

Influence of Temperature on Incubation Rates of Coho Salmon (*Oncorhynchus kisutch*) from Ten Washington Populations

Abstract

Coho salmon embryos from 10 Washington populations were incubated under controlled conditions to determine the levels of variation in time to hatch among populations and families within populations. The average incubation rate was somewhat slower than that estimated from a quantitative model derived from British Columbia populations, and was slightly faster than that predicted by a Washington model. Significant variation in incubation rates among the Washington populations was detected, consistent with results from other studies. Dates of first hatching of families within populations ranged more than two weeks at 6°C. Within families, the first and last individuals to hatch ranged over 1-3 weeks. The variation in incubation rate among populations likely reflects local adaptation to the thermal regimes of the rivers. The variation within populations and families will contribute to the variation in emergence date of fry, which will affect their growth and survival.

Introduction

Water temperatures in streams are chiefly influenced by local air temperature, shade, stream depth and groundwater inputs (Sullivan *et al.* 1990). Although stream temperatures are naturally dynamic, human activities such as timber removal can alter thermal regimes (Holby 1988, Thedinga *et al.* 1989). Recent physico-geomorphic models (Sullivan *et al.* 1990) can forecast the effects of such human activities on stream temperatures but the biological consequences of temperature changes on stream fishes are imperfectly understood. Wide-spread landscape alterations in the Pacific Northwest have generated concern over the status of fishes in general and Pacific salmon (*Oncorhynchus* spp.) in particular (Nehlsen *et al.* 1991).

Temperature regimes are a major factor contributing to the local adaptation and isolation of salmon populations (Ricker 1972, Murray *et al.* 1990). Temperatures directly affect the rate of embryonic development, hatch rates, survival and size of embryos (Tang *et al.* 1987, Beacham and Murray 1990, Murray *et al.* 1990). The time of year when adults spawn also is related to the temperature regime that the embryos will experience and the period of peak food abundance in spring (Godin 1982, Beacham and Murray 1987, Brannon 1987). Increased incubation temperature can result in early emergence, longer growing season, larger size and higher over-winter survival rates of stream-resident species such as coho salmon, *O. kisutch* (Holby 1988), but they also can lead to a mis-match between the timing of downstream

migration and adequate levels of marine food resources, leading to reduced marine survival (Holby 1988, Holby and Scrivener 1989).

Species-specific models (e.g., Beacham and Murray 1990) have been developed to project hatch times and developmental stage of salmon embryos, given a known or simulated temperature regime (e.g., Sullivan *et al.* 1990). These projections can aid in assessing potential consequences of early emergence (Holby 1988), physical disturbance in streams (Johnson *et al.* 1989), or dewatering of streams (Graybill *et al.* 1979, Becker *et al.* 1983) on developing salmon. However, the variation in temperature among streams and the tendency of salmon populations to evolve local adaptations (Ricker 1972, Taylor 1991) indicates that species-specific models must be used with caution, as populations may vary considerably in time to hatch (Brannon 1987, Beacham and Murray 1989). Most of the information on incubation rate has been reported for populations of salmon in B.C. (e.g., sockeye: Brannon 1987, chinook, pink and chum: Beacham and Murray 1989, 1986, 1987, coho: Murray *et al.* 1990).

The purpose of this study was to examine the amount of variation in time to hatch among and within populations of coho salmon in Washington state. Coho salmon were selected because: (1) altered incubation temperatures may affect subsequent life-history events (Holby 1988); (2) many populations in Washington (Washington Department of Fisheries *et al.* 1993) and Oregon (Nickelson *et al.* 1992) are in jeopardy; and (3) the British Columbia data may not be representative of populations in Washington. Specifically, we

examined variation in incubation rate under different temperature regimes among populations, among families within populations, and among individuals within families.

Materials and Methods

Gametes from 10 coho salmon populations in Washington were collected in fall and winter of 1989-1992 (Figure 1). Fish representing both the early and late spawning run of coho in the Solduc River were also sampled in 1990. Gametes were transported to either the University of Washington hatchery facility in Seattle or the University's research facility located at Big Beef Creek, Seabeck, Washington. In 1989, one female from each river was crossed with one male to form a single full sibling cross. This provided general information of the variance of individual hatch rates about the true mean of a single family.

The females collected in 1990-91 were each mated with two males from their respective populations to form half sibling crosses. Usually this type of cross is made and replicated to allow statistical partitioning of the paternal, maternal, and interactive genotypic effects on the phenotype, in this case, time to hatch. Due to hatchery space constraints, crosses were not replicated, thus rigorous statistical treatment of the genotypic data was not possible.

The 1989 and 1990 crosses were each divided into four lots of approximately 250 eggs. Embryos were incubated at 6, 8, 10, and 13°C ($\pm 0.5^\circ$) in 1989 and at 6, 9, and 12°C ($\pm 0.5^\circ$) in 1990. Embryos were incubated in polyvinyl chloride (PVC) cups (7.6 cm diameter and 6.4 cm high) with plastic mesh bottoms. Ten cups were placed centrally on plastic grids approximately 7 cm above the incubation trough (1.0 x 0.5 x 0.15 m) floor. A 2.5 cm dia. x 0.5 m long perforated PVC pipe was installed at the head of the trough to evenly distribute flows (8 l min⁻¹). Dechlorinated municipal water was chilled by an immersion-coil cooler or warmed by a steam heat exchanger. The 1991 crosses were divided into lots of approximately 500 and each lot was individually incubated (6°C \pm 0.3) in a vertically stacked Heath tray.

Embryos were checked every two days to monitor hatch rates and remove dead eggs and alevins. Days and thermal units or TUs ($^\circ\text{C} \times$ number of incubation days) to different hatching stages were noted for all crosses. Dissolved oxygen levels were

monitored in the troughs and Heath trays and were consistently at or near saturation. Temperatures were controlled automatically, and continuously recorded electronically. Embryos were incubated in total darkness except when light was needed to monitor hatching.

Results

Single crosses (one female crossed with one male) from the Toutle, Elochoman, Baker and Clark rivers were incubated at 6, 8, 10 and 13°C in 1989. The number of TUs required to obtain 50% hatching of Toutle River embryos increased with increasing temperature (Figure 2). Elochoman and Baker River eggs required slightly fewer TUs to 50% hatch at the lower and higher (6° and 13°) than at intermediate temperatures (Figure 2). Clark Creek embryos required slightly more TUs to 50% hatch at 6°C than embryos from the other rivers and 100% mortality was observed in the 13°C treatment. The number of TUs required from first to 50% hatch decreased with increasing temperature for all families. For example, Elochoman River eggs required 138 TUs from first to 50% hatch at 6°C, and only 39 TUs at 13°C.

Five populations (represented by 2-6 families per population) incubated at 6, 9 and 12°C (Table 1) exhibited considerable variation in incubation rate at a given temperature. For example, embryos from the Toutle, Snow and Cowlitz rivers required, on average, more TUs to 50% hatch at 9°C than at 6°C, whereas embryos from the early and late runs of the Solduc River required the same or fewer. Embryos collected after 27 November (Solduc-late run, Snow, and Cowlitz rivers) required fewer TUs to reach 50% hatch than embryos collected on 30 October from the Solduc early run. The Toutle River embryos, collected 1 November, had similar 50% TU requirements to the later spawning populations at 6 and 12°C, but required more TUs to 50% hatch at 9°C than the other populations. The Toutle River incubation rates were the least protracted at 6 and 12°C and the most protracted at 9°C, relative to all other populations.

We compared incubation rates of embryos collected from the early (30 October 1990) and late (27 November 1990) spawning runs of coho in the Solduc River (Table 1). The early run embryos incubated at 6°C required, on average, 135 more TUs to realize first hatch and an additional 135

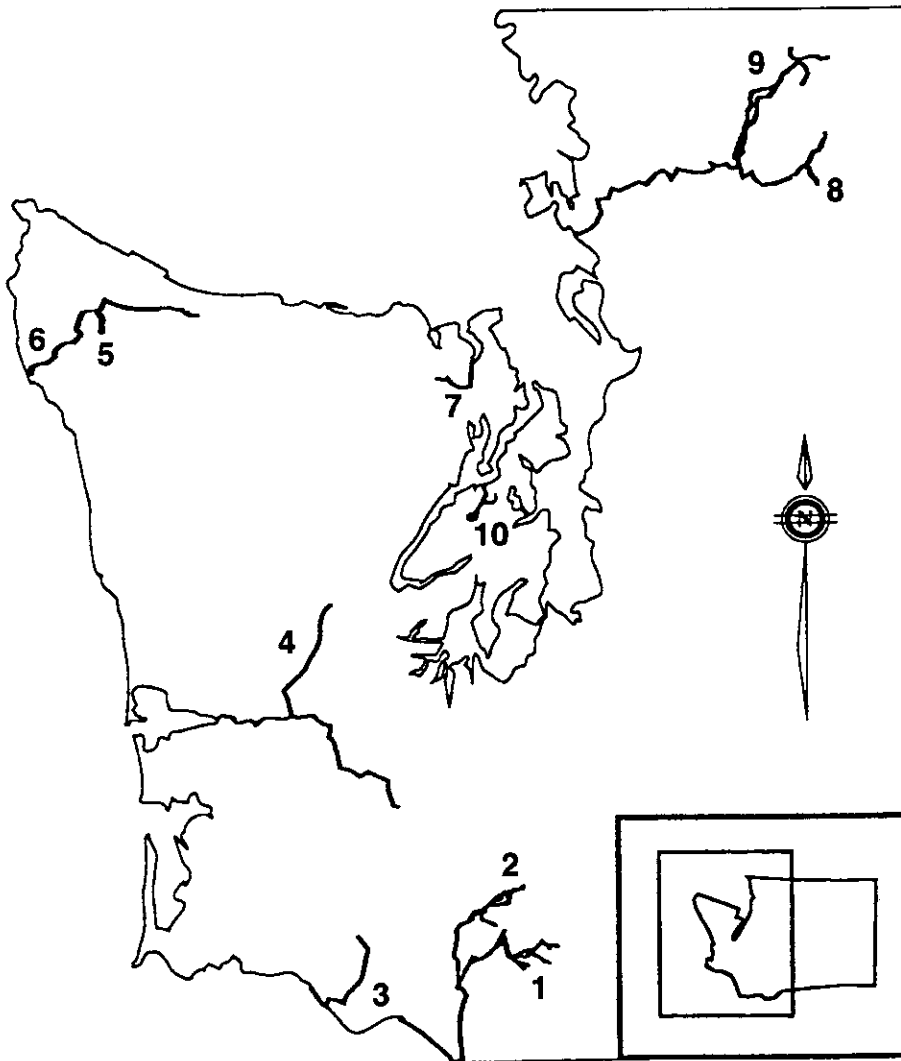


Figure 1. Map of western Washington, indicating sites where gametes were collected for coho salmon incubation studies: (1) Toutle River, (2) Cowlitz River, (3) Elochoman River, (4) Bingham Creek, (5) Bockman Creek, (6) Soldue River, (7) Suow Creek, (8) Clark Creek, (9) Baker River and (10) Big Beef Creek.

TUs to reach 50% hatch than the late run embryos. The early run embryos still required more TUs to 50% hatch than the late run at higher incubation temperatures (9 and 12°), but the TUs to first hatch were similar.

We examined time to hatch at 6°C in more detail, as this is more representative of coho salmon incubation regimes than the higher temperatures. Analysis of data from six populations with at least four families each revealed significant variation (ANOVA, $F = 4.11$, $P < 0.01$) in TUs to hatch

(Table 2). A posteriori analysis (least squares means) revealed that the incubation rate of Cowlitz River coho salmon was slower than that of the other populations, accounting for the most of the variation. There was also variation in TUs to 100% hatch among the three populations with at least 10 families (ANOVA $P < 0.001$, Table 3).

In addition to variation among populations and families, there was also variation within families in hatching time. This was examined in detail in the three populations with the largest numbers of

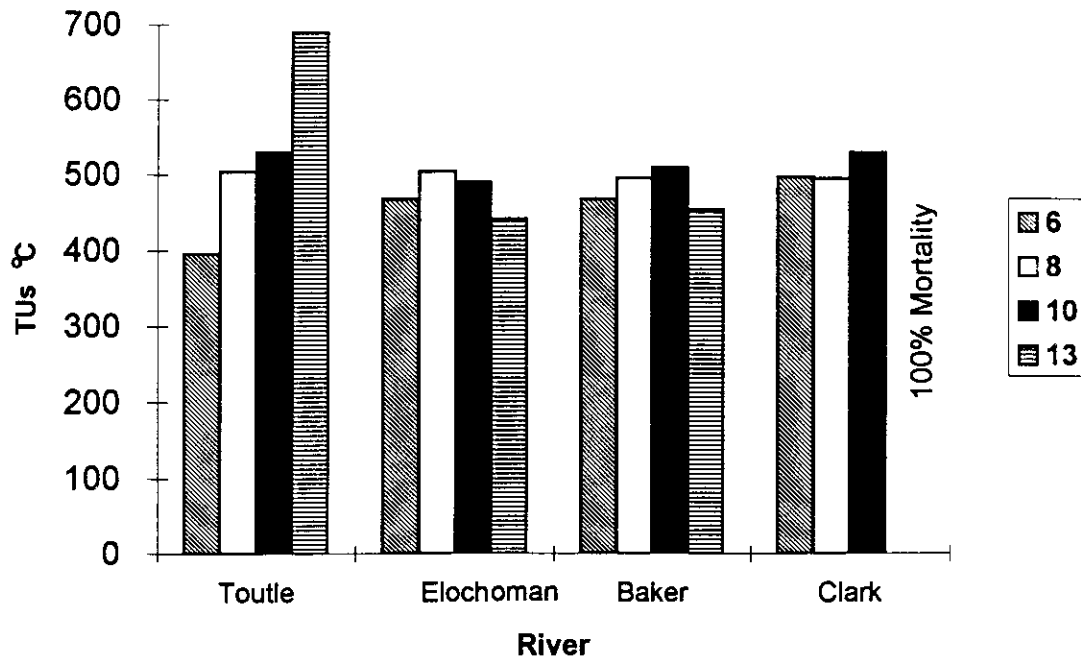


Figure 2. Number of centigrade temperature units (TUs) required for 50% of the embryos from four Washington coho salmon populations to hatch at constant temperatures.

TABLE 1. Average number of temperature units (TUs) to first and 50% hatch in five populations of coho salmon incubated at one of three constant temperatures in 1990. The number of families within each population is designated in parentheses and the range of TUs among families within populations are also indicated.

Population (spawn date)		Incubation Temperature		
		6	9	12
Toutle (6) (1 Nov.)	first:	447 (432-456)	396 (387-405)	432 (420-444)
	50%	471 (450-492)	551 (513-613)	458 (456-468)
Solduc-early (2) (30 Oct.)	first:	513 (510-516)	423 (423)	480 (468-492)
	50%	606 (606)	549 (549)	540 (540)
Solduc-late (5) (27 Nov.)	first:	374 (294-462)	439 (432-450)	478 (456-504)
	50%	471 (456-504)	468 (459-486)	514 (492-540)
Snow (2) (30 Nov.)	first:	423 (420-426)	423 (414-432)	426 (420-432)
	50%	462 (462)	486 (468-504)	482 (477-486)
Cowlitz (4) (5 Dec.)	first:	327 (246-414)	401 (387-423)	414 (408-420)
	50%	438 (420-468)	491 (450-567)	462 (444-480)
Average of populations	first	416.8	416.4	446.0
	50%	489.6	508.2	492.0

families (Big Beef, Bockman and Bingham creeks). Within families, the dates of first and last hatching spanned about 9-14 days (Table 3). Bockman Creek families had the most protracted hatch times and required the most TUs to realize 100% hatch.

We separated families into two groups based on paternal half sibling crosses and evaluated the potential effect male genotype had on TUs to first and 100% hatch (Table 4). The average number of TUs required to first and 100% hatch did not

TUs as the Big Beef population which had the smallest eggs.

As with sockeye salmon (Brannon 1987), and other species (Beacham and Murray 1990), coho salmon incubation generally displays a compensatory response to increasing temperatures up to about 10°C. That is, while incubation requires fewer days at higher temperatures, more TUs are required so that development does not proceed as rapidly as would occur if a fixed number of TUs were required. The effect of this compensation is to reduce the variation in emergence date for a given distribution of spawning dates. However, this compensatory relationship was much more pronounced in some populations than others, hence projections of incubation rate based on general models will have some error. Moreover, the compensation is most obvious at temperatures below those in our study (e.g., Tang *et al.* 1987). Little compensation was observed over the range of temperatures that we used and some reverse compensation (i.e., fewer TUs at high temperatures) was observed (e.g., Figure 2), consistent with Tang *et al.* (1987).

A species-specific model of coho salmon incubation, based primarily on British Columbia data (Model 4 of Beacham and Murray 1990), predicted somewhat earlier hatching than we observed. The model estimated 460 TUs to 50% hatch at 6°C compared with the mean of 490 (i.e., 5 days) from five populations (Table 1). The 50% dates were not recorded for the Bingham, Bockman and Big Beef creek populations but interpolated 50% dates were 494, 513 and 516 TUs, respectively. Tang *et al.* (1987) reported 492 TUs to 50% hatch for coho from Washington's Dungeness River, similar to our average. However, the populations that we studied incubated more rapidly than the Skagit River coho salmon reported by Graybill *et al.* (1979), which required 573 TUs to 50% hatch at 6.1°C. Populations from colder regions tend to require fewer TUs to hatch than those from warmer regions (Beacham and Murray 1989, Murray *et al.* 1990). Assuming that British Columbia temperatures are likely to be colder than those in Washington, the tendency for Washington

populations to incubate more slowly than British Columbia populations is not unexpected.

In addition to the variation among populations and families in incubation rate, we also observed variation in hatching date among individuals within families. The first and last individuals to hatch within a family were separated by about 9–14 d. The variation can be magnified at emergence, as Mason (1976) reported variation in emergence from a simulated redd of 20–23 d within full-sibling families. Experiments with Atlantic salmon (*Salmo salar*) indicated that the variation in first feeding date within families leads to differences in social dominance, growth rate and duration of freshwater residence (Metcalf and Thorpe 1992).

Coho salmon populations in the Pacific Northwest often show very protracted spawning periods (Sandercock 1991). Temperature compensation and variation in TUs to emergence between early and late spawners (Brannon 1987) will tend to compress the time of fry emergence. However, the range of spawning dates and variation in development among and within families will generally result in an extended period of emergence. This pattern, combined with variation in fry size related to egg size and family-specific differences in growth and distribution (Quinn *et al.* 1994), may lead to great variation among families in fry size and social status at the end of the summer. Size is also related to overwinter survival in freshwater (Hartman *et al.* 1987), duration of freshwater residence (Holtby 1988) and marine survival (Holtby *et al.* 1990) in coho salmon. Thus, factors that affect the average incubation rate or the variation among and within families may substantially affect the fitness of young salmon.

Acknowledgements

John T. Konecki was in the process of completing this research as part of his doctoral dissertation when he lost his life in an airplane accident. We are grateful to the U.S. Fish and Wildlife Service, the Washington Forest Protection Association and the H. Mason Keeler endowment for supporting this work.

Literature Cited

- Beacham, T. D., and C. B. Murray. 1986. Comparative developmental biology of pink salmon, *Oncorhynchus gorbuscha*, in southern British Columbia. *J. Fish Biol.* 28:233-246.
- . 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Can. J. Fish. Aquat. Sci.* 44:244-261.

- . 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. *Can. J. Zool.* 67:2081-2089.
- . 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Trans. Amer. Fish. Soc.* 119:927-945.
- Becker, C. D., D. A. Neitzel, and C. S. Abernethy. 1983. Effects of dewatering on chinook salmon redds: tolerance of four developmental phases to one-time dewatering. *N. Amer. J. Fish. Mgmt.* 3: 373-382.
- Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. *Can. Sp. Publ. Fish. Aquat. Sci.* 96:120-124.
- Godin, J.-G. J. 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. In E. L. Brannon and E. O. Salo, (eds.). *Proceedings of the salmon and trout migratory behavior symposium*. School of Fisheries, University of Washington, Seattle, Washington. pp. 22-50.
- Graybill, J. P., R. L. Burgner, J. C. Gislason, P. E. Huffman, K. H. Wyman, R. C. Gibbons, K. W. Kurko, Q. J. Stober, T. W. Fagnan, A. P. Stayman and D. M. Eggers. 1979. Assessment of the reservoir-related effects of the Skagit project on downstream fishery resources of the Skagit River. Final Report for City of Seattle, Department of Lighting, Seattle, Washington. Univ. of Washington, College of Fisheries, Fisheries Research Institute.
- Hartman, G., J. C. Scrivener, I. B. Holtby, and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish populations processes in Carnation Creek, a coastal rain forest stream in British Columbia. In E. O. Salo and T. W. Cundy, (eds.). *Streamside management: forestry and fishery interactions*. Institute of Forest Resources, Univ. of Washington, Seattle. pp. 330-372.
- Holtby, I. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 45:502-515.
- Holtby, I. B. and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia. *Can. Sp. Publ. Fish. Aquat. Sci.* 105:62-81.
- Holtby, I. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 47:2181-2194.
- Johnson, S. C., G. A. Chapman, and D. G. Stevens. 1989. Relationships between temperature units and sensitivity to handling for coho salmon and rainbow trout embryos. *Prog. Fish-Cult.* 51: 61-68.
- Mason, J. C. 1976. Some features of coho salmon, *Oncorhynchus kisutch*, fry emergence from simulated redds and concurrent changes in photobehavior. *Fish. Bull.* 74:167-175.
- Metcalfe, N. B., and J. E. Thorpe. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* 41(Suppl. B):93-99.
- Murray, C. B., T. D. Beacham, and J. D. McPhail. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. *Can. J. Zool.* 68:347-358.
- Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- Nickelson, T.E., J.W. Nicholas, A.M. McGie, R.B. Lindsay, D.L. Bottom, R.J. Kieser and S.F. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Dept. Fish & Wildlife. 83 p.
- Quinn, T.P., A.H. Dittman, N.P. Peterson and E. Volk. 1994. Spatial distribution, survival and growth of sibling groups of juvenile coho salmon (*Oncorhynchus kisutch*) in an experimental stream channel. *Can. J. Zool.* 72: 2119-2123.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In R.C. Simon and P.A. Larkin, (eds.), *The stock concept in Pacific salmon*. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver. pp. 19-160.
- Saunderscock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In C. Groot and L. Margolis, (eds.), *Pacific salmon life histories*. University of British Columbia Press, Vancouver. pp. 395-445.
- Sullivan, K. J., J. L. Tooley, K. Doughty, J. E. Caldwell, and P. Knudsen. 1990. Evaluation of prediction models and characterization of stream temperature regimes in Washington. *Timber/Fish/Wildlife Rep. No. TFW-WQ3-90-006*. Olympia, Washington, Wash. Dept. Nat. Resources. 224 p.
- Tang, J., M. D. Bryant, and E. L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. *Prog. Fish-Cult.* 49:167-174.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98:185-207.
- Theedinga, J. F., M. L. Murphy, J. Heifitz, K. V. Koski, and S. W. Johnson. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) in southeast Alaska streams. *Can. J. Fish. Aquat. Sci.* 46:1383-1391.
- Washington Department of Fisheries, Washington Department of Wildlife, and Western Washington Treaty Indian Tribes. 1993. 1992 Washington state salmon and steelhead stock inventory. Olympia, Washington. 212 p.
- Withler, F. C., and R. B. Morley. 1970. Sex-related parental influences on early development of Pacific salmon. *J. Fish. Res. Board Can.* 27:2197-2214.
- Wood, C. C. and C. J. Foote. 1990. Genetic differences in the early development and growth of sympatric sockeye salmon and kokanee (*Oncorhynchus nerka*), and their hybrids. *Can. J. Fish. Aquat. Sci.* 47:2250-2260.

Received 29 June 1993

Accepted for publication 21 November 1994