may reflect some adaptation to thermal regimes encountered during development. As in previous examples, significant interactions between family and temperature were observed in all fry size characters (all $P < 0.01$) (Fig. 7).

No significant interactions between flesh colour and temperature were observed for any of the fry size characters in the Quesnel River stock (all $P > 0.05$). There was some indication that white fry grew less well at 15°C than red fry. For example, tissue weight of white fry was heavier at emergence than that of red fry at temperatures of 4 (452 vs. 441 mg), 8 (427 vs. 408 mg), and 12°C (390 vs. 383 mg), but at 15°C red fry were heavier than white fry (331 vs. 341 mg).

Discussion

Substantial differences in developmental characters occurred between interior- and coastal-spawning stocks of sockeye and chinook salmon. Egg size was smaller in interior-spawning stocks compared with coastal-spawning stocks. Egg size in Pacific salmon is generally related to female size (Bilton and
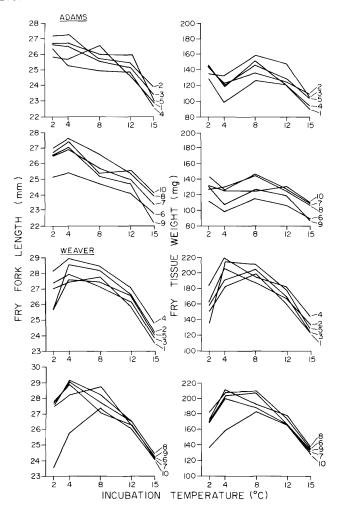
FIG. 6. Fork length and tissue weight of fry at 50% emergence for Adams River and Weaver Creek sockeye salmon incubated at 2, 4, 8, 12, and 15°C.
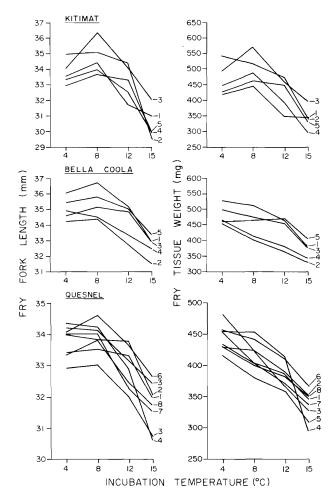

FIG. 7. Fork length and tissue weight of fry at 50% emergence for Adams River, Bella Coola River, and Quesnel River chinook salmon incubated at 4, 8, 12, and 15°C.

Jenkinson 1966; Bilton and Smith 1973; Beacham and Murray 1985); however, females in the interior-spawning sockeye salmon stock that we examined were longer than those in the coastal stock, so this is an inadequate explanation for stock variation in egg size. Egg size may also reflect stock variation in fecundity, with more fecund stocks having smaller eggs. In sockeye salmon, mean fecundity in the Cultus Lake stock in the lower Fraser River is 4100 eggs (Foerster 1968), whereas fecundity in the upper river Chilko Lake stock is less than 3500 eggs (Williams 1977). As lower Fraser River sockeye salmon stocks tend, on average, to have larger eggs than upper river stocks (Brannon 1987), the expectation that more fecund stocks should have smaller eggs is not supported. It may be that interior-spawning stocks have a longer freshwater migration than coastal-spawning stocks, and consequently they expend greater energy during their migration (Gilhousen 1980). This greater expenditure of energy may be diverted from egg production, resulting in smaller eggs at maturity.

Interior-spawning stocks of sockeye and chinook salmon had higher embryo survival rates at low incubation temperatures than did coastal spawning stocks. These results suggest that interior stocks are better adapted to low water temperatures during development, presumably a result of selection to lower water temperatures experienced during the winter. Variation among stocks in embryo survival rate has also been observed for pink (Beacham and Murray 1988) and chum salmon

(Beacham and Murray 1987) and has been interpreted to reflect adaptation to local environmental conditions.

No chinook salmon embryos survived at 2°C, whereas survival rates in excess of 95% were observed at 4°C in two of the three stocks examined. The temperature of 50% embryo mortality is probably thus near 3°C, similar to the conclusion of Alderdice and Velsen (1978). The lower temperature of 50% mortality for sockeye salmon embryos varied among stocks, but probably ranges between 1 and 3°C. Our observed survival rate of 33% for Weaver Creek embryos incubated at 2°C is in close agreement with the 40% rate observed by Murray and McPhail (1988) for the same stock under a 2°C incubation regime, providing further evidence this stock is not adapted to low water temperatures during embryonic development. Murray and McPhail (1988) reported that chinook salmon embryos from the interior-spawning Babine River stock in northern British Columbia survived at a rate of 14% under a 2°C incubation temperature, compared with the complete mortality observed in northern coastal stocks or in the southern interior stock in our study. These observations provide further evidence that variation in survival rates during development likely reflect adaptations to local environmental conditions.

White-fleshed chinook salmon embryos were less viable at 15°C than red-fleshed embryos. Craik (1985) suggested that carotenoids in the egg may have some role in metabolism if oxygen is limited in the environment. Our results tend to support this hypothesis, with lowest dissolved oxygen concentra-

tions expected at the highest incubation temperature. White-fleshed alevins also survived more poorly at 15°C than red-fleshed ones, but it is difficult to account for this difference as a result of oxygen deprivation. Lower survival of white-fleshed embryos incubated at temperatures between 1.7 and 9.0°C has been observed (Hard 1986). White-fleshed embryos and alevins may be less viable than red-fleshed ones, but a completely satisfactory explanation is not yet available.

Hatching and emergence timing of alevins and fry varied among the stocks, with interior-spawning (and later-spawning) stocks having faster development rates than coastal-spawning stocks. Stock variation in development rate has been described for pink and chum salmon by Beacham and Murray (1987, 1988) and has been interpreted to reflect adaptations to spawning environments. Pink and chum salmon generally do not migrate far upstream during spawning migration. However, chum salmon in the Yukon River migrate up to 2800 km upstream (Milligan et al. 1986) and spawn in October, but their development rate is much faster than that of a comparable British Columbia stock spawning in October (Beacham et al. 1988). Development rates of specific stocks likely reflect adaptations to timing of spawning and thermal regimes experienced during development (Beacham and Murray 1987; Brannon 1987).

Interior-spawning stocks had proportionately larger alevins or fry at low incubation temperatures relative to their performance at 8°C than did coastal-spawning stocks. This indicates that they were more efficient at metabolizing yolk at low incubation temperatures, perhaps reflecting adaptations to thermal environments during development. Differential efficiency of yolk conversion to body tissue among stocks has been reported for pink (Beacham and Murray 1988) and chum salmon (Beacham and Murray 1987), and has been interpreted as adaptation to colder thermal environments during development. In summary, as salmon home to their natal streams to spawn at specific times each year, distinct stocks have developed, and given the diversity of spawning habitats, it is not unreasonable to expect that adaptations to local environmental conditions should occur in many of their life-history characters.

Acknowledgements

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