Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins

C. B. MURRAY AND J. D. MCPHAIL[1]

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

Received March 6, 1987

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.

Embryo and alevin survival, time to hatching and emergence, and alevin and fry size of five species of Pacific salmon (*Oncorhynchus*) were observed at five incubation temperatures (2, 5, 8, 11, and 14°C). No pink (*Oncorhynchus gorbuscha*) or chum (*O. keta*) salmon embryos survived to hatching at 2°C. Coho (*O. kisutch*) and sockeye (*O. nerka*) salmon had higher embryo survival at 2°C than chinook (*O. tschawytscha*) salmon. At 14°C, chum, pink, and chinook salmon had higher embryo survival than coho or sockeye salmon. In all species, peaks of embryo mortality occurred at specific developmental stages (completion of epiboly, eye pigmentation, and hatching). Alevin survival to emergence was high for all species, except for coho and pink salmon at 14°C. Hatching and emergence time varied inversely with incubation temperature, but coho salmon hatched and emerged sooner at all temperatures than the other species. Coho and sockeye salmon alevins were larger at 2°C, pink, chum, and chinook salmon alevins were larger at 5 and 8°C. Coho salmon fry were larger at 2°C, chinook and chum salmon fry were larger at 5°C, and sockeye and pink salmon fry were larger at 8°C. High incubation temperatures reduced fry size in all species. Each species of Pacific salmon appears to be adapted to different spawning times and temperatures, and thus indirectly to specific incubation temperatures, to ensure maximum survival and size and to maintain emergence at the most favorable time each year.

MURRAY, C. B., et 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.

La survie des embryons et des alevins, le temps nécessaire à l'éclosion et à l'émergence, ainsi que la taille des larves (alevins vésicules) et des alevins ont été mesurés chez cinq espèces de saumons du Pacifique (*Oncorhynchus*) gardés à cinq températures différentes d'incubation (2, 5, 8, 11 et 14°C). Aucun des embryons de Saumon rose (*Oncorhynchus gorbuscha*) ou de Saumon keta (*O. keta*) n'a survécu jusqu'à l'éclosion à 2°C. À cette température, les embryons du Saumon argenté (*O. kisutch*) et du Saumon nerka (*O. nerka*) avaient un meilleur taux de survie que ceux du Saumon chinook (*O. tschawytscha*). À 14°C, les embryons des saumons keta, rose et chinook ont survécu mieux que ceux des saumons argenté et nerka. Chez toutes les espèces, la mortalité embryonnaire était maximale à des stades spécifiques du développement (fin de l'épibolie, pigmentation de l'oeil et éclosion). La survie des larves était élevée chez toutes les espèces, sauf chez le Saumon argenté et le Saumon rose à 14°C. Les temps nécessaires pour atteindre l'éclosion et l'émergence étaient inversement proportionnels à la température d'incubation et ce sont les Saumons argentés qui sont parvenus le plus rapidement à l'éclosion et à l'émergence, à toutes les températures. Les larves des saumons argenté et nerka ont atteint leur taille maximale à 2°C, et celles des saumons keta, rose et chinook, à 5 et à 8°C. Les alevins du Saumon argenté étaient plus grands à 2°C, ceux des saumons chinook et keta à 5°C, ceux des saumons nerka et rose à 8°C. Les températures élevées diminuaient la taille des alevins chez toutes les espèces. Chacune des espèces semble adaptée à des périodes particulières de fraye et à des températures spécifiques et, conséquemment, à des températures déterminées d'incubation; cela leur assure une survie maximale et restreint l'émergence à la période la plus favorable chaque année.

[Traduit par la revue]

Introduction

Temperature is one of the primary physical factors influencing the life history traits of Pacific salmon (*Oncorhynchus*) (Brett 1956, 1969; Smirnov 1975). It affects the time of migration in adults and thus the time of spawning (Killick 1955; Andrew and Geen 1960; Burger *et al.* 1985). In turn, the time of spawning influences the incubation temperature regime, and incubation temperatures influence survival rates (Brannon 1965; Bams 1967, 1969; Fowler 1972), development rates (Embody 1934; Alderdice and Velsen 1978), and growth (Gray 1928; Hamor and Garside 1977; Heming 1982) of embryos and alevins.

Temperature is clearly an important environmental factor for Pacific salmon, and its influence on survival, development time, and size of alevins and fry have been studied in individual species (Smirnov 1975; Heming 1982; Beacham and Murray 1986*a*, 1986*b*). There are, however, no data that allow interspecific comparisons for all five North American species of *Oncorhynchus* reared under similar conditions over a wide temperature range. Our study provides such a data set by comparing embryo and alevin survival, development time to hatching and emergence, and alevin and fry size in five *Oncorhynchus* species reared at a series of controlled temperatures.

Material and methods

Coho salmon (*Oncorhynchus kisutch*) were obtained from Rosewall Creek (49°27′ N, 124°46′ W) and held until mature at the Biological Sciences Branch, West Vancouver Laboratory. The eggs from a single female were fertilized at 9.0°C with milt from a single male. Chinook salmon (*Oncorhynchus tshawytscha*) eggs were taken from several Babine River (55°21′ N, 126°41′ W) females and fertilized at 14.0°C with milt from several males. Pink salmon (*Oncorhynchus gorbuscha*) eggs were collected from a single female from the Chilliwack River (49°06′ N, 121°29′ W) and fertilized at 12.0°C with milt from a single male. Sockeye salmon (*Oncorhynchus nerka*) and chum salmon (*Oncorhynchus keta*) eggs from single females were taken at Weaver Creek (49°20′ N, 121°53′ W) and fertilized at 11.0°C with milt from single males of each species.

[1]Present address: Department of Zoology, 6270 University Boulevard, 2204 Main Mall, University of British Columbia, Vancouver, B.C., Canada V6T 2A9.

Printed in Canada / Imprimé au Canada

All eggs were fertilized on site, water hardened for 1 h, and then transported to the laboratory in an insulated ice chest containing ice. Transit time was less than 12 h. In the laboratory, eggs were divided into five equal lots, adjusted to the appropriate incubation temperature over a 4-h period, and then reared at each of five controlled temperatures (2.0, 5.0, 8.0, 11.0, and 14.0°C).

The incubation system consisted of a water-filled refrigeration unit operating at 1.0°C and containing a coil that cooled dechlorinated water to 2.0°C. Initially, this system supplied chilled water to the 2, 5, and 8°C baths, while the 11 and 14°C baths received water directly from the main water supply. Temperature control was maintained by heating each temperature bath to the desired temperature. However, maintaining 2.0°C during a test period was difficult, so the 2°C bath was placed directly into the water-filled refrigeration unit. The incubation units in each temperature bath were 0.7-L wide-mouth jars with lift pipes embedded in 8.0 cm of peagravel and fitted with screen lids to retain the alevins after hatching and to exclude foreign material. Aerated water circulated from the temperature bath through each incubation unit at 29.9 ± 0.85 L/h (±1 SD), equivalent to an apparent velocity of 534 cm/h. Oxygen levels were determined on a regular basis, and were always greater than 85% air saturation. These conditions were well within the recommended ranges for the incubation of salmon embryos and alevins (Bams and Simpson 1977). Water temperatures were recorded daily, and the mean temperatures throughout the study were 2.3 ± 0.97, 5.1 ± 0.78, 8.1 ± 0.85, 11.2 ± 0.98, and 13.9 ± 0.94°C (±1 SD). All incubators were kept in darkness except for a brief examination period each day.

The incubators were checked daily, and dead eggs were removed except during epiboly (Johnson *et al.* 1983) and preserved in Stockard's solution (Rugh 1952). Hatching was used to distinguish between embryos and alevins, and emergence was used to distinguish between alevins and fry (Velsen 1980). During hatching, alevins were removed and counted into a new incubation unit on a daily basis. The time of hatching was taken as the time when 50% of the eggs were hatched. Within 1 d of 50% hatching we removed, anesthetized, and preserved in 10% formalin a sample of 15 alevins, except for chinook salmon at 2°C, where survival was low and all the alevins were allowed to develop through to emergence. Emergence timing of the fry was investigated using fry emergence traps modified from Mason (1976). Each emergence trap received water from the appropriate temperature bath. At 75% yolk absorption (stage 35, Vernier 1969), the alevins were transferred to the dark compartment of the emergence trap. An alevin emerged when it left the dark compartment by swimming under a baffle, crossed the adjacent light compartment (12 h light each day), and swam over a second baffle into the second light compartment. Newly emerged fry were photopositive and neutrally buoyant (Bams 1969). Each day the newly emerged fry were removed from the trap and counted. Within 1 d of 50% emergence a sample of 15 fry was removed, anesthetized, and preserved in 10% formalin.

The samples were preserved for at least 90 d to ensure that increases in weight (9−14%) and decreases in length (3−5%) had ceased (Murray 1980; Heming and Preston 1981). The samples were measured to the nearest 0.1 mm with Vernier calipers. Alevin and fry length was measured from the tip of the snout to the end of the hypural plate, which corresponds to standard length in adults (Hubbs and Lagler 1958). Weights were taken by blotting the sample dry and weighing to the nearest 1.0 mg. All dead eggs were inspected to determine which were fertilized, or to determine the stage of development (Vernier 1969) within a period of development (e.g., fertilization to epiboly) at which mortality had occurred.

Survival was calculated as the percentage of fertilized eggs or alevins that survived from one development period to the next. Heterogeneity of embryo and alevin survival rates both among and within species and temperatures were compared using the likelihood ratio (G-test) (Sokal and Rohlf 1981). An approximate F-ratio (G-statistic/degrees of freedom) was used to test the relative magnitude of the sources of variation. The 50% hatching and emergence times were calculated using the method of Colby and Brooke (1969).

Differences in alevin and fry standard length (SL) or wet weight (WWT) at 50% hatching and emergence among species and temperatures were analyzed using a random effects analysis of variance model:

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

where Y = length, weight, or days to 50% hatching or 50% emergence; μ = overall mean length, weight, or days to 50% hatching or 50% emergence for all species and temperatures combined; S_i = the effect of species ($i = 1-5$); T_j = the effect of temperature ($j = 1-5$); ST_{ij} = species−temperature interaction ($i = 1-5, j = 1-5$); e_{ijk} = error term for kth observation in subgroup ij.

Time to 50% hatching or 50% emergence was examined with a similar model without the interaction term. The effect of temperature on variation in alevin and fry length or weight within a species was analyzed with a one-way analysis of variance model. The predicted means were tested with Duncan's multiple range test.

Results

Survival

Coho and chinook salmon embryo survival from fertilization to hatching was high at 5, 8, and 11°C but declined sharply at 14 and 2°C (Table 1). In coho salmon, embryo survival was higher at 2°C than at 14°C, but in chinook salmon, embryo survival was higher at 14°C than at 2°C. In both species, alevin survival from hatching to emergence was high, except for a decline in coho salmon alevin survival at 14°C.

Embryo survival in sockeye salmon was highest at 8°C and declined towards both temperature extremes. This decline, however, was not uniform, and sockeye salmon embryo survival was higher at 2°C than at 14°C. Alevin survival in sockeye salmon was high at all temperatures, but again there was a slight tendency towards reduced alevin survival at both temperature extremes.

Embryo survival was higher in chum salmon at 11°C and higher in pink salmon at 8°C than at 5 or 11°C. For both species, no embryos survived to hatch at 2°C. Pink and chum salmon alevin survival was high at all temperatures except 14°C, where there was a slight decline in chum salmon and a sharp decline in pink salmon alevin survival.

The patterns of embryo survival differed among the species and suggest specific temperature adaptations (Fig. 1). Coho salmon embryos suffered low mortality and sockeye and chinook salmon embryos higher mortality from fertilization to epiboly when incubated at 2°C. In contrast, pink and chum salmon embryos incubated at 2°C suffered almost total mortality during this period of development. This suggests an inability of pink and chum salmon embryos to tolerate low incubation temperatures immediately after fertilization. The mortality peaks from epiboly to eye pigmentation and eye pigmentation to hatch in all species were associated with higher rearing temperatures. Mortality from eye pigmentation to hatch at 14°C was particularly high in chinook, coho, and chum salmon, and severe in sockeye salmon.

We compared the variation in embryo and alevin survival among species with the variation among temperatures. Variability in survival of embryos and alevins among temperatures was greater than among species (Table 2). Variability in embryo survival within temperatures and among species was lowest at 8°C, and the variability in embryo survival increased towards 2 and 14°C. Embryos incubated at 8°C had higher survival for all species than those incubated at the other temperatures. The increase in variability of embryo survival at 2 and 14°C was largely the result of complete mortality of pink and chum salmon embryos at 2°C and the reduced survival of chinook, coho, and sockeye salmon embryos at 14°C. Within

TABLE 1. Survival and development times for five species of *Oncorhynchus* incubated at controlled water temperatures

	Temperature (°C)	N^a	Survival (%)			Development time (d)	
			Fertilization to hatch	Hatch to emergence	Fertilization to emergence	Fertilization to 50% hatch	Fertilization to 50% emergence
Coho	14.0	447	0.17	0.64	0.11	31.5	61.2
	11.0	391	0.84	0.86	0.72	42.0	73.7
	8.0	458	0.86	0.93	0.80	62.7	109.1
	5.0	394	0.85	0.96	0.82	86.9	138.5
	2.0	433	0.62	0.90	0.56	114.7	228.0
Chinook	14.0	229	0.48	0.97	0.46	38.4	63.0
	11.0	248	0.90	0.96	0.87	46.9	84.0
	8.0	243	0.94	0.95	0.90	67.1	115.0
	5.0	240	0.83	1.00	0.83	101.5	191.0
	2.0	231	0.14	1.00	0.14	202.0	316.0
Sockeye	14.0	430	0.10	0.80	0.08	47.0	72.0
	11.0	366	0.40	1.00	0.40	51.8	90.3
	8.0	381	0.79	1.00	0.79	76.9	120.5
	5.0	392	0.40	1.00	0.40	119.5	173.0
	2.0	462	0.40	0.94	0.38	206.4	282.2
Chum	14.0	474	0.64	0.78	0.50	46.2	86.0
	11.0	479	0.70	0.84	0.59	52.4	98.0
	8.0	460	0.67	1.00	0.67	66.6	124.2
	5.0	446	0.58	0.95	0.55	96.6	160.7
	2.0	507	0.00	0.00	0.00	—	—
Pink	14.0	229	0.52	0.42	0.22	39.8	72.1
	11.0	219	0.96	0.88	0.84	47.2	90.8
	8.0	203	0.97	1.00	0.97	72.2	120.2
	5.0	211	0.94	1.00	0.94	99.0	173.2
	2.0	272	0.00	0.00	0.00	—	—

[a]Number of fertilized eggs.

species among temperatures, pink and chum salmon had the greatest variability in embryo survival. Again, this was largely the result of the complete mortality of pink and chum salmon embryos at 2°C. High and low incubation temperatures had a greater effect on embryo survival than intermediate temperatures.

Differences in alevin survival were less than those for embryo survival (Table 2). Variability in alevin survival within temperatures among species was greater at 14 than at 2°C. This was the result of higher mortality of alevins among species after hatching at 14 than at 2°C. Within species among temperatures, pink and chum salmon had the greatest and chinook salmon the least variability in alevin survival. Continued mortality of pink and chum salmon alevins after hatching at 11 and 14°C increased the variability in survival, whereas very few chinook salmon alevins died after hatching. High incubation temperatures reduced alevin survival compared with intermediate and low temperatures.

Development time

Days to 50% hatching and 50% emergence for all five species of Pacific salmon embryos and alevins varied inversely with mean incubation temperature (Table 1). All alevins and fry hatched or emerged at similar morphological stages of development. There were significant differences in the time from fertilization to 50% hatching among temperatures (F = 41.01; df = 4,22; $P < 0.01$) and among species (F = 5.38; $P < 0.01$). Coho salmon eggs hatched sooner at all temperatures than the other species. Sockeye salmon eggs hatched later at 2, 5, and 8°C than the other species. Emergence timing of fry was dependent upon temperature (F = 96.99; $P < 0.01$) and species (F = 6.17; $P < 0.01$). Coho salmon alevins maintained a rapid rate of development and coho fry emerged sooner at all temperatures than the other species. Pink salmon alevins required the longest time to reach 50% emergence at 8, 11, and 14°C, while chinook salmon alevins required the longest time to reach 50% emergence at 2 and 5°C.

Alevin and fry size

Alevin length and weight at hatching were variable among temperatures within a species (Table 3). Maximum alevin length occurred in coho (F = 254.06; df = 4,70; $P < 0.01$) and sockeye salmon (F = 108.62; $P < 0.01$) at 2°C, in pink salmon (F = 42.80; df = 3,56; $P < 0.01$) at 5°C, and in chum (F = 72.33; $P < 0.01$) and chinook salmon (F = 26.40; $P < 0.01$) at 8°C. Alevins were heaviest in coho salmon (F = 64.65; $P < 0.01$) at 2 and 8°C, sockeye salmon (F = 79.69; $P < 0.01$) at 5°C, and chinook salmon (F = 43.43; $P < 0.01$) at 5 and 8°C. The alevins of these species were lightest at 14°C. Pink salmon alevins were of similar weights at 8, 11, and 14°C, but significantly lighter at 5°C (F = 5.77; $P < 0.01$). Chum salmon alevins were of similar weights at all temperatures (F = 2.19; $P > 0.05$).

As with alevin size, species may show different trends in fry size with respect to incubation temperature (Table 3). Maximum fry length occurred in coho salmon (F = 140.32; df = 4,70; $P < 0.01$) at 2°C, in chinook (F = 72.12; $P < 0.01$) and chum salmon (F = 42.15; df = 3,56; $P < 0.01$) at 5°C, and in sockeye (F = 49.52; df = 4,70; $P < 0.01$) and pink salmon (F = 38.16; df = 3,56; $P < 0.01$) at 8°C. In all species, minimum fry length occurred at 14°C. Coho (F = 559.28; $P < 0.01$) and sockeye salmon (F = 244.05; $P < 0.01$) fry were heaviest at 2°C and chinook (F = 187.80; $P < 0.01$), chum (F = 1142.53; $P < 0.01$), and pink salmon (F =

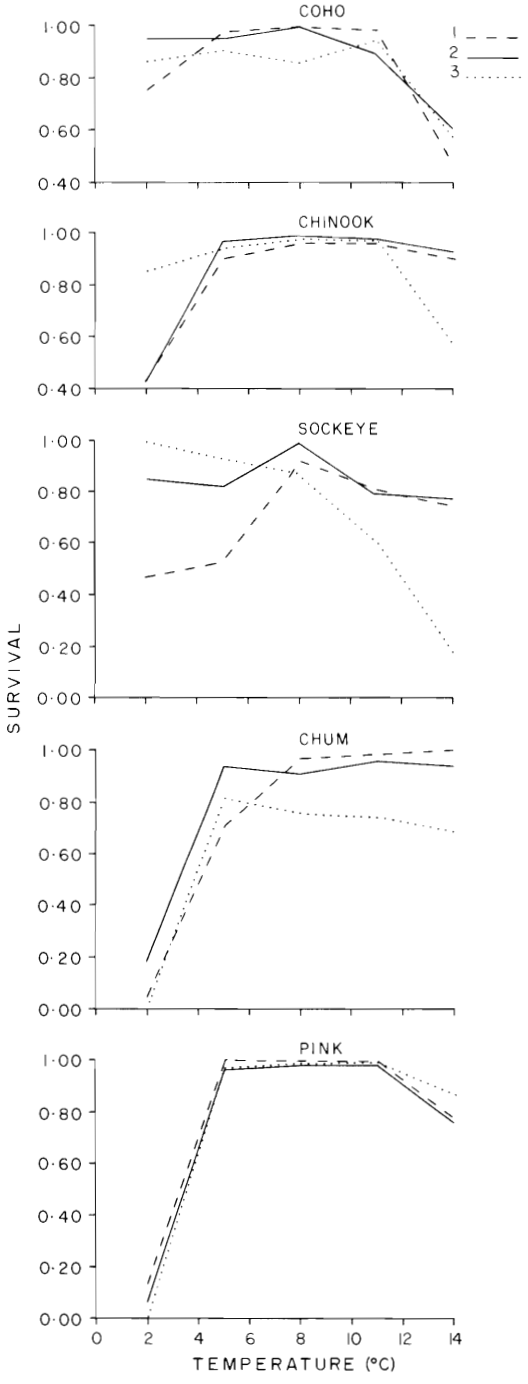

FIG. 1. Survival for five species of *Oncorhynchus* incubated at controlled water temperatures. Periods of development are (1) fertilization to epiboly, (2) epiboly to eye pigmentation, and (3) eye pigmentation to hatch. The number of fertilized eggs for each species and temperature can be found in Table 1.

172.18; $P < 0.01$) fry were heaviest at 5°C. Coho, sockeye, chum, and pink salmon fry were lightest at 14°C, while chinook salmon fry were lightest at 2°C.

Discussion

Two aspects of salmon reproduction fundamental to survival are incubation conditions (O_2, water velocity, substrate, and density) and the size of fry at emergence (Bams 1972). Generally, salmon are thought to migrate and spawn at a time of year that, under average conditions, provides an incubation environment suitable for successful embryonic development (Killich 1955; Andrew and Geen 1960; Foerster 1968). Salmon spawning times are at least partially dependent on water temperature (Sheridan 1962; Brannon 1984; Burger *et al.* 1985), and spawning will be interrupted if temperatures exceed a certain level (Smirnov 1975). The duration of the incubation period is controlled by temperature (Alderdice and Velsen 1978), and there is evidently strong selective pressure (Ricker 1972; Miller and Brannon 1982) to ensure that emergence occurs at the most favorable time each spring (Godin 1982). Fry size at emergence is also affected by incubation temperature (Gray 1928; Peterson *et al.* 1977; Heming 1982), and in turn fry size influences swimming performance (Bams 1967), vulnerability to predators (Mead and Woodall 1968), and growth (Fowler 1972), and thus the probability of survival.

Many investigators have studied the high and low threshold temperatures for the normal development of Pacific salmon embryos and alevins. Incubation of coho salmon embryos at ambient temperatures above 12°C increased mortality (Shapovalov and Berrian 1940; Shaw and Magh 1943; Allen 1957). In our study, coho salmon embryos suffered increased mortality above 11°C. Chinook salmon embryos reared at 1.1 and 1.7°C or above 15°C did not survive (Combs and Burrows 1957; Heming 1982; Garling and Masterson 1985). Our results are consistent; we found poor survival at 2°C and only moderate survival at 14°C. Incubation of sockeye salmon embryos at ambient temperatures with initial incubation between 5.1 and 15.6°C (Andrew and Geen 1960; Mead and Woodall 1968; Withler and Morley 1970) and at constant temperatures between 4.4 and 12.8°C resulted in high survival, but below 4.4°C survival was low (Combs 1965). Combs concluded that sockeye salmon embryos were apparently more tolerant of low temperatures and less resistant to high temperatures than chinook salmon embryos. We also observed similar results to those of Combs (1965) for sockeye and chinook salmon embryos. Pink salmon embryos initially incubated below 4.5°C had high mortality, with no survival at 2.0°C (Bailey and Evans 1971). Kwain (1982) found that survival to hatching for freshwater pink salmon embryos from the Great Lakes varied from 13 to 27%, and that 15°C was near the upper limit for successful incubation. Beacham and Murray (1986*a*, 1986*b*) reported that pink and chum salmon survival rates were higher at 8°C than at 4 or 12°C, and that survival rates among stocks and families of pink and chum salmon surveyed could be extremely variable (14–100%), particularly at 4°C. We observed complete mortality of pink and chum salmon embryos at 2°C, and higher survival in chum salmon than in pink salmon at 14°C.

Our survival results are similar, in general, to those of other researchers, except that our sockeye salmon data show only moderate survivals at 8°C, and our chum salmon data show only moderate survivals at temperatures from 5 to 14°C, and survivals at 8°C were lower than expected when compared with those of the other species at 8°C. We attribute this reduced survival in both species to the use of single families and the possibility of extreme variability in survival among families (Kanis et al. 1976; Beacham and Murray 1986*a*, 1986*b*), rather than to other incubation factors (O_2, velocity, substrate, light) that were common to all the species.

We conclude from our results and those of other researchers that except for coho salmon, 2°C is clearly at, or close to, the

TABLE 2. Likelihood ratio (G-test) of heterogeneity of survival of embryos from fertilization to hatch and of alevins from hatch to emergence for five species of Pacific salmon in British Columbia

		Fertilization to hatch		Hatch to emergence	
	df	G	Standardized statistic	G	Standardized statistic
Among species	4	378.19	94.55	129.11	32.28
Among temperatures	4	1868.70	467.18	361.89	90.47
Within temperatures, among species	20	1983.81	99.19	272.24	13.61
14.0°C	4	415.19		100.72	
11.0°C	4	330.30		63.72	
8.0°C	4	145.24		66.54	
5.0°C	4	316.45		33.67	
2.0°C	4	776.63		7.55	
Within species, among temperatures	20	3474.37	173.72	504.76	25.24
Coho	4	690.42		62.90	
Chinook	4	523.78		15.18	
Sockeye	4	424.89		60.27	
Chum	4	889.20		122.33	
Pink	4	946.08		244.08	
Total	24	3852.57		633.87	

NOTE: All cases $P < 0.05$.

lower limit for normal development. Likewise, 14°C is at, or near, the upper limit for normal development of all the species except chum salmon.

Data on hatching times for individual species of Pacific salmon are available from many sources, covering wide geographic areas, incorporating many stocks, and including both ambient and controlled temperature regimes (Foerster 1968; Smirnov 1975; Alderdice and Velsen 1978; Murray 1980; Heming 1982; Kwain 1982; Beacham and Murray 1985, 1986*a*, 1986*b*). However, comparisons of these hatching times with our data indicate that hatching times within a species can be very similar. The greatest differences in development time to hatching occur at lower incubation temperatures and between ambient and controlled temperature regimes. Alderdice and Velsen (1978) concluded that early imposition of low, constant incubation temperatures slowed the development rate of chinook salmon below the rates occurring at ambient temperatures with the same mean values. Beacham and Murray (1986*a*, 1986*b*) found very little variation within species' hatching times at the same incubation temperatures for 32 families from seven stocks of chum salmon and for 27 families from five stocks of pink salmon. These results suggest that at any given temperature, hatching times can be highly conservative within a species.

There are only a few published studies that compare the rate of development to hatching for different species of Pacific salmon incubated under similar conditions. Ievleva (1951) concluded that the development time to hatching increased progressively in coho, chum, pink, and sockeye salmon. Withler and Morley (1970) also found the same order of hatching for chum, pink, and sockeye salmon. Smirnov (1975) reports that the order of hatching was coho, chum, chinook, pink, and sockeye salmon. Our data indicate a similar pattern for development time to hatching. Coho salmon have the fastest and sockeye salmon the slowest development time to hatching.

Comparisons of emergence times can be very difficult because the time required for alevins to reach maximum alevin weight and to emerge can be affected by initial egg weight (Smith 1958; Beacham *et al.* 1985; Rombough 1985). Differences in egg size may explain why development times from fertilization to emergence for chinook salmon in our study were slower than those reported for Campbell River chinook salmon (Heming 1982) and faster than those reported for Big Qualicum River chinook salmon (Rombough 1985). Beacham and Murray (1985) also found that egg size had a considerable effect on the emergence time of chum salmon fry. The period of incubation from fertilization to emergence was longer for alevins from larger eggs than for alevins from smaller eggs, because there was more yolk to be absorbed at the same incubation temperature. They concluded that variations in egg size and spawning time within a species appear to be a mechanism by which fry emergence timing is regulated, as later-spawning chum salmon tend to have smaller eggs than those spawning earlier.

There are no published studies that compare development time to emergence for the different species of Pacific salmon incubated under similar conditions. Our data indicate that coho salmon maintain a rapid rate of development, and emerge sooner at all temperatures than the other species. Coho salmon also spawn later and at lower temperatures than the other species, and this suggests that the rapid rate of development in coho salmon is a mechanism for maintaining fry emergence timing similar to that of the other species in the spring (Lister and Genoe 1970; Smirnov 1975; Murray 1980).

Incubation temperatures affect the size of both alevins and fry (Beacham and Murray 1985). Low incubation temperatures produce larger alevins and fry than higher incubation temperatures (Gray 1928; Timoshina 1972; Hamor and Garside 1977; Peterson *et al.* 1977). Our study clearly illustrates that species may show different trends in alevin and fry size with respect to incubation temperature. Coho and sockeye salmon alevins

TABLE 3. The effect of temperature on standard length and wet weight for five species of Pacific salmon at 50% alevin hatching and 50% fry emergence

(A) Alevins

Temperature (°C)	Coho	Chinook	Sockeye	Chum	Pink
14.0					
SL	15.3 (0.16)	18.7 (0.24)	15.1 (0.26)	17.2 (0.27)	15.8 (0.33)
WWT	182.0 (6.58)	342.0 (9.62)	104.0 (10.2)	223.5 (9.11)	168.9 (7.08)
11.0					
SL	16.0 (0.23)	18.5 (0.27)	16.1 (0.17)	17.9 (0.47)	16.8 (0.22)
WWT	188.6 (6.07)	350.0 (13.66)	113.0 (9.62)	225.3 (7.59)	168.7 (9.62)
8.0					
SL	17.4 (0.15)	20.1 (0.31)	17.1 (0.23)	19.9 (0.31)	17.5 (0.25)
WWT	200.0 (10.12)	375.0 (10.63)	117.6 (7.59)	229.2 (8.60)	171.4 (6.58)
5.0					
SL	18.4 (0.24)	19.4 (0.27)	17.2 (0.41)	19.5 (0.31)	17.8 (0.25)
WWT	195.6 (9.62)	372.1 (13.16)	120.0 (8.60)	224.3 (9.62)	163.8 (8.10)
2.0					
SL	19.1 (0.15)	—*	17.8 (0.24)	—†	—†
WWT	202.3 (10.12)	—*	117.4 (6.58)	—†	—†

(B) Fry

Temperature (°C)	Coho	Chinook	Sockeye	Chum	Pink
14.0					
SL	23.9 (0.26)	27.3 (0.18)	20.7 (0.37)	30.0 (0.54)	26.0 (0.28)
WWT	231.5 (7.08)	465.0 (11.64)	126.6 (10.63)	307.8 (13.66)	221.6 (9.11)
11.0					
SL	24.9 (0.29)	28.6 (0.30)	22.9 (0.50)	31.0 (0.51)	27.1 (0.25)
WWT	224.2 (6.58)	494.3 (8.60)	154.0 (9.62)	334.4 (10.63)	254.5 (7.08)
8.0					
SL	25.9 (0.23)	28.5 (0.25)	24.4 (0.31)	31.4 (0.62)	28.4 (0.20)
WWT	251.5 (6.58)	491.0 (10.63)	168.9 (8.60)	360.1 (11.64)	266.3 (10.63)
5.0					
SL	27.1 (0.28)	30.7 (0.42)	23.4 (0.39)	32.6 (0.45)	26.8 (0.42)
WWT	270.4 (9.62)	526.7 (15.18)	173.2 (11.13)	442.8 (15.18)	269.7 (9.63)
2.0					
SL	27.9 (0.28)	29.0 (0.42)	23.6 (0.39)	—†	—†
WWT	302.4 (10.12)	440.0 (13.66)	179.2 (8.60)	—†	—†

NOTE: N = 15 for alevins and fry; 95% confidence limits are in parentheses. SL, standard length (mm); WWT, wet weight (mg).
*No sample taken.
†No survival.

were larger at 2°C, pink, and chum and chinook salmon alevins were larger at 5 and 8°C. The smallest alevins for all species were produced at 14°C. The pattern of fry size at emergence differed from that of alevin size at hatching. Coho salmon fry were still larger at 2°C, but chinook and chum salmon fry were now larger at 5°C and sockeye and pink salmon fry were larger at 8°C. As with alevins, high incubation temperatures reduced fry size in all species. Maximum conversion efficiencies of yolk to body tissue for chinook salmon have been reported at 6°C or below (Heming 1982; Rombough 1985). Beacham and Murray (1985, 1986*a*) concluded that the maximum efficiency of conversion for several chum salmon stocks was probably between 6 and 10°C, with certain chum salmon families among stocks having maximum conversions at 4°C. Vancouver Island pink salmon obtained maximum conversion at 12°C, whereas Fraser River pink salmon obtained maximum conversion at 8°C (Beacham and Murray 1986*b*). We suggest that maximum conversion of yolk to tissue is probably near 2°C for coho salmon, between 2 and 5°C for sockeye salmon, and between 5 and 8°C for the other species.

Our study clearly illustrates that there is significant variation among species in embryo and alevin survival, development time, and alevin and fry size. These results suggest that each species is adapted to different spawning times and temperatures, and thus indirectly adapted to specific incubation temperatures, to ensure maximum survival and size and to maintain emergence at the most favorable time each year.

Acknowledgments

This study would not have been possible without the help and cooperation of many individuals and organizations. We express our thanks to Bob Carveth, Marvin Rosenau, Dave Peacock, Ruth Withler, and Darlene Balford for their help, comments, and encouragement. The help of the Department of Fisheries and Oceans, Canada, and the International Pacific Salmon Fisheries Commission in obtaining salmon eggs and

sperm is greatly appreciated. Drs. D. F. Alderdice and T. D. Beacham provided many helpful suggestions to improve the manuscript. This research was supported by Natural Sciences and Engineering Research Council of Canada grant A3451.

ALDERDICE, D. F., and VELSEN, F. P. J. 1978. Relation between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. **35**: 69–75.

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

ANDREW, F. J., and GEEN, G. H. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Int. Pac. Salmon Fish. Comm. Bull. No. 11.

BAILEY, J. E., and EVANS, D. R. 1971. The low-temperature threshold for pink salmon eggs in relation to a proposed hydroelectric installation. Fish. Bull. **69**: 587–593.

BAMS, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. **24**: 1117–1153.

——— 1969. Adaptations in sockeye salmon associated with incubation in stream gravels. *In* Symposium on Salmon and Trout in Streams. H. R. MacMillan Lectures in Fisheries. *Edited by* T. G. Northcote. University of British Columbia, Vancouver. pp. 71–87.

——— 1972. A quantitive evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates natural conditions. J. Fish. Res. Board Can. **29**: 1151–1167.

BAMS, R. A., and SIMPSON, K. S. 1977. Substrate incubators workshop, 1976: Report on current state-of-the-art. 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*a*. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. **43**: 252–262.

——— 1986*b*. Comparative developmental biology of pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia. J. Fish. Biol. **28**: 233–246.

BEACHAM, T. D., WITHLER, F. C., and MORLEY, R. B. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*). Can. J. Zool. **63**: 847–850.

BRANNON, E. L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 12.

——— 1984. Influence of stock of origin on salmon migratory behavior. *In* Mechanisms of migration in fishes. *Edited by* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Meill. Plenum Press, New York. pp. 103–112.

BRETT, J. R. 1956. Some principles in the thermal requirements of fishes. Q. Rev. Biol. **31**: 75–87.

——— 1969. Temperature and fish. Chesapeake Sci. **10**: 275–276.

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.

COLBY, P. J., and BROOKE, L. T. 1969. Survival and development of lake herring (*Coregonus artedii*) eggs at various incubation temperatures. *In* Biology of coregonid fishes. *Edited by* C. C. Lindsey and C. G. Woods. University of Manitoba Press, Winnipeg. pp. 417–428.

COMBS, B. D. 1965. Effects of temperature on the development of salmon eggs. Prog. Fish-Cult. **27**: 134–137.

COMBS, B. D., and BURROWS, R. E. 1957. Threshold temperatures for the normal development of chinook salmon eggs. Prog. Fish-Cult. **19**: 3–6.

EMBODY, G. C. 1934. Relation of temperature to the incubation periods of the eggs of four species of trout. Trans. Am. Fish. Soc. **64**: 281–291.

FOERSTER, R. E. 1968. The sockeye salmon *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. No. 162.

FOWLER, L. G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. Prog. Fish-Cult. **34**: 66–69.

GARLING, D. L., JR., and MASTERSON, M. 1985. Survival of Lake Michigan chinook salmon eggs and fry incubated at three temperatures. Prog. Fish-Cult. **47**: 63–66.

GRAY, J. 1928. The growth of fish. Part III. The effect of temperature on the development of eggs of *Salmo fario*. J. Exp. Biol. **6**: 125–130.

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

HAMOR, T., and GARSIDE, E. T. 1977. Size relations and yolk utilization in embryonated ova and alevins of Atlantic salmon *Salmo salar* L. in various combinations of temperature and dissolved oxygen. Can. J. Zool. **55**: 1892–1898.

HEMING, T. A. 1982. Effects of temperature on utilization of yolk by chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. Can. J. Fish. Aquat. Sci. **39**: 184–190.

HEMING, T. A., and PRESTON, R. P. 1981. Differential effect of formalin preservation on yolk and tissue of young chinook salmon (*Oncorhynchus tshawytscha* Walbaum). Can. J. Zool. **59**: 1608–1611.

HUBBS, C. L., and LAGLER, K. F. 1958. Fishes of the Great Lakes region. Cranbrook Inst. Sci. Bull. No. 26.

IEVLEVA, M. Y. 1951. Morphology and rate of embryonic development of Pacific salmon. *In* Pacific salmon. Selected articles from Soviet periodicals. pp. 236–244. (English translations, Israel Program for Scientific Translation, Jerusalem, 1961.)

JOHNSON, S. C., CHAPMAN, G. A., and STEVENS, D. G. 1983. Sensitivity of steelhead trout embryos to handling. Prog. Fish-Cult. **45**: 103–104.

KANIS, E., REFSTIE, T., and GJEDREM, T. 1976. A genetic analysis of egg, alevin and fry mortality in salmon (*Salmo salar*), sea trout (*Salmo trutta*) and trainbow trout (*Salmo gairdneri*). Aquaculture, **8**: 259–268.

KILLICK, S. R. 1955. The chronological order of Fraser River sockeye salmon during migration, spawning and death. Int. Pac. Salmon Fish. Comm. Bull. No. 7.

KWAIN, W. 1982. Spawning behavior and early life history of pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes. Can. J. Fish Aquat. Sci. **39**: 1354–1360.

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.

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.

MEAD, R. W., and WOODALL, W. L. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels and natural spawning areas. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 20.

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, University of Washington. *Edited by* E. L. Brannon and E. O. Salo. School of Fisheriers, University of Washington, Seattle. pp. 296–309.

MURRAY, C. B. 1980. Some effects of temperature on zygote and alevin survival, rate of development and size at hatching and emergence of Pacific salmon and rainbow trout. M.Sc. thesis, Uni-

versity of British Columbia, Vancouver.

PETERSON, R. H., SPINNEY, H. C. E., and SREEDHARAN, A. 1977. Development of Atlantic salmon (*Salmo salar*) eggs and alevins under varied temperature regimes. J. Fish. Res. Board Can. **34**: 31–43.

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. *Edited by* R. C. Simon and P. A. Larkin. University of British Columbia, Vancouver. pp. 27–160.

ROMBOUGH, P. J. 1985. Initial egg weight, time to maximum alevin wet weight, and optimal ponding times for chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **42**: 287–291.

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

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

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. *Edited by* N. J. Wilimovsky. University of British Columbia, Vancouver. 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.)

SMITH, S. 1958. Yolk utilization in fishes. *In* Embryonic nutrition. *Edited by* D. Rudnick. University of Chicago Press, Chicago, IL. pp. 33–53.

SOKAL, R. R., and ROHLF, F. J. 1981. Biometry. The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Co., San Francisco, CA.

TIMOSHINA, L. A. 1972. Embryonic development of the rainbow trout (*Salmo gairdneri irideus* Gibb.) at different temperatures. J. Ichthyol. (Engl. Transl.), **12**: 425–432.

VELSEN, F. P. J. 1980. Embryonic development in eggs of sockeye salmon, *Oncorhynchus nerka*. Can. Spec. Publ. Fish Aquat. Sci. No. 49.

VERNIER, J.-M. 1969. Chronological table of the embryonic development of rainbow trout. Ann. Embryol. Morphog. **2**: 495–520. (Can. Fish. Mar. Serv. Transl. Ser. No. 3913.)

WITHLER, F. C., and MORLEY, R. B. 1970. Sex related parental influence on early development of Pacific salmon. J. Fish. Res. Board Can. **27**: 2197–2214.