

Thermal Tolerance and Rate of Development
of Coho Salmon Embryos

by
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Abstract

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By John N. Dong

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College of Fisheries

Coho salmon eggs from the University of Washington Hatchery (UW) and the Dungeness River, WA, were incubated in constant temperatures ranging from 0.1° to 17.0°C from fertilization to yolk absorption. The lower lethal threshold for embryonic development was established at between 0.6° and 1.3°C for UW coho. The upper lethal threshold was between 12.5° and 14.5°C for UW coho and between 10.9° and 12.5°C for Dungeness River coho. Incubation temperatures between 4.0° and 6.5°C produced fry with the greatest dry body weight and yolk absorption efficiency. Pace of development inferred by the number of thermal units required to reach hatching and yolk absorption was not constant throughout the temperature range. Development per unit of temperature was greater at low temperatures than at high temperatures. Fewer thermal units were required at low temperatures than at high temperatures to reach yolk absorption. Best-fit equations of the least square regression of the dependent variable of temperature and the independent variables of both the number of days and thermal units to reach both 50% hatching and yolk absorption showed that they are not linearly related. Developmental compensation behavior was compared between the two stocks of coho and to that of sockeye and pink salmon.

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INTRODUCTION

Coho salmon, Oncorhynchus kisutch, generally spawn in small tributary streams that are subject to greater diel and annual temperature variations than would normally be experienced in larger rivers. This species generally spawns later in the fall than the other Pacific salmon when river temperatures are cooling rapidly. Its eggs experience colder water temperatures during spawning and early incubation than do early-fall spawning species, such as sockeye, O. nerka, and pink salmon, O. gorbuscha.

As poikilotherms, developmental rates of salmon eggs are affected by temperature changes in the stream environment. However, coho salmon eggs may be more influenced by environmental perturbations than other salmon species because of their more variable incubation habitat. A one- or two-degree change in winter low temperatures may significantly alter hatching time and ultimately influence emergence timing of coho salmon fry.

There is currently very little published data on the effects of temperature upon the development of coho eggs. What is the range of temperatures tolerated by incubating coho embryos? How do coho embryos cope with extreme changes in stream temperatures? Is the relative pace of development constant over the entire temperature range experienced by incubating coho? And is the response of coho embryos to temperature different from that exhibited by early-fall spawning species?

This study was undertaken to further investigate the influence of temperature on coho development. The objectives were defined as follows:

- 1) Provide baseline data on the rate of development of coho eggs at various constant temperatures ranging from near freezing to 17°C.
- 2) Establish the upper and lower temperature limits for successful coho incubation.
- 3) Determine whether the effect of temperature on the pace of development of coho embryos is the same as that of other salmon embryos.

REVIEW OF SELECTED LITERATURE

The effects of temperature on the speed of development of fish eggs have long been of intense interest to fish biologists. The thermal sums hypothesis was one of the first rules to be applied to the development of living organisms by fish biologists. The hypothesis states that development is the sum total of an organisms's thermal experience and can be expressed by the formula $\underline{y}x = \underline{k}$, where $\underline{y}$ is time of development, $\underline{x}$ is temperature, and $\underline{k}$ is a constant. The product of time and temperature is constant at all normal temperatures and the graph of $1/y = kx$ is a straight line. This rule formed the basis for many subsequent hypotheses.

One of the first to document the effect of temperature on fish egg development was Ainsworth, who in 1859 experimented with eggs of the speckled brook trout, Salvelinus fontinalis. He incubated brook trout eggs in average water temperatures ranging from 37° to 54°F and noted the number of days required to hatching at these temperatures. His data showed that fewer days were required as temperature increased (Norris 1868; Embury 1934).

An often quoted "rule of thumb" was stated by Seth Green (1870): "Trout eggs will hatch in 50 days at a mean water temperature of 50°F and for each degree colder or warmer five days more or less will be required, the difference, however, increasing the farther we recede from 50 degrees." This rule was widely embraced by fish culturists until 1901, when Wallich offered a more quantitative method for monitoring fish egg development. He called it the "temperature or thermal unit system." Based on the thermal sums hypothesis, a temperature

unit (t.u.) was defined as 1°F above 32°F for a period of 24 hours. Thus, eggs incubating at a mean daily temperature of 50°F would accumulate 18 t.u. per day of incubation. Working with chinook salmon eggs, O. tshawytscha, Wallich concluded that the number of t.u. required from fertilization to hatching was constant over all temperatures that were normal to the eggs. He found that about 900 t.u. were needed for eggs to hatch at incubation temperatures between 42° and 51°F . The temperature unit system offered a convenient way of monitoring development and is still widely used by fish culturists today.

Reibisch (1902) argued that since the eggs of cod and plaice were shown to be capable of development at temperatures below freezing, temperature units should be reckoned from some point below freezing, or the lowest point at which some development could occur. This he termed the "threshold temperature". His arguments were based on data presented by Dannevig (1894), who successfully incubated cod eggs at -1°C for about one month. These eggs later hatched normally when transferred to 6°C .

Apstein (1909) proposed an alternate thermal unit system. His temperature unit was called a "Tagesgrade." A tagesgrade is the product of temperature in centigrade and days. It differed from Wallich's temperature unit in that it was reckoned from the lowest point at which development could occur and not from the freezing point of water.

Van't Hoff (1884) observed that the velocity of certain chemical reactions progressed at a geometric rate when the temperature was increased at an algebraic rate. Van't Hoff's Q_{10} proved to be unsatisfactory when applied to the data of Dannevig by Johansen and Krogh

(1914), who concluded that the reciprocal of the number of days to hatching and temperature were linearly related. That is, the speed of development was simply proportional to increases in temperature. This finding was essentially a restatement of the thermal sums hypothesis.

Johansen and Krogh (1914) also concluded that the egg did not derive its energy for development from heat supplied by the environment but rather from the metabolism of egg tissue. This view differed from that of Reibisch, who thought that some heat from the outside was necessary for development.

It has been shown that temperature certainly has an effect on the development of fish eggs. It acts as a catalyst for the chemical reactions that are necessary for the development of the embryo. The complexity of the living cytoplasm and its response to temperature makes it almost impossible to express satisfactorily the speed of development by a mathematical formula. Belehradek (1929) recognized this problem and pointed out the deficiencies of the formulas of Van't Hoff and Arrhenius, which are essentially the same. Both assume that a given difference in temperature will result in a proportional difference in the speed of development that is constant throughout the temperature range of an animal. Belehradek modified the thermal sums hypothesis to the form

$$y = \frac{k}{x^b}$$

where b is a new constant. According to Belehradek, this formula takes into account the greater effect of a 1° increase in temperature at low temperatures than at temperatures near the optimum. This relationship he felt better approximated real life.

Seymour (1956), working with chinook salmon eggs at the University of Washington, found that the speed of development in constant temperatures ranging from 40° to 58°F was adequately expressed by either the thermal sums hypothesis, the Belehradek equation, or an equation of the logistic curve (Davidson, 1944). In a more recent paper, Alderdice and Velsen (1978) assembled data from the literature on chinook salmon incubation and fitted them to different forms of the same three equations used by Seymour. They found the log-inverse form of Belehradek's equation best fitted the data. They also found that at temperatures below 4°C, the thermal sums hypothesis tended to overestimate hatching time. This suggests that the rate of development is not constant in relation to temperature throughout the range of temperatures compatible with the egg. Specifically, chinook eggs developed at a faster rate than would be expected at temperatures below 4°C.

This apparent acceleration of development at low temperatures was observed by Embury (1934) in the brook trout. He plotted log days against temperature and found that there was a change in the slope of the curve at temperatures below 3°C and above 10°C. He concluded that brook trout eggs developed faster than normal below 3°C and slower than normal at temperatures above 10°C. He believed that temperatures between 3° and 10°C produced a normal rate of development. He also observed a similar speeding up of development in the rainbow trout, Salmo gairdneri, at temperatures above 9°C.

Price (1940) found that the speed of development of the whitefish, Coregonus clupeaformis, embryos to hatching differed at temperatures above and below 6°C. An increase of 1°C at temperatures below 6°C

increased the speed 1.205 times, whereas a 1°C increase at temperatures above 6°C increased the speed by only 1.157 times.

Brannon (International Pacific Salmon Fisheries Commission, manuscript), working with sockeye and pink salmon eggs, found that an increase in temperature units is required to reach yolk absorption as temperature increases; more than three times the t.u. accumulated at 34°F were required at 60°F. He concluded that development was faster at low temperatures than at high temperatures. Otherwise, the number of temperature units required would be about equal at all temperatures.

A distinction needs to be drawn between the rate of development defined by the number of (or a transformation of) days required to hatching and what may be called the pace of development that is implied by an interpretation of the number of thermal units required to hatching. The former definition involves a measurement of time (incubation period) whereas the latter is a more general indicator of the relative amount of embryonic growth per unit of temperature experienced at different temperatures. By the first definition, a faster rate of development is inferred if the incubation period of eggs at a particular temperature decreases (with increasing temperature) by an amount less than that expected from a proportional decrease at another temperature. This was essentially how the previously mentioned investigators, with the exception of Brannon, interpreted their data on egg development. A greater pace of development, on the other hand, may not be directly reflected in the incubation period of the egg. The incubation period

still decreases with increasing temperature but the number of t.u. required to reach hatching should remain about the same over all temperatures if the pace of embryonic growth is constant (Wallich 1901). A greater pace of development at temperature A than temperature B is inferred if the number of t.u. required to hatching at temperature A is less than that required at temperature B. In other words, the amount of development produced by the accumulation of one t.u. is greater at temperature A than at temperature B. Confusion can arise when one ponders the apparent contradiction of a greater pace of development at cold temperatures with a corresponding lengthening of the incubation period.

It is apparent that the relationship between speed of egg development and temperature cannot be described satisfactorily by a linear equation. Garside (1966) criticized the practice of many investigators who have tended to consider only the central or linear portion of the developmental curve. Many extrapolated the curve to determine the threshold temperature, which usually resulted in a subzero temperature. But the lower lethal temperature of most fish eggs is usually above 0°C. Granted, the central portion of the "real-life" developmental curve is, in all probability, linear, as is evident in the works of the aforementioned investigators. But it is the nonconformity of the extremities of the curve that is of special interest. Many investigators considered these outlying temperatures as being "abnormal." But winter low temperatures in many streams often decrease to these levels. To the developing embryo, these temperatures represent a stress that has to be dealt with

not just in terms of survival, but also in terms of how it may affect emergence timing.

MATERIALS AND METHODS

1977

The study was conducted over a two-year period. In the first year, 1977, constant temperature incubation experiments were conducted using coho eggs from the College of Fisheries, University of Washington (UW) Hatchery and the Dungeness River Hatchery on Washington's Olympic Peninsula. These two populations of coho were chosen for this study because of their distinctly different thermal history.

The UW coho originated from a stock inhabiting a stream with relatively mild temperatures. Since their introduction, the UW coho have been exposed to even warmer incubation conditions (Donaldson and Brannon, 1976).

The Dungeness River, on the other hand, provides a much colder environment for its residents. Winter low temperatures often remain at near freezing levels. Incubation temperatures in the Dungeness River are generally about 6°C cooler than those of the UW Hatchery (Brannon, personal communication). A comparison of the thermal tolerance and rate of development of these two populations of coho salmon will provide insight on the early life environmental physiology of this species.

Incubation Tables

A total of nine incubation tables were built from plywood that had been coated with fiberglass. Three tables each had a capacity of 64 lots of eggs and the other six each had a 16-lot capacity. The three larger tables were built to accommodate the large number of egg lots required for another study. The construction of an incubation

table similar to the larger ones was described by Hickey, Hershberger, and Dong (1979).

Briefly, each large table was a hollow box measuring 2' x 8' and 3" deep with sixty-four holes drilled in the table top. Each hole was made to accommodate an incubation cup 2 1/2" deep made from 4 1/2" diameter PVC pipe. Fiberglass screening was glued to the bottom of the cup with PVC cement so that eggs could be placed inside. The cups were set into the holes in the table top and held secure by an "O" ring made from surgical tubing. Thus, each cup could be moved easily in and out of the hole.

Water was introduced to each table from a submerged perforated pipe running the entire length of the table. Water upwelled through the fiberglass screening, bathing the eggs, and exited out the top of each cup. A 3" wall around the table top kept the water level above the tops of the cups. Two exhaust holes were drilled at each end of the wall to allow even drainage from the table top.

The six smaller tables measured 2' x 2' and 3" deep and were of similar construction as the larger ones. All nine tables were fitted with covers made from wood molding and black plastic to provide darkness for the eggs.

Temperature Control

A steam-heat exchanger warmed water pumped into the UW Hatchery from Lake Washington. Chilled water was provided by cooling filtered city water in a 300-gallon Sunset brand milk cooler (Model No. MC-300PX) driven by a 1 1/2-ton compressor. The cooling power of the milk cooler was supplemented by an immersion-coil cooler driven by a 1/2-ton

compressor. Both the heat exchanger and milk cooler were equipped with thermostats and outlet temperatures were maintained at 17.0 and 1.3°C, respectively.

The two tempered waters were piped via separate PVC piping to each incubation table. The desired temperature and flow rate to each table were attained by mixing the two waters by means of PVC valves. The whole water system worked by gravity flow. Flow rates were 3.5 l/min in the large tables and 1.0 l/min in the small tables. The above flows were more than adequate for incubation, especially since eggs were placed only one layer deep in the cups. Dissolved oxygen ranged from 8 to 12 ppm and pH from 6.8 to 7.0. Dissolved oxygen measurements were made every two weeks during the first two months of the experiment and about once a month thereafter.

There was a slight difference in the incubation temperatures experienced by the UW and Dungeness eggs due to the manner by which tempered water entered the tables. Because water entered at one end of the table, a temperature gradient existed between the "inlet" and the "outlet" ends of the tables. The gradient was more pronounced in the three longer tables. At times, this gradient was as high as 1°C; however, it did not alter the incubation temperatures of the duplicate lots of each population in the tables because they were always placed in adjacent holes. The UW lots were placed at the "inlet" end, whereas the Dungeness eggs were placed near the "outlet" end. Eggs were also incubated inside the milk cooler to take advantage of the coldest water available. (Eggs were placed in incubation cups and then suspended by stainless steel wire.)

The actual temperatures experienced by each population in the incubation tables were as follows:

UW eggs: 1.3° (inside cooler), 2.5°, 3.0°, 4.0°, 6.1°, 8.4°, 10.2°, 12.4°, 14.4°, 17.0°C.

Dungeness eggs: 1.3° (inside cooler), 2.4°, 3.1°, 4.7°, 6.5°, 8.3°, 10.9°, 12.5°, 14.4°, 17.0°C.

Temperature was measured at the level of the eggs with a mercury-filled thermometer calibrated to 0.1°C intervals. Temperature in each table was recorded at least three times a day and then averaged. The range was 0.5°C at all temperatures. Two Bristol thermograph recorders continuously monitored the water temperature at the milk cooler and heat exchanger outlets.

Experimental Procedure

On November 25, 1977, eggs were stripped from fourteen ripe female coho salmon from the UW Hatchery homing pond and then thoroughly mixed to insure a homogeneous sample. Using 50-ml graduated cylinders, I divided the eggs into 50-ml egg lots and placed them in small styrofoam cups. Milt containing sperm from ten males was mixed together and 0.5 ml of milt was injected into each cup with a syringe. The egg and sperm mixture was stirred and water-activated, and duplicate lots were placed in the appropriate incubation tables.

Dungeness eggs taken from six females and fertilized with milt from four males arrived at the UW Hatchery on December 9, 1977. These eggs had been fertilized about four hours before arrival and were transported in quart-size glass jars filled with river water. The eggs were divided into lots and placed in the incubation tables.

Duplicate lots were placed in adjacent holes in the incubation table to minimize experimental variation.

Mortality in each cup was recorded daily. Egg samples were taken every week -- more frequently at the higher temperatures -- and placed in Stockard's solution to examine the embryonic development. Time to 50% hatching (H50) was determined by counting the number of hatched eggs each day. After hatching was complete, the number of alevins in each incubation cup was decreased to 100 to reduce crowding. Alevins were incubated until nearly "buttoned up" and then preserved in 10% formalin solution for at least seven days before analysis.

At the buttoned-up stage, there is usually a small amount of yolk still remaining in the yolk sac. However, if the fish were allowed to incubate much past this stage, they could absorb this residual amount of yolk and then begin to metabolize body tissue to maintain body functions. Therefore, the termination of the experiment at each temperature had to occur before all the fish were buttoned up. The experiment was terminated when approximately thirty individuals in each incubation cup had reached the buttoned-up stage.

Twenty-five fish drawn randomly from each temperature were dried and weighed to determine percent yolk absorption and efficiency. Yolks were separated from the fish and the two parts were dried for 24 hours at 90°C. Dry weights were made on a Mettler Gram-matic balance to the nearest 0.01 mg. All samples were kept in a desiccator during the weighing process to minimize moisture absorption.

Percent yolk absorption was calculated as follows:

$$\% \text{ yolk absorption} = \frac{Y_i - Y_t}{Y_i} \times 100$$

where Y_i^* = average dry weight of undeveloped egg
(without the chorion)

Y_t = dry weight of yolk remaining at termination
of experiment.

Yolk absorption efficiency, expressed as a percentage, is defined as follows:

$$\% \text{ yolk absorption efficiency} = \frac{\text{dry fry weight}}{Y_i - Y_t} \times 100$$

100% yolk absorption efficiency would be achieved if an alevin converted all of the yolk material it absorbed into body tissue.

The number of days required to reach 100% yolk absorption had to be estimated due to the improbability of obtaining alevins that would have absorbed 100% of their yolk on precisely the day the experiment was terminated. This estimate was based on the rate of absorption up to the point of termination:

* Since it was not feasible to determine Y_i of a live experimental fish, Y_i was estimated by averaging the yolk weights of twenty-five undeveloped eggs.

$$\text{estimated days to 100\% yolk absorption} = \frac{(D_t - D_{H50}) \times 100}{\% \text{ absorption at termination}} + D_{H50}$$

where D_t = number of days to termination of experiment

D_{H50} = number of days to 50% hatch.

This equation assumed that absorption of the remaining yolk would have proceeded at the same rate as during the period from hatching to termination.

Egg and alevin mortality at each temperature were used to determine the viability of these two populations of coho at those temperatures. Upper and lower lethal thresholds were established based on the following criteria: A particular temperature was considered to be lethal to incubation coho salmon embryos if 1) more than 50% of the eggs died, or 2) more than 50% of the alevins perished. In other words, a temperature was considered compatible to coho embryos only if both egg and alevin survival was greater than 50%.

Analysis of Variance and the Student-Newman-Keuls multiple comparisons procedure were used to test for the most compatible temperatures for egg incubation for each population based on dry fry weight and yolk absorption efficiency.

Development was monitored using the temperature unit system in degrees centigrade. This "centigrade unit" (c.u.) was adopted to facilitate the data recording process. A c.u. can be converted to the t.u. by the formula:

$$t.u. = 9/5 \times c.u.$$

Best-fit equations for the least squares regression of days or c.u. to reach both H50 and yolk absorption were generated to compare the development of these two coho populations to each other and to that of sockeye and pink salmon, which are early fall spawners.

1978

Results from the experiments conducted in 1977 indicated that the lower lethal threshold for coho salmon egg incubation was colder than 1.3°C. It was decided to incubate additional eggs at even lower temperature. The milk cooler was adjusted to 0.6°C for this purpose. In addition, eggs were placed in an ice bath at a temperature of 0.1°C. The ice bath was made with water from the milk cooler, and the eggs-water-ice mixture was placed in a 1/2-gallon covered plastic container and then refrigerated. Once a day, some of the water from the ice bath was carefully replaced with fresh water and ice. Dissolved oxygen in the ice bath was measured on days 3 and 9 and found to be 7.0 mg/ml and 6.7 mg/ml, respectively.

On December 11, 1978, small amounts of eggs from each of ten female coho salmon from the UW hatchery were fertilized with milt collected from seven males. The eggs were fertilized and divided into egg lots using the same procedure as described for 1977. Duplicate lots were placed in the milk cooler and in the water-ice mixture. The experiment was terminated when all eggs had perished in each lot.

RESULTS

For UW coho, experimental lots at 17.0°, 0.6°, and 0.1°C suffered 100% mortality with the majority perishing before blastopore closure (Table 1). There were no survivors to the eyed stage at 17.0°C. Only seven eggs (3.2%) developed to that stage at 0.6°C and all of them died shortly thereafter. All eggs incubating in 0.1°C had died after 19 days. Fixation of these eggs in Stockard's solution revealed very little development had occurred up to that time. Only four eggs (2%) showed a cell mass that could be considered a blastodisc. Incubation temperature of 14.4°C also appeared to be lethal to UW coho; only about 15% of the eggs hatched successfully and these showed a high alevin mortality. Temperatures between 12.4° and 1.3°C seemed to be compatible with normal embryonic development. Hatching success and alevin mortality were comparable at all temperatures within this range. Alevin abnormality was low at these temperatures. However, the incidence of labored, head-first hatching was high at temperatures colder than 4.0°C. At warmer temperatures, notably 17.0° and 14.4°C, many of the eggs erupted with yolk material extruding.

Constant temperature incubation data for Dungeness coho are presented in Table 2. Again, both lots at 17.0°C suffered 100% mortality, and 14.4°C was also lethal to Dungeness eggs. Only 1% of the eggs hatched successfully and the alevins died within 8 days of hatching. A temperature of 12.5°C also was too warm for successful incubation. Although egg mortality was not extremely high at that temperature, both experimental lots suffered alevin mortality in excess of 50%.

Table 1. Data on the survival and incubation characteristics of UH coho salmon eggs and alevins in water of constant temperatures.

Temp. °C	Egg mortality %	% hatched	No. of abnor- malities	Alevin mortality %	Days to 50% hatch	to 50% hatch		Days to termination	% yolk absorption at term.	Estimated days to 100% absorption	Estimated to 100% absorption	
						C.U.	T.U.				C.U.	T.U.
17.0	100											
17.0	100											
14.4	84.8	15.2	0	35.0	32	462	831					
14.4	85.8	14.2	0	20.0	32	462	832	59	91.3	62	899	1618
12.4	13.0	87.0	0	9.0	37	459	826	63	86.9	67	835	1504
12.4	21.4	78.6	0	5.0	38	472	850					
10.2	18.9	81.1	0	1.0	46	470	846	74	85.0	79	810	1458
10.2	7.5	92.5	0	5.0	47	461	866					
8.4	10.0	90.0	0	0	58	487	877	90	87.5	96	795	1430
8.4	7.0	93.0	0	1.0	58	487	877					
6.1	15.1	84.9	0	2.0	83	494	871	122	87.3	128	761	1370
6.1	16.5	83.5	0	1.0	83	494	871					
4.0	5.6	94.4	0	2.0	114	453	815	162	84.3	171	678	1221
4.0	0.8	99.2	0	0	115	457	823					
3.0	5.8	84.2	0	1.0	144	436	785					
3.0	3.7	96.3	1 Sp	1.0	147	445	801					
2.5*	4.1	95.9	1 Sp	0	162	404	727	230	86.2	241	595	1071
1.3*	10.0	90.0	2 Sp	0	188	253	456	292	82.4	307	394	709
0.6	100.0											
0.6	100.0											
0.1	100.0											
0.1	100.0											

* Only one lot was incubated at this temperature
Sp = spinal

Table 2. Data on the survival and incubation characteristics of Dungeness coho salmon eggs and alevins in water of constant temperatures.

Temp. °C.	Egg mortality %	% hatched	No. of abnor- malities	Alevin mortality %	Days to 50% hatch	to 50% hatch		Days to termination	% yolk absorption at term.	Estimated days to 100% absorption	Estimated to 100% absorption	
						C.U.	T.U.				C.U.	T.U.
17.0	100											
17.0	100											
14.4	99.0	1.0	0	100	32	462	832					
14.4	99.0	1.0	0	100	30	433	779					
12.5	26.0	74.0	0	59.0	37	461	830	66	84.6	71	888	1598
12.5	20.8	79.2	0	51.0	37	461	830					
10.9	10.6	89.4	0	3.0	42	456	821	68	84.3	73	792	1426
10.9	8.7	91.3	0	3.0	42	456	821					
8.3	8.5	91.5	0	0	59	488	878	90	86.4	95	790	1422
8.3	12.0	88.0	0	0	60	496	893					
6.5	6.3	93.7	0	0	78	505	909	117	86.9	123	793	1427
6.5	6.5	93.5	2 Sp	1.0	80	518	932					
4.7	6.4	93.6	0	0	101	473	851					
4.7	4.3	95.7	0	1.0	104	486	875	154	89.6	160	748	1346
3.1	8.3	91.7	1 Tw	3.0	146	452	814					
3.1	6.0	94.0	0	1.0	146	452	814					
2.4	6.3	93.7	1 Tw	0	176	416	749	243	84.1	256	611	1100
2.4	5.9	94.1	0	2.0	176	416	749					
1.3*	10.2	89.8	2 Sp	1.0	196	258	464	283	84.1	299	382	688

* Only one lot was incubated at this temperature.

Sp = spinal
Tw = twin

Table 2. Data on the survival and incubation characteristics of Dungeness coho salmon eggs and alevins in water of constant temperatures.

Temp. °C.	Egg mortality %	% hatched	No. of abnor- malities	Alevin mortality %	Days to 50% hatch	to 50% hatch		Days to termination	% yolk absorption at term.	Estimated days to 100% absorption	Estimated to 100% absorption	
						C.U.	T.U.				C.U.	T.U.
17.0	100											
17.0	100											
14.4	99.0	1.0	0	100	32	462	832					
14.4	99.0	1.0	0	100	30	433	779					
12.5	26.0	74.0	0	59.0	37	461	830	66	84.6	71	888	1598
12.5	20.8	79.2	0	51.0	37	461	830					
10.9	10.6	89.4	0	3.0	42	456	821	68	84.3	73	792	1426
10.9	8.7	91.3	0	3.0	42	456	821					
8.3	8.5	91.5	0	0	59	488	878	90	86.4	95	790	1422
8.3	12.0	88.0	0	0	60	496	893					
6.5	6.3	93.7	0	0	78	505	909	117	86.9	123	793	1427
6.5	6.5	93.5	2 Sp	1.0	80	518	932					
4.7	6.4	93.6	0	0	101	473	851					
4.7	4.3	95.7	0	1.0	104	486	875	154	89.8	160	748	1346
3.1	8.3	91.7	1 Tw	3.0	146	452	814					
3.1	6.0	94.0	0	1.0	146	452	814					
2.4	6.3	93.7	1 Tw	0	176	416	749	243	84.1	256	611	1100
2.4	5.9	94.1	0	2.0	176	416	749					
1.3*	10.2	89.8	2 Sp	1.0	196	258	464	283	84.1	299	382	688

* Only one lot was incubated at this temperature.

Sp = spinal
Tw = twin

Incubation temperatures of 10.9°C and below appeared to be compatible with normal development.

The incubation period of both populations of coho decreased with increasing temperature. For UW coho the number of days required to H50 ranged from 188 days at 1.3°C to only 32 days at 14.4°C. Estimated number of days to reach 100% yolk absorption were 307 and 62 at those respective temperatures. The incubation period of Dungeness coho similarly decreased with increasing temperature. At 1.3°C, 196 days were required to reach H50 and an estimated 299 days were needed to reach 100% yolk absorption. At 12.5°C, only 37 days were needed to reach H50 and an estimated 71 days to reach 100% yolk absorption.

On the other hand, the number of centigrade units required to reach H50 and 100% yolk absorption increased with increasing temperature. For UW coho, the number of c.u. required to H50 ranged from a low of 253 at 1.3°C to a high of 462 at 14.4°C. The estimated number of c.u. accumulated to 100% yolk absorption was 394 and 899 at those respective temperatures. That is a difference of well over two-fold. Similarly for Dungeness coho, eggs required only 258 c.u. to reach H50 at 1.3°C but 461 c.u. were needed at 14.4°C. Estimated c.u. to reach 100% yolk absorption were 382 and 888 at those two respective temperatures, again a difference of over two-fold.

In this study, the number of c.u. required to hatching and yolk absorption at each temperature was analyzed to reveal any differences in the rate and pace of development of coho eggs. The statistical technique of least squares regression was employed to generate a set of best-fit equations for the independent variable of incubation temperature

and the dependent variables of number of days required to reach H50, number of c.u. required to H50, number of days to 100% yolk absorption, and number of c.u. to 100% yolk absorption. The results are presented in Figures 1 to 8.

For both populations of coho salmon, the incubation of alevins at the highest temperature at which some fish survived to termination (14.4°C for UW coho and 12.5°C for Dungeness coho) produced the smallest fry (Tables 3 and 4). On the other hand, 1.3°C produced a fry that was closer in size to those reared at more moderate temperatures. For UW coho salmon, the lowest dry fry weight was recorded at 14.4°C. For Dungeness River coho salmon, both average fry length and dry weight were lowest at 12.5°C.

Yolk absorption efficiency followed the same pattern. Alevins in the highest incubation temperature showed the poorest efficiency (Tables 3 and 4). At 1.3°C, alevin yolk absorption efficiency was very comparable to those of other temperatures; and in many cases, it was higher. In the case of UW coho, the efficiency at 1.3°C was higher than those of other temperatures except at 4.0° and 6.1°C.

Analysis of variance of the alevin data and subsequent multiple range tests using the Student-Newman-Keuls procedure revealed that for UW coho, dry fish weight at termination was lowest at 14.4° and 2.5°C and highest at 4.0°C ($P = 0.05$). Yolk absorption was least efficient at 14.4°C and most efficient at 1.3, 4.0 and 6.1°C ($P = 0.05$). For Dungeness coho, dry fish weight was lowest at 12.5°C and highest at 4.7 and 6.5°C ($P = 0.05$). Yolk absorption efficiency at 12.5°C was significantly lower ($P = 0.05$) than at the other temperatures.

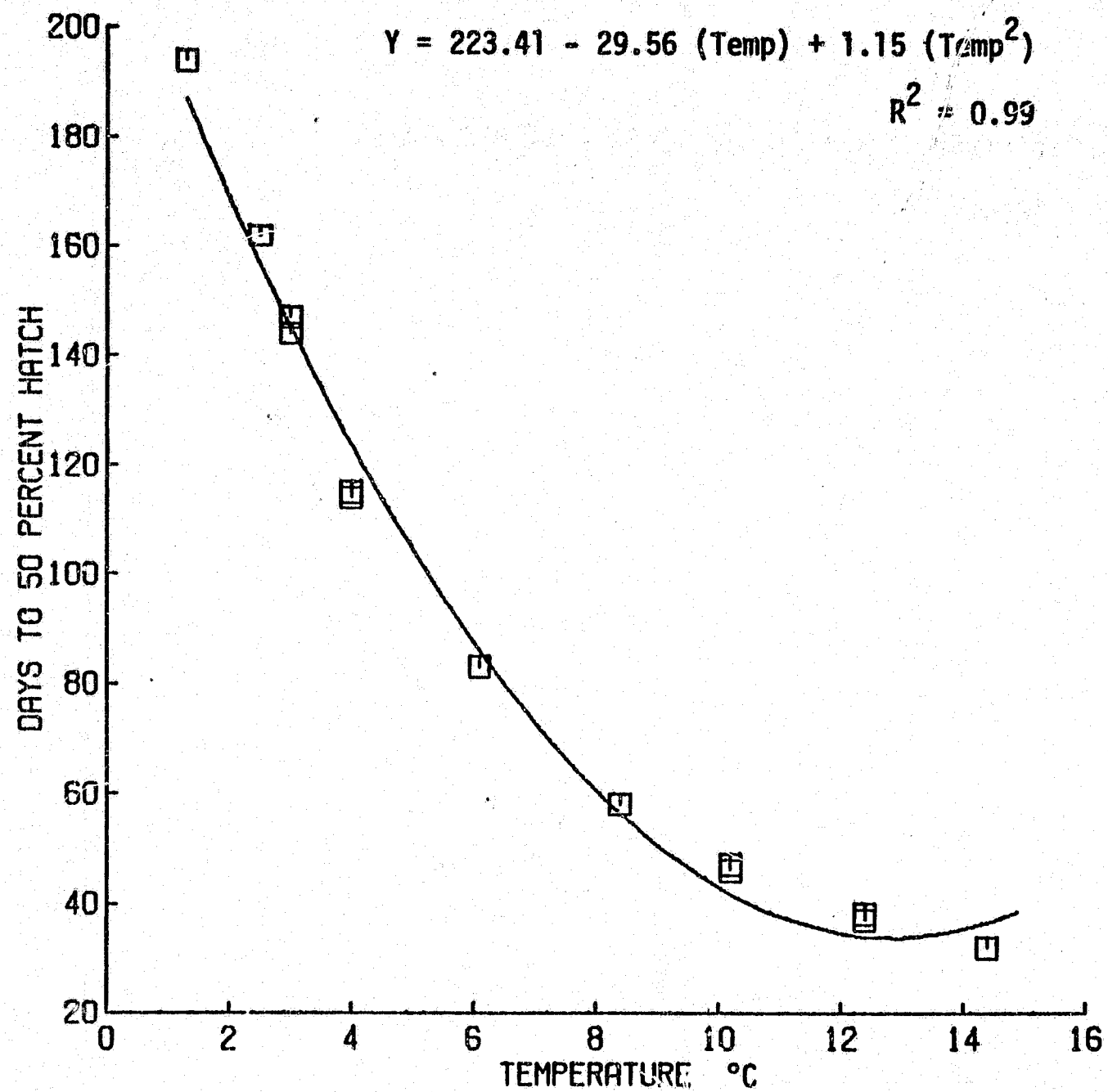


Figure 1. A plot of the quadratic line of the regression of days to H50 vs. temperature. UW Coho.

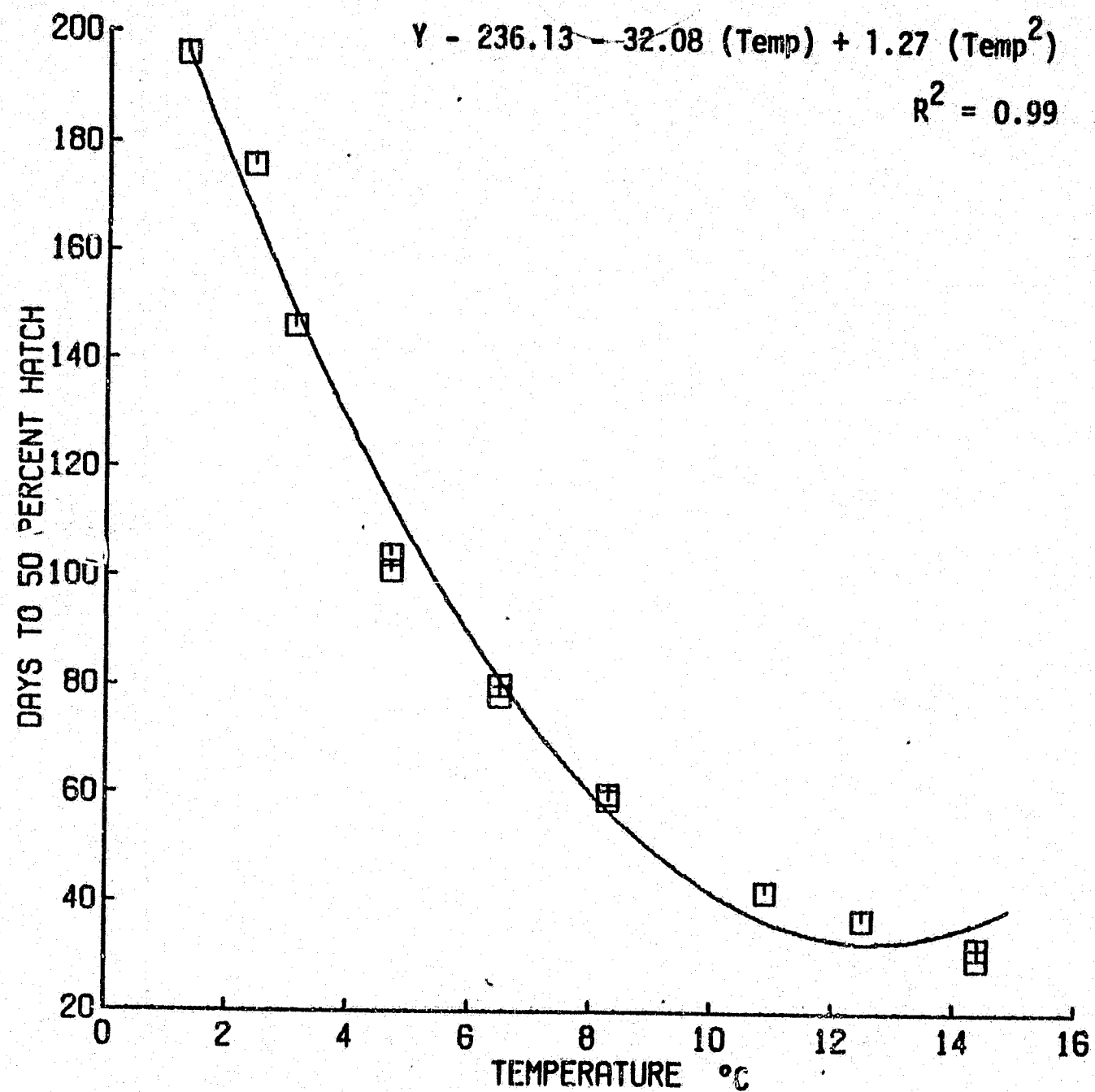


Figure 2. A plot of the quadratic line of the regression of days to H50 vs. temperature. Dungeness Coho.

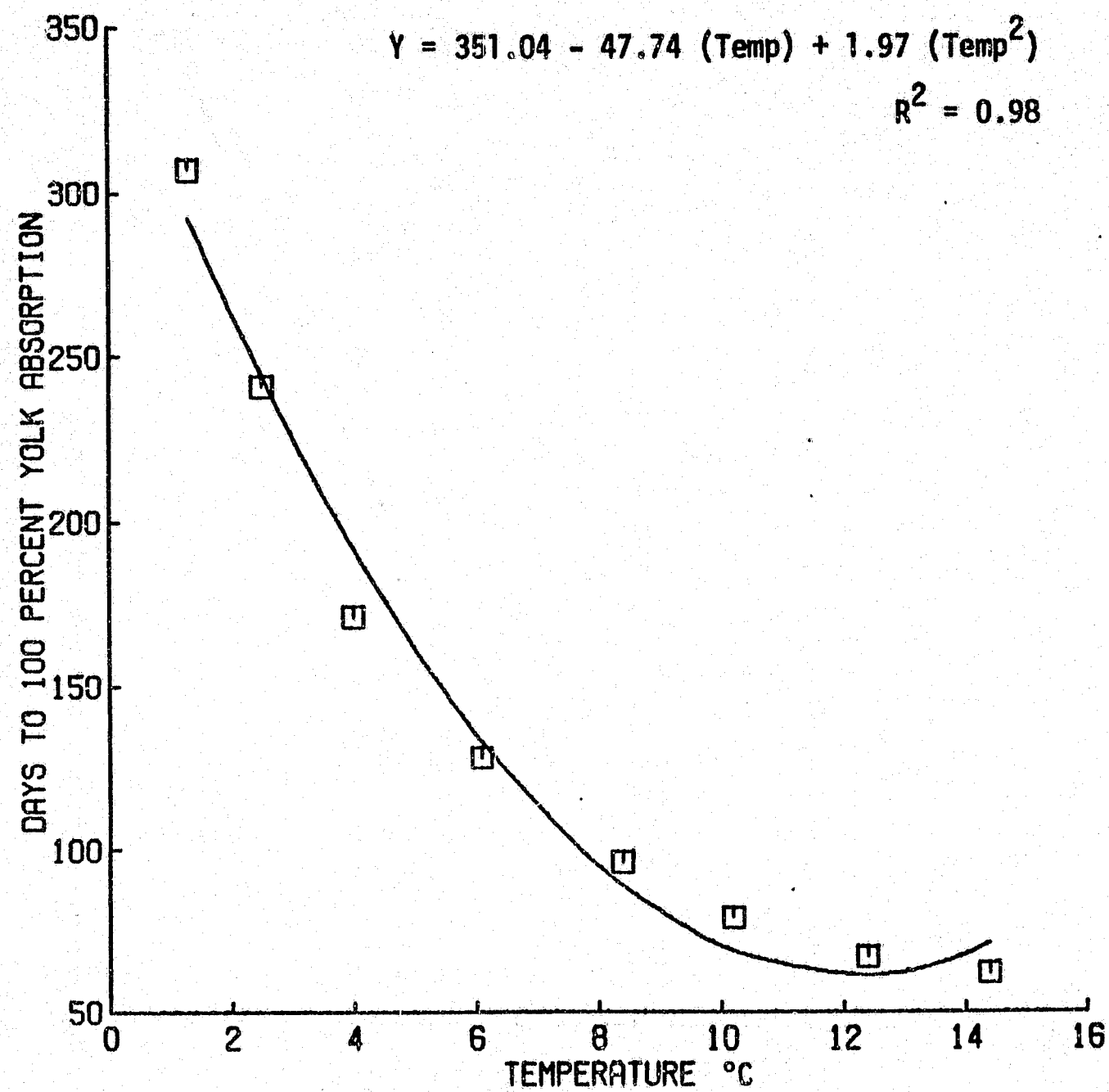


Figure 3. A plot of the quadratic line of the regression of days to 100% yolk absorption vs. temperature. UW Coho.

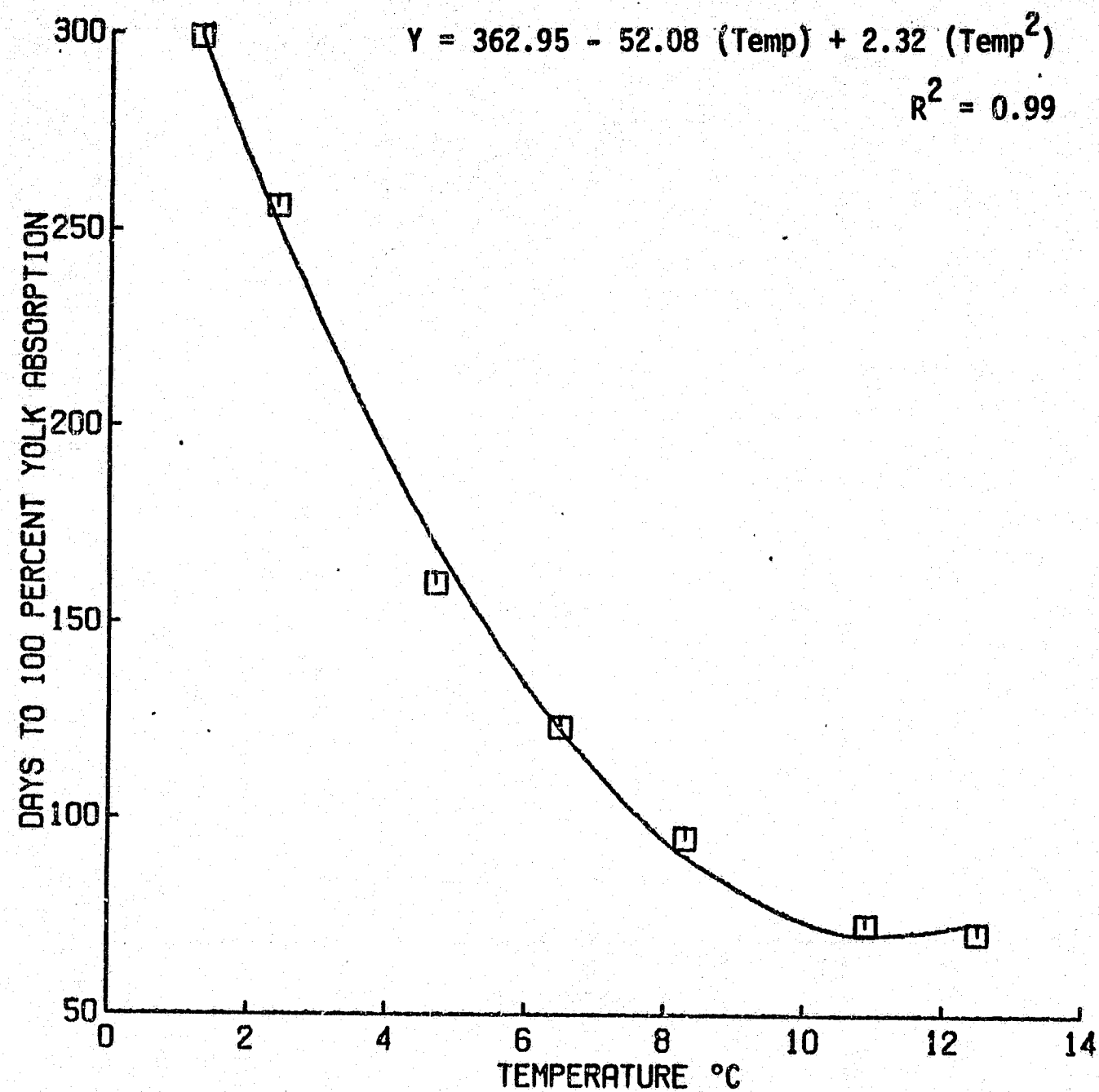


Figure 4. A plot of the quadratic line of the regression of days to 100% yolk absorption vs. temperature. Dungeness Coho.

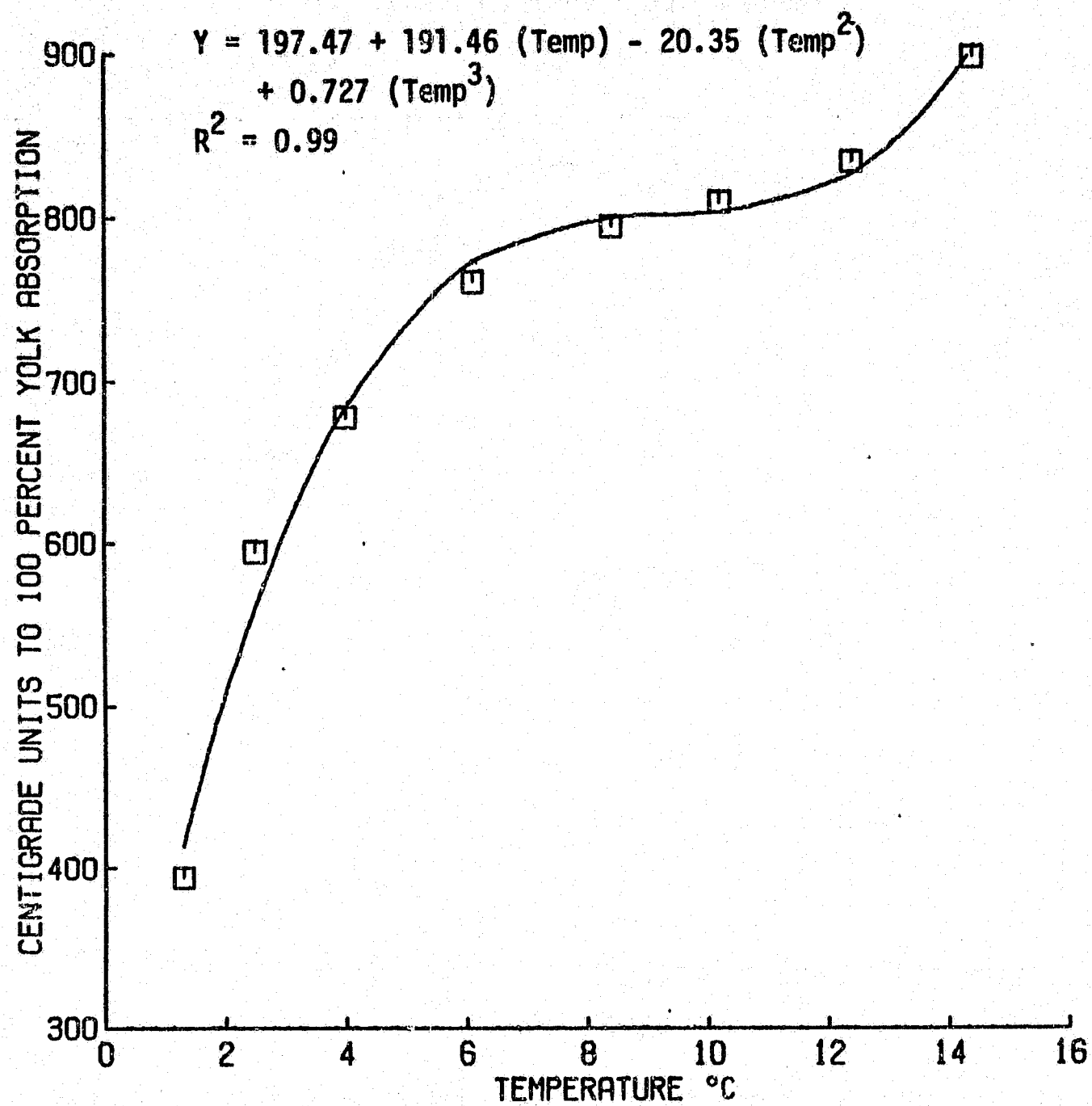


Figure 5. A plot of the cubic line of the regression of C.U. to 100% yolk absorption vs. temperature. UW Coho.

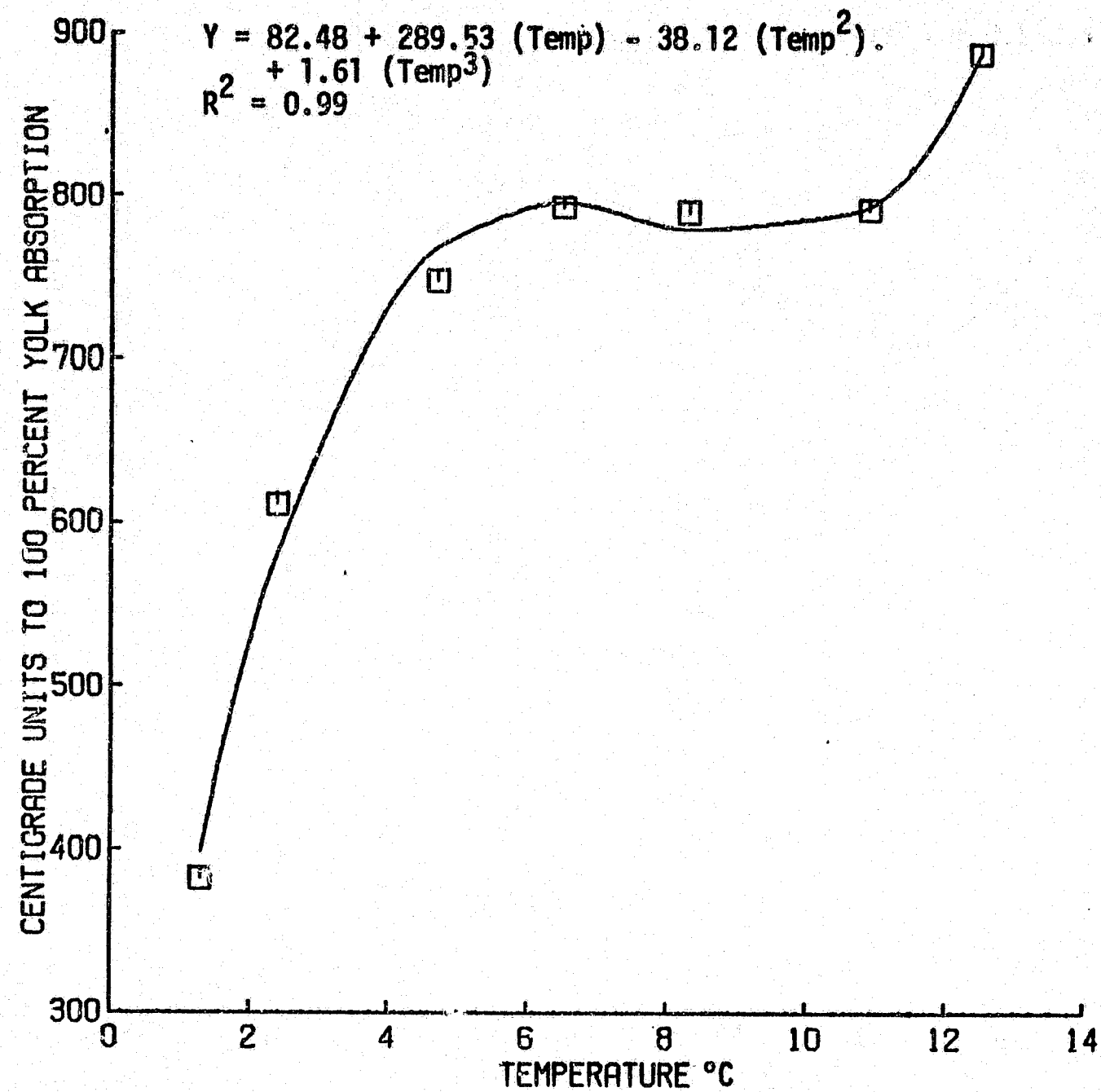


Figure 6. A plot of the cubic line of the regression of C.U. to 100% yolk absorption vs. temperature. Dungeness Coho.

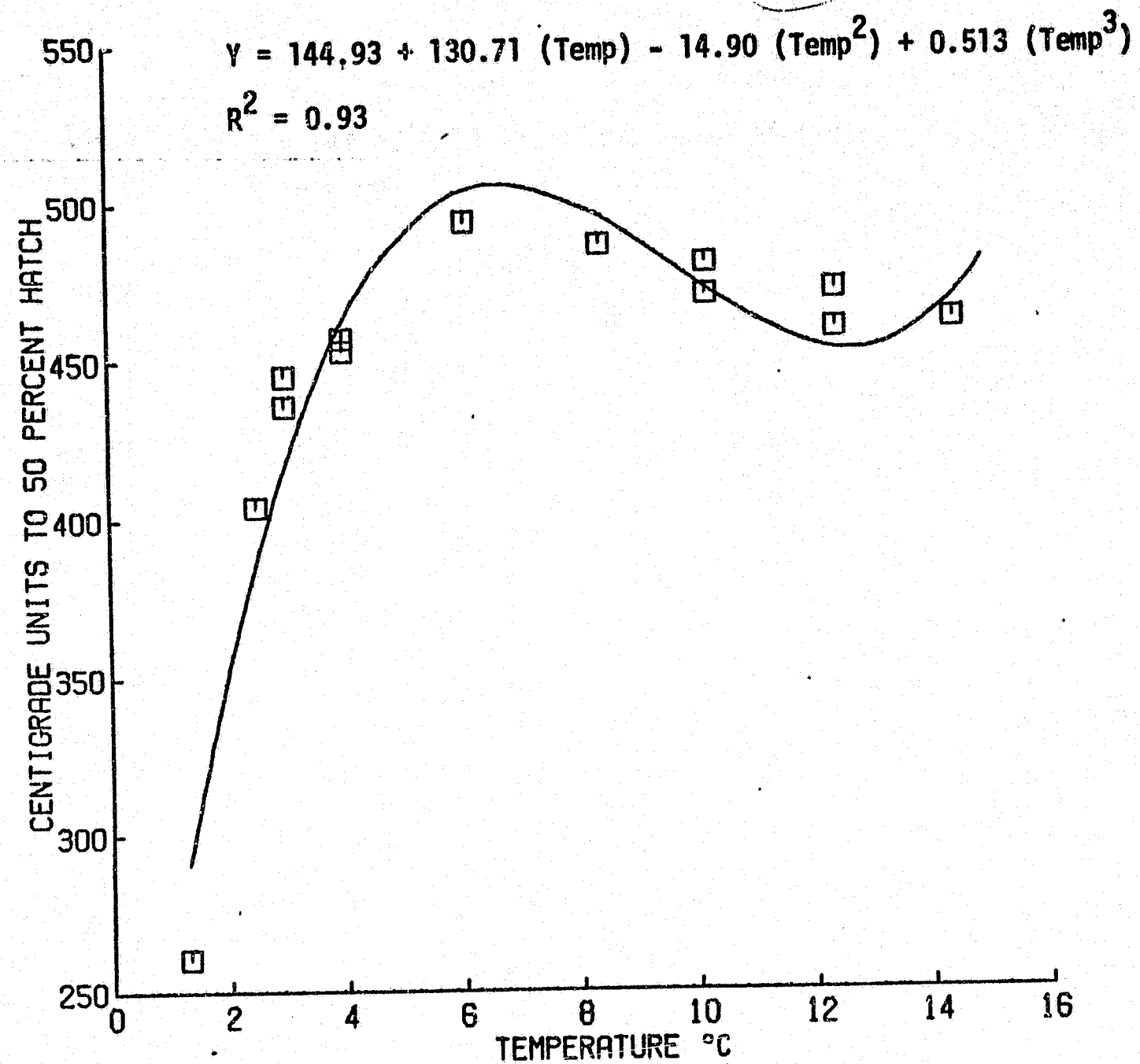


Figure 7. A plot of the cubic line of the regression of C.U. to H50 vs. temperature. UW Coho.

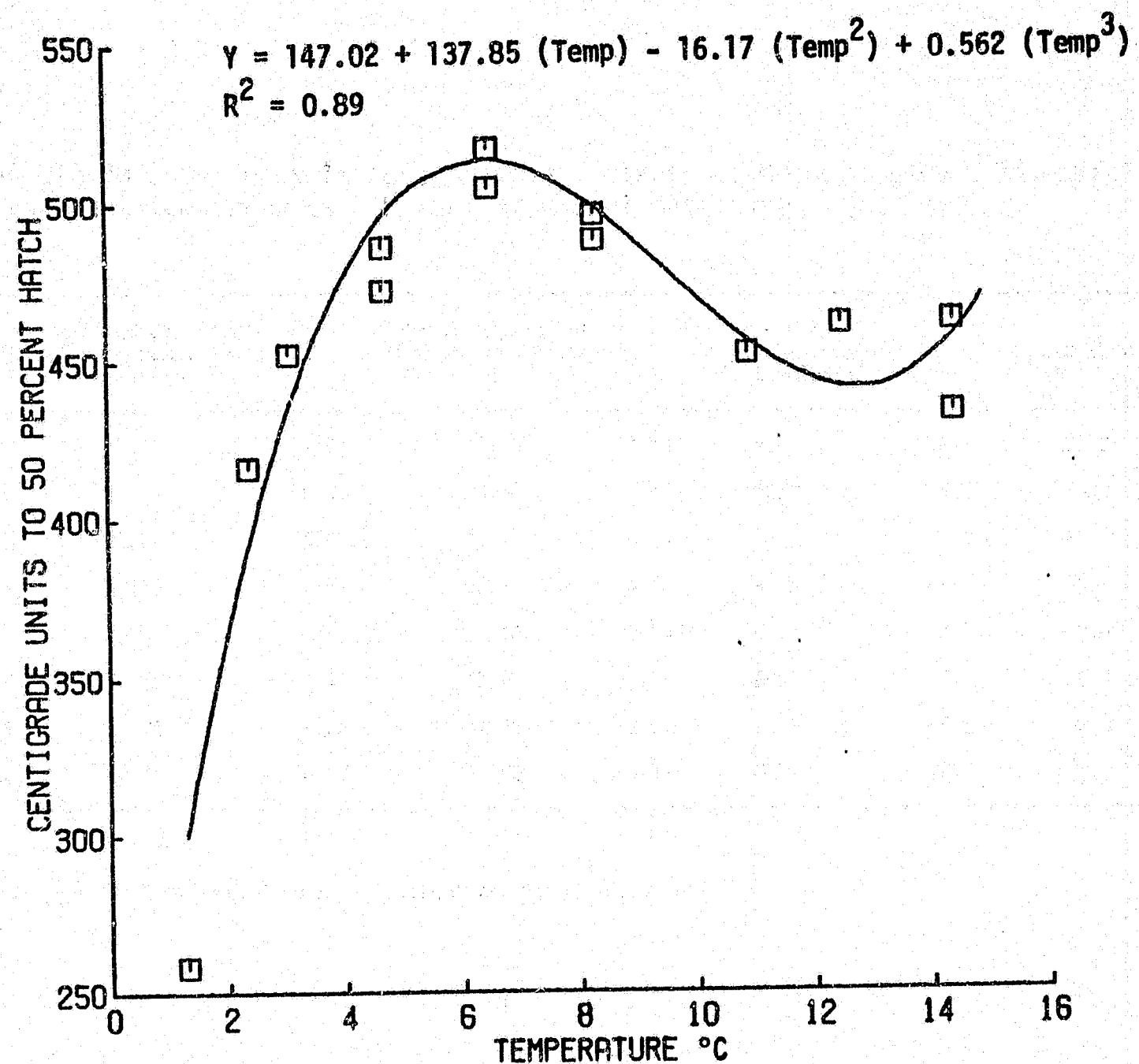


Figure 8. A plot of the cubic line of the regression of C.U. to H50 vs. temperature. Dungeness Coho.

Table 3. Summary of alevin size and yolk absorption efficiency of UW coho salmon incubated in water of constant temperatures. N = 25 at each temperature.

Temp. °C.	Average Length (mm)	<u>s</u>	Average dry weight of yolk remaining at termination (mg)	<u>s</u>	Average dry wt. of fish at termination (mg)	<u>s</u>	% yolk absorption at termination	<u>s</u>	% yolk absorption efficiency	<u>s</u>
14.4	Not avail.		7.12	4.25	38.06	5.16	91.3	5.2	50.7	5.2
12.4	30.6	1.0	10.74	6.90	44.66	4.6	86.9	8.4	63.3	10.0
10.2	30.6	1.1	12.29	6.01	43.18	5.69	85.0	7.3	62.7	12.2
8.4	31.0	0.8	10.21	6.21	46.77	4.26	87.5	7.6	66.1	12.7
6.1	31.9	1.1	10.41	5.8	51.14	7.54	87.3	7.1	72.6	15.9
4.0	32.1	1.0	12.88	7.45	47.91	6.82	84.3	9.1	71.0	17.0
2.5	30.4	1.1	11.34	4.22	41.26	5.21	86.2	5.1	58.8	10.2
1.3	32.7	1.6	14.4	6.47	46.86	6.17	82.4	7.9	70.4	13.9

s = standard deviation

Average initial yolk weight (Y_i) of 25 unfertilized eggs (without chorion) = 81.97 mg.

Table 4. Summary of alevin size and yolk absorption efficiency of Dungeness coho salmon incubated in water of constant temperatures. N = 25 at each temperature.

Temp. °C.	Average Length (mm)	<u>s</u>	Average dry weight of yolk remaining at termination (mg)	<u>s</u>	Average dry wt. of fish at termination (mg)	<u>s</u>	% yolk absorption at termination	<u>s</u>	% yolk absorption efficiency	<u>s</u>
12.5	28.8	1.5	10.74	8.83	34.41	8.66	84.6	12.6	58.7	13.5
10.9	30.9	1.2	10.97	3.59	43.40	4.94	84.3	5.1	74.1	10.7
8.3	30.8	1.7	9.51	5.11	43.26	8.16	86.4	7.3	72.9	17.5
6.5	31.7	1.3	9.17	2.62	46.47	6.73	86.9	3.8	76.8	12.5
4.7	31.9	1.9	7.15	3.59	44.58	8.61	89.8	5.1	71.5	15.1
2.4	30.8	1.9	11.14	5.01	38.99	6.25	84.1	7.2	67.2	13.8
1.3	31.3	1.2	11.12	3.82	41.19	4.75	84.1	5.5	70.4	9.7

s = standard deviation

Average initial yolk weight (Y_1) of 25 unfertilized eggs (without chorion) = 69.95 mg.

DISCUSSION

Constant Temperature Incubation

Using the criteria set up previously, the upper lethal threshold for UW coho salmon incubation falls between 12.4° and 14.4°C. The lower threshold is between 1.3° and 0.6°C. An extrapolation of the curve of UW coho egg mortality (Fig. 9) to the temperature axis suggests that 50% mortality would occur at about 13.5°C and 1.0°C. Although the lethal thresholds cannot be determined exactly, it can be concluded that they fall within the range of temperature outlined above.

Dungeness coho appear to be more sensitive to warm incubation temperatures than do UW coho salmon. For Dungeness coho, the upper limits for egg incubation fall in the same range as that of UW coho, but alevin mortality in excess of 50% indicates that temperatures cooler than 12.5°C are required for normal development. The upper lethal threshold for Dungeness coho incubation is between 10.9° and 12.5°C. Extrapolation of the alevin mortality curve (Fig. 10) suggests that 50% mortality would occur at about 12.4°C. One suspects that the true upper lethal threshold temperature is nearer to 12.5°C than to 10.9°C.

The greater sensitivity of Dungeness coho eggs to high temperatures is consistent with the fact that winter temperatures in the Dungeness River are generally much cooler than the hatchery water at the UW. It would have been informative to have incubated Dungeness coho eggs at temperatures below 1.3°C. Total mortality of egg and alevin combined for both stocks of coho is presented in Fig. 11.

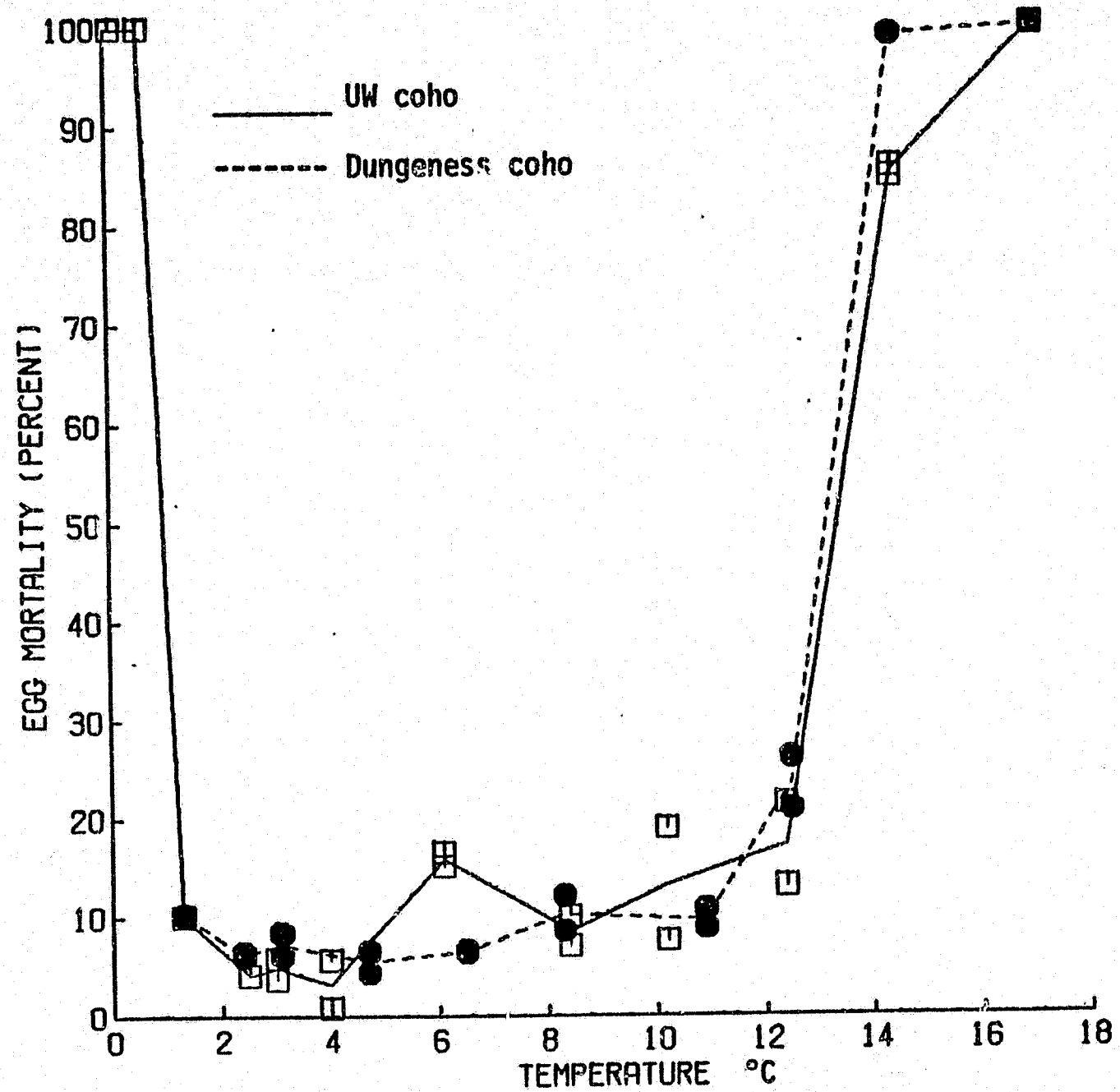


Figure 9. A plot of the mortality of UW and Dungeness Coho salmon eggs incubated at constant temperatures.

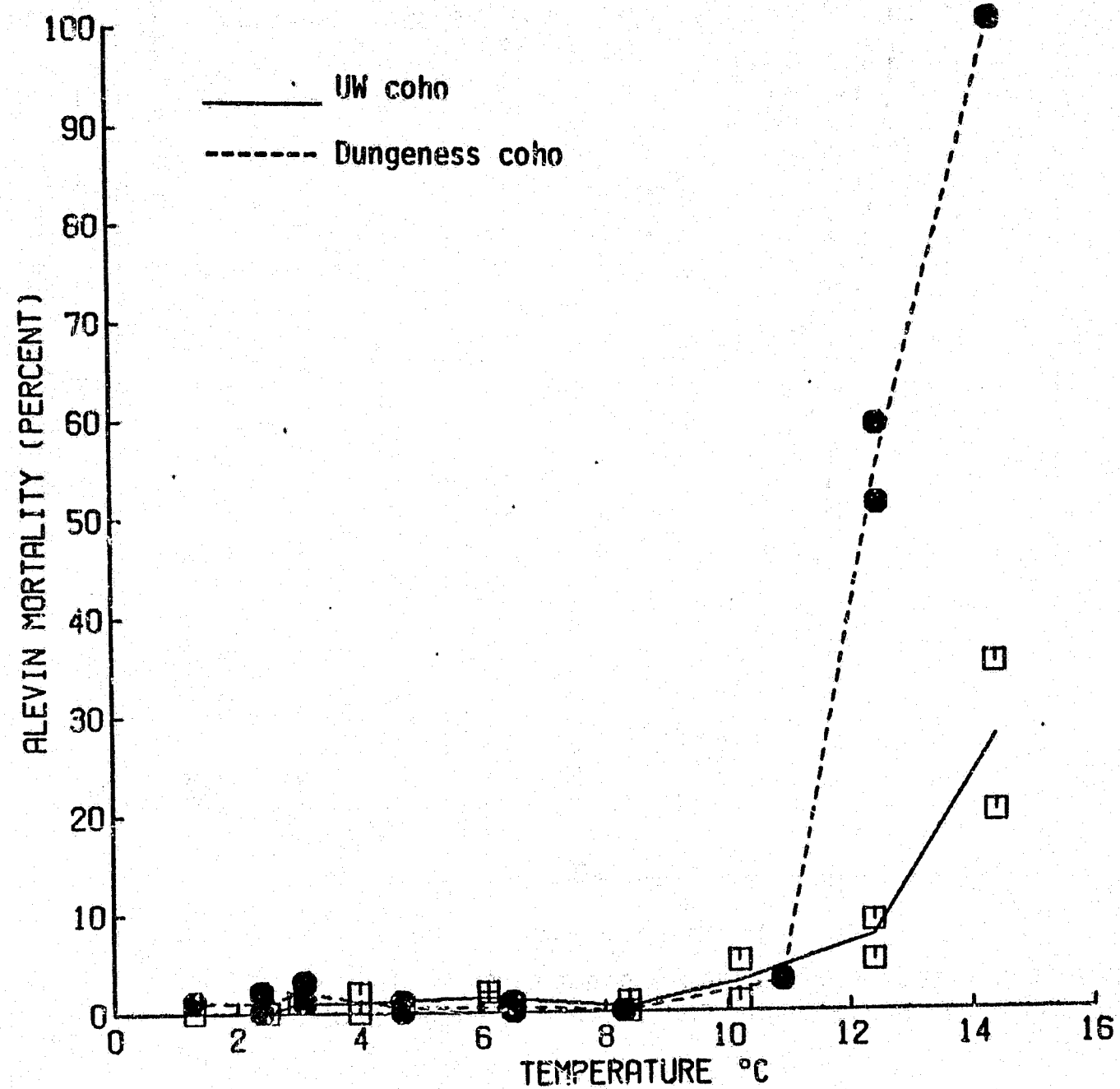


Figure 10. A plot of the mortality of UW and Dungeness Coho salmon alevins incubated at constant temperatures.

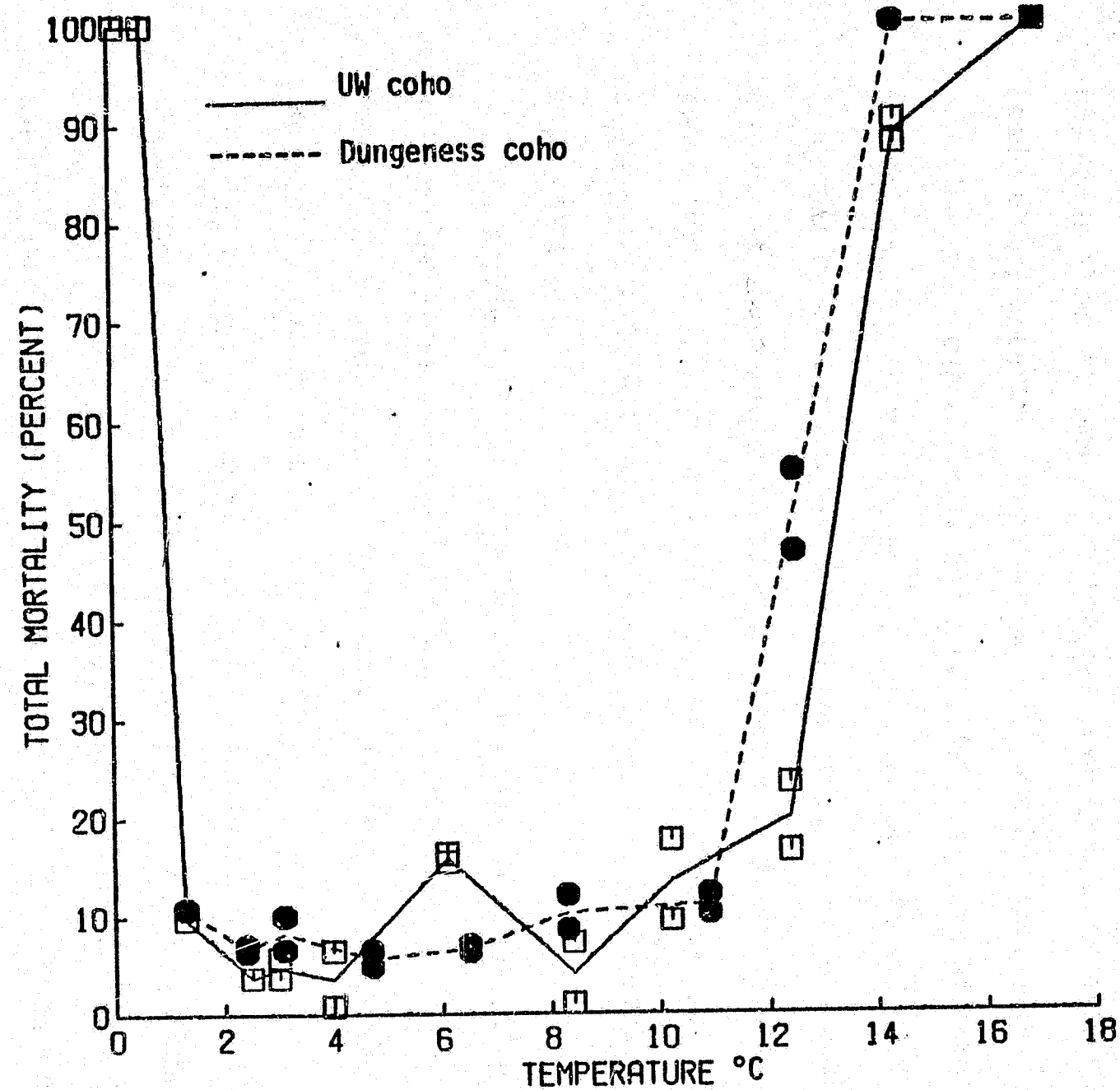


Figure 11. A plot of the combined mortality of egg and alevin of UW and Dungeness Coho salmon incubated at constant temperatures.

It should be emphasized that these threshold temperatures were derived under constant temperatures. It is unlikely that coho eggs would experience such extreme temperatures in nature immediately after fertilization. The tolerance of salmon eggs to extreme temperatures has been shown to improve if initial development was allowed to proceed at more moderate temperatures (Fish and Burrows, 1939; Combs, 1965).

The small overall size and poor yolk absorption efficiency of fry at high incubation temperatures (14.4°C for UW coho and 12.5°C for Dungeness coho) are consistent with the low survival of eggs and alevins at those temperatures. The greater size and efficiency of yolk absorption of fry at the colder temperatures indicate that coho salmon alevins are better able to tolerate unusually cold temperatures than high temperatures.

This tolerance for cold temperatures may be a selective advantage to the coho alevin since stream temperature generally remain cold throughout the winter. A winter cold snap lowers atmosphere temperature which will tend to lower stream temperature.

Conversely, the sensitivity of coho alevins to high temperatures places the species in a vulnerable position to any long-term increase in stream temperature. Stream temperature can be increased by natural events (such as volcanic activity) or by man's activities (such as mixing of the heated effluent of power plants with stream water and the damming of once free-flowing streams).

From the analysis of dry fish weight and yolk absorption efficiency, it appears that temperatures between 4° and 6.5°C produced the most robust fry. These temperatures may encourage the alevin to invest more

of the energy derived from the yolk material in tissue building than in maintaining body functions.

Variation in yolk absorption efficiency within each temperature is high due to the great variation of dry yolk weights of fry samples. The fish were at various stages of being buttoned up when the experiments were terminated, ranging from just beginning to button up to having used most of the residual yolk.

The necessity of estimating Y_f by the average weight of eggs that were not actually used in obtaining yolk absorption efficiencies results in the inflation of the efficiency of eggs that are larger than the average and an underestimation of the efficiency of eggs that are smaller than the average. The effect of this source of error could be reduced by an increase in sample size. Nevertheless, significant differences in yolk absorption efficiencies were obtained with a sample size of twenty-five at each temperature. It is of interest to note that the yolk absorption efficiencies obtained in this study are noticeably higher than those obtained by Hayes and Pelluet (1945).

In general, coho seem to adapt well to a wide range of incubation temperatures. Furthermore, they are able to tolerate incubation temperatures that are colder than those tolerated by early fall spawning salmon. Combs and Burrows (1957) found that an incubation temperature of 35°F (1.7°C) resulted in 100% mortality of chinook eggs from the Entiat River, WA. There was poor survival at temperatures below 40°F (4.4°C). Sockeye salmon eggs from the same river suffered 80% mortality when incubated at 35°F (Combs, 1965). Only 63% survived at a temperature of 37.5°F (2.5°C). The ability of coho salmon to tolerate

lower incubation temperatures is consistent with the fact that this species spawns later in the fall when river temperature is cooling rapidly.

Developmental Compensation

Best-fit equations for the least squares regression of days or c.u. to reach H50 and yolk absorption were generated with data collected from the 1977 experiments, since none of the eggs in the 1978 experiments ever hatched. Although the results were based on data from only one year, they are significant because of the high degree of correlation between the tested variables (see R^2 values in Figs. 1-8). However, the equations presented here are used primarily as tools to better understand the relationship between development and temperature in coho salmon and not as predictors of hatching time and emergence.

The number of days required to reach H50 and yolk absorption appear not to be linearly related to temperature, as evident from a plot of the data points. The best fit line from the step-wise regression was the equation with a quadratic term (Figs. 1-4). The rise of the curve at the highest temperature in each case is an artifact of the quadratic curve. It is very unlikely that the number of days to reach H50 and yolk absorption would increase at temperatures higher than this. However, the question is academic since coho salmon eggs cannot live at those higher temperatures. The non-linear character of the curves shows that the rate of development (as defined by the incubation period) is not constant over all incubation temperatures.

X The decrease in the number of centigrade units required to reach H50 and yolk absorption with decreasing temperature suggests that there

was a greater amount of development per unit of temperature accumulated at cold temperatures than at warm temperatures. This compensation results in the pace of development being greater at low temperatures and less at high temperature. The net result is a rate of development (as measured by the incubation period) that is not constant over the range of tolerable incubation temperatures. X

The relationship between the number of c.u. to reach yolk absorption and temperature, based on data from the present experiment, is sigmoid. The regression equation with three variables (cubic) would best fit this relationship (Figs. 5 and 6). For comparison, the number of c.u. to reach H50 is also fitted by a cubic equation (Figs. 7 and 8).

There doesn't appear to be any noticeable difference in the series of regression curves between the two populations of coho. The shape and slope of the curves are very similar. However, an examination of the curves for the number of c.u. to H50 and those for the number of c.u. to 100% yolk absorption shows that a difference in shape exists between the curves for these two developmental stages.

The number of c.u. required to hatching showed an unexpected decrease at temperatures between about 8° and 13°C (Figs. 7 and 8). However, this decrease was not observed at 100% yolk absorption (Figs. 5 and 6). There are two possible explanations for this difference.

The first explanation is that incubation temperatures between 8° and 13°C can overwhelm the underlying mechanism of developmental compensation which is operative in the egg at temperatures below 8°C. After hatching, the alevin "corrects" for the lack of compensation in

the egg by absorbing the yolk material at a slower rate, thereby restoring the more typical shape of the sigmoid curve at 100% yolk absorption.

An alternative explanation is that the decrease in the number of c.u. required to hatching at temperatures above 8°C results from the early hatching of eggs at those temperatures. Early hatching may be a mechanism by which the eggs meet their increased demand for oxygen as they develop to near hatching. If the level of dissolved oxygen becomes critical, especially at warm temperatures, it may be more advantageous for the embryo to hatch "prematurely" than to continue to exist inside the egg shell (Bams, 1969). Low dissolved oxygen levels trigger the release of hatching enzymes which break down the egg membrane (Hayes, 1942). It has been shown that at near hatching, Salmo salar embryos without the egg membrane can extract two times more oxygen from the water environment than unhatched embryos when both are incubating in the same oxygen pressure (Hayes et al., 1951).

It is therefore possible that coho eggs incubating at temperatures above 8°C had hatched prematurely because of a decreased level of dissolved oxygen at these relatively warm temperatures, resulting in the leveling of the curve of the number of c.u. to H50 and temperature at temperatures above 8°C.

Developmental compensation at hatching also may be of little adaptative value to the fish. To an incubating embryo, hatching may not be as important a stage, in terms of its overall survival, as yolk absorption. Hatching can be delayed or hastened by abnormal temperatures and dissolved oxygen levels but after hatching the alevins continue to

live in the protected environment of the redd. Yolk absorption, on the other hand, is closely associated with emergence from the gravel and thus affects the survival of the fry. This would account for the apparent greater effect of developmental compensation at yolk absorption than at hatching.

Incubation of sockeye and pink salmon eggs to yolk absorption at different temperatures has been shown to require less temperature units as temperature increases (Table 5) (Brannon, International Pacific Salmon Fisheries Commission, manuscript). The relationship is sigmoid and slightly different between the two species at higher temperatures (Fig. 12). The data show that a strong compensation exists in the relative pace of development, especially at low and high temperatures.

This compensatory behavior is similar to that shown by coho salmon, although incubation time for the former two species is much longer.

However, some noticeable differences in developmental compensation to temperature between these salmon species do exist. Coho embryos do not appear to have the same degree of compensation over the entire range of suitable incubation temperatures as do sockeye embryos (Fig. 12). For Dungeness coho, compensation is most evident at temperatures below 4.5° and above 11°C. From 6.0° to 11°C, there is little effect on pace of development due to compensation. UW coho shows much the same behavior. This pattern of compensation contrasts to the one shown by sockeye salmon, which compensates over the entire range of incubation temperatures.

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Table 5. Days and temperature units required during incubation from fertilization to yolk absorption for sockeye salmon and pink salmon. (Data taken from Brannon, International Pacific Salmon Fisheries Commission, manuscript.)

Temp. °F Constant	°C	Sockeye			Pink		
		days	T.U.	C.U.	days	T.U.	C.U.
34	1.1	341	682	379			
36	2.2	278	1112	618			
38	3.3	238	1428	793			
40	4.4				190	1520	844
42	5.6	169	1690	939	169	1690	939
44	6.7				148	1776	987
46	7.8	130	1820	1011			
48	8.9				124	1984	1102
50	10.0	106	1908	1060			
52	11.1	94	2068	1149	101	2222	1234
56	13.3	91	2184	1213			
58	14.4	88	2288	1271			
60	15.6	85	2380	1322			

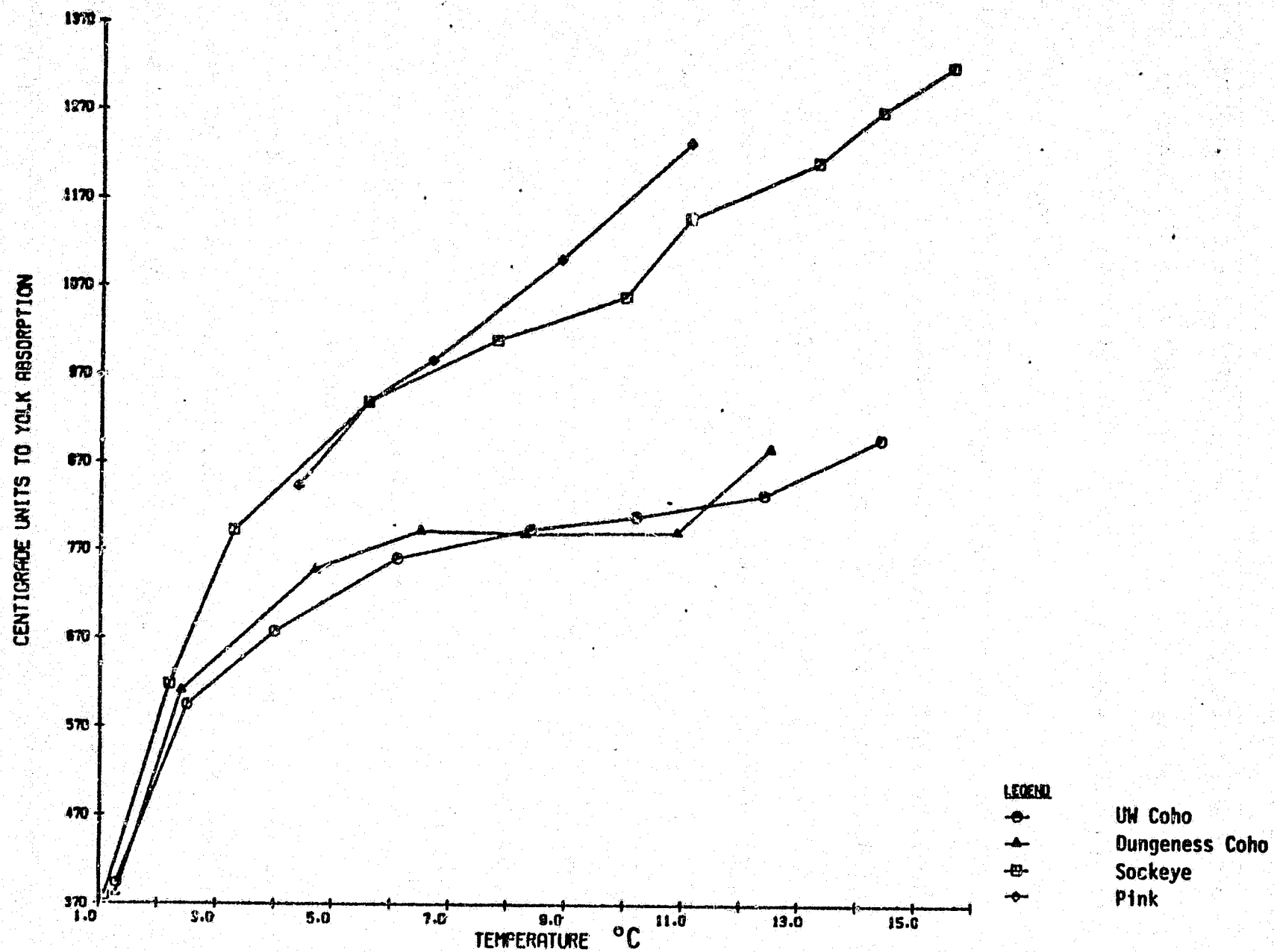


Figure 12. The number of centigrade units required to reach yolk absorption for the embryos of coho, sockeye and pink salmon incubated at constant temperatures.

The difference in compensation may be explained by the fact that coho salmon are late fall spawners and their eggs normally incubate over a much shorter period of time than do sockeye eggs. With a short incubation period, compensation may exert only a minimal influence on development in terms of the number of days required to emerge. Its role becomes more important only when incubation temperatures are well below (or above) normal.

In general, greater development per unit of temperature at low temperatures and lesser development at high temperatures per unit of temperature enables salmon, which incubate over a wide range of fall and winter temperatures, to somewhat reduce the influence of such a range in temperature on the fry's emergence timing. This compensatory behavior helps to ensure that most of the offspring will emerge within a few days of each other and at the optimum time in the spring.

A narrow span in time of emergence activity in the early spring is advantageous to the fish if it is synchronized with a corresponding peak of productivity in the stream. This timing of emergence is predetermined by the timing of spawning of the adults in the fall. The timing of spawning is in turn influenced by factors that are both genetically controlled and environmentally induced. The instinctive timing of spawning that has been fine-tuned to the temperature regime of the native stream can be modified by unfavorable water conditions. Adult salmon may delay or hasten their timing of spawning depending on stream flows and temperature. This behavior encourages the adults to select a spawning time, based on the environmental information available

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to them in the fall, that will result in an optimum time of emergence of fry in the spring.

As soon as the eggs are safely buried in the redd, the responsibility of the parents ends. But developmental compensation, like a built-in, self-adjusting timer, provides a safeguard that can modify the pace of development to buffer the influence of any unforeseen fluctuation in the temperature regime of the stream during incubation.

The findings of this study once again point to the major shortcoming of the thermal sums hypothesis and Wallich's system; that is, the assumption that the speed of development is constant at all temperatures that are tolerated by incubating eggs. In the case of coho, sockeye and pink salmon, the pace of development is not constant over the entire range of temperatures. The accumulation of one t.u. at lower temperatures results in a greater amount of development than at median temperatures. Conversely, at high temperatures, one t.u. results in less development.

Most past experiments on salmon egg development have been conducted with temperatures in the median range and were usually terminated at hatching. But the results of the present study shows that the response of the embryo to temperature at the median portion of its range is very different from that at the extreme portions. Furthermore, hatching may not be an appropriate stopping point for experimentation since this stage has little adaptive meaning to the fish. Incubation of embryos to yolk absorption would provide more valuable insight on the response of salmon embryos to temperatures.

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SUMMARY

- 1) The lower lethal threshold for the normal development of UW coho eggs is between 0.6° and 1.3°C. The upper threshold is between 12.4° and 14.4°C. Good survival of both eggs and alevin occurred at incubation temperatures between 1.3° and 12.4°C.
- 2) Dungeness River coho, a population with a colder thermal history than UW coho, did not survive high incubation temperatures as well as UW coho. Good survival occurred only at incubation temperatures below 12.5°C. Alevin mortality in excess of 50% at 12.5°C indicates that the upper lethal threshold is between 10.9° and 12.5°C.
- 3) Incubation temperatures between 4° and 6.5°C produced the best fry in terms of fish body weight and efficiency of yolk absorption.
- 4) The rate of development of coho, measured by the incubation period, was accelerated at high temperatures and slowed at cold temperatures.
- 5) The relative pace of development at various temperatures, inferred by the number of thermal units required to reach yolk absorption, is greater at low temperatures than at high temperatures. The accumulation of one temperature unit at low temperatures results in a greater amount of development than the accumulation of one temperature unit at high temperatures.
- 6) A plot of the number of centigrade units required to reach yolk absorption and temperature shows that embryos at low temperatures required fewer than one-half the number required at high

temperatures. The relation is sigmoid and is similar between the two populations of coho salmon.

- 7) This compensation in the pace of development of coho salmon embryos helps to ensure that young fry will emerge at the optimum time in the spring. It is a safeguard against any unforeseen fluctuations in water temperature during incubation.
- 8) Developmental compensation in sockeye and pink salmon, both early fall spawning species, has been shown to occur throughout the range of incubation temperatures. On the other hand, coho salmon, a late fall spawning species, compensates in its development only when incubation temperatures are at the low or high end of its range.

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