INFLUENCE OF TEMPERATURE ON FRESHWATER FISHES: A LITERATURE REVIEW WITH EMPHASIS ON SPECIES IN ALASKA

By
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Technical Report 91-1

Alaska Department of Fish & Game
Division of Habitat

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ABSTRACT

Small (1-5°C) changes in water temperature may have consequential effects on fish, depending upon the time of year the changes occur, the magnitude and duration of the changes, and the fish species and life stage of the fish affected. Changes in water temperature affect survival at all life stages, rates of egg development and growth, timing of smolting, and mortality rates during overwintering. Increases or decreases in water temperature may influence reproduction by changing the timing of the spawning run; influencing fish to seek other spawning areas, increasing egg mortality and the occurrence of deformed alevins, changing the time for egg development; or causing fish to avoid certain streams or stream reaches. Changes in temperature have been shown to affect the number of eggs that are successfully fertilized when fish are delayed in migrating to spawning areas.

In Alaska, elevations in temperature may be particularly harmful to fishes that are adapted to coldwater conditions and rarely experience significant summer warming. Many of the studies that relate changes in temperature to effects on fish examine higher ranges than are usually experienced by fish in Alaska. Therefore, acceptable upper and lower temperature ranges from published literature are often not applicable to fish naturally occurring at higher latitudes. This report examines much of the published literature on coldwater species of fish that inhabit freshwater. Summaries are given of the effects of changes on temperature on different life stages. The final section of this report presents recommendations for optimal temperatures for various fish life stages.

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INTRODUCTION

Temperature is one of the primary physical factors influencing the life history of coldwater fishes. Increases or decreases in water temperature may change the timing of migration, influence fish to seek other spawning areas, or prompt fish to avoid certain streams or stream reaches. Delayed or advanced migration may change the time of spawning, and thus the available incubation temperature (Graybill et al. 1979). Incubation temperature above or below a suitable range will lengthen or shorten the time for egg development, increase egg mortality, and increase the occurrence of deformed alevins. Changes in water temperature may affect growth, timing for juvenile fish to smolt and migrate to salt water (Jonsson and Ruud-Hansen 1985), and overall survival (Brett 1952, Hokanson et al. 1977).

Stream and lake water temperature may be altered by a number of development activities. Management concerns in Alaska that may result in cooler water include such activities as construction of upstream impoundments and subsequent release of cold hypolimnetic water or placement of liquified gas pipelines beneath rivers. Removal of riparian vegetation may result in warmer water during summer and cooler water in winter. Drawdown may cause rivers to cool faster and freeze earlier in the fall and to warm more in the summer.

This report is a review of literature on effects of temperature changes on coldwater freshwater fish species that occur in Alaska and northwest Canada. Examples from published literature are used to describe effects of altered temperature regimes on growth and development of different fish species and to estimate preferred or optimal temperature.

The discussion uses common names of fish; both common and scientific names of all fishes mentioned in this review and identification of those species that occur in Alaska are presented in Table 1. The distinction between Dolly Varden (*Salvelinus malma*) and Arctic char (*S. alpinus*) has changed since many of the papers cited in this literature review were published; I did not attempt to interpret which species the author was discussing, but reported the fish species as given in a specific paper. In 1989, the American Fisheries Society reclassified rainbow trout from *Salmo gairdnerii* to *Oncorhynchus mykiss*; I used the recent name.

Table 1. Common and scientific names of fish discussed in this review.

Scientific Name	Common Name	Alaska sp.
Catostomus catostomus	longnose sucker	yes
Coregonus clupeaformis	lake whitefish	yes
Coregonus lavaretus	whitefish	European
Esox lucius	northern pike	yes
Gasterosteus aculeatus	3-spined stickleback	yes
Lota lota maculosa	burbot	yes
Oncorhynchus gorbuscha	pink salmon	yes
Oncorhynchus keta	chum salmon	yes
Oncorhynchus kisutch	coho salmon	yes
Oncorhynchus nerka	sockeye salmon	yes
Oncorhynchus tshawytscha	chinook salmon	yes
Oncorhynchus mykiss (formerly *Salmo gairdneri*)	rainbow trout	yes
Osmerus mordax	rainbow smelt	yes
Prosopium cylindraceum	round whitefish	yes
Prosopium williamsoni	mountain whitefish	no
Salmo clarki	cutthroat trout	yes
Salmo salar L.	Atlantic salmon	Eastern US
Salmo trutta	brown trout	no
Salvelinus alpinus	Arctic char	yes
Salvelinus malma	Dolly Varden	yes
Salvelinus namayush	lake trout (lake char)	yes
Salvelinus fontinalis	brook trout	no
Stenodus leucichthys	Inconnu (sheefish)	yes
Thymallus thymallus	grayling	European
Thymallus arcticus	Arctic grayling	yes
Thaleichthys pacificus	euchalon	yes

TEMPERATURE PREFERENCES OF COLDWATER FISHES

Although freshwater fish occur in habitats that range from below 0°C to 44°C, no species can survive over this entire range. Each species and each life stage within a species has an optimal temperature range with upper and lower lethal limits. Freshwater fish in temperate regions usually live within the range of 0° to 30°C.

Under natural conditions, fish may experience large diurnal temperature changes. For example, rearing sockeye salmon fry may migrate to warm lake surface waters at dusk to feed (where temperature reported in one study by Brett (1971) was about 17°C), then migrate to cooler hypolimnetic waters at daylight (5°C in Brett's study). Within a natural stream environment, diel fluctuations may be as great as 12°C (Hokanson et al. 1977). Sub-optimal thermal conditions for fish occur when water is too warm or too cool for a specific age, size, or life function or if no alternate habitat is available for the fish to retreat.

The "optimum temperature range" is the range over which feeding occurs and no external signs of abnormal behavior exist (i.e., thermal stress is not obvious) (Elliott 1981). The "preferred temperature" is the average temperature fish most frequently seek when they move freely in a temperature gradient. Variability in the ranges of optimal or preferred temperature reported by different researchers may be due to differences in acclimation, age, size, genetic strain, and physiological conditions of the fish (Brett 1971, McCauley and Tait 1971), food availability (Mac 1985), and to local environmental adaptations. A "critical temperature range" is the range over which a fish shows definite signs of thermal stress (Elliott 1981, Wedemeyer and McLeay 1981).

Elliott (1981) described the stress response of fish to increased temperature as three progressive phases. The first external signs of stress are reluctance to feed, sudden bursts of activity with disrupted navigation (e.g., frequent collisions with the side of the laboratory tank), rolling and pitching, defecation, and rapid ventilatory movements. In the second phase, the fish becomes quiet with short bursts of weak swimming, often floats on its side or back, may rapidly change color, and increases ventilatory movements. Elliott (1981) found that fish transferred to cooler, well-oxygenated water rapidly recover from the first two phases. In the third phase, fish cease all movement, except for limited movement of the opercula, pectoral fins, and eyes, then die.

Short-term, sublethal exposure to elevated temperature may have detrimental effects on fish by increasing their vulnerability to predation. Coutant (1973) found that young rainbow trout and chinook salmon lost equilibrium and were unable to swim upright after exposure to elevated temperature (in the range of 25°C+). When returned to cool water, the fish continued to exhibit disorientation and erratic bursts of swimming. Thermally stressed fish were more susceptible to predation than were control fish. Coutant (1973) documented similar effects in natural conditions: juvenile prey fish that passed through thermal plumes were consumed by predators at higher rates than juvenile fish swimming around thermal plumes.

Temperature also may influence a fish's ability to adjust to changes in salinity, especially by larval fish. deMarch (1989) reported broad whitefish larvae tolerated stressful salinities (>15 $^{o}/oo$) at 15°C more easily than at 10° or 5°C. Mortality was greatest in fish exposed to increased salinity at 10°C.

Decreases in stream water temperature also can be harmful. A rapid decrease in temperature over a sufficiently large range can cause mortality from "cold-shock" (Ash et al. 1974). Cold-shocked fish usually show loss of equilibrium, fanning of the gill opercula (Brett 1952), and inactivity. Cold-shocked fish either die within a few seconds after exposure to coldwater (primary chill coma), or die after the cold has penetrated internally to the central nervous system (secondary chill coma). This second effect can occur within minutes or in several days. Because of their limited body mass, smaller fish appear to be more susceptible to primary chill coma (Brett 1952).

Ash et al. (1974) reported mortality in adult northern pike resulting from cold shock. These fish were acclimated to 21.8°C in a thermal discharge channel. When the heated effluent was shut off, the water temperature dropped to 4.9°C and the fish died. Although northern pike died when water temperature dropped to 4.9°C, this temperature is not necessarily the lower lethal limit. Casselman (1978) reported that subadult northern pike survived in water of 0.1°C when acclimated to cold water and when cooling occurred slowly with seasonal freezeup.

Brett (1952) found that the lower lethal temperature for a given species of fish was strongly dependent on the acclimation temperature of the fish. For example, chinook, coho, sockeye, and chum salmon fry acclimated to 23°C underwent cold shock and experienced at least 50% mortality when exposed to 7.4°, 6.4°, 6.7°, and 7.3°C, respectively. Fish acclimated to 10°C died when suddenly exposed to 2° or 3°C water.

Neither coho nor sockeye salmon fry could survive 0°C, even after being acclimated to 5°C.

The temperature preferred by a given fish species may be affected by time of year (Sullivan and Fisher 1953), age, and spawning condition (Ihnat and Bulkley 1984). Mountain whitefish selected warmer water in the spring when photoperiod lengthened, regardless of whether acclimation temperatures were increasing, decreasing, or constant. This could be due to "anticipation of greater food intake associated with rising spring temperature after a long period of reduced feeding . . . [and] changing photoperiod" (Ihnat and Bulkley 1984).

The effects of acclimation in influencing the fish's preferred temperature appears to be short-term. After 2-3 days, mountain whitefish seek a temperature that is independent of the prior acclimation temperature (Ihnat and Bulkley 1984). The authors concluded that acute temperature preferences of fish should not be based on data from any one time of year. Observations of preferred temperature should be made during all seasons so that periods of fasting, rapid growth, and different stages of sexual maturation are included.

Reported optimum and upper and lower critical (or avoidance) temperature ranges often are from fish populations adapted to temperate areas south of Alaska, and preferred temperature ranges in Alaska may be lower than in those studies. Different authors may report different upper or lower critical temperatures for the same species. These differences may be due to the initial acclimation temperature: fish acclimated to low temperature exhibit stress or death at lower temperature than fish acclimated to high temperature. Optimal temperature ranges of fish that occur in Alaska are usually below 15°C (Figure 1). Studies of temperature tolerance in rainbow trout usually are conducted on hatchery fish and may not be representative of temperature tolerances under natural conditions; therefore, these fish were excluded from the figure.

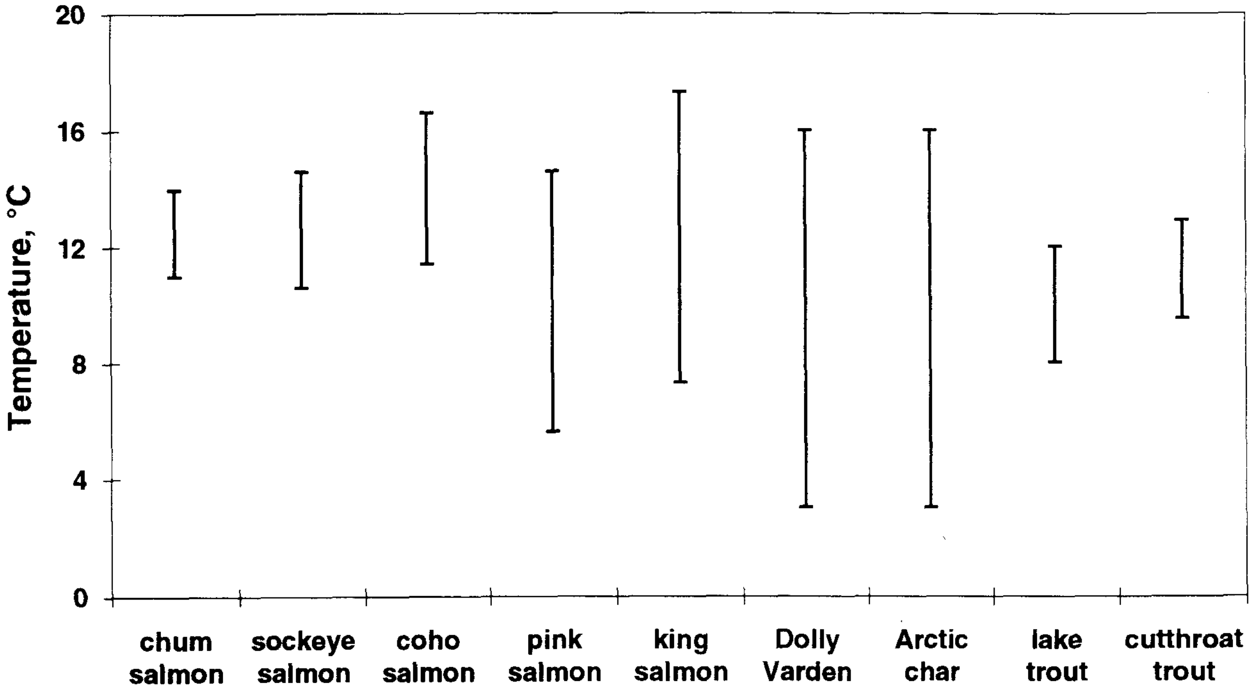

Figure 1. Lowest and highest optimum temperatures reported from the literature for different freshwater species of fish (excluding rainbow trout) occurring in Alaska. Refer to Appendix I for complete data with references.

TEMPERATURE AND SPAWNING

Natural variation in annual water temperature of a specific spawning stream is usually in the range of only a few degrees (Alt 1967). Usually a given species of fish migrates and spawns within a fairly narrow temperature range (Figure 2, Appendix II). Large changes in water temperature (usually more than about 5°C) may change the timing of spawning migration in fish (Bernatchez and Dodson 1985, Reiser and Bjornn 1979, Sheridan 1962), cause fish to stray to another river when returning to spawn, or spawn in suboptimal conditions (Hartman and Holtby 1982).

Water temperature also may limit how far upstream fish may migrate for spawning, either because the upstream habitat is not suitable for spawning or fish cannot swim as efficiently in warmer or cooler water (Bernatchez and Dodson 1985). The idea of optimal temperature for spawning migration suggests that fish select temperatures that lower energy requirements of swimming and optimize swimming performance. Migration patterns of lake whitefish and cisco in the Eastmain River, James Bay, Canada exemplify temperature selectivity to optimize energy demands (Bernatchez and Dodson 1985). Both species enter the Eastmain River in mid-July when water temperature is 17°C, and migrate about 2.7 km upstream. The fish remain there until mid-August to mid-September, when water temperature decreases to 10°C. They then migrate upstream through 6 km of rapids. Both whitefish and cisco hold on the spawning grounds until water temperature drops below 5°C; then they spawn. Bernatchez and Dodson (1985) found that both lake whitefish and ciscos migrate when water temperatures are optimal for energetic requirements. They found that lake whitefish and ciscos fatigue faster at 5°C than at 12°C. Thus, migrating at 12°C is more efficient, and probably results in more successful spawning, than migrating at 5°C.

Changes in water temperature during spawning may delay the time of spawning or decrease the number of fertile eggs. Berlin et al. (1977) estimated that temperature increases of 1°, 2° or 3°C above normal spawning temperature would delay lake whitefish spawning by 5, 11, or 20 days, respectively. Pokrovskii (1961, reported in Berlin et al. 1977) found that when autumn temperature was warm for prolonged periods, whitefish males left the spawning grounds before the mass arrival of females, and eggs deposited by the females were not fertilized.

In Interior and Arctic Alaska, salmon, whitefish, and Dolly Varden spawn in summer or fall and eggs incubate over the winter when stream water temperatures usually are less than 5°C, and often near freezing. Other fish, including Arctic grayling, northern pike, and longnose suckers, spawn in spring when water temperatures are rising. Some whitefish north of the Brooks Range probably spawn in mid- to late summer (Scott and Crossman 1973) and their eggs incubate until spring.

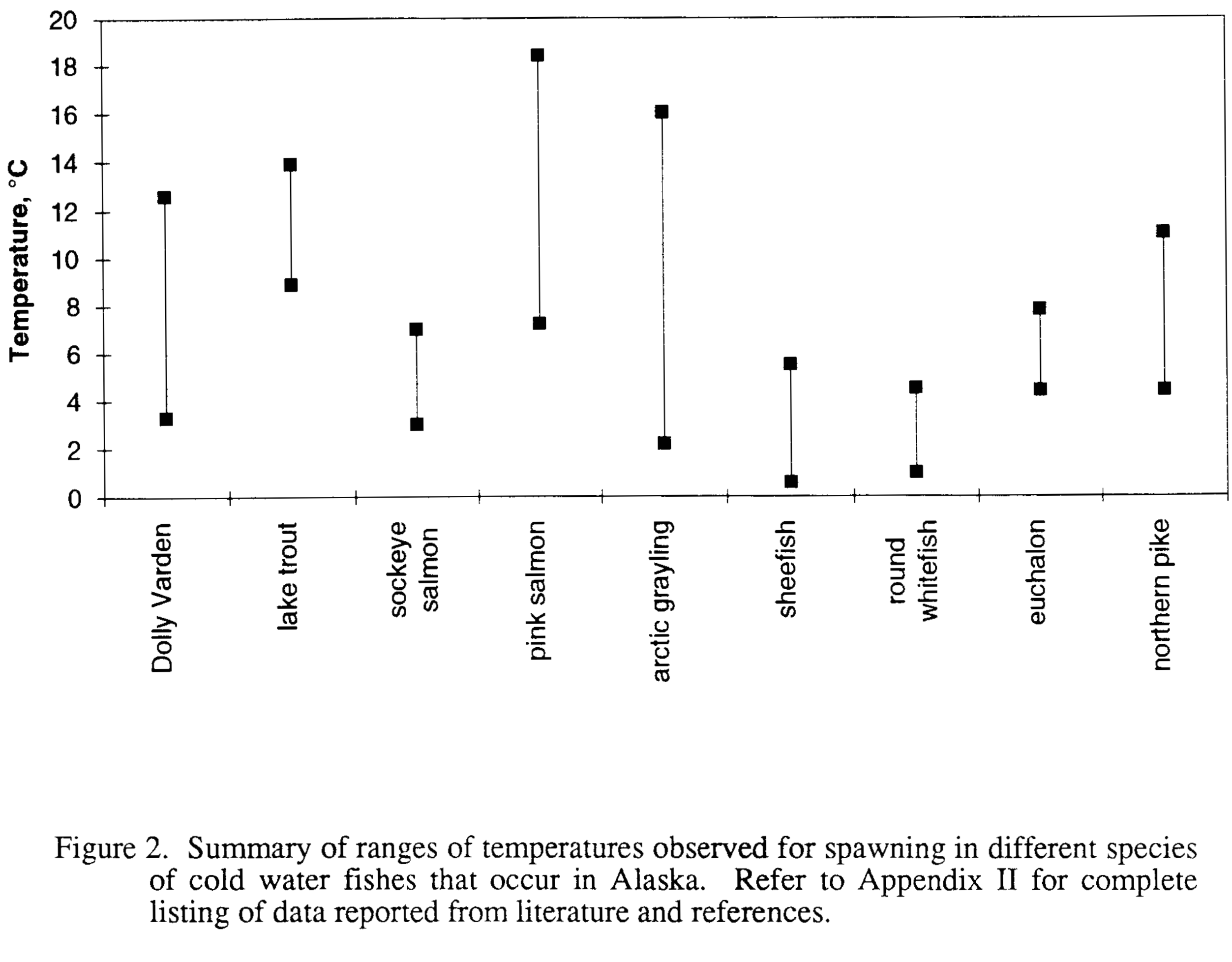

Figure 2. Summary of ranges of temperatures observed for spawning in different species of cold water fishes that occur in Alaska. Refer to Appendix II for complete listing of data reported from literature and references.

TEMPERATURE AND INCUBATION

The process from fertilization to hatch involves two distinct, yet closely related processes: egg incubation and alevin development (Crisp 1981). Temperature changes may affect both of these processes by altering time from egg fertilization to hatching and emergence, and by increasing egg mortality and the occurrence of deformed alevins. The two processes of egg development and alevin development are discussed separately.

Temperature and Egg Development

Several factors influence egg development rates for fish: average water temperature, (Crisp 1981, Graybill et al. 1979), fluctuations in water temperature (Alderdice and Velson 1978), and whether water temperature is increasing or decreasing (Murray and Beacham 1985). Development rates also vary among fish species (Murray 1980) and among stocks within species (Beacham and Murray 1986, 1987).

Comparisons of number of days to hatching for coho, chinook, chum, and pink salmon show a large decrease in the number of days to hatching for each degree change in temperature between 0° and about 4-5°C; an increase of even 1° or 2°C in this range will shorten hatching for most salmonid fishes by about 80-100 days (Figures 3 through 7). Above 10-12°C, increases in temperature produce smaller changes in number of days to hatch. Although most authors reported the greatest change in the number of days to 50% hatch occur between 0°C and 4-5°C, there are few data in that temperature range (Appendix III). Figure 5 for chum salmon, Figure 6 for coho salmon, and Figure 7 for sockeye salmon contain the best representation of the influence of low temperature on rates of egg development.

Rates of egg development appear to be slower when temperature is constant than when temperature fluctuates but maintains the same long-term average. For example, Alderdice and Velsen (1978) reported hatching times of chinook salmon eggs averaged 106.9 days when held at constant 5°C, and averaged 98.3 days when ambient temperature fluctuated around, but averaged, 5°C.

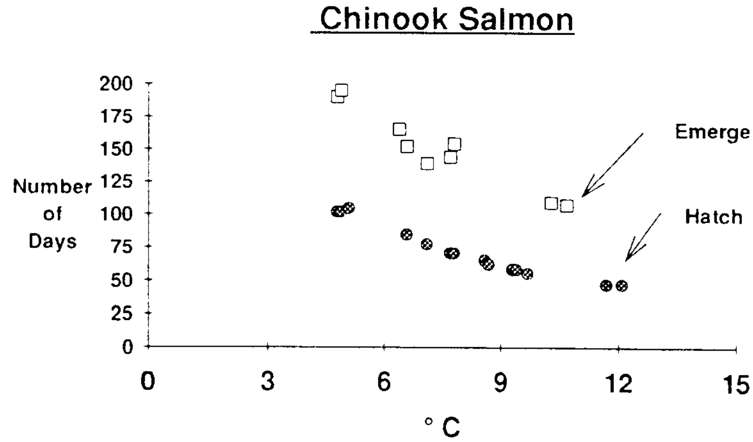

Figure 3. Number of days required for 50% of chinook salmon eggs to hatch and emerge at different incubation temperatures. Refer to Appendix III for complete data and references.

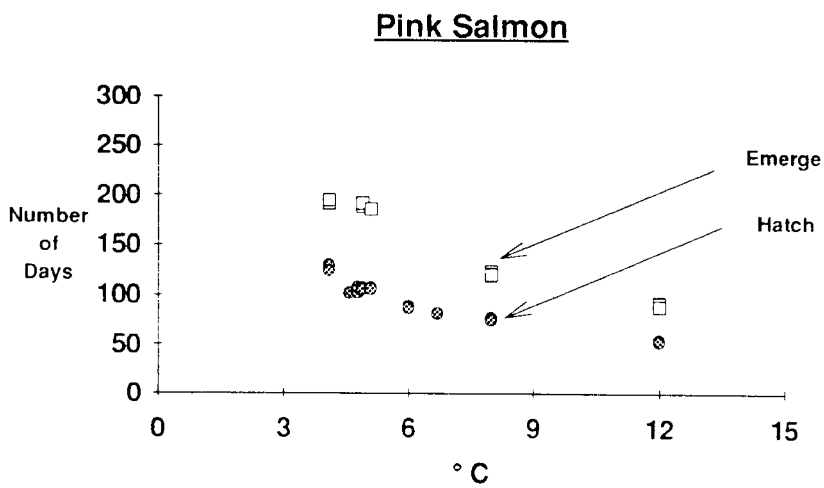

Figure 4. Number of days required for 50% of pink salmon eggs to hatch and emerge at different incubation temperatures. Refer to Appendix III for complete data and references.

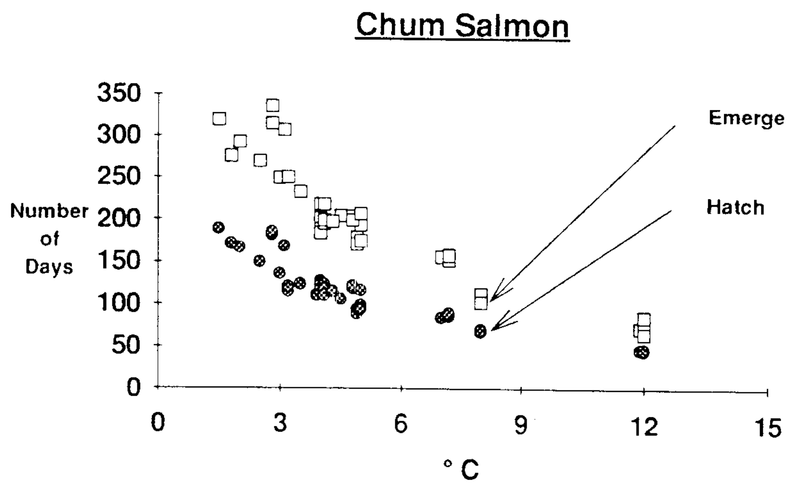

Figure 5. Number of days required for 50% of chum salmon eggs to hatch and emerge at different incubation temperatures. Refer to Appendix III for complete data and references.

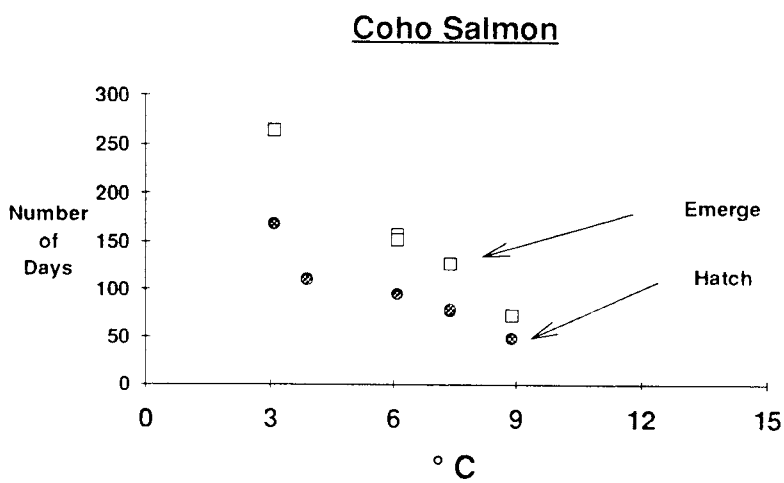

Figure 6. Number of days required for 50% of coho salmon eggs to hatch and emerge at different incubation temperatures. Refer to Appendix III for complete data and references.

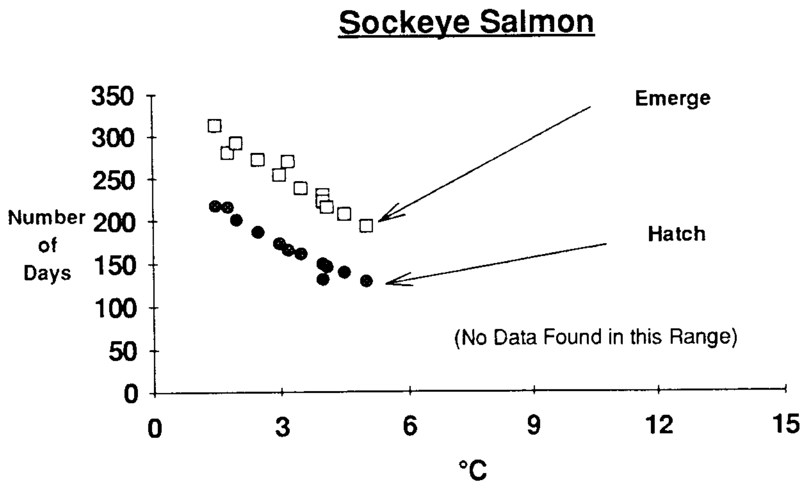

Figure 7. Number of days required for 50% of sockeye salmon eggs to hatch and emerge at different incubation temperatures. Refer to Appendix III for complete data and references.

Salmon eggs develop faster at decreasing temperature than at constant temperature with the same average (Murray and Beacham 1985). For example, at a constant temperature of 5.1°C, hatching of pink salmon eggs took 96.9 days, while incubation at a decreasing temperature regime (11°C to 2°C, with a mean temperature of 5.2°C), hatching took 87.7 days. Eggs developed even more slowly when incubated under increasing temperature than under decreasing or constant temperature (average incubation temperatures were the same in experiments with decreasing, constant, and increasing temperatures). Increases in temperature during the first few weeks of incubation slow egg development more than rising temperature during the mid or late stages of egg development (Alderdice and Velson 1978, Murray and Beacham 1985).

The range in optimum temperature for egg incubation is often narrow (Table 2), and incubation above or below this range may increase egg mortality and the frequency of deformed alevins (Colby and Brooke 1970, Murray and McPhail 1988). Colby and Brooke (1970) found optimal incubation temperature for lake herring (*Coregonus artedii*) at 2°C to 8°C. Incubation at water temperatures outside this range resulted in alevins with various spinal deformities, including scoliosis. The incidence of abnormality was 35% at 1.7°C and 83% at 9.9°C. Price (1940) reported that lake whitefish eggs incubate successfully between 0.5°C and 6.0°C, the optimum at 0.5°C. Lake whitefish incubated at 8°C and 10°C had respective abnormalities of 25% and 50-100% (Price 1940). Murray and McPhail (1988) examined egg and alevin survival rates of Pacific salmon at constant temperature between 2°C and 14°C. The researchers reported that coho salmon and sockeye salmon (Figure 8) were more tolerant of low temperature (2°C and 5°C) and less resistant to high temperature (14°C) than the other salmon species (Figure 9). Chinook and chum salmon eggs incubated at 2°C did not survive and chinook, coho, or sockeye salmon incubated above 14°C did not survive.

Cold shock is more damaging to incubating eggs in early stages of development than later in development. However, incubation in warm temperature (around 12°C) during the first few days following fertilization causes increased egg mortality during later stages of development, from eye pigmentation to hatching (Beacham and Murray 1986a). Exposure of salmonid eggs to low temperature during initial stages of egg incubation (before the formation of the tail bud) produces increased egg mortality and alevin spinal deformity (Bailey and Evans 1971). Bailey and Evans (1971) reported that pink salmon eggs required initial water temperature above 4.5°C through the gastrula stage. The authors found incubation during the first month in water temperatures of 4.5°C and 3.0°C caused egg mortality of 10% and 75%, respectively, and increased spinal deformity among alevins. All pink salmon eggs incubated at 2.0°C died. No egg mortality or alevin spinal deformity occurred in eggs incubated for the first month at 8.5°C. After pink salmon eggs reach the gastrula stage they can tolerate water temperature as low as 0°C, provided the water does not freeze. McNeil and Bailey (1975) reported that chum salmon eggs held in cold water (less than 4.4°C) during the first month of incubation had higher rates of mortality and deformity than chum salmon eggs held in warmer water (near 6°C).

Table 2. Reported optimal and critical temperatures for egg incubation. Data from various sources, as noted.

Species and life stage (if specified)	Optimal Temp. °C	Lower Critical Temp. °C	Upper Critical Temp. °C	Reference
lake whitefish	0.5-6.5		10	Scott & Crossman 1973
	0.5		6.0	Price 1940
lake trout	0.3-1.0			Scott & Crossman 1973
Arctic char	0-2.2		7.8	Scott & Crossman 1973
pink salmon				
even year		3.5		Beacham and Murray 1990
odd year		4.5		Beacham and Murray 1990
1st month dev.		5.5	14-15.6	Combs 1965
through gastrula		4.5		Bailey & Evans 1971
after gastrula		~0		Bailey & Evans 1971
early stage	5-<14	4.5	14	Murray & McPhail 1988
sockeye salmon	4.4-12.8	<4	>14	Murray & McPhail 1988
		1		Beacham and Murray 1990
chinook salmon	4-12	<4	>14	Murray & McPhail 1988
	<12		>12	Heming 1982
		3		Beacham and Murray 1990
chum salmon	4.4-13.3			Bell 1973
through gastrula		4.4		McNeil & Bailey 1975
after gastrula		~0		McNeil & Bailey 1975
(Vedder R. stock)	4			Beacham & Murray 1986a
(Chehalis R. stock)	8			Beacham & Murray 1986a
coho salmon	5-11		14	Murray & McPhail 1988
		1		Beacham and Murray 1990
mountain whitefish	6		9	Rajagopol 1979

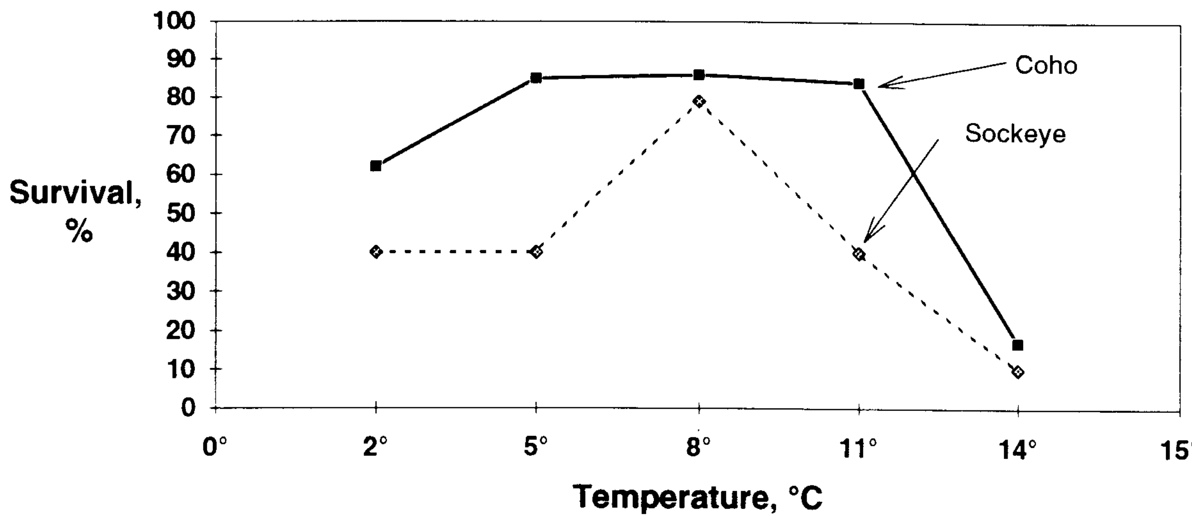

Figure 8. Survival of coho and sockeye salmon eggs from fertilization to hatching at different temperatures. Data from Murray and McPhail (1988).

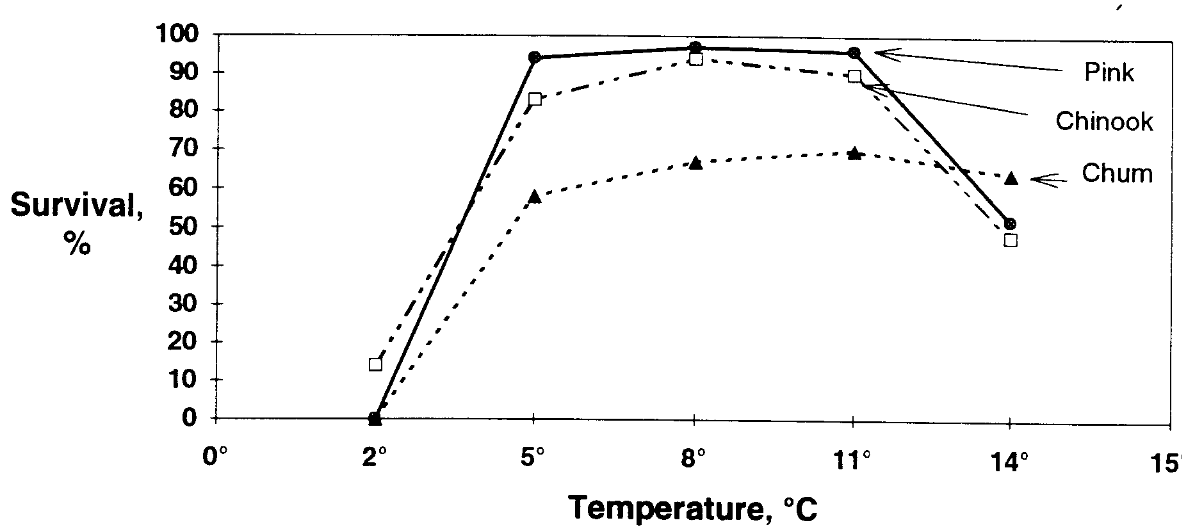

Figure 9. Survival of chinook, chum, and pink salmon eggs from fertilization to hatching at different temperatures. Data from Murray and McPhail (1988).

Few data were found for spring-spawning fish such as Arctic grayling and steelhead trout. (Studies on rainbow trout often were conducted on hatchery fish that may be genetically different and have different temperature tolerances than natural stocks.) Spring-spawning fish reproduce when stream temperature is cold (around 4-7°C for Arctic grayling) and rising. No studies were found that document effects of static or fluctuating temperature on egg development and survival of these species.

Temperature and Alevin Development

Many coldwater species of fish, including salmonids, hatch from the egg with yolk still attached. At this stage of growth, the fish are called alevins. The alevins stay within the gravel interstices until the yolk is partially or completely absorbed. This yolk provides nutrition and energy until the alevin can feed on other sources. Fish size at emergence from the gravel depends on the amount of yolk present in the egg, rate of yolk absorption, and efficiency in metabolizing yolk. Temperature strongly influences rates of alevin development (Figures 3-7, Appendix III).

When alevins are incubated within the optimal temperature range for their species and stock, yolk is converted to tissue with maximum efficiency. Energy consumption, estimated by the amount of oxygen consumed per unit weight of tissue, increases directly with increasing temperature. Murray and McPhail (1988) reported that Pacific salmon alevins hatched from eggs incubated near the optimal temperature for their species had a greater total body length (Figure 10) than fish incubated at higher or lower temperature regimes. Beacham and Murray (1986a) reported similar results for chum salmon: maximum alevin and fry tissue weights occurred at the optimal incubation temperature of 8°C. They cautioned that this temperature range applies to the stocks they tested, and may be different for other stocks that may be adapted to their local environment.

Chinook salmon alevins reared at higher temperature (12°C) absorbed yolk more rapidly than alevins reared at lower temperatures (6-10°C) (Heming 1982). Warmer water shortened alevin development time and increased energy requirements for growth and development. As a result, salmon alevins reared at 12°C required more energy than was available in the remaining yolk; the fish resorbed body tissue during final stages of alevin development. Chinook salmon incubated above 10°C had higher mortality, hatched and emerged precociously, and were smaller at hatching, as alevins, and as fry than were chinook salmon incubated and reared at lower temperatures.

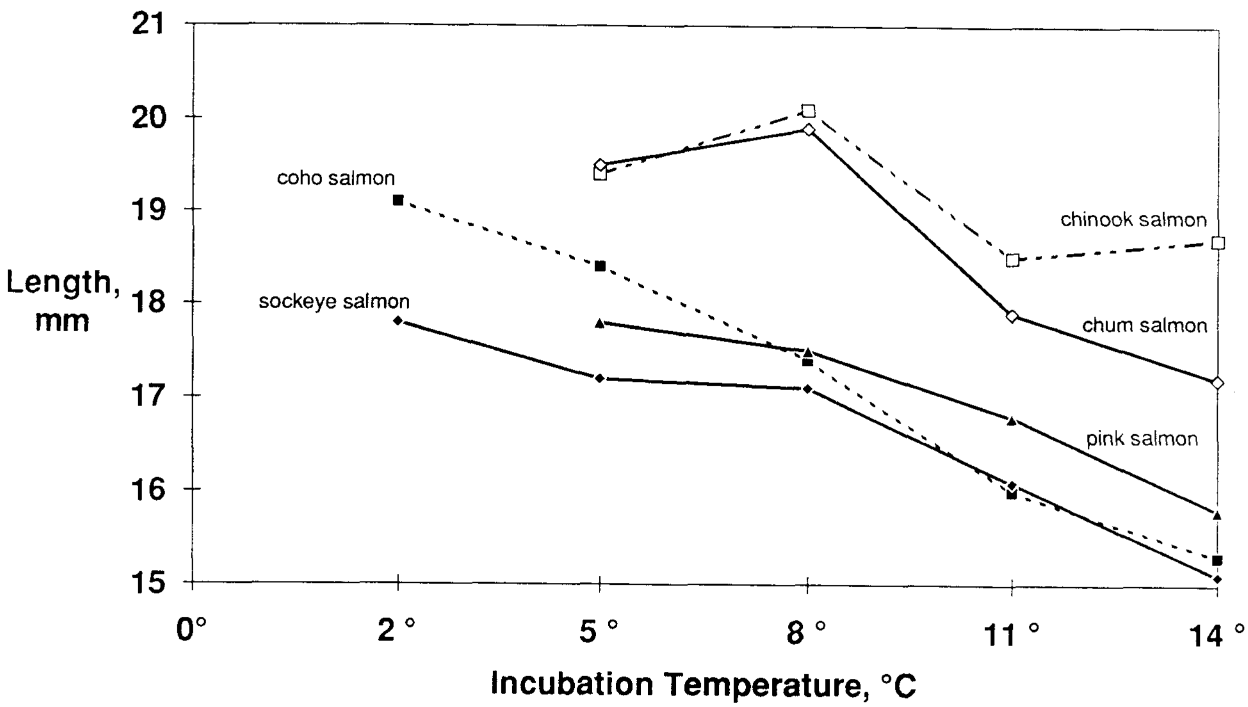

Figure 10. The effect of temperature on total body length for five species of Pacific salmon at 50% alevin hatching. Data from Murray and McPhail (1988).

The developmental stage at which Pacific salmon alevins emerge from the gravel may depend on temperature. Heming (1982) reported that chinook salmon alevins emerged from stream gravels at an earlier stage of development when reared at 10° or 12°C than at 6° or 8°C. Precocious emergence may impart alevins with certain territorial advantages and offer some benefit to growth by enabling alevins to begin feeding earlier in development. Precocious emergence also may confer several disadvantages, including reduced swimming ability, decreased foraging ability or emergence before suitable prey species are available, and increased susceptibility to predation. Heming (1982) estimated that maximum growth efficiency for alevin chinook salmon occurs below 6°C. Berlin et al. (1977) reported similar effects of elevated temperature on whitefish alevins. An increase in temperature of 1-3°C over natural conditions caused whitefish alevins to develop more rapidly and hatch earlier. Fry were smaller than those incubated at lower temperatures. Berlin et al. (1977) suggested that coregonid fry that hatch early may have to search for food when light intensity is below optimum for feeding and when suitable prey are not available.

Few researchers have reported on effects of fluctuating temperature on alevin development. Murray and Beacham (1985) found that a decreasing temperature regime produced larger pink salmon alevins and fry than an increasing temperature regime. Temperature regimes that approximate conditions experienced by pink salmon eggs and alevins during natural incubation (i.e., decreasing temperature to low levels at hatching followed by increasing temperature) produced larger fry than any other temperature regime.

TEMPERATURE AND GROWTH

Each fish species has an optimum temperature for growth that maximizes the fish's efficiency in converting food into tissue. As temperature increases, fish expend more energy to meet metabolic requirements. Above optimum temperature, growth may slow or cease because fish cannot eat or metabolize enough calories to meet increased energy demands. Temperature probably is the most important physical factor determining growth rate of fish (Dwyer and Piper 1987). Optimum temperature for growth usually is the same as the optimum temperature reported in Figure 1 and Appendix I for different species of fish.

Growth rates of fish increase with increasing temperature up to an optimal temperature, then decline (Casselman 1978, Reiser and Bjornn 1979, Dwyer and Piper 1987). Reiser and Bjornn (1979) found that growth rate of chinook salmon parr increased as water temperature increased from 10.0°C to 15.7°C; above 15.7°C, growth rate decreased. Casselman (1978) reported that northern pike grew optimally at 19°C; growth was slow at 2.6°C, increased rapidly with increasing temperature above 10°C, and decreased rapidly above the optimum 19°C.

The effects of temperature on fish growth are controlled primarily by the amount of energy available to the fish. McCormick et al. (1972) reported that optimal temperature for growth and survival of young brook trout (alevins through juveniles) is from 9.8 to 15.4°C when food is not limited. When food was limited, salmonid fish in cool water (9.8°C) exhibited faster rates of growth than fish in warm water (15.4°C) because their energy requirements were lower. Temperature of 18°C or above reduced growth and increased mortality, despite adequate food, because the metabolic requirements exceeded the amount of energy the fish normally consumed.

Brett et al. (1982) conducted detailed studies on rates of growth and energy conversion efficiency of two stocks of juvenile chinook salmon at different temperatures. Growth was measured as percent weight gain per day and energy conversion efficiency was measured as the ratio of dry weight of food consumed to dry weight of growth achieved. The authors reported that in laboratory studies both growth rate (Figure 11) and energy conversion efficiency (Figure 12) increased with increased temperature up to an optimum temperature, then rapidly declined. With unlimited food, juvenile chinook salmon grew fastest at about 19°C; however, under natural riverine conditions with limited food, chinook salmon achieved optimal rates of growth at 15°C (Brett et al. 1982).

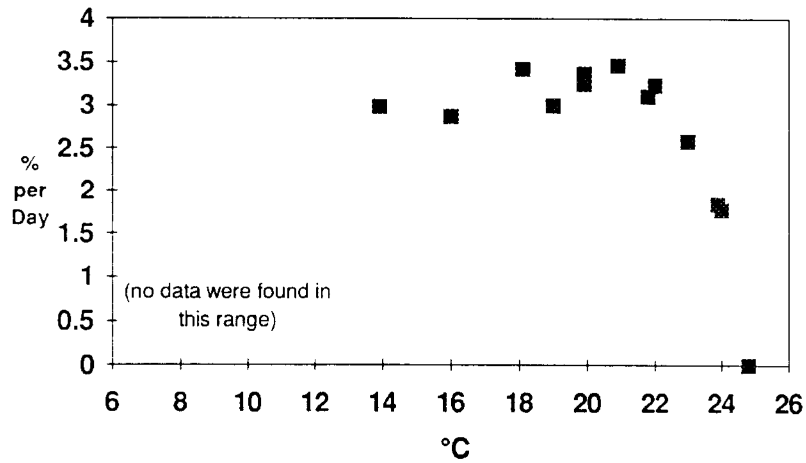

Figure 11. Rates of growth of two populations of juvenile chinook salmon held at different temperatures for 28 days. Data from Brett et al. (1982).

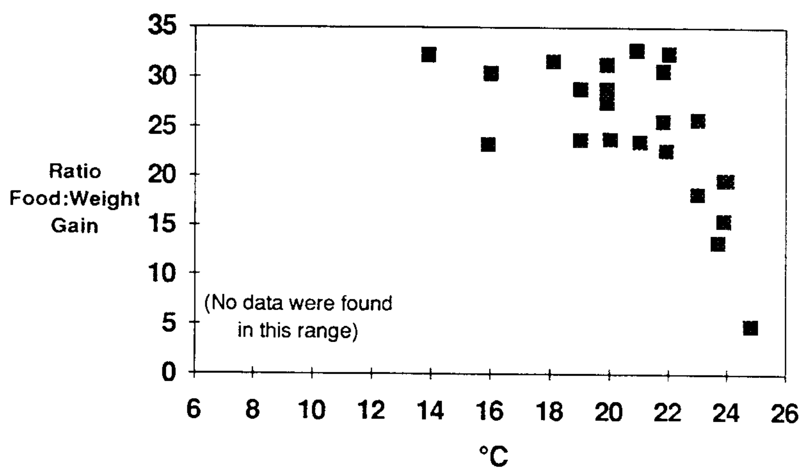

Figure 12. Growth efficiency of two populations of juvenile chinook salmon held at different temperatures for 28 days. Data from Brett et al. (1982).

Fish may seek cooler water as food becomes more limited (Javaid and Anderson 1967). Mac (1985) examined the effects of different ration quantities on preferred temperature of lake trout to determine if fish would select cooler water when food was restricted. He reported that lake trout were equally active when fed different amounts of food, but that fish fed limited rations showed strong selectivity for cooler water. Metabolic energy costs to yearling lake trout could be reduced as much as 35% by lowering residence temperature from 9.2°C to 5°C (unpublished data reported in Mac [1985]). A reduction in metabolic energy demands produces an increase in energy available for growth.

When food is not limited, temperature may affect condition as well as growth of rearing fish. For example, Wandsvik and Jobling (1982) examined tissue content of Arctic char reared at 2.9°C and 13.1°C on satiation diets. Fish reared at high temperature contained about twice as much body fat (by percent total body weight) than fish reared at low temperature. Protein, moisture, and ash content of these two groups were similar.

Slight increases in water temperature during winter and spring caused earlier-than-normal smolting among salmon (Holtby 1988), which may result in younger smolts that migrate to saltwater. In studies of logged areas around Carnation Creek, British Columbia, Holtby (1988) found that most smolts reared in warmer water were yearlings, whereas smolts reared in cooler water were predominantly 2 years old. Smolts that migrated to saltwater as yearlings had lower survival rates than smolts that migrated as 2-year olds. Holtby concluded that increased growth during summer and higher winter survival due to slightly elevated temperature did not improve survival of smolts after migration to saltwater.

Anadromous fish that rear in freshwater respond to extremely cold temperature by extending rearing time until sufficient growth and development occurs. Atlantic salmon in persistently coldwater systems may take up to 7 or 8 years to smolt because growth is slow (Jensen and Johnsen 1986). In extremely cold rivers where water temperature rarely exceeds 10°C, the low temperature limit for growth of Atlantic salmon is around 6.3°C. Jensen and Johnsen (1986) suggest that a lower temperature limit for growth is not a fixed temperature, but varies from river to river according to temperature conditions and population characteristics of the fish.

Fish growth probably is not adversely affected by fluctuating temperature, provided lethal limits are not reached. Thomas et al. (1986) investigated effects of daily fluctuations, such as those that result from clear-cut logging. The authors subjected both starved and fed coho salmon pre-smolts to water fluctuating between 6.5° and 20°C, between 9° and 15°C, and at a constant 11°C. Thomas et al. reported that pre-smolts exposed to large daily fluctuations of up to 14°C showed no change in liver weight or liver glycogen, both indicators of stress. Fish continued to feed and grow in fluctuating temperature that approached but remained below lethal limits.

TEMPERATURE AND OVERWINTERING FISH

Seasonal decreases in water temperature signal many fish species to begin migration to overwintering areas. Juvenile Dolly Varden, for example, move upstream in Starrigavin Creek, southeast Alaska, when water temperature decreases from about 7°C to 4°C (Elliott and Reed 1974). Within a stream, juvenile salmonids seek refuge under vegetation and within rubble substrate, and remain inactive during seasonal low water temperature. Gibson (1978) reported that fish in northern Quebec began sheltering in rubble at 10°C, and at 9°C the majority had disappeared beneath cover.

Overwintering fish actively seek cooler water, presumably to lower their metabolic requirements. Bustard and Narver (1975) gave coho salmon a choice of different water temperatures in simulated winter habitat. Coho salmon preferred water between 2°C and 5°C over water from 5.5°C to 9°C. In Arctic and sub-Arctic climates, rivers and streams often become a series of disconnected pools and unfrozen water is limited; thus, fish may not have a choice of water temperature.

Both oxygen and food may become limiting during winter months, especially if the waterbody is ice-covered, rates of photosynthesis are low, and oxygen demands are high. Thus, overwintering fish survive best when metabolic and energy requirements are low. In high latitude areas, fish often concentrate in larger pools or in active aufeis channels where dissolved oxygen concentrations are above zero and temperature may be as low as -1°C (Adams and Cannon 1987). Most coldwater fish species can withstand prolonged exposure to water at or near freezing, provided the water does not freeze and there is sufficient dissolved oxygen.

TEMPERATURE AND AVOIDANCE

Lake trout are well known for their active migration to avoid warmer conditions. In homothermal lakes, lake trout are often evenly distributed throughout the water column; however, in stratified lakes, lake trout migrate to greater depths as surface waters warm in spring or early summer (Martin and Olver 1980). Martin and Olver reported studies of lake trout migrating from shallow White Trout Lake, Ontario to deeper Big Trout Lake beginning in late May as surface temperatures in the smaller lake reached 9-12°C. In other lakes, lake trout were found evenly distributed throughout the water column until surface waters warmed to 14-15°C, then the lake trout moved down to deeper areas of the lake. Martin and Olver (1980) reported that the majority of lake trout in various Ontario lakes were distributed below 6°C.

For many fish species, acclimation temperature may be an important factor determining the high or low temperature at which a fish species shows avoidance (Table 3). Coldwater species, such as rainbow trout, showed a stronger relationship between acclimation and avoidance temperatures than did warmwater species (Stauffer et al. 1984). Upper avoidance temperature approaches upper critical temperature, especially if the acclimation temperature is high (in the range of 18-24°C for rainbow trout). Brett (1952) reported a simpler relationship for avoidance temperatures in Pacific salmon: salmon avoided temperatures greater than 15°C, regardless of acclimation temperatures.

Table 3. Summary of lower and upper avoidance temperatures for different freshwater species of coldwater fish.

Species Size or age	Acclim. Temp. °C	Lower Avoid. Temp. °C	Upper Avoid. Temp. °C	Reference
lake whitefish				
17.8 mm	--	12	17	Hoagman 1974
23.1 mm	--	14.5	19	Hoagman 1974
lake trout	--	--	13	Cooper & Fuller 1945
	--	--	11	Rawson 1956
young	--	--	15	McCauley & Tait 1970
young	--	--	14	Goddard and Tait 1976
Arctic char				
adult	--	--	13.5-14	Jensen 1981
rainbow trout				
fry	--	14	22	McCauley & Pond 1971
fry	6	5	13	Cherry et al. 1975
fry	9	8	15	Cherry et al. 1975
fry	12	11	17	Cherry et al. 1975
fry	15	13	19	Cherry et al. 1975
fry	18	13	19	Cherry et al. 1975
fry	21	16	23	Cherry et al. 1975
fry	24	19	25	Cherry et al. 1975
fry	6	--	18	Stauffer et al. 1984
fry	18	--	24	Stauffer et al. 1984
fry	24	--	27	Stauffer et al. 1984
sockeye salmon	--	--	21	Coutant 1977
	--	--	>15	Brett 1952
chum salmon	--	--	>15	Brett 1952
coho salmon	--	--	>15	Brett 1952
chinook salmon	--	--	>15	Brett 1952
pink salmon	--	--	>15	Brett 1952

SUMMARY AND RECOMMENDATIONS

The effects of temperature on egg incubation and development of the alevins are complex. Both temperature and its fluctuation are important determinants in the number of days required for incubation and emergence. An increase of 1° to 2°C within the temperature range of 0° and 5°C will shorten hatching times of most salmonid fishes by 80-100 days. Above 10° to 12°C, increases in temperature produce smaller changes in number of days to hatch; an increase of 2°C between 10°C and 12°C may shorten incubation times by 20 days.

Incubation of eggs at higher or lower temperatures than the optimum range will increase mortality of eggs and the occurrence of deformed alevins. After the egg has reached the gastrula stage, water temperatures can drop to near freezing, with no ill effects for many species.

Short-term exposure to sublethal temperature changes may weaken fish, leaving them more vulnerable to predation or less able to adjust to other environmental changes, such as increases in salinity. If water temperatures are higher than natural conditions in winter months, fish will probably smolt earlier and migrate to saltwater at a smaller size. These fish have higher mortality rates than fish that smolt later and migrate at larger sizes.

Each fish species has an optimum temperature for growth that is related to the fish's efficiency in converting food into tissue. Fish use more energy for growth and metabolism in warm water than cool water. Growth rates of fish increase with increasing temperatures up to an optimal temperature; then growth rates decline or cease when metabolic demands for maintenance are greater than demands for growth. When food is limiting, fish in cooler water will survive better than fish in warm water because their energy requirements are lower. Optimal growth temperatures for most salmonids are in the range of 10°C to 15°C. Upper lethal temperatures for most salmonids are in the range of 20°C to 25°C.

Most coldwater species of fish exhibit avoidance when temperatures are within 2-3°C of the upper or lower lethal temperatures.

Overwintering fish may seek cooler water to reduce their metabolic energy requirements. Fish survive better if metabolic and energy requirements are as low as possible during periods when flows, dissolved oxygen concentrations, and available food are low.

The following conclusions can be made from published literature on effects of temperatures on coldwater species of fish:

Spawning Migration

Effect	If stream water temperatures are altered from the natural conditions, spawning may be delayed, males may leave the spawning areas before the arrival of females, fish may seek other drainages.
Recommended Temperature	Maintain seasonal patterns of warming and cooling, do not depress or elevate temperatures more than 5°C over natural conditions.

Egg Development

Effect	Exposure to cold temperatures in the early stages of development of eggs from late summer and fall spawning species may increase mortality and rates of deformed alevins. Exposure to warm temperatures in later stages of development of eggs from late summer and fall spawning species may increase mortality and rates of deformed alevins. Temperature regimes that approximate the natural condition will result in highest survival rates.
Recommended Temperature	Maintain seasonal temperature patterns of warming and cooling and natural temperature fluctuations. Do not depress water temperatures during initial stages of development for most coldwater fish species. Do not elevate water temperatures above 12-14°C for most coldwater fish species.

Alevin Development

Effect	Alevins incubated at higher temperatures may exhaust their stored energy supplies and be smaller upon emergence than alevins incubated at cooler temperatures.
Recommended Temperature	Optimum temperatures for alevin development range between 5° and 8°C for most species of Pacific salmon. Temperatures should not exceed 12-14°C. For other species of coldwater fish, do not elevate temperatures more than a few degrees over natural conditions and maintain natural seasonal patterns of warming or cooling.

Growth

Effect	Generally, fish will grow faster in warmer temperatures up to a maximum level. Growth will slow or cease when metabolic requirements of higher temperatures exceed the amount of energy consumed. When food is limited, fish inhabiting cooler temperatures will have higher survival rates.
Recommended Temperature	For most stocks of Pacific salmon, optimal growth occurs below 15°C, and even lower when food is limited. For northern pike, optimal growth occurs below 19°C.

Overwintering

Effect	Overwintering fish survive best when metabolic and energy requirements are low, water does not freeze, there is sufficient cover and dissolved oxygen, and no abrupt changes in temperature.
Recommended Temperature	Avoid abrupt changes in temperatures. Fish can withstand lower winter temperatures if they are acclimated slowly. Therefore, natural seasonal fluctuations in stream water temperatures and patterns of cooling should be maintained.

Avoidance

Effect	Acclimation temperature appears to be the single most important factor determining the temperature at which a fish will exhibit avoidance. If acclimation temperature is high, fish will exhibit avoidance to temperatures approaching the upper critical level.
Recommended Temperature	Avoidance usually occurs slightly above the optimal temperature for a specific fish species or population; for Pacific salmon, avoidance may occur at temperatures exceeding 15°C. Lower avoidance temperatures are not well documented.

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APPENDIX I.

Summary of optimum temperature ranges, and upper critical ranges for different freshwater species of fish occurring in Alaska.

Species size or age (if given)	Acclimation Temp. °C	Optimum Temp. Range °C	Upper Critical Temp. °C	Reference
rainbow trout		10-22	19-30	Elliott 1981
		7.3-14.6	24.1	Reiser and Bjornn 1979
fry		13	24	Scott & Crossman 1973
fry		22		Javaid & Anderson 1967
fry		18-19		McCauley & Pond 1971
fry		18		Cherry et al. 1975
starved fry		18		Javaid & Anderson 1967
adult		18.9-21.1		Horak & Tanner 1964
adult		13		Garside & Tait 1958
adult		16.5		Spigarelli 1975
coho salmon		11.8-14.6	25.8	Reiser and Bjornn 1979
fry	10	12-14	23.7	Brett 1952
fry	15	12-14	24.3	Brett 1952
fry	20	12-14	25.0	Brett 1952
fry	23	12-14	25.0	Brett 1952
adult		11.4		Reutter & Herdendorf 1975
adult		16.6		Spigarelli 1975
chinook salmon		7.3-14.6	25.2	Reiser and Bjornn 1979
fry	5	12-14	21.5	Brett 1952
fry	10	12-14	24.3	Brett 1952
fry	15	12-14	25.0	Brett 1952
fry	20	12-14	25.1	Brett 1952
fry	24	12-14	25.1	Brett 1952
fry		12-14		Scott & Crossman 1973
adult		17.3		Spigarelli 1975
sockeye salmon		11.2-14.6	24.6	Reiser and Bjornn 1979
		10.6-12.8		Horak & Tanner 1964
fry		12-14	24.4	Scott & Crossman 1973
fry	5	11-14	22.2	Brett 1952
fry	10	11-14	23.4	Brett 1952
fry	15	11-14	24.4	Brett 1952
fry	20	11-14	24.8	Brett 1952
fry	23	11-14	24.3	Brett 1952

Appendix I, continued.

Species size or age (if given)	Acclimation Temp. °C	Optimum Temp. Range °C	Upper Critical Temp. °C	Reference
chum salmon fry		11-14	23.8	Brett 1952
pink salmon		5.6-14.6	10.1	Reiser and Bjornn 1979
emerged		11.7-12.8		Hurley & Woodall 1968
50 da		9.3		Hurley & Woodall 1968
fry		11.7		Brett 1952
fry		12-14	23.9	Scott & Crossman 1973
fry	5	11-14	21.3	Brett 1952
fry	10	11-14	22.5	Brett 1952
fry	15	11-14	23.1	Brett 1952
fry	20	11-14	23.9	Brett 1952
fry	24	11-14	23.9	Brett 1952
fry		11.2-14.6	25.8	Reiser and Bjornn 1979
adult spawners			17.0	Kruger 1981a
cutthroat trout		9.5-12.9	23.0	Reiser and Bjornn 1979
Arctic char		5-16	*c.*22-27	Elliott 1981
		3-16		Jensen et al. 1989
lake trout		14		Kennedy 1941
		10		Martin 1952
		15.5		Galligan 1951
fry			23.5	Evans, et al. 1991
fry		10-16		MacLean, et al. 1990
young		11.7		McCauley & Tait 1970
young		11.5		Goddard and Tait 1976
adult		11.8		Spigarelli 1975
adult		8-12		Evans, et al. 1991
adult		10		Scott & Crossman 1973
Arctic grayling				
sac fry	8.5±1		21.5-24.2	LaPerriere & Carlson 1973
young of year	8.5±1		>24.5	LaPerriere & Carlson 1973
>10 cm	4+1		20.0-24.0	LaPerriere & Carlson 1973
>20 cm	8+1		22.5-24.5	LaPerriere & Carlson 1973

Appendix I, concluded.

Species size or age (if given)	Acclimation Temp. °C	Optimum Temp. Range °C	Upper Critical Temp. °C	Reference
lake whitefish		11.9		Cooper & Fuller 1945
small		12.7		Ferguson 1958
larvae		17		Reckahn 1970
12.9 mm		12-16		Hoagman 1974
17.8 mm		13.5		Hoagman 1974
23.1 mm		15.5		Hoagman 1974
round whitefish		17.5		Cooper & Fuller 1945
longnose sucker			11.6	Cooper & Fuller 1945
burbot		11.4		Cooper & Fuller 1945
northern pike		9-25	30-34	Elliott 1981
subadult		19	29.4	Casselman 1978
3-spined stickleback		4-20	22-37	Elliott 1981

APPENDIX II

Temperatures in which different species of coldwater fish were observed spawning at various locations.

Fish Species	Time of Spawning or Location	Temperature °C	Reference
lake whitefish	Nov.-mid-Dec.	1.4 to 1.6	Bryan & Kato 1975
	Lake Erie	7.8	Scott & Crossman 1973
	L.Michigan	4.4	Berlin et al. 1977
round whitefish	November	1-2	Bryan & Kato 1975
	USSR	~0	Hale 1981
	fall	4.5	Scott & Crossman 1973
Inconnu (sheefish)	Alaska late Sept	2.6-4.6	Alt 1967
	Alaska early Oct	0.8-3.7	Alt 1987
	Alaska late Sept	0.6-5.5	Alt 1987
rainbow trout	April-June	10	Scott & Crossman 1973
sockeye salmon	Sept-Oct	3-7	Scott & Crossman 1973
pink salmon	Alaska	7.2-18.4	Sheridan 1962
	Alaska	10	Kruger 1981a
	Alaska	13	McNeil 1962
	Alaska	7.2-12.8	Kruger 1981a
	Alaska:Itkillik Lk	6.0	Bendock 1979
cutthroat trout	Feb-May	10	Scott & Crossman 1973
Dolly Varden	Sept-Nov	7.8	Scott & Crossman 1973
	Alaska	4.4-12.6	Armstrong 1967
	Alaska	6.1-11.1	Armstrong & Winslow 1968
	Alaska	3.3-4.4	Armstrong & Kissner 1969
Arctic char	Sept-Dec	4.0	Scott & Crossman 1973
	August	4.0	Yoshihara 1973
	Sept	3.0-5.0	Yoshihara 1973
lake trout	Oct	8.9	Scott & Crossman 1973
	S.Saskatchewan	10.6-13.9	Scott & Crossman 1973
	Alaska	<10	Burr, pers. comm. 1991

Appendix II, concluded.

Fish Species	Time of Spawning or location	Temperature °C	Reference
arctic graying	spring	3.3	Kruger 1981b
	Alaska spring	3.9-10.0	Tack 1972
	spring	4.0-10.0	Kruse 1959
	spring	2.2-10.0	Kruse 1959
	Alaska spring	3.9-16.0	Craig & Poulin 1974
	Alaska spring	6.7	McCart et al. 1972
	Alaska spring	5.6	Reed 1964
	Alaska spring	5.0-9.0	Bendock 1979
	Alaska spring	5.0	Bendock 1979
	Alaska spring	4.0	Alt 1977
euchalon	various locations	4.4-7.8	Scott & Crossman 1973
northern pike	April-May	4.4-11.1	Scott & Crossman 1973

APPENDIX III

Number of days from fertilization to 50% hatch and 50% emergence for different fish species. Note that some of these species of fish do not occur in Alaska; data are included on non-Alaska species to compare influences of temperatures with hatching times.

Species	Temp. °C	50% Hatch (days)	50% Emergence (days)	Reference
Atlantic salmon	8.0	63	99	Gunnes 1979
	10.0	49	79	Gunnes 1979
	12.0	38	62	Gunnes 1979
Arctic char				
fall spawners	4	97		Johnson 1980
	6	76		Johnson 1980
	8	54		Johnson 1980
	10	41		Johnson 1980
	12	36		Johnson 1980
spring spawners	4	95		Johnson 1980
	6	74		Johnson 1980
	8	55		Johnson 1980
	10	45		Johnson 1980
lake trout	2-2.5	141-156		Evans et al. 1991
	5	100-117		Evans et al. 1991
	10	50		Evans et al. 1991
brown trout	0	213		Crisp 1988*
	1	179		Crisp 1988*
	2	151		Crisp 1988*
	3	127		Crisp 1988*
	4	108		Crisp 1988*
	5	95		Crisp 1988*
	5.2	85	163	Elliott 1984
	5.5	83	155	Elliott 1984
	5.75	76	147	Elliott 1984
	6.7	68	125	Elliott 1984
	6	78		Crisp 1988*
	7	66		Crisp 1988*
	8	56		Crisp 1988*
	9	48		Crisp 1988*
	10	41		Crisp 1988*
	11	35		Crisp 1988*

Appendix III, continued.

Species	Temp. °C	50% Hatch (days)	50% Emergence (days)	Reference
brook trout	0	191		Crisp 1988*
	1	165		Crisp 1988*
	2	143		Crisp 1988*
	3	124		Crisp 1988*
	4	108		Crisp 1988*
	5	94		Crisp 1988*
	6	82		Crisp 1988*
	7	72		Crisp 1988*
	8	63		Crisp 1988*
	9	55		Crisp 1988*
	10	49		Crisp 1988*
	11	43		Crisp 1988*
	12	38		Crisp 1988*
	13	33		Crisp 1988*
	14	30		Crisp 1988*
	15	26		Crisp 1988*
rainbow trout	0	251		Crisp 1988*
	1	182		Crisp 1988*
	2	138		Crisp 1988*
	3	107		Crisp 1988*
	4	86		Crisp 1988*
	5	71		Crisp 1988*
	6	59		Crisp 1988*
	7	50		Crisp 1988*
	8	43		Crisp 1988*
	9	37		Crisp 1988*
	10	32		Crisp 1988*
	11	28		Crisp 1988*
	12	25		Crisp 1988*
	13	22		Crisp 1988*
	14	20		Crisp 1988*
	15	18		Crisp 1988*
coho salmon	3.1	168	261	Graybill et al. 1979
	3.1	168	264	Graybill et al. 1979
	6.1	94	157	Graybill et al. 1979
	3.9	110		Graybill et al. 1979
	3.9	109		Graybill et al. 1979
	6.1	94	152	Graybill et al. 1979
	7.4	76	127	Graybill et al. 1979
	7.4	78	127	Graybill et al. 1979
	8.9	48	72	Graybill et al. 1979

Appendix III, continued.

Species	Temp. °C	50% Hatch (days)	50% Emergence (days)	Reference
chinook salmon	4.8	101	190	Graybill et al. 1979
	4.9	101	195	Graybill et al. 1979
	5.1	104		Graybill et al. 1979
	6.4		165	Graybill et al. 1979
	6.6	84	152	Graybill et al. 1979
	7.1	77	139	Graybill et al. 1979
	7.7	70	144	Graybill et al. 1979
	7.8	70	154	Graybill et al. 1979
	8.6	65		Graybill et al. 1979
	8.7	62		Graybill et al. 1979
	9.3	58		Graybill et al. 1979
	9.4	58		Graybill et al. 1979
	9.7	55		Graybill et al. 1979
	10.3		109	Graybill et al. 1979
	10.7		107	Graybill et al. 1979
	11.7	47		Graybill et al. 1979
	12.1	47		Graybill et al. 1979
pink salmon	4.1	128	194	Beacham & Murray 1985
	4.1	129	191	Beacham & Murray 1985
	4.1	123	194	Beacham & Murray 1985
	4.6	101		Graybill et al. 1979
	4.8	101		Graybill et al. 1979
	4.8	107		Graybill et al. 1979
	4.9	106	188	Graybill et al. 1979
	4.9	105	191	Graybill et al. 1979
	5.1	106	185	Graybill et al. 1979
	5.1	105	185	Graybill et al. 1979
	6.0	88		Graybill et al. 1979
	6.0	86		Graybill et al. 1979
	6.7	80		Graybill et al. 1979
	6.7	81		Graybill et al. 1979
	8.0	76	119	Beacham & Murray 1985
	8.0	76	123	Beacham & Murray 1985
	8.0	76	121	Beacham & Murray 1985
	8.0	74	121	Beacham & Murray 1985
	8.0	74	120	Beacham & Murray 1985
	12.0	53	90	Beacham & Murray 1985
	12.0	53	92	Beacham & Murray 1985
	12.0	54	91	Beacham & Murray 1985
	12.0	53	88	Beacham & Murray 1985
	12.0	52	88	Beacham & Murray 1985

Appendix III, continued.

Species	Temp. °C	50% Hatch (days)	50% Emergence (days)	Reference
chum salmon	2.8	180	335	Graybill et al. 1979
	2.8	184	314	Graybill et al. 1979
	3.1	167	307	Graybill et al. 1979
	3.2	114		Graybill et al. 1979
	3.9	110		Graybill et al. 1979
	4.0	114		Graybill et al. 1979
(Vedder early stock)	4.0	127	198	Beacham & Murray 1986a
(Vedder middle stock)	4.0	127	201	Beacham & Murray 1986a
(Vedder late stock)	4.0	126	188	Beacham & Murray 1986a
(Chehalis late stock)	4.0	123	183	Beacham & Murray 1986a
(Chehalis early stock)	4.1	122	197	Beacham & Murray 1986a
(Alouette stock)	4.1	122	195	Beacham & Murray 1986a
(Jones stock)	4.1	123	199	Beacham & Murray 1986a
	4.1	117		Graybill et al. 1979
	4.3	114	197	Graybill et al. 1979
	4.8	118	203	Graybill et al. 1979
	4.8	121	199	Graybill et al. 1979
	4.9	92	179	Graybill et al. 1979
	4.9	93	178	Graybill et al. 1979
	4.9	88	170	Graybill et al. 1979
	5.0	94	174	Graybill et al. 1979
	5.0	116	206	Graybill et al. 1979
	7.0	84	156	Graybill et al. 1979
	7.2	85	152	Graybill et al. 1979
	7.2	85	158	Graybill et al. 1979
	7.2	89	157	Graybill et al. 1979
(Jones stock)	8.0	68	112	Beacham & Murray 1986a
(Alouette stock)	8.0	69	112	Beacham & Murray 1986a
(Vedder early stock)	8.0	70	112	Beacham & Murray 1986a
(Vedder middle stock)	8.0	69	106	Beacham & Murray 1986a
(Vedder late stock)	8.0	67	104	Beacham & Murray 1986a
(Chehalis early stock)	8.0	69	112	Beacham & Murray 1986a
(Chehalis late stock)	8.0	69	102	Beacham & Murray 1986a
(Vedder late stock)	11.9	46	72	Beacham & Murray 1986a
(Jones stock)	12.0	45	83	Beacham & Murray 1986a
(Alouette stock)	12.0	45	83	Beacham & Murray 1986a
(Vedder early stock)	12.0	46	84	Beacham & Murray 1986a
(Vedder middle stock)	12.0	46	78	Beacham & Murray 1986a
(Chehalis early stock)	12.0	46	85	Beacham & Murray 1986a
(Chehalis late stock)	12.0	47	65	Beacham & Murray 1986a

Appendix III, concluded.

Species	Temp. °C	50% Hatch (days)	50% Emergence (days)	Reference
sockeye salmon	1.5	217	313	Wangaard & Burger 1983
	1.8	215	280	Wangaard & Burger 1983
	2.0	200	292	Wangaard & Burger 1983
	2.5	186	272	Wangaard & Burger 1983
	3.0	172	254	Wangaard & Burger 1983
	3.2	165	270	Wangaard & Burger 1983
	3.5	160	238	Wangaard & Burger 1983
	4.0	130	230	Wangaard & Burger 1983
	4.0	148	222	Wangaard & Burger 1983
	4.1	145	215	Wangaard & Burger 1983
	4.5	138	207	Wangaard & Burger 1983
	5.0	128	193	Wangaard & Burger 1983
rainbow smelt	6	29		Scott & Crossman 1973
	7.1	25		Scott & Crossman 1973
	9	19		Scott & Crossman 1973

* These are estimated values based upon a regression relationship developed by Crisp (1988).