Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia

C. B. MURRAY AND T. D. BEACHAM

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

AND

J. D. MCPHAIL

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, B.C., Canada V6T 2A9

Received November 30, 1988

MURRAY, C. B., BEACHAM, T. D., and MCPHAIL, J. D. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. Can. J. Zool. **68**: 347–358.

Coho salmon (*Oncorhynchus kisutch*) stocks in British Columbia spawning from October to April were surveyed for variation in developmental characteristics at incubation temperatures from 1.5 to 15°C. There were no trends in embryo or alevin survival rates associated with spawning time or spawning temperature. The highest embryo and alevin survival rates occurred at 4 or 5°C and complete mortality generally occurred at 14 or 15°C. Vancouver and Queen Charlotte Island stocks had lower survival rates at 1.5 and 2°C than did mainland stocks. Time to 50% hatching and 50% emergence varied inversely with incubation temperature. Alevin hatching time for the Pallant Creek stock on the Queen Charlotte Islands was later than for all other stocks. Stocks had different trends in alevin and fry length and weight with respect to incubation temperature. Northern stocks tended to be more efficient than southern stocks at converting yolk to body tissue at 1.5 and 2°C, as were mainland stocks compared with island stocks.

MURRAY, C. B., BEACHAM, T. D., et MCPHAIL, J. D. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. Can. J. Zool. **68** : 347–358.

Des stocks de Saumons argentés (*Oncorhynchus kisutch*) de Colombie-Britannique qui frayent d'octobre à avril ont été inventoriés dans le but de déterminer les variations de croissance à des températures d'incubation de 1,5 à 15°C. Les taux de survie des embryons et des alevins ne suivent pas de tendance particulière en fonction du moment de la fraye ou de la température au moment de la fraye. Les taux de survie maximaux des embryons et des alevins se produisent à 4 ou 5°C et la mortalité est généralement de 100% à 14 ou 15°C. Les stocks de l'Île de Vancouver et des Îles de la Reine-Charlotte ont des taux de survie à 1,5 et 2°C plus faibles que ceux des stocks du continent. Le temps écoulé jusqu'à l'éclosion de 50% des embryons ou jusqu'à l'émergence de 50% des alevins varient en fonction inverse de la température d'incubation. L'éclosion des alevins se produit plus tard au sein du stock de Pallant Creek, dans les Îles de la Reine-Charlotte, que dans tous les autres stocks. La longueur et la masse des alevins vésiculés et des alevins plus âgés suivent des tendances différentes selon la température d'incubation. Les stocks nordiques ont un pouvoir de conversion de vitellus en tissu plus efficace que les stocks du sud à 1,5 et 2°C; de même, les stocks continentaux sont plus efficaces que les stocks insulaires.

[Traduit par la revue]

Introduction

Pacific salmon return to their natal stream to spawn and this results in the segregation of spawning adults in both time and location, which leads to the formation of discrete stocks (Ricker 1972). Pacific salmon also appear to be genetically adapted to specific spawning times, locations, and temperatures (Ricker 1972; Miller and Brannon 1982; Burger *et al.* 1985; Brannon 1987) and thus, indirectly to specific incubation temperatures. Adaptation to specific incubation temperatures ensures maximum fry survival and size (Beacham and Murray 1985, 1986, 1987; Murray and McPhail 1988) and maintains fry emergence at the most favourable time each year (Godin 1982; Brannon 1987). Transplants of Pacific salmon within what was thought to be their normal range have been relatively unsuccessful in producing new stocks (Withler 1982). Adaptations to local environments may explain some of these unsuccessful transplants (Helle 1981). Transplants may be more successful if donor stocks are better matched to proposed environments (Beacham and Murray 1987).

In British Columbia, coho salmon (*Oncorhynchus kisutch*) spawn in over 970 rivers and streams, with spawning concentrated mainly in coastal systems and in small systems rather than large ones (Aro and Shepard 1967). Spawning of coho salmon in British Columbia typically peaks in November and December when autumn rains have raised water levels, but spawning may continue at low levels into January or as late as March at temperatures from 0.8 to 14.4°C (Godfrey 1965). In this study, we examine the effects of incubation temperature on survival, development time, and alevin and fry size of coho salmon in British Columbia. We also present evidence which illustrates that coho salmon in British Columbia have stock specific developmental traits that may be adaptations to different environments.

Materials and methods

Coho salmon gametes were collected from 13 different stocks (Table 1) with the specific locations shown in Fig. 1. Postorbital-hypural length of females was measured to the nearest mm. Eggs from single females were fertilized with sperm from single males, producing up to five full-sib families per stock. A sample of 30 water-hardened eggs from each female was preserved for at least 3 months in 10% formalin for subsequent determination of egg size. Egg diameter was measured along the longest axis to the nearest 0.1 mm and weight was obtained by first blotting the egg dry and then weighing it to the nearest mg.

The incubation system we used from 1976 to 1979 has been described by Murray and Beacham (1986). Briefly, it consists of two water-filled refrigeration units operating at 1°C that contained the temperature baths. Temperature control was maintained by heating the temperature baths to 2, 5, 8, 11, or 14°C. The eggs were incubated in submerged aquarium filters half filled with pea gravel and compressed air circulated water through each filter. Single egg lots from each family were incubated at each temperature.

The incubation system we used in 1986 has been described by Beacham and Murray (1985). The eggs were incubated in vertical stack

TABLE 1. Collection date, water temperature, postorbital-hypural length (POHY), and egg diameter and weight for 49 females from 13 stocks of coho salmon in British Columbia (N is the number of females or eggs examined; standard deviations are in parentheses)

Stock and collection date	Water temperature (°C)	Female		Egg size		
		N	POHY (mm)	N	Diameter (mm)	Weight (mg)
Capilano River						
Dec. 4, 1976	6.5	1	477(—)	30	7.2(0.25)	224.4(11.85)
Nov. 18, 1979	9.0	2	489(6.4)	60	7.0(0.28)	215.8(10.83)
Coho Creek						
Dec. 19, 1976	6.0	2	508(17.7)	60	7.0(0.22)	235.8(8.94)
Nov. 16, 1979	9.0	1	546(—)	30	7.6(0.31)	212.4(10.87)
Salmon River						
Nov. 11, 1977	9.0	2	531(10.6)	60	7.5(0.20)	243.6(11.42)
Nov. 7, 1979	6.5	1	499(—)	30	7.0(0.22)	214.9(12.70)
Elk Creek						
April 6, 1977	10.0	1	459(—)	30	6.7(0.30)	171.6(9.16)
Nov. 24, 1979	6.0	2	446(50.9)	60	6.2(0.31)	169.7(26.38)
Nathan Creek						
Nov. 7, 1979	6.5	1	482(—)	30	7.1(0.25)	221.0(12.58)
Gosden Creek						
Nov. 19, 1979	6.0	1	598(—)	30	8.1(0.19)	302.6(12.22)
Spius Creek						
Oct. 31, 1986	6.0	5	501(31.4)	150	6.6(0.45)	132.8(21.51)
Pallant Creek						
Nov. 7, 1986	4.0	5	577(38.0)	147	8.7(0.51)	348.2(30.40)
Kitimat River						
Nov. 14, 1986	1.5	5	597(21.9)	150	7.5(0.40)	219.2(30.77)
Robertson Creek						
Nov. 19, 1986	5.0	5	617(17.6)	150	8.0(0.40)	262.7(30.40)
Bella Coola River						
Nov. 29, 1986	2.0	5	593(23.8)	148	7.6(0.37)	215.1(25.99)
Chehalis River						
Dec. 4, 1986	3.0	5	505(28.4)	150	7.2(0.37)	174.2(22.15)
Big Qualicum River						
Dec. 10, 1986	4.0	5	518(38.4)	150	7.5(0.39)	206.8(29.54)

incubators maintained at 1.5, 2, 4, 8, 12, and 15°C, with each tray containing 20 plexiglass containers. The bottom and lid of each container were covered with screen. Two egg lots from each family were assigned to each temperature, with each replicate in a separate tray. Water velocities and oxygen tensions for both series of experiments were within the recommended ranges for the incubation of salmonid embryos and alevins (Bams and Simpson 1977).

In both series of experiments, dead eggs were removed and preserved in Stockard's solution (Rugh 1952), and later inspected to remove unfertilized eggs. Embryo survival rates were then calculated based upon the number of fertilized eggs. Once hatching began in each family, we recorded the number of newly hatched alevins daily, and within 1 day of 50% hatching, we anesthetized and then preserved, for at least 3 months, 25-30 alevins per family (15 alevins per replicate in 1986) in 10% formalin for subsequent determination of alevin length and weight. Standard length was recorded to the nearest 0.1 mm. Total wet weight was recorded to the nearest mg and, for the 1986 experiment, yolk was separated from the rest of the body and weighed (mg). Tissue weight was determined by subtracting yolk weight from total weight. Dead alevins were removed and counted to determine alevin survival rates. The timing of fry emergence for each family was determined by placing 20 alevins in an emergence trap (modified from Mason (1976) and Godin (1980)). Alevins in the trap were classified as newly emergent fry when they became neutrally buoyant and positively phototactic. Within 1 day of 50% emergence, all the fry remaining in the incubator for each family were anesthetized and then preserved in 10% formalin. A sample of 25–30 fry (15 fry per replicate in 1986) from each family was subsequently measured and weighed, using the methods outline for alevins.

Variation in egg size for all stocks was analyzed with the analysis of variance model (all effects random)

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

where Y_{ijk} = egg diameter or weight, μ = mean, S_i = effect of stock ($i = 1,13$), F_{ij} = effect of female within stock ($j = 1,5$), and e_{ijk} = error term for k^{th} observation in subgroup ij.

For the analysis of stock and temperature effects on embryo and alevin survival for all coho salmon stocks surveyed in British Columbia during 1976–1986, we calculated survival rates for each group as proportions and then used the arcsine square root transformation. We then used a one-way analysis of variance model to analyze variation in survival rates for stocks from 1976–1979 and a model similar to the egg size model for stocks in 1986, except that Y_{ijk} = embryo or alevin survival rates and S_i = effect of stock ($i = 1,7$). In both analyses, temperatures were considered separately.

Variation in 50% hatching and emergence times for all coho salmon

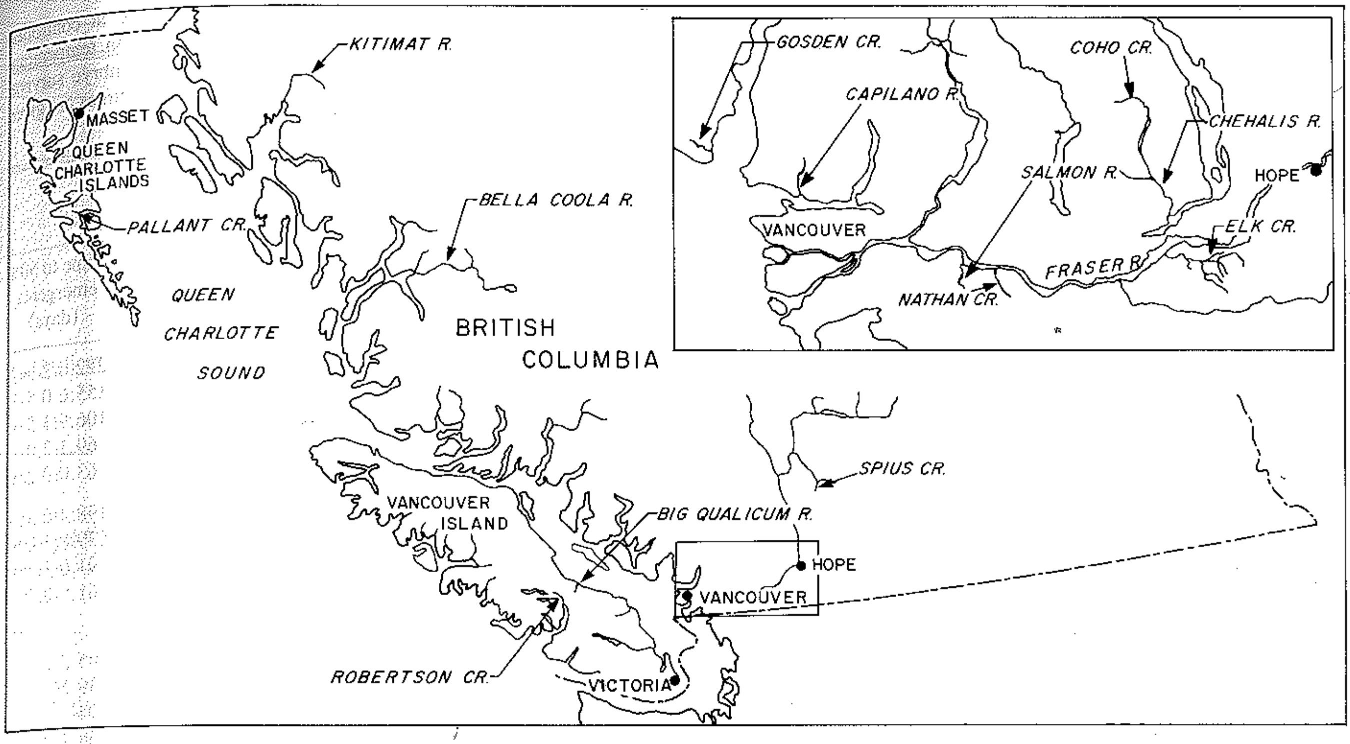


FIG. 1. Location where coho salmon gametes were collected in 1976–1986.

stocks was examined with the model

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

where Y_{ijk} = observed 50% hatching or emergence times, μ = overall mean, S_i = effect of stock (i = 1,13), T_j = effect of temperature (j = 1,9), ST_{ij} = interaction between stock and temperature, and e_{ijk} = error term for k^{th} observation in subgroup ij.

Variation in alevin and fry length and weight for coho salmon stocks surveyed during 1976–1979 or 1986 was exmained with the model

$$Y_{ijkl} = \mu + S_i + T_j + ST_{ij} + F_{ik} + FT_{ijk} + e_{ijkl}$$

where Y_{ijk} = observed length or weight, μ = overall mean, S_i = effect of stock, T_j = effect of temperature, ST_{ij} = interaction between stock and temperature, F_{ik} = effect of family within stock (k = 1,5), FT_{ijk} = interaction between families within stock and temperature, and e_{ijkl} = error term for l^{th} observation in subgroup ijk. Temperature was considered fixed and other effects random. Satterthwaite's (1946) approximation was necessary to calculate an appropriate mean square to test the effect of stock.

Regional differences in alevin and fry tissue weight for stocks surveyed in 1986 were investigated by analysis of covariance with the model

$$Y_{ij} = \mu + R_i + B(\bar{W}_{ij} - W) + e_{ij}$$

where Y_{ij} = alevin or fry tissue weight, μ = overall mean, R_i = effect of region (i = 1,2 for northern vs. southern stocks and for island vs. mainland stocks), B = regression coefficient of alevin or fry tissue weight on mean egg size, W_{ij} = mean egg weight by stock (j = 1,3 for northern and island stocks and 1,4 for southern and mainland stocks), W = overall mean egg weight, and e_{ij} = error term for j^{th} observation in subgroup i. Temperatures were considered separately in the analysis.

Results

Egg size

There were no clear regional or seasonal trends in egg size among the 13 coho salmon stocks surveyed (Table 1). However, egg diameters and weight in coho salmon were dependent upon female postorbital-hypural length. As mean female body length increased, mean egg diameter (r = 0.79; df = 11; $P < 0.01$) and weight (r = 0.64; $P < 0.05$) also increased. Significant differences were observed among stocks in mean egg diameter (F = 10.24; df = 12,36; $P < 0.01$) and weight (F 12.92; $P < 0.01$), where variation among stocks in egg diameter and weight accounted for 65 and 74% of the total variance, respectively. There were also significant differences among females within stocks in both egg diameter (F = 80.96; df = 36, 1416; $P < 0.01$) and weight (F = 231.62; $P < 0.01$), accounting for 26 and 23% of the total variance, respectively. The stock and female components accounted for more of the total variance in egg weight (96%) than in egg diameter (91%).

Survival rates

Survival rates of coho salmon embryos from fertilization to hatching were variable for the 13 stocks examined (Table 2). The highest embryo survival rates for most stocks were recorded at 4 or 5°C and were usually over 85% at 2, 4, 5, and 8°C. Complete mortality was recorded at 14 and 15°C except for two Coho Creek families in 1979 (Fig. 2) and one Spius Creek family in 1986 (1.7%). Survival rates for coho salmon embryos during 1976–1979 were not significantly different among stocks within temperatures ($P > 0.10$). In 1986, embryo survival rates were significantly different among stocks within temperatures at 1.5, 2, 4, and 8°C ($P < 0.05$), but not at 12°C. The lowest embryo survival rates at 1.5°C were recorded in the Pallant Creek and Robertson Creek stocks and, although not significant, in the Kitimat River stock at 12°C (Table 2). Within a stock, there were marked differences in embryo survival among families (Fig. 2), with the greatest differences occurring at the extreme incubation temperatures. In 1976–1979 these differences were greatest at 11°C, where embryo survival rates for three families in both the Salmon River and Elk Creek stocks ranged from 76 to 92% and 73 to 95%, respectively. Similar differences were recorded for the five Bella Coola River families at 12°C in 1986. At 1.5°C, embryo survival rates for

TABLE 2. Survival rates of embryos and alevins for 13 stocks of coho salmon sampled from 1976 to 1986 and incubated at controlled temperatures of 1.5, 2, 4, 5, 8, 11, 12, 14, and 15°C; time to 50% hatching of alevins, 50% emergence of fry, and mean temperature observed under each controlled temperature regime for each stock is also indicated (*N* is the number of fertilized eggs (for embryo survival rates) or alevins hatching (for alevin survival rates); standard deviations of mean temperatures and 50% hatching and emergence times are given in parentheses)

	Embryo				Alevin				
		Survival rate				Survival rate			
Stock	Water temperature (°C)	*N*	Fertilization to hatch	Time to 50% hatching (days)	Water temperature (°C)	*N*	Hatching to emergence	Fertilization to emergence	Time to 50% emergence (days)
Coho Creek	2.3(0.75)	593	0.960	164.6(2.57)	2.2(0.73)	569	1.000	0.960	222.0(2.96)
	5.0(0.20)	587	0.954	90.2(0.74)	5.0(0.16)	560	0.996	0.951	155.6(0.51)
	7.9(0.30)	595	0.936	61.2(1.06)	8.0(0.23)	557	0.993	0.929	106.9(1.53)
	10.9(0.47)	614	0.876	43.4(1.35)	10.7(0.25)	536	0.985	0.860	69.1(2.07)
	13.8(0.36)	428	0.554	31.0(0.07)	13.9(0.25)	237	0.903	0.500	63.0(0.28)
Salmon River	2.1(0.57)	627	0.960	158.8(0.17)	2.1(0.49)	602	1.000	0.960	198.4(0.55)
	5.1(0.28)	617	0.955	86.2(1.68)	5.1(0.26)	589	0.998	0.953	139.8(1.00)
	8.0(0.13)	657	0.933	53.6(1.97)	8.0(0.10)	613	0.980	0.915	91.0(1.39)
	10.9(0.38)	632	0.842	38.3(0.57)	10.9(0.26)	532	0.890	0.748	61.9(0.50)
	13.8(0.39)	629	0.000	— —					
Elk Creek	2.2(0.30)	619	0.730	150.7(7.21)	2.1(0.48)	452	0.958	0.700	265.3(2.11)
	5.0(0.28)	627	0.982	87.2(1.00)	5.1(0.22)	616	1.000	0.982	139.5(2.12)
	8.1(0.30)	607	0.886	61.1(1.98)	8.0(0.27)	538	0.994	0.881	94.2(1.72)
	10.9(0.32)	592	0.861	42.3(0.97)	11.0(0.17)	510	0.953	0.821	68.1(0.82)
	13.9(0.59)	608	0.000	— —					
Capilano River	2.3(0.87)	629	0.900	152.2(2.22)	2.1(0.78)	566	0.926	0.833	265.3(1.54)
	5.0(0.28)	652	0.962	80.5(0.86)	5.0(0.33)	627	0.989	0.951	147.5(0.92)
	8.1(0.30)	657	0.988	51.3(0.82)	8.0(0.22)	649	0.995	0.983	97.8(0.35)
	10.9(0.32)	658	0.953	38.8(0.46)	10.9(0.31)	627	0.974	0.929	69.1(1.62)
	13.9(0.59)	649	0.000	— —					
Nathan Creek	2.3(0.40)	220	0.945	149.8(—)	2.1(0.58)	208	0.880	0.832	196.6(—)
	5.0(0.27)	201	0.975	74.6(—)	5.1(0.22)	196	0.990	0.965	137.3(—)
	7.9(0.29)	289	0.958	53.5(—)	8.0(0.27)	277	0.940	0.910	92.8(—)
	10.9(0.44)	250	0.960	38.4(—)	10.8(0.45)	240	0.871	0.836	67.4(—)
	13.8(0.37)	241	0.000	— —					
Gosden Creek	2.0(0.51)	205	0.878	149.5(—)	2.1(0.49)	180	0.900	0.790	214.9(—)
	5.1(0.32)	185	0.973	87.8(—)	5.0(0.35)	180	1.000	0.973	153.5(—)
	8.0(0.25)	201	0.975	57.6(—)	8.0(0.30)	196	0.995	0.970	109.7(—)
	10.9(0.37)	225	0.951	38.7(—)	11.0(0.35)	214	0.902	0.858	78.4(—)
	14.0(0.49)	207	0.000	— —					
Spius Creek	1.4(0.15)	1102	0.984	189.5(1.75)	1.4(0.14)	1084	0.975	0.959	280.0(1.89)
	2.0(0.07)	1004	0.968	158.7(1.58)	2.0(0.07)	972	0.984	0.952	230.0(0.00)
	3.8(0.32)	1033	0.981	105.6(1.08)	3.9(0.31)	1013	0.996	0.977	154.8(3.02)
	7.9(0.39)	1157	1.000	58.1(0.54)	7.8(0.34)	1157	0.997	0.997	88.7(5.53)
	11.9(0.30)	1042	0.958	36.6(0.15)	12.0(0.36)	998	0.998	0.946	57.9(0.09)
	14.9(0.23)	1051	0.031	28.0(0.06)	14.9(0.27)	33	0.485	0.015	53.0(0.00)
Pallant Creek	1.4(0.15)	1679	0.634	217.4(2.02)	1.4(0.13)	1064	0.497	0.315	350.0(7.82)
	2.0(0.06)	1561	0.858	185.5(1.42)	2.0(0.10)	1339	0.964	0.827	264.9(1.59)
	3.9(0.32)	1643	0.998	123.8(1.12)	3.9(0.33)	1639	0.981	0.979	169.0(1.34)
	7.8(0.37)	1730	0.998	67.7(0.82)	7.8(0.34)	1710	0.968	0.957	99.3(1.24)
	11.9(0.31)	1668	0.865	41.2(0.60)	12.0(0.34)	1442	0.784	0.677	73.7(1.76)
	14.9(0.27)	1916	0.000	— —					
Kitimat River	1.4(0.15)	1332	0.978	198.0(2.13)	1.4(0.14)	1303	0.921	0.901	295.4(8.34)
	2.0(0.06)	1278	0.988	168.6(1.76)	2.0(0.10)	1263	0.988	0.971	237.3(0.00)
	3.9(0.31)	1214	0.972	112.3(1.06)	3.9(0.33)	1181	0.993	0.965	154.3(2.11)
	7.8(0.39)	1164	0.979	61.2(0.51)	7.8(0.35)	1140	0.989	0.968	94.6(0.86)
	12.0(0.32)	1218	0.646	37.9(0.46)	12.0(0.35)	787	0.882	0.570	62.8(1.37)
	14.9(0.31)	1249	0.000	— —					
Bella Coola River	1.4(0.13)	1170	0.987	195.1(3.14)	1.5(0.12)	1155	0.972	0.960	299.6(9.15)
	2.0(0.07)	1095	0.990	171.8(2.49)	2.0(0.07)	1084	0.977	0.967	245.3(2.75)
	3.9(0.33)	1158	1.000	110.3(0.79)	3.9(0.39)	1158	0.997	0.997	156.3(7.91)

TABLE 1 (*concluded*)

Stock	Embryo: Water temperature (°C)	Embryo: N	Embryo: Survival rate, Fertilization to hatch	Embryo: Time to 50% hatching (days)	Alevin: Water temperature (°C)	Alevin: N	Alevin: Survival rate, Hatching to emergence	Alevin: Survival rate, Fertilization to emergence	Alevin: Time to 50% emergence (days)
	7.8(0.39)	1145	0.996	61.1(0.39)	7.8(0.36)	1140	0.989	0.984	89.2(1.82)
	12.2(0.34)	1126	0.878	37.6(0.59)	12.1(0.34)	989	0.930	0.817	60.8(0.86)
	14.9(0.26)	1139	0.000	— —					
Big Qualicum River	1.4(0.11)	2142	0.950	188.0(2.13)	1.4(0.10)	2035	0.585	0.556	318.2(4.73)
	2.0(0.07)	2272	0.974	163.3(3.65)	2.0(0.10)	2214	0.880	0.857	237.5(3.54)
	3.9(0.31)	2125	0.988	104.1(1.56)	3.9(0.41)	2099	0.988	0.976	152.7(0.94)
	7.9(0.32)	2125	0.956	57.9(0.53)	7.8(0.34)	2031	0.834	0.797	91.2(4.30)
	12.1(0.35)	1986	0.834	37.8(0.41)	12.1(0.29)	1657	0.923	0.770	62.8(1.27)
	15.1(0.20)	1935	0.000	— —					
Robertson Creek	1.4(0.15)	2358	0.660	198.1(2.01)	1.4(0.12)	1556	0.789	0.521	323.8(6.20)
	2.0(0.06)	2366	0.861	168.9(2.69)	2.0(0.10)	2037	0.951	0.819	244.4(2.07)
	3.9(0.31)	2458	0.984	112.1(1.06)	4.0(0.32)	2419	0.995	0.979	157.1(2.11)
	7.8(0.39)	2408	0.915	61.5(0.39)	7.8(0.35)	2204	0.975	0.893	96.1(3.64)
	12.1(0.35)	2375	0.899	37.1(0.34)	12.0(0.32)	2134	0.836	0.751	67.7(1.62)
	14.8(0.26)	2303	0.000	— —					
Chehalis River	1.4(0.13)	2221	0.973	190.0(1.88)	1.4(0.11)	2160	0.930	0.904	308.8(6.19)
	2.0(0.07)	2270	0.979	164.7(2.45)	2.0(0.07)	2220	0.983	0.963	230.8(1.03)
	3.8(0.33)	2185	0.999	105.2(0.77)	3.9(0.32)	2182	0.999	0.998	149.3(3.32)
	7.9(0.39)	2037	0.992	58.3(0.51)	7.8(0.34)	2021	0.994	0.986	92.0(3.26)
	11.9(0.28)	2066	0.924	36.4(0.47)	12.0(0.36)	1908	0.887	0.819	61.5(1.83)
	14.9(0.24)	1922	0.000	— —					

five families in both the Pallant and Robertson Creek stocks ranged from 20 to 97% and 16 to 94%, respectively, and similar differences were recorded for the three Elk Creek families at 2°C (32–95%) (Fig. 2). Incubation temperature had a marked effect on subsequent embryo survival and, within a stock, families apparently were not all equally adapted to survive in similar environments.

As with embryos, the highest alevin survival rates were recorded at 4 or 5°C and were usually over 90% at 2, 4, 5, and 8°C. Coho salmon alevins incubated at 1.5 and 12°C had lower survival rates than did those at the other incubation temperatures examined. Alevin survival rates in 1976–1979 were not significantly different among stocks within temperatures, except at 2°C where the Coho Creek and Salmon River stocks had higher survival rates than the other stocks examined. In 1986, survival rates of coho salmon alevins differed among stocks within incubation temperatures at 1.5, 2, 8, and 12°C (all $P < 0.05$), but not at 4°C. The lowest alevin survival rates at 1.5°C were recorded in the Pallant Creek, Big Qualicum River, and Robertson Creek stocks, and at 12°C in the Pallant and Robertson Creek stocks (Table 2). As with embryos, there were marked differences in alevin survival rates among families within stocks, with the differences most apparent at the extreme incubation temperature (Fig. 2). Very low and high incubation temperatures reduced the survival of coho salmon embryos and alevins.

The 13 coho salmon stocks surveyed in British Columbia covered a wide geographic range and diverse spawning temperatures, but spawning times were very similar among stocks (November–December), except for the one family from the Elk Creek stock that spawned in April. No clear trends in survival rates from fertilization to emergence were associated with spawning time or spawning temperature. Survival rates within a region and over several years were relatively consistent (Table 2, Fig. 2). For example, within the Chehalis River drainage, overall survival rates for the Coho Creek stock at 2 and 8°C were 96 and 93%, respectively, and 96 and 98% for the Chehalis River stock. There was significant regional variation in overall survival rates for coho salmon stocks in British Columbia, with the Queen Charlotte Island stock (Pallant Creek) and both Vancouver Island stocks (Robertson Creek and Big Qualicum River) having lower survival rates from fertilization to emergence at 1.5 and 2°C than the mainland stocks examined. Coho salmon survival rates clearly differ among incubation temperatures, among stocks, and among families within stocks.

Development time

Time to 50% hatching and 50% emergence for all coho salmon stocks surveyed in 1976–1979 varied inversely with mean incubation temperature (Table 2). As expected, there were significant differences among temperatures in the time from fertilization to 50% hatching ($F = 1461.38$; df = 8,42; $P < 0.01$), with hatching at 8 and 2°C requiring 51–68 and 149–185 days, respectively. Significant differences occurred among stocks ($F = 10.90$; df = 12,42; $P < 0.01$), with coho salmon alevins from Pallant Creek on the Queen Charlotte Islands hatching later at all temperatures than those in the other stocks surveyed. Significant interactions occurred among stocks and incubation temperatures ($F = 37.15$; df 42,348; $P < 0.01$), so that stocks hatching sooner at one incubation temperature did not necessarily hatch sooner at another temperature. Because of these interactions there were no clear regional (except for Pallant Creek) or seasonal trends associated with hatching time.

There were significant differences in the time from fertilization to 50% emergence among incubation temperatures ($F = 490.92$; df = 8,42; $P < 0.01$) and among stocks ($F = 3.67$;

TABLE 3. Standard length, total wet weight, yolk weights, and tissue weights for coho salmon alevins and fry incubated at 1.5, 2, 4, 5, 8, 11, 12, 14, and 15°C (*N* is the number of alevins or fry measured and weighed for all families combined in each stock; standard deviations are in parentheses)

		Alevin					Fry				
Stock	Water temperature (°C)	*N*	Standard length (mm)	Total wet weight (mg)	Yolk weight (mg)	Tissue weight (mg)	*N*	Standard length (mm)	Total wet weight (mg)	Yolk weight (mg)	Tissue weight (mg)
Coho Creek	2.0	75	18.8(0.62)	188.6(30.42)			75	26.4(1.82)	285.0(16.33)		
	5.0	75	17.2(1.22)	184.3(30.11)			75	27.4(1.33)	329.2(20.62)		
	8.0	75	17.7(1.08)	179.4(29.91)			75	27.3(1.25)	290.5(29.03)		
	11.0	75	16.5(0.54)	172.1(31.78)			75	25.6(1.42)	270.6(14.54)		
	14.0	50	15.6(0.86)	151.0(31.50)			50	23.7(1.03)	242.4(12.43)		
Salmon River	2.0	75	19.2(1.11)	201.8(38.05)			75	27.0(0.92)	297.6(68.62)		
	5.0	75	17.6(0.93)	199.1(34.32)			75	27.4(0.65)	347.8(98.23)		
	8.0	75	17.7(1.07)	200.4(31.34)			75	27.7(0.95)	327.4(81.04)		
	11.0	75	16.7(0.64)	191.1(28.46)			75	26.2(1.02)	304.1(47.32)		
Elk Creek	2.0	75	16.5(0.83)	125.7(24.92)			75	24.8(1.53)	205.7(49.92)		
	5.0	75	16.8(0.89)	124.6(25.73)			75	25.0(1.58)	205.8(81.67)		
	8.0	75	16.7(0.84)	125.1(28.80)			75	24.6(1.44)	204.4(49.2)		
	11.0	75	15.8(0.95)	123.6(27.80)			75	23.9(1.45)	197.3(45.26)		
Capilano River	2.0	75	17.9(0.74)	176.2(20.32)			75	26.4(0.97)	256.1(19.42)		
	5.0	75	17.2(0.65)	169.7(20.42)			75	26.6(0.99)	211.1(31.63)		
	8.0	75	16.7(0.73)	172.3(13.72)			75	26.2(1.12)	227.7(10.86)		
	11.0	75	15.4(0.52)	159.6(17.84)			75	25.0(1.05)	231.5(14.37)		
Nathan Creek	2.0	25	17.9(0.41)	160.9(9.62)			25	26.3(0.65)	241.5(15.35)		
	5.0	25	17.6(0.56)	167.0(8.94)			25	27.3(0.78)	225.0(17.72)		
	8.0	25	17.4(0.54)	168.2(9.20)			25	27.3(0.62)	226.5(12.88)		
	11.0	25	16.5(0.73)	160.2(9.25)			25	28.3(0.77)	320.3(10.83)		
Gosden Creek	2.0	25	21.9(0.42)	268.4(12.23)			25	29.6(0.42)	328.2(9.12)		
	5.0	25	21.6(0.56)	275.3(14.92)			25	30.3(0.78)	321.6(13.55)		
	8.0	25	20.6(0.39)	273.3(12.84)			25	29.5(0.53)	319.0(9.29)		
	11.0	25	19.4(0.52)	260.2(9.22)			25	38.2(0.77)	320.3(10.84)		
Spius Creek	1.5	149	17.5(0.91)	137.8(19.42)	64.6(12.91)	73.2(9.12)	150	23.3(1.22)	175.7(29.93)	14.8(7.02)	161.0(27.92)
	2.0	139	16.9(0.92)	134.7(21.65)	63.3(15.16)	71.4(9.43)	147	24.7(1.44)	208.8(34.07)	16.2(6.31)	192.5(31.74)
	4.0	150	17.7(1.04)	158.6(25.91)	68.6(17.62)	90.0(13.15)	150	25.9(1.17)	270.4(42.22)	7.9(5.55)	262.6(38.72)
	8.0	142	17.9(0.97)	152.4(23.22)	70.6(17.14)	31.8(9.17)	142	26.0(1.33)	255.5(38.81)	5.5(5.06)	250.0(38.01)
	12.0	144	16.7(1.06)	149.8(22.75)	86.1(18.35)	63.7(9.00)	144	25.7(1.05)	219.5(39.82)	0.6(2.73)	218.9(39.30)
	15.0	18	14.4(0.86)	124.7(16.94)	63.9(4.92)	60.8(16.14)	13	21.6(1.15)	164.0(19.56)	9.5(5.54)	154.5(20.30)
Pallant Creek	1.5	140	18.8(0.92)	306.2(48.33)	180.0(35.35)	126.2(16.82)	118	27.1(1.72)	326.1(57.11)	56.6(26.21)	269.5(48.00)
	2.0	149	20.8(0.73)	302.6(52.31)	175.9(36.92)	126.7(18.03)	150	30.5(1.11)	468.5(83.01)	36.6(14.22)	431.9(72.27)
	4.0	145	21.4(0.74)	356.5(54.97)	194.0(42.07)	162.5(18.21)	150	30.5(1.01)	540.0(78.21)	62.6(14.93)	477.4(67.41)
	8.0	149	20.7(0.86)	341.6(54.62)	208.2(42.87)	133.4(22.72)	150	30.7(1.02)	527.3(72.22)	59.0(20.97)	468.4(57.60)
	12.0	148	18.3(0.92)	330.5(49.55)	229.8(49.63)	100.6(14.92)	150	29.6(1.11)	487.3(73.31)	49.6(27.85)	437.7(68.32)
Robertson Creek	1.5	143	19.4(0.61)	237.3(29.21)	136.0(23.52)	101.3(10.11)	114	25.9(0.82)	270.6(36.41)	30.4(13.42)	240.2(35.00)
	2.0	149	19.6(0.65)	246.6(26.51)	145.8(22.81)	100.7(13.21)	150	28.3(1.32)	380.8(40.92)	31.8(10.77)	348.9(34.62)

	4.0	150	20.3(0.73)	284.8(32.84)	156.0(24.44)	128.8(16.82)	150	29.0(1.11)	438.8(39.27)	47.1(17.02)	391.7(28.26)
	8.0	149	19.9(0.77)	276.3(34.95)	164.7(28.81)	111.6(17.02)	150	29.8(1.02)	439.1(41.65)	23.3(20.33)	415.9(39.41)
	12.0	150	18.0(0.78)	262.3(30.92)	180.2(32.24)	82.1(21.77)	150	29.0(1.04)	372.1(48.22)	24.2(24.36)	347.9(42.00)
Kitimat River	1.5	150	19.0(0.82)	208.0(25.31)	113.1(18.41)	95.0(10.81)	150	26.1(1.22)	273.2(31.77)	27.8(9.81)	245.3(29.72)
	2.0	147	19.0(0.85)	210.2(24.32)	112.5(20.42)	97.7(10.11)	150	27.2(0.97)	325.4(39.71)	21.7(10.32)	303.6(33.72)
	4.0	150	19.2(1.01)	244.2(31.33)	122.9(23.31)	121.3(14.11)	150	27.6(1.13)	391.2(46.11)	36.5(12.01)	354.7(42.11)
	8.0	150	19.2(0.65)	237.9(29.10)	133.4(24.11)	104.5(10.00)	150	28.3(0.92)	393.1(42.91)	23.8(10.62)	369.3(36.32)
	12.0	120	17.1(0.69)	214.9(23.61)	135.4(16.63)	79.5(12.31)	119	26.3(1.14)	332.0(38.84)	34.0(17.22)	298.0(45.34)
Bella Coola River	1.5	150	19.2(0.84)	211.3(27.52)	115.1(18.72)	96.2(14.82)	150	26.1(1.13)	276.7(33.62)	22.3(11.76)	254.4(33.52)
	2.0	149	19.0(0.93)	205.4(26.41)	110.9(17.43)	94.5(15.17)	150	27.2(1.27)	339.7(42.17)	26.6(11.22)	313.0(41.00)
	4.0	150	19.5(0.75)	242.7(28.52)	121.6(17.84)	121.1(13.92)	150	27.7(1.13)	385.5(44.33)	27.8(14.37)	357.7(44.80)
	8.0	150	19.3(0.77)	243.9(29.44)	129.2(19.21)	114.8(14.67)	150	27.7(0.58)	395.6(38.63)	28.4(10.04)	367.1(32.66)
	12.0	150	17.3(0.76)	233.0(28.92)	141.2(22.21)	91.6(14.32)	147	26.9(1.00)	362.2(50.66)	31.2(10.72)	331.0(48.11)
Big Qualicum River	1.5	145	18.6(0.82)	200.0(25.01)	115.9(19.43)	84.1(15.10)	141	25.0(0.92)	232.2(29.84)	27.4(12.22)	204.9(26.84)
	2.0	121	18.9(0.84)	200.4(27.62)	114.1(24.63)	86.3(13.42)	130	27.0(1.23)	312.5(36.61)	28.8(13.22)	283.8(28.44)
	4.0	148	18.9(0.88)	232.4(28.34)	122.9(18.32)	109.5(14.65)	149	27.6(1.11)	372.0(44.63)	25.1(8.64)	346.9(38.75)
	8.0	126	19.0(0.89)	235.3(28.52)	127.4(16.13)	108.0(16.53)	127	28.0(0.72)	388.2(41.02)	24.6(14.93)	363.6(33.82)
	12.0	127	17.8(0.72)	230.8(25.84)	139.2(19.33)	91.6(11.42)	128	27.1(1.15)	352.9(41.33)	24.1(13.00)	328.8(45.21)
Chehalis River	1.5	149	18.1(0.83)	167.0(21.34)	89.1(15.82)	77.9(8.11)	150	24.1(1.06)	204.6(31.91)	17.3(8.44)	187.4(31.32)
	2.0	150	18.1(0.87)	167.9(19.52)	86.5(14.43)	81.4(9.22)	150	25.8(0.86)	275.1(31.72)	20.9(6.92)	254.3(29.44)
	4.0	150	19.0(0.72)	200.5(23.41)	93.9(15.72)	106.7(11.65)	150	27.0(0.72)	326.9(38.81)	21.5(9.07)	305.4(34.82)
	8.0	150	18.8(0.65)	197.1(22.62)	100.7(16.64)	96.4(10.43)	150	27.3(0.91)	318.6(45.01)	7.6(8.22)	311.0(41.32)
	12.0	150	17.4(0.54)	191.0(24.51)	109.4(19.32)	81.6(14.74)	150	26.7(1.24)	297.8(41.82)	11.8(12.54)	286.1(47.52)

df = 12,42; $P < 0.01$). In addition, there were no clear regional or seasonal trends associated with emergence time because of the significant interactions among stocks and temperatures ($F = 49.45$; df = 42,348; $P < 0.01$). Emergence at 8 and 2°C required 84–109 and 197–265 days, respectively. The trend of Pallant Creek coho salmon hatching later at all temperatures was not maintained at emergence.

Alevin size

Alevin size at hatching for stocks surveyed in 1976–1986 was variable among stocks within an incubation temperature and among temperatures within a stock (Table 3, Fig. 3). For stocks surveyed in 1976–1979, there were significant differences among temperatures for alevin standard length ($F = 12.86$; df = 4,15; $P < 0.01$) and total wet weight ($F = 24.1$; $P < 0.01$), but no significant differences among stocks for either size characteristic. Alevin length and weight generally increased with decreasing incubation temperatures. Significant variation also occurred among families within a stock for both length and weight, but this variation was probably the result of differences in female egg size within stocks. Interactions were observed between families within stocks and incubation temperature, but not between stock and temperature, for both length and weight. Families within a stock responded differently to incubation temperatures (Fig. 3), suggesting that families within a stock are not necessarily adapted to the same environmental conditions.

We compared trends in alevin size for stocks surveyed in 1986 with replicates for each family at each temperature combined. As indicated for the stocks surveyed in 1976–1979, alevin standard length clearly differed among incubation temperatures ($F = 25.60$; df = 5,24; $P < 0.01$), with the longest alevins generally produced at 4 and 8°C (19.4 and 19.3 mm, respectively) and those at 12°C being the shortest (17.5 mm). Alevins hatching at 4 and 8°C had similar total weights (245.2 and 241.3 mg, respectively) with total weight declining at 1.5 and 2°C to 208.7 and 210.6 mg, respectively. Alevin tissue weights were heavier at 4°C (119.8 mg), intermediate at 1.5 and 2°C (93.1 and 94.5 mg, respectively), and lighter at 12°C (84.5 mg). Incubation temperatures clearly affect alevin length, weight, and the conversion of yolk to body tissue, with the longest and heaviest alevins generally produced at 4°C. Alevin yolk weights at hatching also varied significantly among incubation temperatures ($F = 31.38$; $P < 0.01$), with alevin yolk weight decreasing with declining incubation temperature. There were no significant stock differences detected for alevin size parameters, except for total weight ($F = 6.24$; df = 6,13; $P < 0.01$). Differences in total weight were largely the result of differences in mean egg size among stocks (Table 1). Heavier alevins were produced by stocks with larger eggs. Significant variation among families within stocks was observed for all alevin size parameters investigated (all $P < 0.01$) (Fig. 3), but this variation was again the result of differences in female egg size within stocks, with longer and heavier alevins produced by females with larger eggs.

Significant interactions were observed between stock and incubation temperature for alevin standard length ($F = 7.10$; df = 24,111; $P < 0.01$), total weight ($F = 5.58$; $P < 0.01$), yolk weight ($F = 7.96$; $P < 0.01$), and tissue weight ($F = 6.90$; $P < 0.01$). Interaction between stock and incubation temperature suggested that stocks were adapted to different environments with respect to incubation temperature. Interactions were also observed among families within stocks and incubation temperatures for all alevin size parameters (all $P < 0.01$) (Fig.

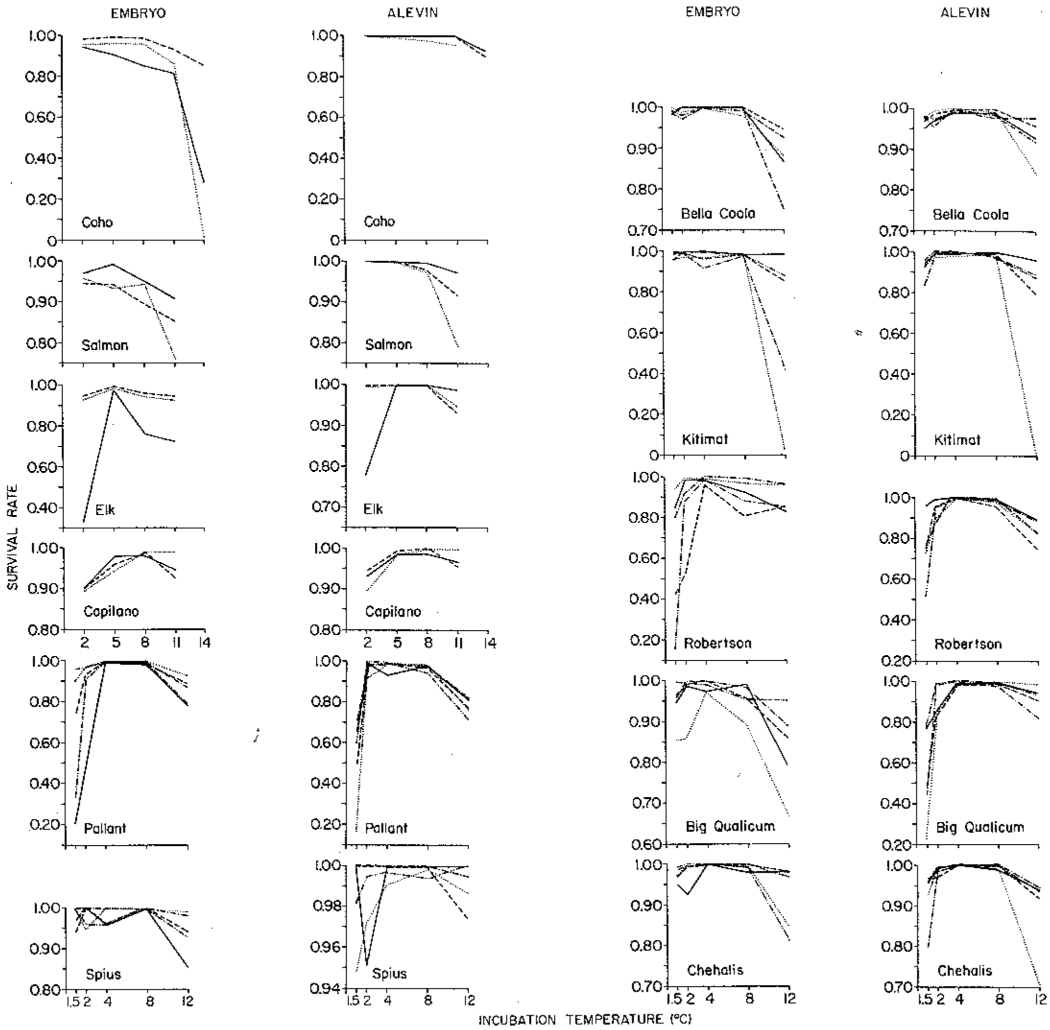


FIG. 2. Survival rates of embryos from fertilization to hatching and of alevins from hatching to emergence for 47 families from 11 stocks of coho salmon. Families are indicated by different lines.

3). Families producing larger alevins at one temperature did not necessarily produce larger alevins at another temperature.

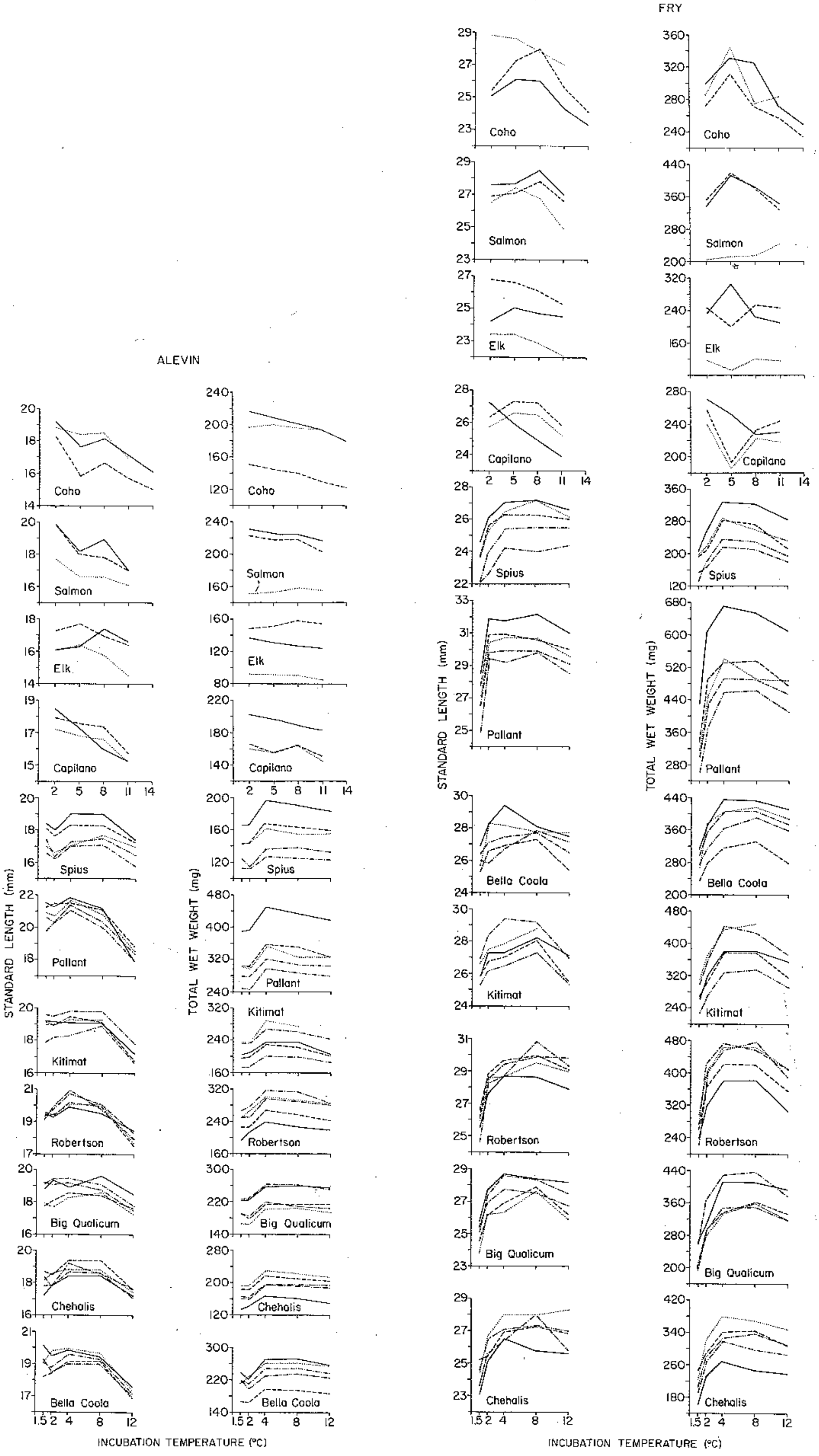
Fry Size

Incubation temperatures had an effect not only on alevin size, but also on fry size for all stocks surveyed (Table 3). At emergence for stocks surveyed in 1976–1979, there were significant differences in fry standard length among incubation temperatures ($F = 23.74$; df = 4,15; $P < 0.01$), and among families within stocks ($F = 11.79$; df = 8,23; $P < 0.01$), but not among stocks ($F = 1.47$; df = 5,10; $P > 0.10$). Fry total weight also varied among families within stocks ($F = 18.20$; df = 8,23; $P < 0.01$), but not among stocks or temperatures ($P > 0.10$). The longest (26.9 mm) and heaviest (273.4 mg) fry were produced at 5°C. As with alevins, differences in fry length and weight at emergence among families within stocks were attributable to variation in egg size among females. Conversely, the similarity in egg size among stocks probably accounts for the lack of stock differences in fry length and weight in 1976–1979. Significant interactions were observed between temperature and families within stocks for fry length and weight ($P < 0.01$), but not between stock and temperature ($P > 0.10$). Trends in fry size with respect to temperature can be dependent upon the family under consideration (Fig. 3).

In 1986, fry standard length at emergence differed among incubation temperatures ($F = 30.3$; df = 5,24; $P < 0.01$), with the longest fry produced at 4 and 8°C (27.9 and 28.3 mm, respectively) and the shortest, at 1.5°C (25.3 mm). Total weight at emergence for fry incubated at 4 and 8°C was 389.3 mg and it declined to 248.3 mg at 1.5°C ($F = 52.6$; $P < 0.01$). On average, fry tissue weights were the heaviest at 8°C (364.5 mg) and they declined at 1.5 and 12°C to 221.3 and 322.3 mg, respectively. There was no significant difference in the amount of residual yolk among temperatures ($F = 1.42$; $P > 0.10$). Incubation temperature had a marked effect on fry size at emergence, with the longest and heaviest fry produced at 8°C.

There were no significant differences in standard length, total weight, and tissue weight among stocks (all $P > 0.10$), but

FIG. 3. Standard length and total weight of alevins at 50% hatching and fry at 50% emergence for 47 families from 11 stocks of coho salmon incubated at 1.5, 2, 4, 5, 8, 11, 12, and 14°C. Families are indicated by different lines.


ALEVIN
FRY
STANDARD LENGTH (mm)
TOTAL WET WEIGHT (mg)
Coho
Salmon
Elk
Capilano
Spius
Pallant
Kitimat
Robertson
Big Qualicum
Chehalis
Bella Coola
INCUBATION TEMPERATURE (°C)
INCUBATION TEMPERATURE (°C)

residual yolk weight was variable among stocks in 1986 ($F = 5.93$; df = 6,22; $P < 0.01$). Fry from stocks with large eggs had more residual yolk (Pallant Creek, 52.7 mg) than fry from stocks with small eggs (Spius Creek, 9.0 mg). Fry size parameters varied among families within stocks (all $P < 0.01$; Fig. 3), but, as with alevins, these differences were attributable to variation in egg size among females.

Trends in fry size with respect to incubation temperature were different among stocks and significant interactions were observed between stock and incubation temperature for all size parameters investigated (all $P < 0.01$). When standard length was compared at 2 and 12°C, Pallant Creek, Kitimat River, and Bella Coola River fry were longer at 2°C, and Spius Creek, Robertson Creek, Chehalis River, and Big Qualicum River fry were longer at 12°C. Spius Creek, Pallant Creek, and Chehalis River fry were the heaviest at 4°C, while Robertson Creek, Kitimat River, Bella Coola River, and Big Qualicum River fry were the heaviest at 8°C. Stocks clearly respond differently to incubation temperatures with respect to fry size.

Interactions were observed among families within stocks and incubation temperatures for all fry size paramters (all $P < 0.01$; Fig. 3). The interactions between families and temperatures were the most apparent in the Robertson Creek stock and the least apparent in the Pallant River stock.

At a common egg size there were no significant differences in the efficiency of converting yolk to alevin or fry tissue between northern and southern or between island and mainland stocks surveyed in 1986 (all $P > 0.10$). However, at 1.5°C, there was a tendency for northern stocks to be more efficient at converting yolk to tissue than southern stocks (alevin, 97 and 91 mg, respectively; fry, 243 and 208 mg, respectively) and for mainland stocks to be more efficient than island stocks (alevin, 96 and 89 mg, respectively; fry, 236 and 205 mg, respectively). Conversely, at 8°C, southern stocks tended to be more efficient than northern stocks (alevin, 107 and 100 mg, respectively; fry, 366 and 349 mg, respectively) and island stocks, to be more efficient than mainland stocks (alevin, 108 and 100 mg, respectively; fry, 372 and 348 mg, respectively. Northern or mainland stocks tend to be more efficient at converting yolk to alevin and fry tissue at low incubation temperatures than southern or island coho salmon stocks.

Discussion

Salmonid species generally segregate into distinct seasonal stocks within a river system, and exhibit differences in spawning time and temperature, size, fecundity, age at maturity, and embryo and alevin survival rates (Ricker 1972; Beacham and Murray 1987; Brannon 1987). Unlike the other salmonids, coho salmon do not seem to form distinct seasonal races within a stream, with characteristic differences in size, fecundity, and age at maturity (Ricker 1972). We observed coho salmon spawning from October to April at temperatures between 1.5 and 10.0°C, and there appeared to be little correlation between the time of entry into a spawning stream and the spawning date or temperature. Early run fish may spawn early or may wait weeks or even months to spawn and, conversely, late run fish may spawn immediately or also wait weeks (Ricker 1972). Differences in the spawning migration of coho salmon seem to be related to flow conditions, where the migration begins when there is a large increase in flow (Neave 1943; Sumner 1953; Shapovalov and Taft 1954; Fraser *et al.* 1983).

Incubation temperatures near the upper and lower thresholds for normal embryonic development substantially reduced coho salmon embryo and alevin survival rates. Except for two Coho Creek families incubated at 14°C and one Spius Creek family incubated at 15°C, coho salmon incubated at 14 and 15°C suffered 100% mortality. Other researchers have observed increased mortality for coho salmon incubated at ambient temperatures between 11 and 12°C (Shapovalov and Berrian 1940; Shaw and Magh 1943; Smirnov 1975; Allen 1957; Murray and McPhail 1988). Tang *et al.* (1987) reported high survival rates to emergence for two Washington State coho salmon stocks incubated between 1.3 and 10.9°C, but at 0.1, 0.6, and 17°C no embryos survived. They also reported that survival to emergence for one stock ranged from 75 to 79% at 12.4°C and from 10 to 11% at 14.5°C, whereas survival to emergence for the other stock ranged from 30 to 39% at 12.5°C and was 0% at 14.4°C. We also found that there were regional differences in survival rates at 1.5 and 2.0°C, with island stocks generally having lower survival rates to emergence than mainland stocks. Mainland stocks may be adapted to colder initial incubation temperatures than island stocks because mainland streams tend to be colder than island streams (Sheridan 1962; Anonymous 1977). Clearly, there are regional, stock, and family differences in survival rates, with the upper threshold for normal development near 14°C and the lower threshold between 0.6 and 1.3°C.

We found no regional trends or differences in coho salmon egg size among stocks, but mature water-hardened egg size was dependent on female length, with small females producing smaller eggs than large females. Similarly, Allen (1958) reported that the diameter of mature water-hardened eggs within a stock was correlated with female length.

Alevin hatching time at each incubation temperature was similar for all coho salmon stocks examined, except for the Pallant River stock from the Queen Charlotte Islands, where hatching was considerbly later than in the other stocks. Chum (*O. keta*) and pink (*O. goruscha*) salmon stocks on the Queen Charlotte Islands also hatch later (Beacham and Murray 1987, 1988) and are genetically distinct from stocks in other areas of British Columbia (Beacham *et al.* 1987, 1988). The Queen Charlotte Islands were a refugium during the last ice age in British Columbia (Warner *et al.* 1982). Salmon stocks indigenous to the Queen Charlotte Islands have thus presumably had a longer time to accumulate genetic differences and adaptations to the environment. This greater time period coupled with higher mean winter water temperatures than comparable mainland areas (Anonymous 1977) may account for the differences between hatching times for Pallant Creek coho salmon and other stocks in British Columbia.

Emergence timing is considered to be a major selective force influencing spawning time and the differentiation of specific stocks (Godin 1982; Miller and Brannon 1982; Beacham and Murray 1987; Brannon 1987). Coho salmon develop faster and emerge sooner at all temperatures than other *Oncorhynchus* species (Murray and McPhail 1988). They also spawn later and at lower temperatures than the other species and their rapid rate of development is thought to be a mechanism for maintaining fry emergence timing similar to that of the other species in the spring (Lister and Genoe 1970; Smirnov 1975; Godin 1982; Brannon 1987; Murray and McPhail 1988).

Spawning later than other species may reduce interspecific competition for spawning areas. It is not uncommon to find coho and chinook (*O. tshawhytcha*) salmon utilizing similar spawning sites, but at different times (Burner 1951; Lister and Genoe 1970; Fraser *et al.* 1982). Pravdin (1940) also observed late spawning coho salmon digging up the eggs of sockeye (*O. nerka*) and chum salmon. Coho salmon fry have an extended freshwater rearing period and frequently cohabit rearing areas with chinook salmon and rainbow (*Salmo gairdneri*) and cutthroat (*S. clarki*) trout (Mason 1976; Miller and Brannon 1982; Rosenau and McPhail 1987). Interspecific competition for rearing areas may make it necessary for coho salmon fry to emerge at a similar time to chinook salmon and cutthroat trout or before rainbow trout in order to establish a territory. Coho salmon fry that cannot establish territories may be displaced into suboptimal rearing areas and thus have lower survival rates (Chapman 1962).

As with other species, coho salmon females with larger eggs produce larger alevins and fry than other females with smaller eggs (Kazakov 1981; Wallace and Aasjord 1984; Beacham and Murray 1985, 1986, 1987). Incubation temperatures also influence alevin and fry size (Beacham and Murray 1987; Murray and McPhail 1988). Northern or mainland stocks generally produced heavier alevins and fry at low incubation temperatures (1.5–2.0°C) than southern or island stocks, with the opposite trends occurring at 8°C. Incubation environments vary among stocks, with mainland and northern stocks on average subjected to lower mean temperatures during development than island or southern stocks (Martin 1959; Sheridan 1962; Beacham and Murray 1987). Tang *et al.* (1987) found that for one coho salmon stock the conversion of yolk to tissue was maximized at 4°C and for another it was maximized at 4.7 and 6.5°C. Murray and McPhail (1988) suggested that maximum conversion of yolk to tissue for a single coho salmon family was near 2°C. Our results from several coho salmon families and stocks suggest that maximum conversion of yolk to tissue occurred between 4 and 8°C. Clearly, coho salmon stocks do not respond identically to changes in incubation temperatures.

Coho salmon stocks in British Columbia differ in egg size, embryonic survival, development time, and alevin and fry size. These differences are adaptations to stock-specific environmental conditions, and genetic mechanisms have evolved through natural selection to stabilize these life-history characteristics to assure maximum fry survival. The unique characteristics of each stock emphasizes the need for management stategies to ensure that, before transplants occur, donor stocks are well matched to the proposed environment.

Acknowledgements

Gary Birch, Bryon Grove, Dave Peacock, and Marvin Rosenau helped with the egg collections in 1976–1979. Funding in 1976–1979 was supplied by a Natural Sciences and Engineering Research Council of Canada grant (A3451) to J.D.M. Sharon Bader and Sarah Lotz weighed and measured the coho salmon eggs, alevins, and fry examined in 1986. Special thanks are due to Wally Barner for maintaining the incubation laboratory and assisting in egg collections in 1986 and for his assistance in data analysis. We are deeply indebted to the managers and staff of the Pallant, Kitimat, Bella Coola, Spius, Robertson, Capilano, Chehalis and Big Qualicum hatcheries for their assistance.

ALLEN, G. H. 1957. Survival through hatching of eggs from silver salmon (*O. kisutch*). Trans. Am. Fish. Soc. **87**: 207–219.

——— 1958. Notes on the fecundity of silver salmon (*Oncorhynchus kisutch*).Prog. Fish-Cult. **20**: 163–169.

ANONYMOUS. 1977. Water temperatures. British Columbia and Yukon Territory. Environment Canada, Inland Waters Directorate.

ARO, K. V., and SHEPARD, M. P. 1967. Salmon of the North Pacific Ocean. Part IV. Spawning populations of North Pacific salmon. 5. Pacific salmon in Canada. Bull. Int. North Pac. Fish. Comm. **23**: 225–327.

BAMS, R. A., and SIMPSON, K. S. 1977. Substrate incubators workshop—1976. Report on current state-of-the-art. Environ. Can. Fish. Mar. Serv. Tech. Rep. No. 689.

BEACHAM, T. D., and MURRAY, C. B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. **42**: 1755–1765.

——— 1986. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. **43**: 252–262.

——— 1987. Adaptive variation in body size, age, morphology, egg size, and development biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. **44**: 244–261.

BEACHAM, T. D., GOULD, A. P., WITHLER, R. E., MURRAY, C. B., and BARNER, L. W. 1987. Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. **44**: 1772–1713.

BEACHAM, T. D., WITHLER, R. E., MURRAY, C. B., and BARNER, L. W. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. Trans. Am. Fish. Soc. **117**: 109–126.

BRANNON, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H. D. Smith, L. Margolis, and C. C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 120–124.

BURGER, C. V., WILMOT, R. L., and WANGAARD, D. B. 1985. Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Can. J. Fish. Aquat. Sci. **42**: 693–700.

BURNER, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fish. Bull. U.S. Fish Wildl. Serv. **52**: 97–110.

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

FRASER, F. J., STARR, P. J., and FEDORENKO, A. Y. 1982. A review of the chinook and coho salmon of the Fraser River. Can. Tech. Rep. Fish. Aquat. Sci. No. 1126.

FRASER, F. J., PERRY, E. A., and LIGHTLY, D. T. 1983. Big Qualicum River salmon development project. Vol. 1. A biological assessment 1959–1972. Can. Tech. Rep. Fish. Aquat. Sci. No. 1189. pp. 1–198.

GODFREY, H. 1965. Salmon of the North Pacific Ocean. Part IX. Coho, chinook and masou salmon in offshore waters. 1. Coho salmon in offshore waters. Bull. Int. North Pac. Fish. Comm. **16**: 1–39.

GODIN, J.-G. J. 1980. Temporal aspects of juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum) emergence from simulated gravel redd. Can. J. Zool. **58**: 735–744.

——— 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, Seattle, June 3–5. 1981. *Edited by* E. L. Brannon and E. O. Salo. School of Fisheries, University of Washington, Seattle, WA. pp. 22–50.

HELLE, J. H. 1981. Significance of the stock concept in artificial propagation of salmonids in Alaska. Can. J. Fish. Aquat. Sci. **38**: 1665–1671.

KAZAKOV, R. V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. J. Fish. Biol. **19**: 353–360.

LISTER, D. B., and GENOE, H. S. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. **27**: 1215–1224.

MARTIN, J. W. 1959. Stream catalog of eastern section of Ketchikan management district of southeastern Alaska. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 305.

MASON, J. C. 1976. Some features of coho salmon, *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes in photobehavior. Fish. Bull. **74**: 167–175.

MILLER, R. J., and BRANNON, E. L. 1982. The origin and development of life history patterns in Pacific salmonids. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, June 3–5, 1981, Seattle. *Edited by* E. L. Brannon and E. O. Salo. School of Fisheries, University of Washington, Seattle, WA. pp. 296–309.

MURRAY, C. B., and BEACHAM, T. D. 1986. Effect of varying temperature regimes on the development of pink salmon (*Oncorhynchus gorbuscha*) eggs and alevins. Can. J. Zool. **64**: 670–676.

MURRAY, C. B., and MCPHAIL, J. D. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Can. J. Zool. **66**: 266–273.

NEAVE, F. 1943. Diurnal fluctuations in the upstream migration of coho and spring salmon. J. Fish. Res. Board Can. **6**(2): 158–163.

PRAVDIN, I. F. 1940. A review of investigations of the far-eastern salmon. Izvestiia TINRO 28: 5–105. Fish. Res. Board Can. Transl. Ser. No. 371.

RICKER, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, Seattle, April 8, 1970. *Edited by* R. C. Simon and P. A. Larkin. University of British Columbia, Vancouver, B.C. pp. 27–160.

ROSENAU, M. L., and MCPHAIL, J. D. 1987. Inherited differences in agonistic behavior between two populations of coho salmon. Trans. Am. Fish. Soc. **116**: 646–654.

RUGH, R. 1952. Experimental embryology. Burgess Publishing Company, Minneapolis, MN.

SATTERTHWAITE, F. E. 1946. An approximate distribution of estimates of variance components. Biom. Bull. **2**: 110–114.

SHAPOVALOV, L., and BERRIAN, W. 1940. An experiment in hatching silver salmon (*O. Kisutch*) eggs in gravel. Trans. Am. Fish. Soc. **69**: 135–140.

SHAPOVALOV, L., and TAFT, A. C. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Fish Game Bull. No. 98.

SHAW, P. A., and MAGH, J. A. 1943. The effect of mining silt on the yield of fry from salmon spawning beds. Calif. Fish Game, **29**: 29–41.

SHERIDAN, W. L. 1962. Relation of stream temperatures to timing of pink salmon escapements in southeastern Alaska. *In* Symposium on Pink Salmon. H. R. MacMillan Lectures in Fisheries, Vancouver, October 13–15, 1960. *Edited by* N. J. Wilimovsky. University of British Columbia, Vancouver, B.C. pp. 87–102.

SMIRNOV, A. I. 1975. The biology, reproduction, and development of the Pacific salmon. Izdatel'stuo Moskovskogo Universiteta, Moskow. Can. Fish. Mar. Serv. Transl. Ser. No. 3861.

SUMNER, F. H. 1953. Migrations of salmonids in Sand Creek, Oregon. Trans. Am. Fish. Soc. **82**: 139–150.

TANG, J., BRYANT, M. D., and BRANNON, E. L. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Prog. Fish-Cult. **49**: 167–174.

WALLACE, J. C., and AASJORD, D. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). J. Fish. Biol. **24**: 427–435.

WARNER, B. G., MATHEWES, R. F., and CLAQUE, J. J. 1982. Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of the late Wisconsin glaciation. Science (Washington, D.C.), **218**: 675–677.

WITHLER, F. C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. No. 1079.