OPTIMAL TIMING OF INITIAL EXOGENOUS FEEDING, AS AFFECTED BY TEMPERATURE, IN CHINOOK SALMON (*Oncorhynchus tshawytscha* Walbaum)

by

THOMAS ARTHUR HEMING

B.Sc., University of Guelph, 1976

A THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

ACCEPTED
FACULTY OF GRADUATE STUDIES
[redacted]
DEAN
DATE Sept 1980

We accept this thesis as conforming
to the required standard

[redacted]

J.E. McInerney

[redacted]

W.R.D. Sewell

[redacted]

E.M. Hagmeier

[redacted]

D.F. Alderdice

UNIVERSITY OF VICTORIA

September 1979

ABSTRACT

Supervisor: Dr. J.E. McInerney

The relationship between timing of initial food presentation, alevin growth and early survival was examined in chinook salmon (Oncorhynchus tshawytscha Walbaum) at 6, 8, 10, and 12 °C. Feeding of test groups of alevins was begun in serial order from shortly after hatching to complete yolk absorption, in relation to progressive wet weight changes observed in unfed alevins. Experimental work at each temperature was terminated when cumulative mortality of unfed fish surpassed 50%. In addition, growth of chinook salmon reared unfed and in commercial incubation trays from hatching to complete yolk absorption, and emergence of alevins from simulated redds were investigated at each of the four temperatures.

Length and tissue weight of unfed alevins increased with time to maxima following hatching. Maximum tissue weight (MTW) and maximum alevin length were reached simultaneously, at 1125.1 tu after fertilization. Yolk reserves remaining at this time averaged 6% of those present at fertilization (dry weight basis). Thereafter, although yolk remained, unfed alevins began to catabolize tissue and tissue weight declined. Alevin length, however, remained unchanged with continued starvation. Over the four temperatures, alevins completed yolk absorption at 1456.1 tu after fertilization. The developmental index (k_D) of unfed alevins at complete yolk absorption averaged 1.96. Generally, the efficiency of yolk utilization from fertilization to MTW decreased at higher temperatures, from 67.1% at 6 °C to 58.6% at 12 °C. Thus, more than a third of the yolk absorbed to MTW was utilized for purposes other than growth. Nevertheless, total wet weight (tissue plus yolk) of unfed alevins

increased with time to a maximum alevin wet weight (MAWW). This increase in total wet weight resulted from absorption of water. Total wet weight reached a maximum and began to decline before MTW was attained at each temperature. Thus, measurement of alevin wet weight was considered a poor indication of growth. Temperature influenced the developmental stage at which MAWW was reached. MAWW occurred earlier in development at higher temperatures, and as a consequence, alevin size decreased and the yolk reserve remaining at MAWW increased from 6 to 12 °C. Yolk reserves remaining at MAWW increased from 9% at 6 °C to 29% at 12 °C (from fertilization, dry weight basis). Over the four temperatures, 50% emergence of alevins from simulated redds occurred within 26.8 tu of MAWW.

Chinook salmon began ingesting external food while retaining 51% of the yolk reserve present at fertilization. Feeding was not dependent on attainment of neutral buoyancy (swim-up); alevins were capable of exogenous feeding before inflating their air bladders. However feeding did not significantly affect growth, when compared with that of unfed alevins, until shortly before MAWW was attained. Alevins presented food initially before attaining MAWW did not exhibit a maximum wet weight; their total wet weight continued to increase while that of unfed fish reached MAWW and then declined. The ultimate size achieved and total survival of feeding alevins were maximized when feeding was initiated before MAWW occurred, regardless of the specific timing of initial food presentation. The ultimate size achieved was reduced when feeding was initiated at or after alevins attained MAWW. Survival was reduced when initial feeding was delayed until alevins attained MTW. Exogenous feeding had no effect on yolk absorption. As well, timing of initial food presentation had no effect on the subsequent growth rate of feeding alevins.

The results establish that chinook salmon are capable of utilizing exogenous food to supplement their endogenous reserves. This "mixed feeding" primarily determined subsequent growth and survival. Natural populations of chinook probably utilize external food prior to emerging from the gravel redd. In fish culture, the optimal time to commence feeding of chinook salmon is before alevins attain MAWW. Occurrence of MAWW can be regarded as a preliminary symptom of starvation, indicating that a greater ultimate size could have been achieved by initiating feeding earlier in development. Estimates of the optimal time (tu after fertilization) to commence feeding at each temperature are given; initiating feeding of chinook salmon at or before these optimal times should maximize subsequent growth and survival. These optimal times were found not to be related to swim-up, button-up (disappearance of the visible yolk sac), MAWW, MTW, or complete yolk absorption.

[redacted]

J.E.McInerney

[redacted]

W.R.D.Sewell

[redacted]

E.M.Hagmeier

[redacted]

D. F. Alderdice

TABLE OF CONTENTS

TABLE OF CONTENTS (cont'd)

LIST OF TABLES

LIST OF TABLES (cont'd)

LIST OF TABLES (cont'd)

LIST OF FIGURES

LIST OF FIGURES (cont'd)

LIST OF FIGURES (cont'd)

ACKNOWLEDGEMENTS

I sincerely thank Dr. D.F. Alderdice and Dr. J.E. McInerney for their encouragement and support throughout the project, and for their critical review of the manuscript. Appreciation also is extended to Mr. R.P. Preston, Mr. D. Gee, and Mr. F.P.J. Velsen for their assistance in carrying out the research.

This research was conducted at the Pacific Biological Station in Nanaimo, British Columbia, in laboratory facilities provided by Dr. D.F. Alderdice. I thank each of the many P.B.S. staff members, who freely offered positive and helpful scientific advice and other tangible assistance.

I also wish to acknowledge the unceasing support of Ms. L.M. Heming, who willingly shared my frustrations as well as my accomplishments during this project.

I. INTRODUCTION

Current fish cultural practices often rely on imperfectly understood biological principles. One of these principles involves the timing of introduction of larval fishes to exogenous food. This study seeks a framework for understanding the relationship between initial feeding, growth and early survival of chinook salmon (Oncorhynchus tshawytscha).

The transition from endogenous feeding, primarily involving utilization of yolk, to exogenous feeding or utilization of external food is a critical period in the larval development of fishes. In the natural environment, availability of adequate external food during the transition is a major determinant of larval mortality (Hjort 1914, 1926, Hempel 1965, Braum 1967, Latta 1969, Ehrlich 1974, May 1974, White 1978). Experimentally, food deprivation during the transition has been associated with a variety of sublethal disabilities, including abnormal behavioural and morphological development, degeneration of the alimentary tract and trunk musculature, and reductions in growth, food utilization efficiency and feeding activity (Palmer et al. 1951, Toetz 1966, Blaxter and Ehrlich 1974, Ehrlich et al. 1976, O'Connell 1976, Theilacker 1978). Deprived larvae eventually reach a "point of no return" (Blaxter 1969), after which they lose the capability of successful exogenous feeding and succumb to the lethal effects of starvation.

Exogenous feeding in salmonids apparently develops during the ontogenetic phase associated with emergence of alevins[1] from the gravel

---

[1] Hubbs' (1943) definition of the term "alevin", as the larval stages from hatching to the juvenile stage, is used in reference to young salmonids.

redd, attainment of neutral buoyancy (popularly termed "swim-up), and completion of yolk absorption. However, the precise timing of initial feeding is unclear. Several authors have related initial feeding with swim-up (Palmer et al. 1951, Bams 1969, Twongo and MacCrimmon 1976). Twongo and MacCrimmon (1977) found that an epithelial tissue plug completely occluded the upper alimentary tract of rainbow trout (Salmo gairdneri) and prevented food ingestion until swim-up. Yet, there is evidence that exogenous feeding, in both wild and cultured salmonids, can occur before attainment of neutral buoyancy and often prior to emergence from the gravel (Disler 1953, Stuart 1953, Salo and Baycliff 1958, Dill 1967, Thomas and Shelton 1968, Simonova 1972, Smirnov 1975, Mason 1976).

Pioneering investigators also related initial exogenous feeding with disappearance of the visible yolk sac (popularly termed "buttoning-up") (White 1915, Leach 1923, Brown 1938). Henshall (1904, 1907) stressed the necessity of feeding cultured salmonids before button-up. However, Atkins (1905, 1906) showed that delaying initial food presentation for a period of five days after button-up improved survival and presented no permanent growth disadvantage to Atlantic salmon (Salmo salar), brook trout (Salvelinus fontinalis), and coho salmon (Oncorhynchus kisutch). As well, Brown and Buck (1939) found no correlation between size or presence of the visible yolk sac and initial food ingestion in a number of salmonids.

Disappearance of the visible yolk sac does not mean that yolk absorption is complete; quantities of yolk can remain internally (Hayes 1949, Blaxter 1969, Twongo and MacCrimmon 1976). While it is recognized that young salmonids may be capable of ingesting external food before their endogenous reserves are exhausted, recent studies have raised questions regarding the significance of such "mixed feeding" (Roley 1974, Twongo and MacCrimmon 1976). Harvey (1966) and Hurley and Brannon (1969) found that sockeye salmon (O. nerka) were capable of food ingestion shortly after hatching, but that exogenous feeding offered no growth advantage until all internal yolk was absorbed. Hurley and Brannon (op. cit.) also reported that feeding before complete yolk absorption increased alevin mortality.

There is evidence, however, that growth and survival of chinook salmon are increased by feeding before complete yolk absorption (Hopley 1974, 1975). As well, in the absence of exogenous food, chinook alevins have been found to lose weight before complete yolk absorption (B. McLean, Quinsam Hatchery, Campbell River, unpublished data). Weight loss, a characteristic of starvation, has been documented before complete yolk absorption in a variety of fishes (Blaxter and Hempel 1963, Marr 1965, 1966, Toetz 1966, Blaxter 1969, Laurence 1969, 1973, Ishibashi 1974). Mixed feeding, involving utilization of external food to supplement endogenous yolk, would seem essential to these fishes. Marr (1965) reported decreases in the wet weight of unfed Atlantic salmon before the visible yolk sac disappeared. He found that alevin survival was maximized when initial feeding coincided with attainment of maximum alevin wet weight.

Temperature is one of the most potent factors influencing piscine growth and development (Brown 1957, Blaxter 1969, Brett 1979). Consequently, temperature can be expected to influence the transition of larval fishes to exogenous feeding. Braum (1967) reported that temperature influenced the timing of initial feeding with respect to morphological development in whitefish (<u>Coregonus</u> <u>warmanni</u>); larvae at higher temperatures began feeding at earlier stages of morphological development. On the other hand, Laurence (1973) found that increased temperature accelerated yolk absorption more than morphological and behavioural development in tautog (<u>Tautoga</u> <u>onitis</u>); larvae at higher temperatures completed yolk absorption before developing the capability of exogenous feeding. Temperature also influences the point of no return (Blaxter 1969); fish at higher temperatures lose the capability of successful feeding more rapidly. Although effects of temperature on the transition to exogenous feeding have not been examined directly among salmonids, it is assumed that temperature influences that transition. This assumption is supported by known effects temperature has on the rate and efficiency of yolk utilization, and on the rate of development in salmonids (Gray 1928a, 1928b, Hayes 1949, Marr 1966, Bams 1969, Vernier 1969, Hamor and Garside 1976, 1977, Peterson et al. 1977, Alderdice and Velsen 1978, Gunnes 1979).

In summary, there is a considerable volume of conflicting evidence in the literature on the timing of initial feeding in salmonids, involving potential species-specific differences and imperfect distinctions between initial ingestion and initial utilization of external food. Futhermore, the influence of temperature on successful commencement of exogenous feeding has not been investigated, but may have important consequences in practical salmonid culture.

The objectives of the current study were to examine the initial feeding strategy of chinook salmon (<u>Oncorhynchus</u> <u>tshawytscha</u>), as affected by temperature, and to define the optimal time to commence feeding in practical chinook culture. For chinook salmon, I hypothesize that exogenous feeding prior to complete yolk absorption determines subsequent alevin growth and survival, and that the optimal time to commence feeding is before maximum alevin wet weight is attained. In this context, "optimal" is defined as the timing of initial feeding that maximizes growth and survival.

Importance of the timing of initial food presentation to chinook was investigated experimentally at temperatures from 6 to 12 °C. Peripheral studies examined growth of unfed alevins in incubation trays and emergence of fish from simulated redds at approximately the same temperatures.

II. MATERIALS AND METHODS

Eggs and alevins of chinook salmon were maintained at temperatures approximating 6, 8, 10, and 12 °C. Collectively, salmon at each temperature are referred to as a temperature group. Alevins of each temperature group were transferred to the experimental tanks after an initial incubation period, lasting from egg fertilization until 50% of the viable eggs hatched. While examination of embryonic (prehatch) development is outside the objectives of the present study, the relationship between the incubation and experimental periods warrants a brief description of egg incubation. The methods associated with investigation of exogenous feeding and alevin emergence are dealt with in subsequent sections. Unless indicated otherwise, standard hatchery techniques were used throughout the study.

A. Egg Incubation

Gametes of chinook salmon were collected from fish captured in the Campbell River (Vancouver Island, British Columbia) during the fall of 1977. The donor adults, 12 females and 13 males (hypural length[1]: ♀ -- 82.8 ± 4.6 cm, ♂ -- 82.6 ± 7.3 cm), were spawned on 4 November 1977 at the Quinsam Hatchery near Campbell River. Ova and sperm were pooled separately in refrigerated containers at 3.5 °C, and airlifted to the Pacific Biological Station (Nanaimo, British Columbia) where the eggs were fertilized (3.9 h after collection). Time of fertilization was taken as the starting point for all records of elapsed time and accumulated thermal units. Thermal units (tu) relate development to water temperature; one tu is accumulated for each degree Celsius above 0 °C experienced over a 24-h period (degree-day). Development during egg incubation also was monitored using the log-inverse Bělehrádek model of Alderdice and Velsen (1978, Table 2, equation 2). Their model estimates the rate of development (percent development per day) of chinook eggs in relation to water temperature, where time to 50% hatching is equivalent to 100% development.

The fertilized eggs (wet weight[2]: 490 ± 32 mg, n = 60) were distributed to 16 incubation trays, using four trays in each of four (8-tray) Heath Incubation Cabinets (Heath Tecna-Plastics, Inc., Auburn, Washington, USA). Each fibreglass tray was subdivided by a grid of

---

[1] Hypural length was measured from the posterior edge of the eye-socket to the base of the last vertebra. It is reported, as are all measurements of central tendency and sample dispersion unless indicated otherwise, as the arithmetic mean ± 1 standard deviation ($\overline{x}$ ± 1 SD).

[2] The eggs were blotted with absorbent tissues and weighed to the nearest 1.0 mg using a Cahn Electrobalance (DTL Millibalance Model 7500).

acrylic panels into 20 compartments ($7.2 \times 7.4 \times 4.9$ cm). Eggs were enumerated volumetrically and distributed approximately 150 eggs per compartment.

The incubators were kept in darkness and were provided dechlorinated Nanaimo city water for the duration of the incubation period. Water temperature and flow rates (Table I) were monitored at least twice daily. Accumulated tu and percent development were calculated as running totals for the temperature experience occurring between successive temperature readings. Averaged over the four temperatures, flow rate was 14.2 ± 0.7 L min^{-1}, equivalent to an apparent velocity of 797.4 ± 37.0 cm h^{-1}.

Dissolved oxygen in the outflow of each incubator was measured twice weekly with an Electronics Instruments Ltd. Oxygen Meter (Model 15A). Dissolved oxygen levels (Table I) averaged 99.3 ± 3.6 % of air saturation throughout the study, and remained within the optimal conditions (Protection level A) for salmonid eggs (Davis 1975, Table 10).

Approximately midway between fertilization and 50% hatching, all eggs were removed from the incubator, pooled, and mechanically shocked by a drop of 5 to 10 cm[3]. Mechanical shocking, a standard hatchery procedure, allows separation of viable eggs from nonviable

---

[3] The eggs were "eyed", equivalent to Vernier's (1969, Table 2) stage 22, when shocked. Averaged over the four temperatures, accumulated tu at that time were 263.3 ± 4.2, and percent development was 50.8 ± 1.3.

Table I. Mean (± 1 SD) water temperature, flow rate, and dissolved oxygen content in the incubation trays from fertilization until 50% hatching of chinook salmon eggs at 6, 8, 10, and 12 °C. Also shown are three scales (± 95% confidence limits) for estimating the developmental age of chinook at the time of 50% hatching, and the total egg mortality during the incubation period.

Temperature group (°C)	Temperature (°C)	Flow rate (L min^{-1})	Dissolved oxygen content (ppm)	Age at 50% hatching: Elapsed time (d)	Age at 50% hatching: Thermal units (tu)	Age at 50% hatching: Development (%)	Mortality (%)
6	5.87 ±0.28	14.04 ±0.81	11.9 ±0.6	94.5 ±0.1	556.1 ±0.6	109.0 ±0.1	7.13
8	7.87 ±0.23	14.27 ±0.76	11.4 ±0.5	70.8 ±0.1	556.0 ±0.8	106.7 ±0.2	8.34
10	9.78 ±0.24	14.25 ±0.54	11.0 ±0.6	54.6 ±0.1	534.1 ±1.0	102.0 ±0.2	9.25
12	11.75 ±0.34	14.30 ±0.54	10.3 ±0.5	44.2 ±0.1	519.5 ±0.6	99.6 ±0.1	10.73

eggs on the basis of a simple colour difference. Following shocking, viable eggs were hand counted and returned to the incubator, 125 eggs per compartment. Surplus eggs were incubated in a fifth tray of the incubator.

Nonviable eggs were enumerated and discarded approximately 12, 25, and 37 tu after fertilization, at shocking, and at least twice weekly thereafter. No attempt was made to differentiate between nonfertile eggs and eggs that died before hatching; all discarded eggs were regarded as dead eggs. After shocking, densities of 125 eggs per compartment were maintained by replacing discarded eggs with viable eggs from the fifth or surplus tray. Mortality at each temperature (Table I) remained within limits documented for salmonid eggs at similar temperatures (Combs and Burrows 1957, Silver et al. 1963, Peterson et al. 1977).

Hatching was monitored in one randomly selected compartment of each tray[4]. Timing of 50% hatching (days after fertilization) and its 95% confidence limits (Table I) were estimated graphically (Litchfield 1949). Accumulated tu and percent development at 50% hatching (Table I) then were calculated using daily temperature records. At 8, 10, and 12 °C, 50% hatching occurred later than predicted by Alderdice and Velsen's (1978) model, so that percent development exceeded 100%.

B. Initial Exogenous Feeding

1. Apparatus Approximately 50 tu after 50% hatching,

---

[4] All random selections and assignments were accomplished using a table of random digits (Snedecor and Cochran 1967, Table A1).

alevins were transferred from the incubator to an experimental unit held at about the same temperature. Each experimental unit consisted of a head box, 20 growth tanks, a waterbath, and a simulated redd (described in Section II(D)). The insulated 79.4-L acrylic head box (Figure 1) controlled water temperature and flow to the 20 growth tanks of each unit. The box was equipped with a YSI Tele-thermometer (Model 73), used in conjunction with a 1000-watt Vycor aquarium heater and a solenoid-controlled cooling system. The cooling system circulated an ethylene glycol solution at 0 °C through an epoxy-coated aluminum alloy cooling coil. Constant and equal water levels were maintained in each box by an internal standpipe of polyvinyl chloride (PVC). Water flowed to the growth tanks through nylon and vinyl tubing from 20 outlets in the front of each box. Outlets were equidistant from the box bottom, providing constant and equal flows to all growth tanks.

The 20 growth tanks of each unit were constructed from 30.5-cm sections of 18.7-cm (inside Diam) black polyethylene pipe (Fig. 2). In addition to solid bottoms, each tank had a raised (4.5-cm) false bottom of fibreglass screening (12 meshes/inch). As well, each was covered with a light-proof top. Water entered the tank through a plastic inlet jet located at the water surface. The inlet flow was tangential to the tank wall, and produced a mild counter-clockwise current estimated to be less than one alevin length (length when transferred) per second. The available water column was 21.0 cm, providing a tank volume of 5.77 L. Water exited from below the false bottom through an external standpipe of chlorinated polyvinyl chloride (CPVC).

Growth tanks of each unit were housed in an insulated 239-L

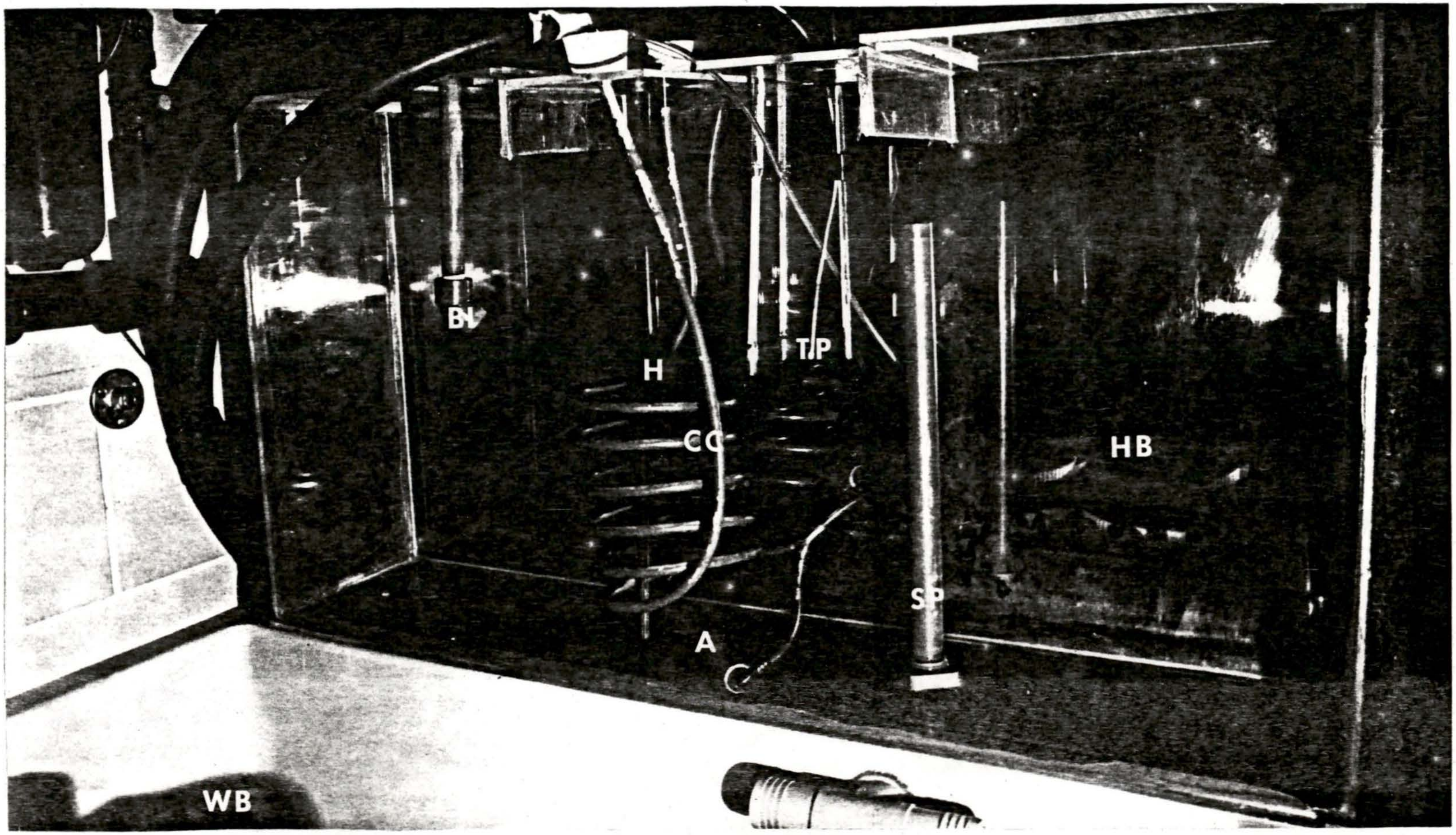


Figure 1. Part of one experimental unit used to study initial feeding in chinook alevins. The front of the head box has been removed to reveal internal construction.
A -- aerator, BI -- box inlet, CC -- cooling coil, H -- heater, HB -- head box, SP -- standpipe, TP -- Tele-thermometer probe, WB -- waterbath.

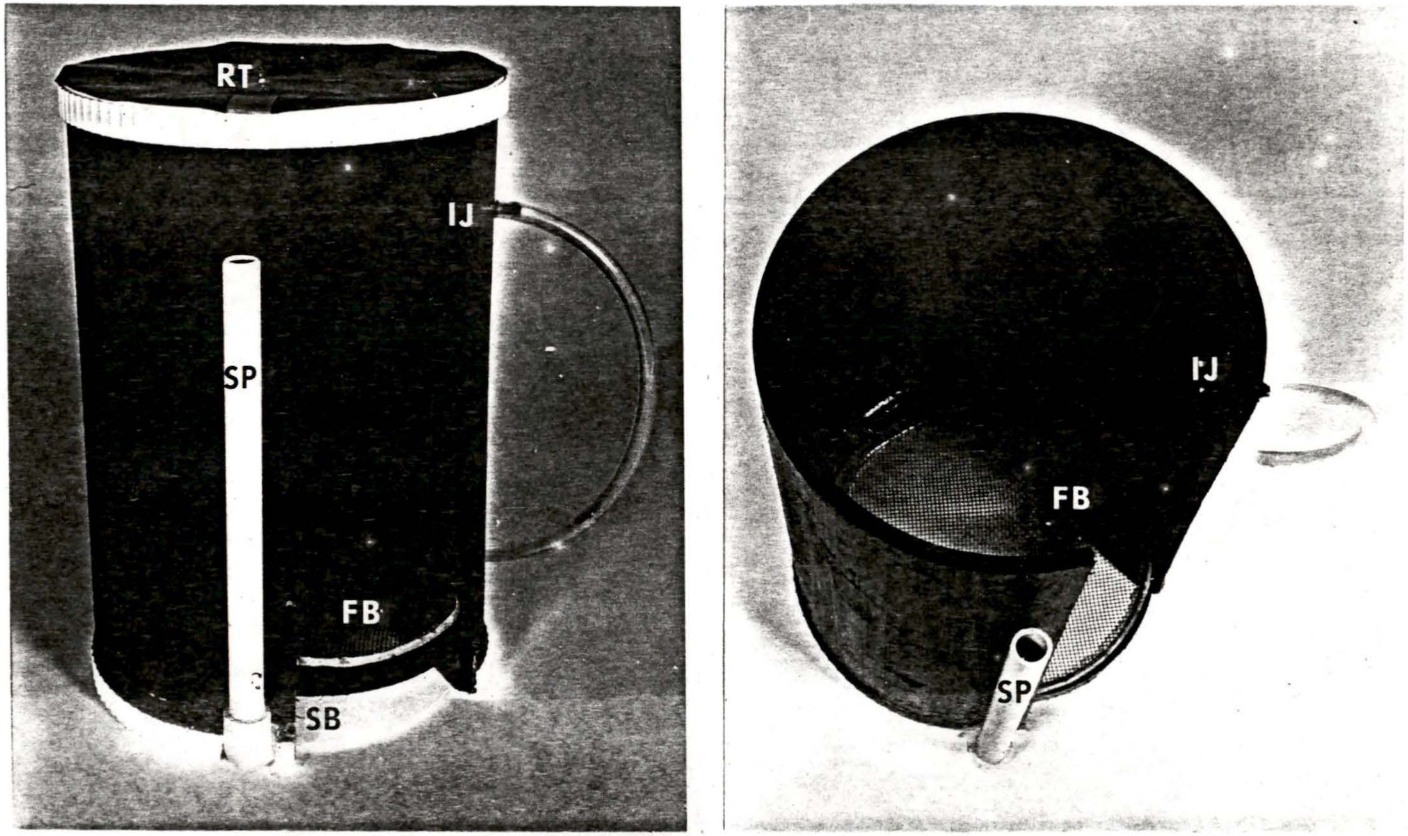


Figure 2. Growth tank used to maintain chinook alevins during the feeding experiments. The side of the tank has been cut away to reveal internal construction. FB -- false bottom, IJ -- inlet jet, RT -- removable top, SB -- solid bottom, SP -- standpipe.

fibreglass waterbath, to minimize temperature differences between tanks. Each waterbath was fed by the outflows of the tanks and by the overflow from the head box. An internal PVC standpipe maintained a water depth of approximately 20 cm in each waterbath, while a stirring impellor ensured adequate circulation. In combination with the temperature control afforded by the head boxes, waterbaths held temperature variations between growth tanks of each unit to within 0.07 $\pm$ 0.03 °C (Appendix Table I).

2. <u>Test Conditions</u> Dechlorinated and filtered (5 μm) Nanaimo city water was used throughout the feeding experiment. Water temperatures (Table II) were monitored at least twice daily in the outflow of one growth tank at each temperature. Accumulated tu were calculated as before. Flow rates to the tanks (Table II) exceeded the 0.05 L min^{-1} requirement calculated from Liao (1971, equations 1-3), and provided 99% water replacement in 0.5 h (Sprague 1973, extrapolation of Fig. 1).

Dissolved oxygen in the outflow of one tank at each temperature was measured weekly using an azide modification of the iodometric method (American Public Health Association et al. 1971). Oxygen levels (Table II) averaged 86.5 $\pm$ 9.6 % of air saturation throughout the study, and remained both above the 5 ppm threshold for normal growth (Brett 1979) and within the optimal conditions (Protection level A) for freshwater salmonid populations (Davis 1975, Table 10).

Each experimental unit was enclosed by black-out curtains, and illuminated by incandescent lights. An 11.4-h light/dark cycle

Table II. Mean (± 1 SD) water temperature, flow rate, and dissolved oxygen content in growth tanks during feeding experiments with chinook alevins at 6, 8, 10, and 12 °C.

Temperature group (°C)	Temperature (°C)	Flow rate (L min^{-1})	Dissolved oxygen content (ppm)
6	6.10 ± 0.27	0.45 ± 0.02	10.0 ± 1.2
8	8.11 ± 0.15	0.45 ± 0.02	10.2 ± 1.1
10	10.03 ± 0.14	0.45 ± 0.02	9.3 ± 1.0
12	11.94 ± 0.22	0.45 ± 0.01	8.7 ± 0.7

was used, with 0.6-h morning and evening periods of "twilight" simulating the annual mean number of twilight hours at 50° North latitude (Brown and Buck 1977). Intensity at the water surface of the tanks during the light phase averaged 39.0 $\pm$ 4.8 lux, an intensity above the threshold at which feeding rates of juvenile salmonids become intensity-dependent (Brett and Groot 1963).

3. Test Fish Alevins from three randomly selected compartments of the incubator were transferred to each tank. During this transfer, obviously abnormal individuals were eliminated. Since no compartment had more than ten structurally abnormal individuals, ten fish were removed from each compartment to maintain constant loading densities. In this way, 345 alevins were transferred to each tank, equivalent to an initial loading density of 30.2 $\pm$ 1.1 g fish L^{-1}. Subsequent loading densities varied depending on alevin numbers and size, but at no time exceeded the 32.0 g fish L^{-1} (2 lb/ft^3) limit mentioned by Liao (1971).

Alevins in the 20 growth tanks at each temperature were assigned randomly to ten treatments; each treatment was replicated once. Treatments differed only in the timing of initial food presentation. Feeding of alevins in treatments 1-9 (referred to as fed alevins) was begun in serial order from shortly after hatching to complete yolk absorption (Fig. 3, Table III). Fish in treatment 10 (referred to as unfed alevins) were held unfed for the duration of the study. Immediately prior to initial food presentation, the tops of the respective tanks were removed permanently. Thus, initial exposure to external food and light was almost simultaneous. This procedure models the ponding of hatchery-reared salmon.

Figure 3. Stylized representation of the experimental scheme for initiating feeding of chinook alevins in treatments 1-9. Alevins in treatment 10 remained unfed. Feeding was begun in serial order in relation to progressive wet weight changes observed in unfed alevins (curve, in figure). The timing of initial food presentation (●) coincides with commencement of sampling in treatments 1-9.

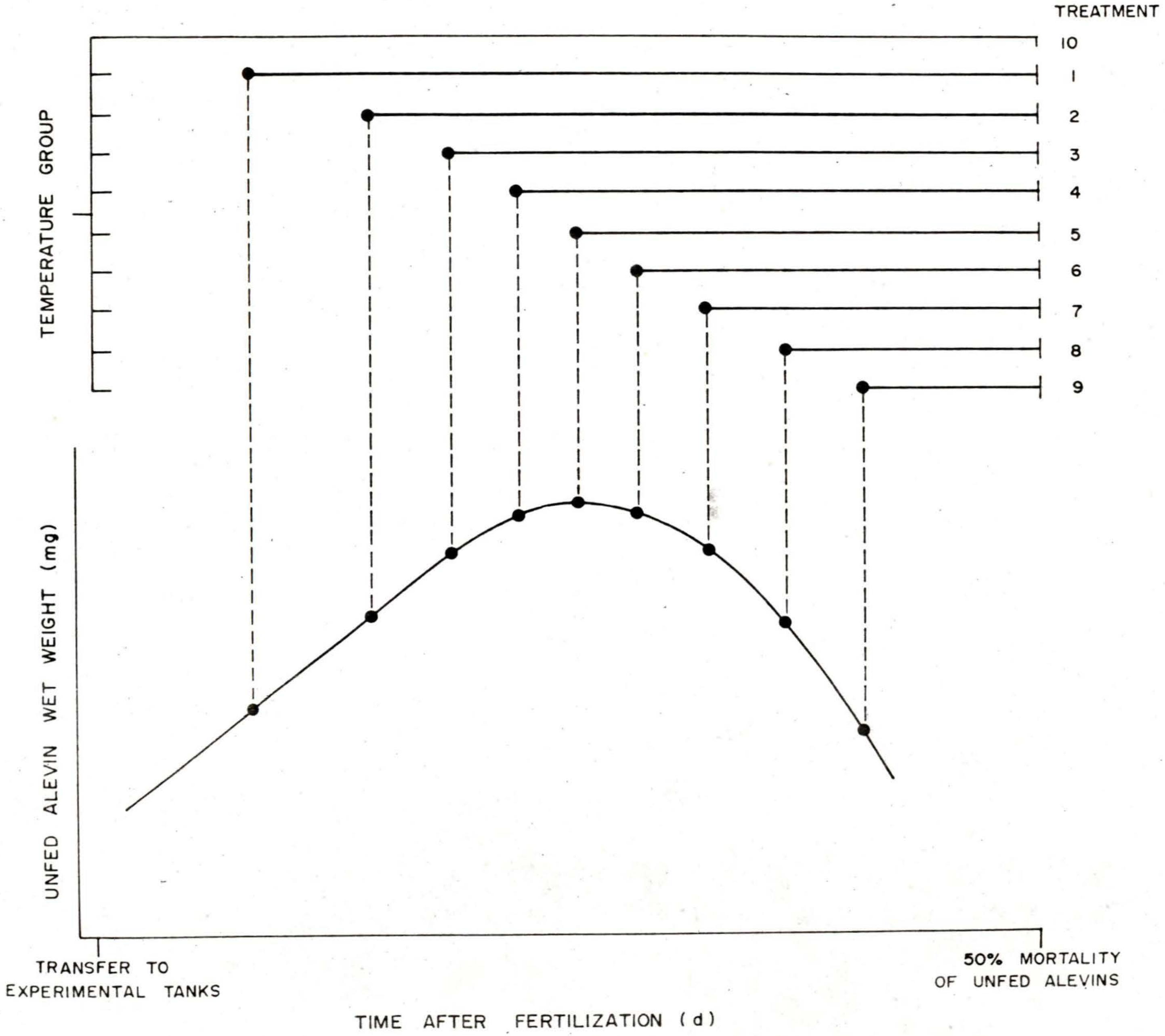

TREATMENT
10
1
2
3
4
5
6
7
8
9
TEMPERATURE GROUP
UNFED ALEVIN WET WEIGHT (mg)
TRANSFER TO EXPERIMENTAL TANKS
50% MORTALITY OF UNFED ALEVINS
TIME AFTER FERTILIZATION (d)

Table III. Timing of initial food presentation to chinook alevins in treatments 1-9 at 6, 8, 10, and 12 °C.

Treatment	Temperature group (°C) 6		8		10		12	
	Elapsed time (d)	Thermal units (tu)	Elapsed time (d)	Thermal units (tu)	Elapsed time (d)	Thermal units (tu)	Elapsed time (d)	Thermal units (tu)
1	124.4	733.7	96.3	761.1	78.0	766.0	63.9	750.8
2	142.8	848.0	109.0	870.3	89.9	884.9	72.6	854.8
3	151.9	903.1	116.8	925.6	96.9	955.2	76.1	896.8
4	155.0	922.3	120.9	958.4	98.9	975.0	78.8	928.6
5	160.0	952.3	124.9	990.7	102.0	1005.9	80.8	952.6
6	168.0	1001.6	131.9	1047.1	105.8	1044.8	86.9	1025.1
7	186.0	1112.2	145.9	1162.9	115.9	1145.9	94.9	1120.0
8	212.0	1269.4	157.0	1252.9	127.9	1265.6	103.9	1228.5
9	247.0	1482.6	182.0	1456.0	142.0	1407.9	118.8	1407.3

4. Diet Alevins were fed Formula II Oregon Moist Pellets (OMP) (Moore-Clark Co., LeConner, Washington, USA) (Hublou 1963). To ensure against nutritional degradation, bulk food was stored frozen. Daily rations were kept at room temperature. Daily feedings were spaced equally between 0900 and 1700 h Pacific Standard Time (PST). "Starter mash" was provided as the base diet for a 78-tu period beginning at the time of initial food presentation. For the first 52-tu portion of this period, starter mash was reduced during successive 13-tu intervals from 100% to 75, to 50, and to 25% of the daily ration by replacement with 1/32-inch (pellet size) OMP. Throughout this 52-tu period, alevins were fed half-hourly. For the following 26 tu, mash was included as 10% of the daily ration and feedings were hourly. Thereafter, alevins were fed according to the OMP Feeding Chart provided by the manufacturer[5].

5. Sampling Test Fish Sampling of fish commenced during their transfer to the growth tanks. At that time, 15 alevins were taken from each tank of treatment 10. Subsequent samples of 15 fish were taken from these tanks at approximate 50-tu intervals. Sampling from treatment 10 was discontinued when unfed alevins completed yolk absorption.

Samples of 15 alevins from tanks of treatments 1-9 were taken at similar 50-tu intervals. To minimize possible density-dependent effects, sampling of these treatments commenced at the same time feeding was initiated (see Figure 3). Hence, the number of

---

[5] The OMP Feeding Chart lists food size, daily ration, and feeding frequency in relation to water temperature and average fish size.

chinook in each treatment was similar when food was presented initially. Sampling from treatments 1-9 was discontinued when cumulative mortality in treatment 10 surpassed 50%.

All sampling was carried out in the early morning (0500 - 0800 h PST), so that at least 12 h elapsed between a sampling period and the previous feeding period. This also permitted adjustment of daily rations so that feeding on a sampling day was never delayed past 1200 h PST.

Sampled fish were killed using tricaine methane sulphonate (MS 222) (Bell 1964). These alevins were blotted with absorbent tissues and weighed to the nearest 1.0 mg using a Cahn Electrobalance (DTL Millibalance Model 7500). These weights were used to estimate succeeding ration levels. Alevins then were preserved in 5% neutral formalin for at least 80 days. Although preservation is known to change the weight and length of fishes (Amosov 1960, Parker 1963, Jones and Geen 1977, Rosenthal et al. 1978), preservation for at least 80 days was found more than adequate to allow standardization of such changes between samples preserved for slightly different periods of time (Appendix Fig. 1).

After removal of alevins from preservative, their wet weights were determined as before. Alevin length[6] was measured to the nearest 0.5 mm using a fish measuring board. All yolk then was removed by

---

[6] Alevin length was measured from the tip of the snout to the fork of the caudal fin, or to the posterior medial edge of the caudal fin if no fork was present.

dissection and weighed as before. Dry weights of alevin and yolk were determined after 48 h at 60 °C. Tissue (body) weights were calculated by subtraction. Water content (percentage of wet weight) of alevins, tissue, and yolk was estimated from the appropriate wet and dry weights.

Preserved weight and length of unfed fish were used to calculate Bams' (1970) developmental index (k_D). This index is based on relative changes in alevin weight and length prior to exogenous feeding, and indicates stage of development. Bams (op. cit.) defines this index as

$$k_D = \frac{10 \times \sqrt[3]{\text{weight in mg}}}{\text{length in mm}} \quad . \tag{1}$$

Gross efficiency of yolk utilization was calculated from fertilization[7] to attainment of maximum tissue weight (Blaxter 1969) as

$$\frac{\text{dry weight increment of tissue}}{\text{dry weight decrement of yolk}} \times 100. \tag{2}$$

Complete yolk absorption was considered to have occurred when no measurable yolk dry weight remained.

Morhological development of preserved alevins was monitored using Vernier's (1969, Table 2) stages (Appendix Table II). As well, internal morphology of alevins was examined during dissection for yolk. Condition of the air bladder, whether uninflated or inflated, and the occurrence of food in the alimentary tract were recorded. Ten percent

---

[7] Yolk dry weight at fertilization, determined as before, was 174 ± 15 mg (n = 60). Tissue dry weight at that time was assumed to be negligible.

of alevins with ingested food in their alimentary tracts were subsampled, and the wet weight of ingested material was measured. Dry weight of this material was estimated as 25.3% of wet weight[8]. Mean weights of ingested food at each sampling period were used to obtain corrected alevin and tissue weights, which were used in data analyses.

Behaviour of fish in the tanks was monitored only superficially. Daily records were made regarding the location of alevins in the water column, predominant activity, and feeding response.

Alevin mortality in the tanks also was recorded daily. Dead alevins were enumerated and discarded. Cumulative percent mortality was calculated as a running total of that occurring between successive sampling periods. Experimental work was terminated at each temperature when cumulative mortality in treatment 10 surpassed 50%.

C. Unfed Alevins in Incubation Trays

To verify that results for fish in growth tanks would be comparable to those found in a practical culture situation, a companion study examined growth and development of chinook alevins maintained unfed in Heath incubation trays from hatching until complete yolk absorption. These alevins hatched from the surplus eggs in the fifth tray of each incubator (see Section II(A)). Water temperatures during their post-hatching development were 6.03 ± 0.47, 8.05 ± 0.32, 9.98 ± 0.33, and 11.93 ± 0.37 °C. Flow rates during the same period averaged 13.9 ± 0.8 L min^{-1}, equivalent to an apparent velocity of 777.7 ± 46.0

---

[8] Solids content of ingested food, after drying to constant weight at 60 °C (48 h), was 25.3 ± 1.4 % of wet weight (n = 100).

cm h^{-1}. Water temperatures and flow rates were measured at least twice daily, and accumulated tu were calculated as before.

Initial loading densities were approximately 1,500 fish per tray. These alevins were sampled at the same time as those in the corresponding temperature group of the feeding experiments, and were handled similarly. In addition, morphological development at 8 °C was examined in samples of ten fish taken at 4-day intervals. Only the Vernier (1969) stages of these alevins were recorded.

D. Emergence of Alevins from Gravel

A simulated redd, modified from Dill (1970) and Godin (1979), was included as part of each experimental unit. Redds were constructed of acrylic and glass panels (25.2 × 51.9 × 31.0 cm), insulated on all sides with 1.9-cm black neoprene sheeting, and filled to a depth of about 21 cm with clean, graded 1.3 - 2.5 cm (1/2 - 1 inch) gravel (Fig. 4). Each redd was provided with an one-way emergence cover, to prevent the re-entry into the gravel environment typical of newly emerged alevins (White 1915, Stuart 1953, Mason 1976). The cover consisted of a clear polyethylene sheet perforated with 36 clear plastic tubes (2-cm Diam, 3-cm height). The tubes were set flush with the underside of the sheet and projected above it. The cover was placed on the gravel surface and sealed to the sides of the redd. Emergence covers of similar construction have been found highly efficient in preventing pink salmon alevins from re-entering the gravel of simulated redds (Godin 1979).

Water flowed to the redd through insulated vinyl tubing from

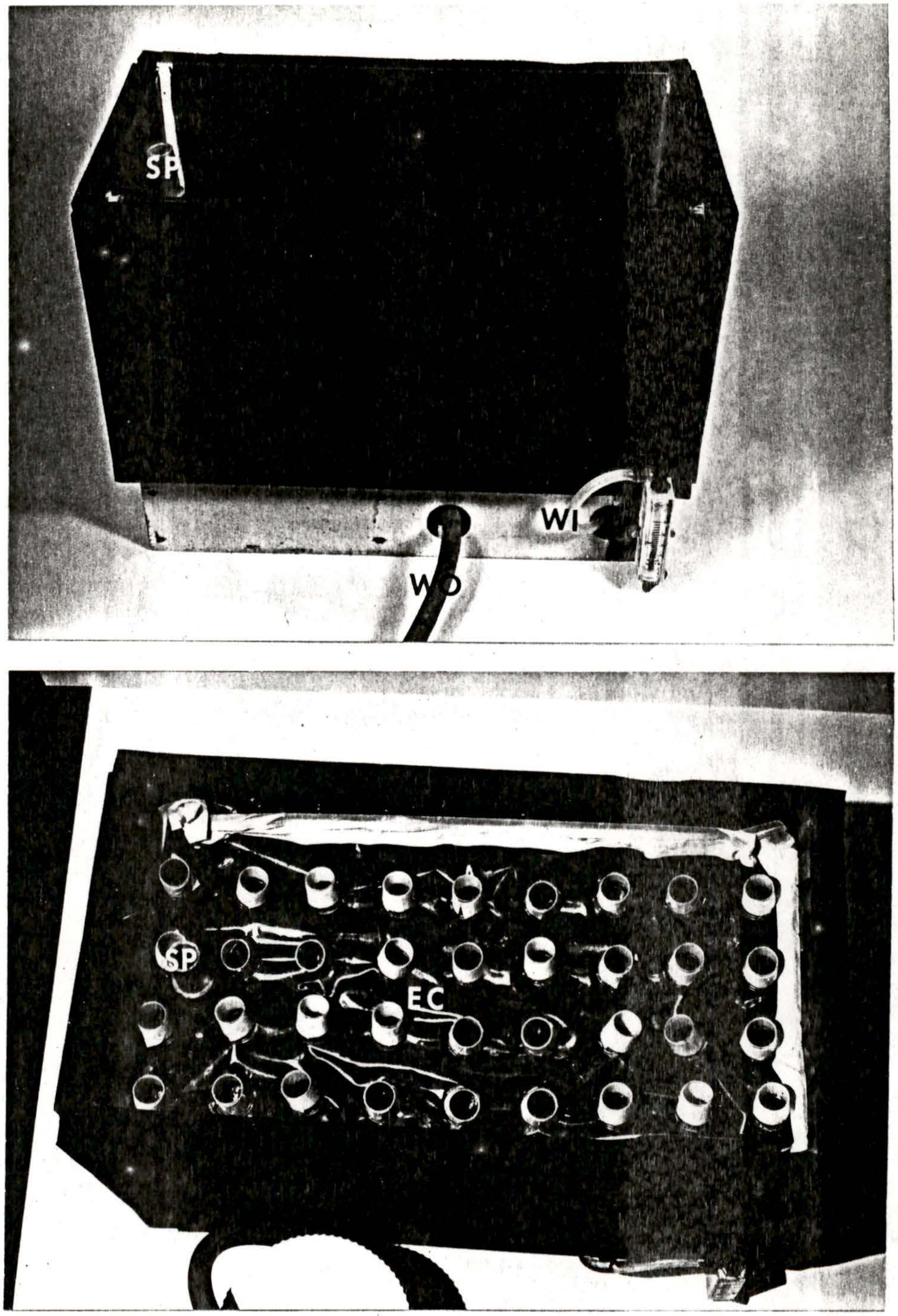


Figure 4. Simulated redd used to examine emergence of chinook alevins. EC -- emergence cover, SP -- standpipe, WI -- water inlet, WO -- water outlet.

an outlet in the front of the head box. A perforated nylon inlet tube located on the bottom of each redd provided an upwelling water flow of 5.2 ± 0.3 L min^{-1}, equivalent to an apparent velocity of 238.6 ± 13.8 cm h^{-1}. This flow rate and apparent velocity exceed the requirements suggested by Bams and Simpson (1977) for the substrate incubation of chinook eggs and alevins. An internal PVC standpipe maintained a water depth above the gravel surface of approximately 6 cm. Water temperatures were measured at least twice daily in the outflow of each redd. Accumulated tu were calculated as before. Temperatures in the redds throughout the experiment were 6.08 ± 0.33, 8.14 ± 0.27, 9.98 ± 0.23, and 11.98 ± 0.31 °C.

Redds were exposed to incandescent lighting within the same light/dark cycle described for the feeding experiments. Illumination at the water surface during the light phase averaged 50.4 ± 0.6 lux.

At each temperature, 345 fish were transferred to the redd at the same time as fish were transferred to the growth tanks. Alevins were introduced 9.5 cm beneath the gravel surface through three 5-cm Diam PVC tubes. These fish were allowed 24 h to disperse into the gravel before the tubes were removed and the emergence cover was installed. Emerged alevins were enumerated daily. Those moving into the outflow were collected in a plastic container; those remaining in the water column above the gravel were removed with a dipnet. The timing of 50% emergence was calculated as described for 50% hatching.

E. Data Analysis and Presentation

General statistical analyses used analysis of variance and covariance, Duncan's New Multiple Range Test, and correlation analysis (Steel and Torrie 1960, Snedecor and Cochran 1967). In all analyses, the lowest level of significance was fixed at 5% ($P \leqslant 0.05$). Differences at the 5% level of probability are designated by *, those at the 1% level ($P \leqslant 0.01$) by **. Where results of analyses pertaining to more than one group are reported simultaneously, subscripts are used to denote the appropriate temperature group.

Variances associated with mean weights and lengths differed significantly between sampling periods (Bartlett's test for homogeneity of variances). In these cases, a natural logarithmic ($\log_e$) transformation of the data was used to stabilize variances and to normalize the data distribution (Bartlett 1947). Means of transformed data were used in all analyses based on the normal distribution. These means are reported as geometric means (means of log-transformed data back-transformed to the original scale), with their 95% confidence limits[9]. As confidence limits are not symmetrical about geometric means, they are reported individually in brackets after each mean (Sokal and Rohlf 1969). In contrast, variances associated with mean water content and k_D did not differ significantly between sampling periods. Consequently, these data are reported as arithmetic means $\pm$ 95% confidence limits ($\overline{x} \pm$ 95% confidence limits),

As no significant differences were found between data from replicate tanks, they were pooled for most analyses. However, since

---

[9] The geometric mean is not directly comparable to the average derived from the original data. For such comparisons, the mean of log-transformed data must be adjusted by addition of 1.15 times the variance of the transformed data, before back-transformation to the original scale (Elliot 1973).

three degrees of freedom are lost during calculation of the partial correlation coefficient ($r_{12.3}$), the degrees of freedom in that calculation were increased by considering replicate data separately.

Growth, the elaboration of tissue, often follows an exponential curve (Hayes 1949, Smith 1956, Brett 1979). The general equation for exponential growth is

$$w = Ae^{bt}, \tag{3}$$

where w is size, t is time, and A and b are derived constants. Analysis of exponential growth is simplified by considering the $\log_e$ transformation of size, as described by the straight-line equation

$$\log_e = bt + \log_e A . \tag{4}$$

The first derivative of equation 4,

$$\frac{\underline{d}w}{w\ \underline{d}t} = b, \tag{5}$$

indicates that the regression coefficient or slope (b) of the $\log_e$ size-time curve (equation 4) is equivalent to the instantaneous rate of change in size per unit time. When multiplied by 100, this represents the specific growth rate (percent change in size per unit time). In this study, changes in the geometric mean dry weight of tissue were considered the most satisfactory measure of growth (Blaxter 1969). Consequently, specific growth rates were estimated from coefficients derived from the regression of $\log_e$ tissue dry weight on time (days after fertilization).

All regression lines were calculated from mean values and were compared using analysis of covariance to test equality of regression coefficients. Comparisons of rates, growth or otherwise, were based on these analyses of regression lines. All rates are reported with their 95% confidence limits. Regression equations from which rates were estimated are presented in Appendix Table III.

III. RESULTS

A. Size at Hatching

Initial size (weight and length) of alevins when transferred to the growth tanks shortly after hatching varied between temperature groups (Table IVa). Initial size decreased significantly in fish hatched at higher temperatures from 6 to 10 °C (Duncan's test). This size reduction was associated with apparent, but not significant, decreases in tissue and yolk weights (Table IVb) (Duncan's test). Yolk at hatching at these temperatures averaged 68.7 $\pm$ 0.6 % of total alevin wet weight. The developmental index (k_D) at hatching (Table IVa) did not vary significantly at 6, 8, and 10 °C (Duncan's test), indicating that fish at these temperatures hatched at a similar developmental stage.

In contrast, 12 °C alevins hatched with a significantly greater k_D (Duncan's test). As well, these fish hatched with significantly less tissue weight and alevin length, and with significantly greater yolk weight (Duncan's test). Yolk at hatching at 12 °C constituted 73.8% of total wet weight. These findings suggest that 12 °C alevins hatched at an earlier developmental stage than fish at lower temperatures. The increased yolk weight at 12 °C was reflected in a significant increase in total alevin weight from 10 to 12 °C (Duncan's test).

Table IV. Characteristics of chinook salmon shortly after hatching at 6, 8, 10, and 12 °C. Means are shown with their 95% confidence limits. F-values (df = 3, 116) for comparison of means between groups are given below each column.
Part a -- Weight, water content, length and developmental index (k_D) of alevins.
Part b -- Weight and water content of tissue and yolk.

Part a.

Temperature group (°C)	Wet weight (mg)	Dry weight (mg)	Water content (%)	Length (mm)	k_D
6	435(421, 448)	166(161, 171)	62.5 ± 0.5	25.8(25.3, 25.9)	2.97 ± 0.05
8	426(409, 442)	159(152, 166)	62.6 ± 0.4	25.6(25.4, 26.1)	2.91 ± 0.05
10	402(388, 417)	149(143, 155)	62.1 ± 0.7	24.9(24.8, 25.1)	2.96 ± 0.05
12	442(427, 456)	166(160, 172)	61.6 ± 0.7	24.6(24.4, 24.8)	3.09 ± 0.04
F	5.76**	3.05**	1.98	21.77**	11.11**

Table IV (cont'd).

Part b.

Temperature group (°C)	Tissue Wet weight (mg)	Tissue Dry weight (mg)	Tissue Water content (%)	Yolk Wet weight (mg)	Yolk Dry weight (mg)	Yolk Water content (%)
6	139(135, 144)	20(19, 21)	85.0 ± 0.7	296(286, 306)	145(138, 152)	50.8 ± 0.7
8	129(126, 133)	20(19, 20)	84.3 ± 0.4	295(282, 310)	139(132, 146)	51.3 ± 0.6
10	126(122, 129)	19(18, 20)	84.7 ± 0.4	276(264, 289)	129(122, 138)	50.9 ± 0.7
12	115(111, 118)	17(16, 18)	84.8 ± 0.5	326(314, 338)	149(143, 155)	52.0 ± 0.8
F	31.12**	11.00**	1.31	9.56**	3.81**	2.26

Initial water content of alevins, tissue, and yolk at hatching did not vary significantly between temperature groups (Table IVa and b). Averaged over the four temperatures, water content of alevins (tissue plus yolk) was 62.3 $\pm$ 1.6 %, while that of tissue and yolk was 84.7 $\pm$ 1.4 % and 51.0 $\pm$ 1.9 %, respectively (n = 120).

B. Development of Unfed and Fed Alevins

Development of behavioural traits and morphological characteristics of chinook salmon was hastened at increased temperatures (Fig. 5 and 6). Alevins remained inactive on the false bottom of the growth tanks following their transfer from the incubators. During this period they remained on their sides, apparently randomly oriented. Fish began to assume and maintain an upright posture by 630 tu after fertilization. Apparent orientation into the current was observed shortly thereafter. By 760 tu, alevins began making short excursions along the bottom. Fish in treatment 1 were first fed about this time. By 800 tu, individuals were found swimming at the water surface. Feeding in treatment 2 commenced shortly thereafter.

Inflated air bladders first were detected after alevins were found swimming at the surface. At 6 and 12 °C, fed fish commenced air bladder inflation before unfed alevins (Fig. 5). As well, at each temperature the number of fed alevins with inflated air bladders was greater initially than that for unfed alevins (Fig. 5). This suggests that some fish exposed to external food and light inflated their air bladders earlier than fish remaining unfed and in darkness.

Alevins were capable of ingesting food prior to inflating their

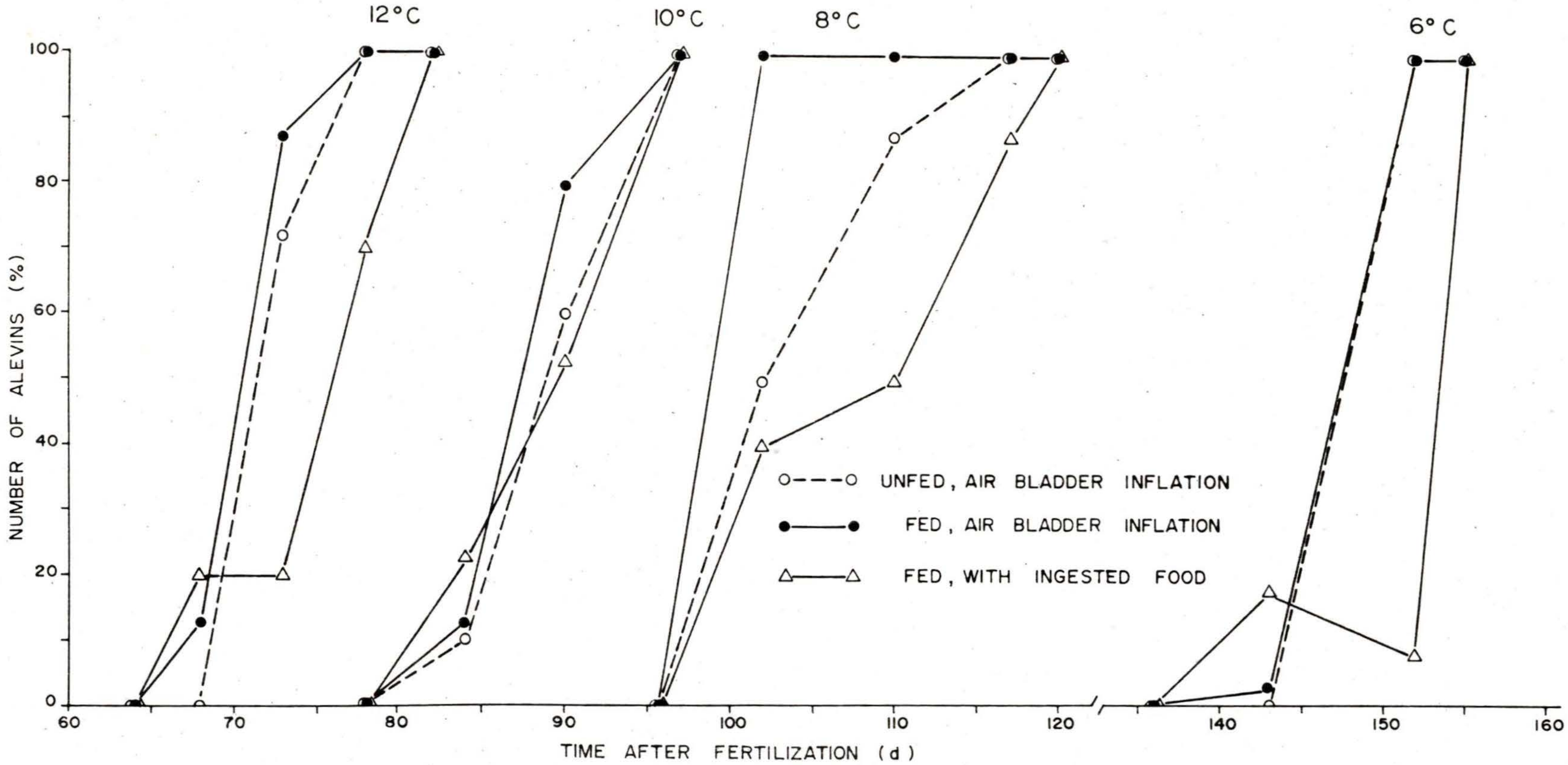


Figure 5. Timing of air bladder inflation for fed (treatment 1) and unfed (treatment 10) chinook alevins, and the occurrence of ingested food in the alimentary tract of alevins at 6, 8, 10, and 12 °C.

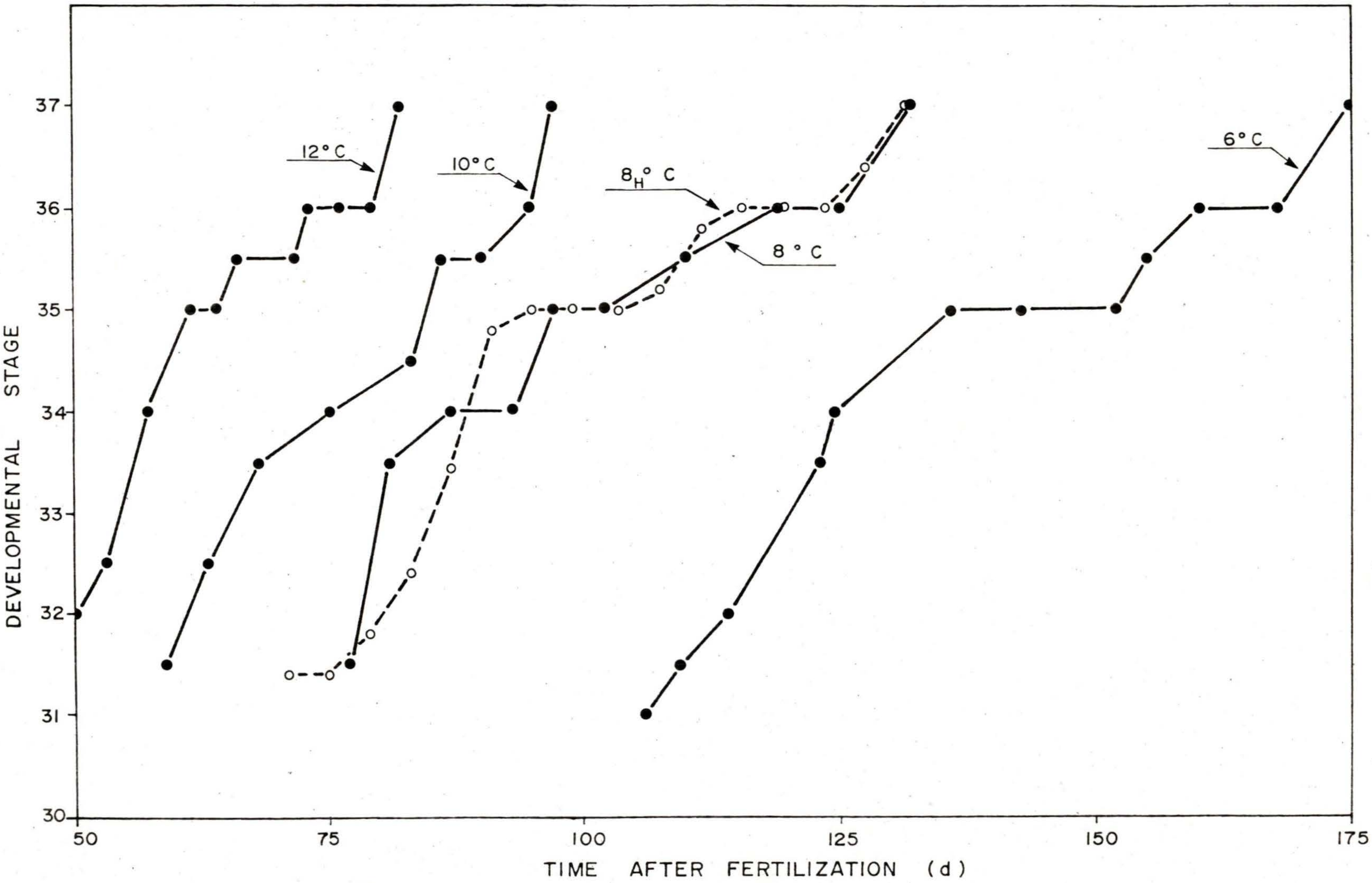


Figure 6. Morphological development of chinook alevins (unfed and fed) in growth tanks at 6, 8, 10, and 12 °C, monitored using Vernier's (1969) stages. Curve 8_H °C is for unfed chinook in a Heath tray at 8 °C (see Section III(F)).

air bladders; 7.8% of fish sampled from treatments 1 and 2 had done so. Averaged over the four temperatures, alevins began consuming food while retaining 51 $\pm$ 2 % of their yolk reserve at fertilization (dry weight). In treatments 3-9, alevins had inflated their air bladders before they were first fed.

Occurrence of Vernier's (1969) stages (Fig. 6, Appendix Table II) did not differ between unfed and fed alevins. Fish were at stages 31-32 when transferred to the tanks, at stages 34-35 when feeding commenced in treatment 1, and at stages 35-36 when air bladders were inflated. When stage 37 (button-up) was reached at the four temperatures, alevins still retained 26 $\pm$ 4 % of their yolk reserve at fertilization (dry weight).

C. Characteristics of Unfed Alevins

Tissue, yolk, and alevin (tissue plus yolk) parameters from treatment 10 varied significantly with time following alevin transfer to the growth tanks. Trends observed for the various parameters were similar at each temperature, and are dealt with in the following sections.

1. <u>Tissue Weight and Water Content of Unfed Alevins</u> Tissue weight (wet and dry) increased with time to a maximum tissue weight (MTW), and then declined (Fig. 7). The specific growth rate (% d^{-1}) to this MTW (Table V) varied between temperature groups and was correlated with temperature ($F = 80.37^{**}$, df = 3, 26; $r = 0.996^{**}$, df = 2). That is, the growth rate increased with increased temperature.

Maximum tissue wet weight and maximum tissue dry weight were

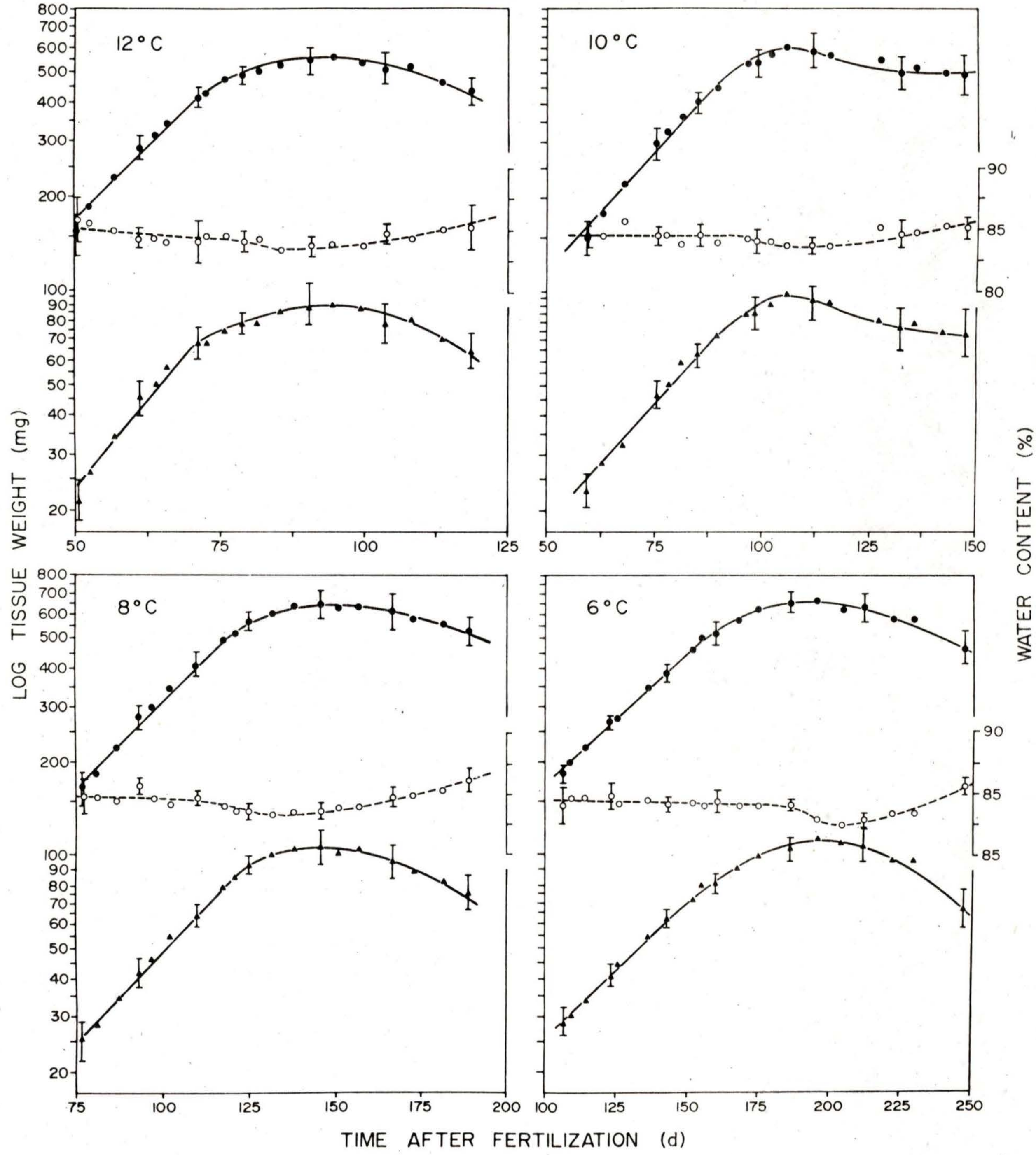


Figure 7. Tissue of unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C: mean wet weight (●——●), dry weight (▲——▲), and water content (○– –○). Sample dispersion is shown as ± 1 SD. Curves fitted by eye.

Table V. Specific growth rate to maximum tissue weight (MTW), geometric mean MTW, and timing of MTW from fertilization for unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C. Rates and means are shown with their 95% confidence limits.

Temperature group (°C)	Specific growth rate ($\% \ d^{-1}$)	Maximum tissue weight: Wet weight (mg)	Maximum tissue weight: Dry weight (mg)	Timing of maximum tissue weight: Elapsed time (d)	Timing of maximum tissue weight: Thermal units (tu)
6	2.07 ± 0.11	655(628, 683)	112(107, 117)	195.9	1172.7
8	2.96 ± 0.32	643(618, 669)	105(100, 111)	145.9	1162.9
10	3.84 ± 0.50	601(583, 620)	98(94, 102)	105.8	1044.8
12	5.10 ± 0.68	562(535, 591)	91(86, 97)	94.9	1120.0

reached simultaneously (Fig. 7). These maxima (Table V) varied between the temperature groups and were negatively correlated with temperature (mean tissue wet weight -- F = 11.78**, df = 3, 116; r = -0.979*, df = 2; mean tissue dry weight -- F 14.62**, df = 3, 116; r = -.0.999** df = 2). Thus, MTW decreased with increased temperature. This trend was not merely a reflection of differences among tissue weights at hatching (Table IVb). Although maximum and initial tissue wet weights were correlated (r = 0.969*, df = 2), no significant relationship was found between maximum and initial tissue dry weights (r = 0.905, df = 2). Furthermore, maximum and initial wet weights no longer were correlated when their common association with temperature was removed statistically ($r_{12.3}$ = -0.228, df = 5). Yet, when differences in initial tissue wet weight were similarly removed, maximum wet weight and temperature remained correlated ($r_{13.2}$ = -0.781*, df = 5). Hence, MTW was determined primarily by temperature after hatching, rather than by tissue weight at hatching.

MTW was reached more rapidly at higher temperatures. Elapsed time to MTW (Table V) decreased with increased temperature (r = -0.968*, df = 2). Accumulated tu to MTW (Table V) showed no significant relationship with temperature (r = -0.612, df = 2), and over the four temperatures averaged 1125.1 ± 58.2 tu.

Tissue weight decreased steadily after MTW was reached at 6,8, and 12 °C. However, the decline at 10 °C appeared to approach an asympote (Fig. 7). By the final sampling period at complete yolk absorption, tissue wet weight had declined 22.1 ± 5.3 % (n = 4), while tissue dry weight had declined 31.2 ± 6.6 % (n = 4).

Tissue water content (Fig. 7) remained constant at 84.4 ± 1.0 %

(n = 36), with time (Duncan's test) and between the temperature groups (F = 0.19, df = 3, 32) from hatching until just prior to MTW. Tissue water content then decreased to an average of 82.6 $\pm$ 0.5 % (n = 120) at MTW at the four temperatures (F = 1.97, df = 3, 116). After MTW, tissue water content increased and by the final sampling period averaged 85.4 $\pm$ 1.5 % (n = 120) over the four temperatures (F = 2.37, df = 3, 116).

In summary, tissue weights increased with time to a maximum tissue weight (MTW), and then declined 22.1-31.2% by the final sampling period at complete yolk absorption. Growth rate to MTW increased with increased temperature, while the maximum weights attained decreased with increased temperature. Hence, MTW was reached more rapidly at higher temperatures. Accumulated tu at that time averaged 1125.1. Tissue water content was constant at 84.4% from hatching until just prior to MTW, and then decreased to 82.6%. After MTW, tissue water content increased and reached 85.4% by the final sampling period.

2. Yolk Weight and Water Content of Unfed Alevins Yolk weight (wet and dry) declined continuously throughout the study (Fig. 8). The rate of yolk utilization (mg d^{-1}) was constant during yolk absorption to a mean wet weight of about 40 mg (approximately 20 mg yolk dry weight). This utilization rate (Table VI) varied between the temperature groups and was correlated with temperature (mean yolk wet weight -- F = 132.07**, df = 3, 43; r = 0.999**, df = 2; mean yolk dry weight -- F = 111.31**, df = 3, 43; r = 0.994**, df = 2). That is, the yolk utilization rate increased with increased temperature.

Although the rate of yolk utilization at each temperature slowed during absorption of the last 40 mg of yolk wet weight (20 mg dry

Figure 8. Yolk of unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C: mean wet weight (●—●), dry weight (▲—▲), and water content (○--○). Sample dispersion is shown as ± 1 SD. Curves fitted by eye. Where some alevins (n = 30) had completed yolk absorption, the number of alevins with yolk is indicated.

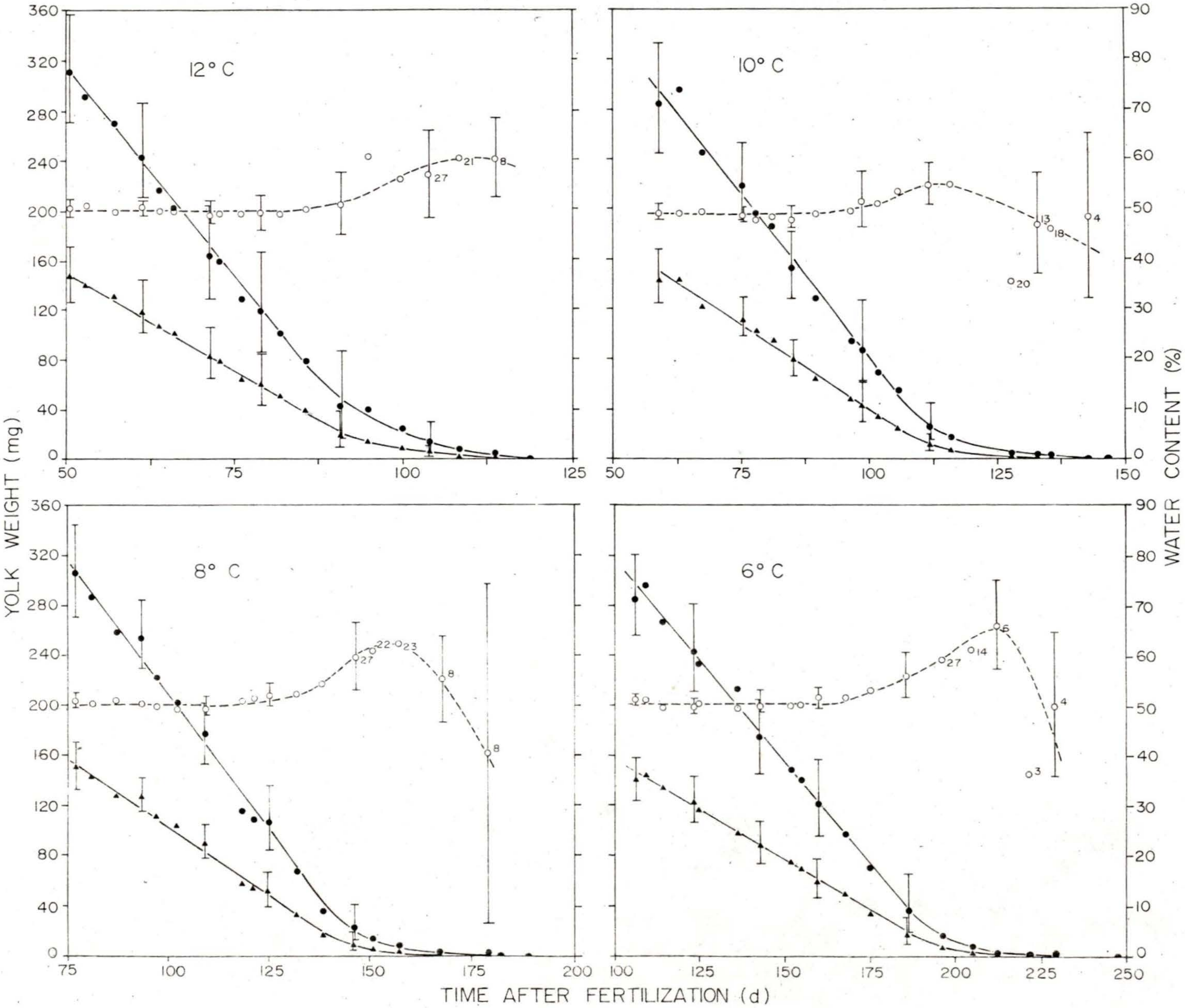

12° C
10° C
8° C
6° C
YOLK WEIGHT (mg)
WATER CONTENT (%)
TIME AFTER FERTILIZATION (d)

Table VI. Yolk utilization rate (± 95% confidence limits) and timing of complete yolk absorption from fertilization for unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C.

	Yolk utilization rate ($mg\ d^{-1}$)		Timing of complete yolk absorption	
Temperature group (°C)	Wet weight basis	Dry weight basis	Elapsed time (d)	Thermal units (tu)
6	3.18 ± 0.14	1.59 ± 0.08	247.0	1480.6
8	4.34 ± 0.28	2.17 ± 0.16	182.9	1456.1
10	5.25 ± 0.36	2.73 ± 0.19	146.9	1459.9
12	6.35 ± 0.35	3.07 ± 0.14	118.8	1427.3

weight) (Fig. 8), yolk absorption was completed more rapidly at higher temperatures. Elapsed time to complete yolk absorption (Table VI) decreased with increased temperature (r = -0.980*, df = 2). Accumulated tu to complete yolk absorption (Table VI) showed no significnat relationship with temperature (r = -0.919, df = 2), and over the four temperatures averaged 1456.1 ± 22.0 tu.

Yolk water content (Fig. 8) remained constant at 50.0 ± 2.0 % (n = 36), with time (Duncan's test) and between the temperature groups (F = 0.72, df = 3, 32) from hatching to a mean yolk wet weight of about 100 mg (approximately 50 mg dry weight). Thereafter, yolk water content increased to 61.2 ± 0.8 % (n = 4), and then decreased to 50.3 ± 4.8 % (n = 4) as yolk absorption was completed. However, comparison of yolk water contents during terminal yolk absorption was desensitized by increased sample variability (Fig. 8). This resulted from decreased sample size as individuals completed yolk absorption at slightly different times, and from increased round-off error as yolk weights approached zero.

In summary, the rate of yolk utilization increased with increased temperature. Hence, yolk absorption was completed more rapidly at higher temperatures. Accumulated tu at that time averaged 1456.1. Yolk water content remained constant at 50.0% during initial yolk absorption following hatching. Yolk water content then increased to 61.2% and, subsequently, decreased to 50.3% as yolk absorption was completed.

3. <u>Tissue-yolk-water Interactions of Unfed Alevins</u> Total

wet weight (tissue plus yolk) increased with time to a maximum alevin wet weight (MAWW), and then declined (Fig. 9). The MAWW achieved (Table VII) varied between the temperature groups and was negatively correlated with temperature ($F = 10.63^{**}$, df = 3, 116; $r = -0.953^{*}$, df = 2). Thus, the maximum weight achieved decreased with increased temperature. MAWW was not correlated with alevin wet weight at hatching (Table IVa) ($r = -0.289$, df = 2). Hence, MAWW was influenced more by temperature after hatching, than by alevin wet weight at hatching.

MAWW was achieved more rapidly and after accumulation of fewer tu at higher temperatures. Both elapsed time and accumulated tu to MAWW (Table VII) were negatively correlated with temperature ($r = -0.988^{*}$, $r = -0.954^{*}$, respectively; df = 2).

The amount of yolk remaining at MAWW (Table VII) varied between the temperature groups ($F = 32.62^{**}$, df = 3, 116). While the yolk residuals at MAWW at 6 and 8 °C were not significantly different, those at higher temperatures were greater (Duncan's test). Yolk residuals at MAWW were not correlated with yolk weight at hatching ($r = 0.442$, df = 2). Thus, regardless of the yolk present at hatching, the yolk residual at MAWW increased at higher temperatures.

In most cases, MAWW occurred before MTW was reached. However, at 10 °C maximum alevin wet weight and maximum tissue weight were reached simultaneously. Still, it is conceivable that tissue weight reached a maximum after MAWW was attained at 10 °C, but that this was not detected by the sampling method. This assumption is supported by the yolk residual present when MTW was attained at the four temperatures. At 6, 8, and 12 °C, yolk reserves at MTW were not significantly different (Duncan's

Figure 9. Changes in unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C, in relation to time: mean wet weight (●—●), dry weight (▲—▲), and water content (○--○). Sample dispersion is shown as $\pm$ 1 SD. Curves fitted by eye.

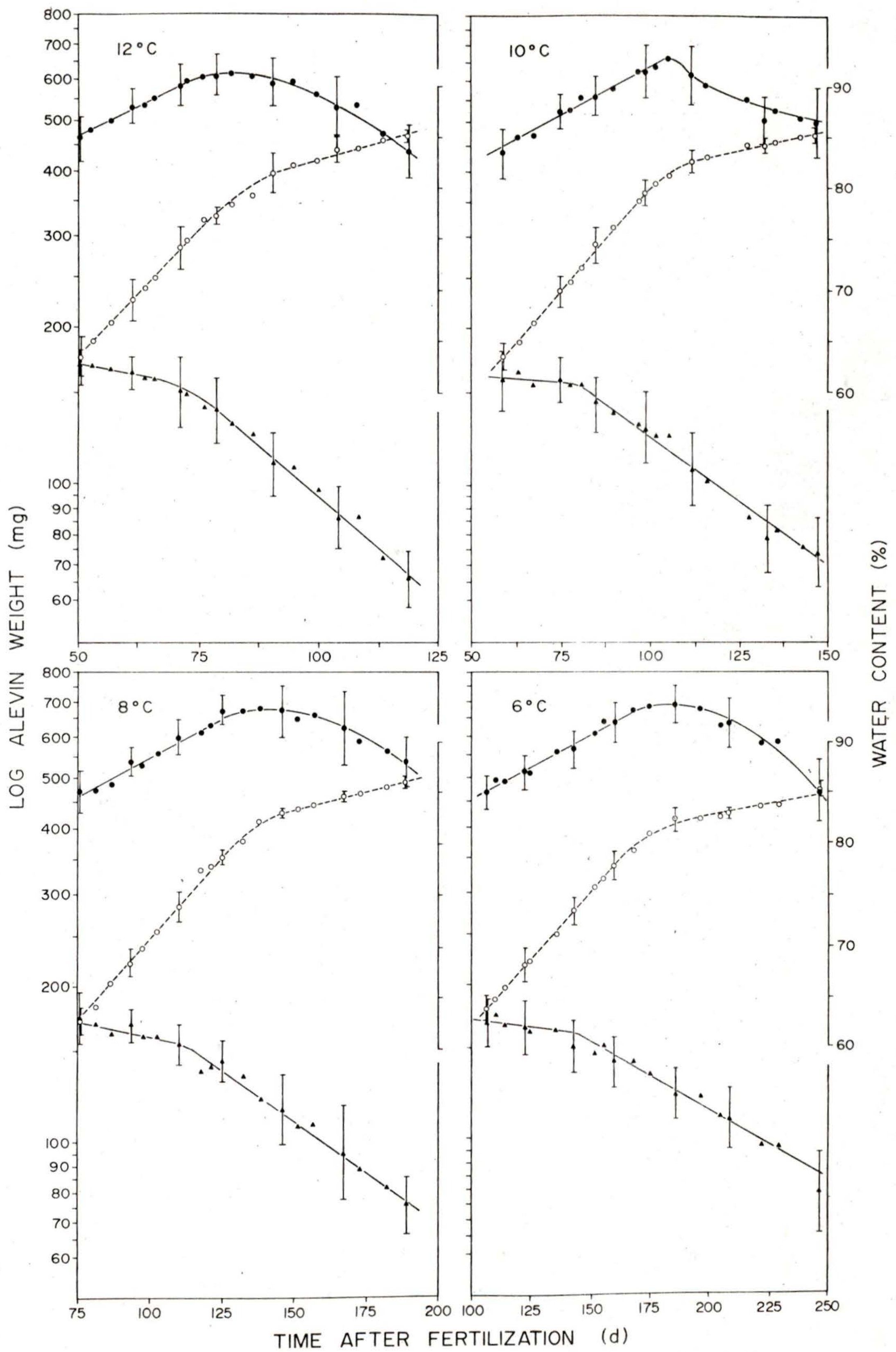

12°C
10°C
8°C
6°C
LOG ALEVIN WEIGHT (mg)
WATER CONTENT (%)
TIME AFTER FERTILIZATION (d)

Table VII. Geometric mean maximum alevin wet weight (MAWW) ($\pm$ 95% confidence limits), timing of MAWW from fertilization, yolk residual at MAWW (percentage of yolk dry weight at fertilization), and gross efficiency of yolk utilization for unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C.

Temperature group (°C)	Maximum weight (mg)	Timing of MAWW: Elapsed time (d)	Timing of MAWW: Thermal units (tu)	Yolk residual at MAWW (%)	Gross utilization efficiency (%)
6	687(666, 709)	186.0	1112.2	9.2	67.1
8	673(642, 706)	138.1	1099.2	9.8	64.6
10	656(633, 680)	105.8	1044.8	14.9	66.7
12	600(580, 620)	81.9	966.2	29.3	58.6

test), and averaged 6 ± 2 % of that at fertilization (dry weight). However, at 10 °C the yolk reserve at MTW was significantly greater (Duncan's test), constituting 15% of that at fertilization (dry weight).

Total wet weight declined steadily after MAWW at 6, 8, and 12 °C, but the decline appeared to approach an asympote at 10 °C (Fig. 9). Total wet weight had declined 26.8 ± 0.1 % from MAWW by the final sampling period at complete yolk absorption ($n = 4$).

The specific rate of tissue growth to MTW was related directly to the rate of yolk utilization ($r = 0.979$*, df = 2). However, total dry weight (tissue plus yolk) declined continually throughout the study (Fig. 9), indicating that during any given time period the amount of tissue synthesized was less than that of yolk utilized. Gross efficiency of yolk utilization from fertilization to MTW (Table VII) showed no clear trend with temperature, but decreased substantially at 12 °C.

Total water content (tissue plus yolk) increased continually from hatching (Fig. 9), and by the final sampling period averaged 85.4 ± 1.5 % ($n = 120$) over the four temperatures ($F = 2.37$, df = 3, 116). Approximately 80% of the overall increase occurred prior to attainment of MAWW.

In summary, total wet weight increased with time to a maximum alevin wet weight (MAWW), and then declined 26.8% by the final sampling period at complete yolk absorption. The maximum wet weight attained decreased at higher temperatures, while the amount of yolk present at MAWW increased at higher temperatures. MAWW was reached before MTW. The specific growth rate to MTW was related directly to the rate of yolk utilization. However, as the tissue synthesized during any given time period was less than the yolk utilized, total dry weight declined continuously. Gross efficiency of yolk utilization averaged 66.1% at the lower temperatures, but decreased to 58.6% at 12 °C. Total water content increased from 62.3% at hatching to 85.4% by the final sampling period.

4. Length and Developmental Index (k_D) of Unfed Alevins

Alevin length increased with time to a maximum (Fig. 10). This maximum length (Table VIII) was reached at the same time MTW was attained (Table V). The maximum length achieved decreased with increased temperature. Maximum length differed between the temperature groups and was negatively correlated with temperature ($F = 19.84^{**}$, df = 3, 116; $r = -0.961^{*}$, df = 2). Maximum length also was correlated with initial length at hatching (Table IVa) ($r = 0.984^{*}$, df = 2). However, direct comparison of maximum and initial lengths is questionable. Measurement of alevin length after hatching was complicated by significant changes in the shape of the caudal fin, as a fork developed in that fin.

At most temperatures, no significant changes in length were detected after a maximum was reached (Duncan's test). However, at 6 °C length decreased significantly with continued food deprivation after the maximum was reached (Duncan's test) (Fig. 10).

The developmental index (k_D) of unfed alevins decreased continually throughout the study (Fig. 10). The k_D when MAWW was reached (Table VIII) varied between the temperature groups and was correlated with temperature ($F = 7.35^{**}$, df = 3, 116; $r = 0.959^{*}$,

Figure 10. Length (●—●) and developmental index (k_D) (○--○) of unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C. Sample dispersion is shown as $\pm$ 1 SD. Curves fitted by eye.

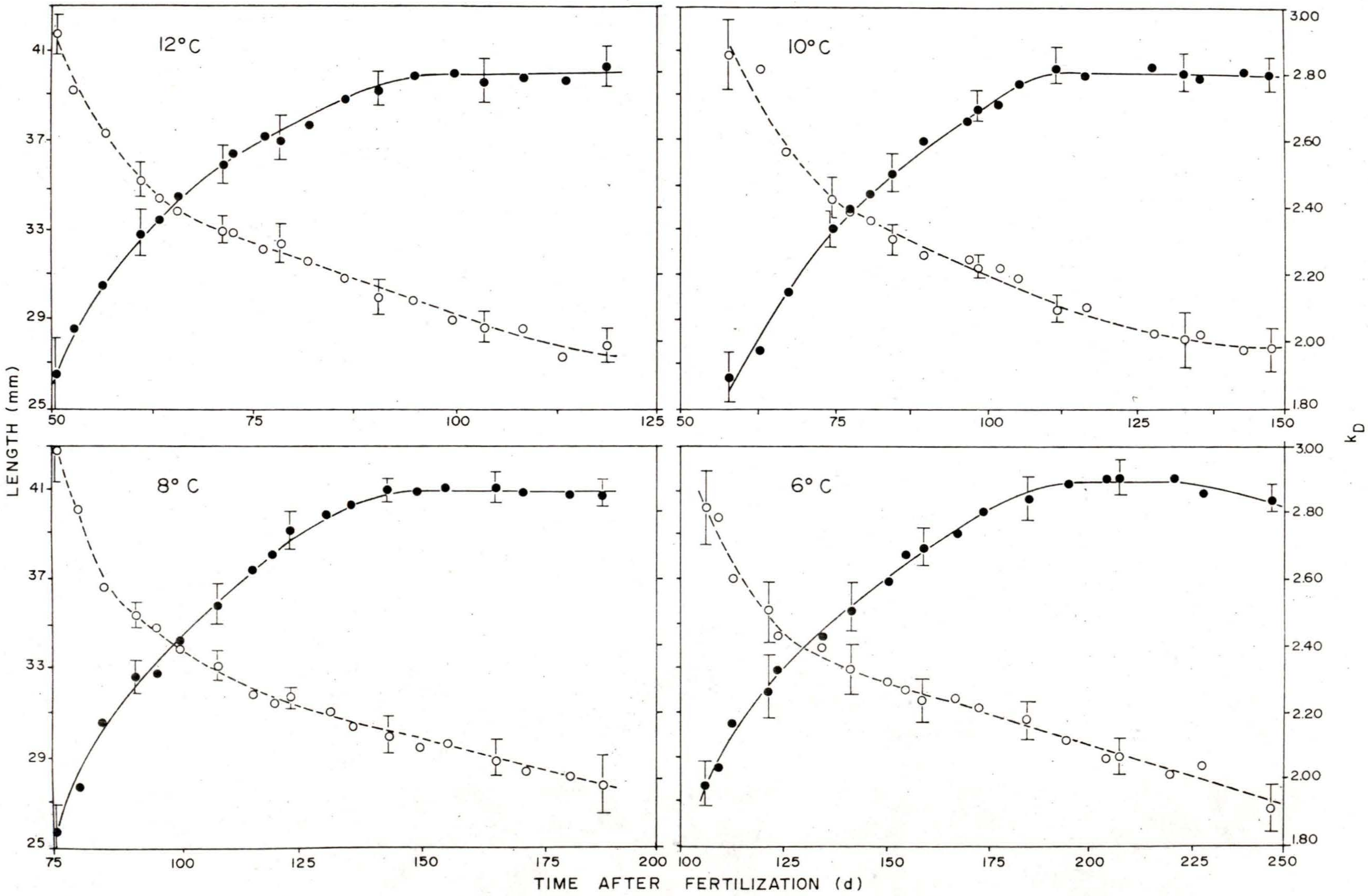

12°C
10°C
8° C
6° C
LENGTH (mm)
k_D
TIME AFTER FERTILIZATION (d)
41
37
33
29
25
50
75
100
125
150
175
200
225
250
3.00
2.80
2.60
2.40
2.20
2.00
1.80

Table VIII. Geometric mean maximum alevin length, and arithmetic mean developmental index (k_D) at maximum alevin wet weight (MAWW), at maximum tissue weight (MTW), and at complete yolk absorption, for unfed chinook alevins (treatment 10) at 6, 8, 10, and 12 °C. Means are shown with their 95% confidence limits.

Temperature group (°C)	Maximum alevin length (mm)	Developmental index (k_D)		
		at MAWW	at MTW	at Complete yolk absorption
6	41.4(41.0, 41.8)	2.17 ± 0.02	2.12 ± 0.02	1.94 ± 0.04
8	41.3(40.8, 41.9)	2.18 ± 0.02	2.13 ± 0.03	1.98 ± 0.04
10	40.3(39.9, 40.6)	2.20 ± 0.02	2.19 ± 0.02	1.96 ± 0.03
12	39.5(39.1, 39.9)	2.24 ± 0.03	2.12 ± 0.03	1.97 ± 0.02

df = 2). Thus, the developmental index at MAWW increased with increased temperature. This indicates that, in terms of k_D, MAWW was reached at an earlier stage of development at higher temperatures.

The k_D when MTW was attained (Table VIII) also varied between the temperature groups, but was not correlated with temperature ($F = 7.29^{**}$, df = 3, 116; $r = 0.230$, df = 2). Differences between temperature groups at this time were attributable to significantly greater k_D at 10 °C, indicating that MTW at 10 °C was reached at an earlier stage of development than at other temperatures.

In contrast, k_D when unfed alevins completed yolk absorption (Table VIII) did not differ between the temperature groups ($F = 2.66$, df = 3, 116). Averaged over the four temperatures, k_D at complete yolk absorption was 1.96 ± 0.02. Hence, alevins completed yolk absorption at a similar developmental stage.

In summary, alevin length increased with time to a maximum. This maximum length was reached at the same time MTW was attained. The maximum length achieved decreased with increased temperature. Lengths at 8, 10, and 12 °C did not change after a maximum was reached. However, at 6 °C length decreased with continued food deprivation.

The developmental index of unfed alevins declined throughout the study. Comparison of this index between temperature groups revealed that MAWW was reached at earlier stages of development at higher temperatures. As well, alevins at 10 °C attained MTW at an earlier developmental stage than fish at other temperatures. Nevertheless, at all temperatures examined alevins completed yolk absorption at a similar developmental stage. The k_D at complete yolk absorption was 1.96.

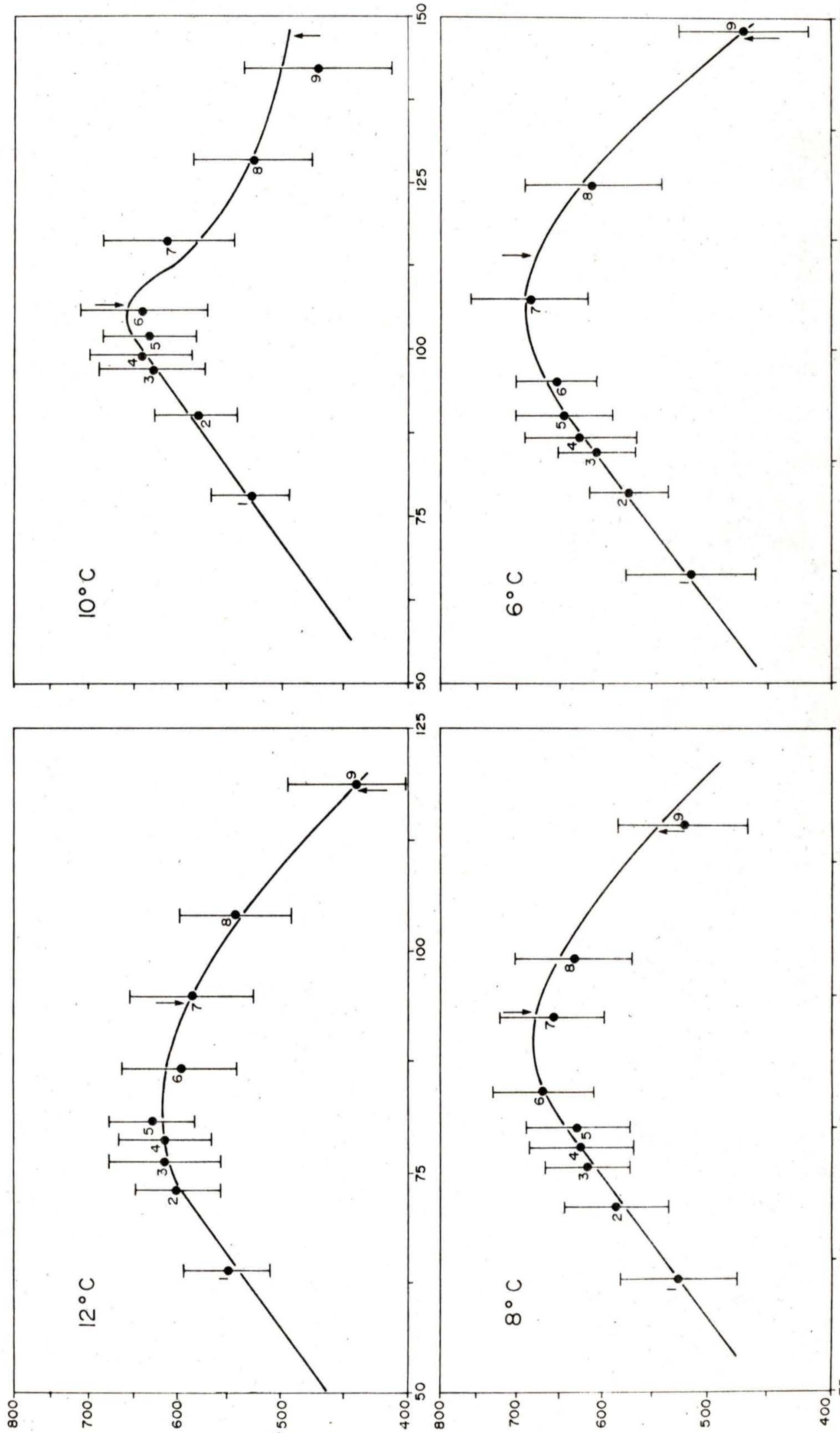
D. Characteristics of Fed Alevins

The tissue, yolk, and alevin (tissue plus yolk) parameters of fish in treatments 1-9, when food was initially presented, did not differ significantly from those of unfed fish. Hence, prior to initial food presentation, alevins in treatments 1-9 underwent changes similar to those described for fish in treatment 10.

Total wet weight (tissue plus yolk) when fish were first fed are presented in relation to changes described previously for weights of unfed alevins in Figure 11. Total wet weight in treatments 7 and 9 at 10 °C at initial food presentation diverged from the sigmoid-shaped trend in the total wet weight-time curve of unfed alevins (Fig. 11). If the total wet weight-time curve of unfed alevins at 10 °C is redrawn incorporating the initial weights in treatments 7 and 9, the resulting curve more closely follows that at 6, 8, and 12 °C. This suggests that the peculiarity of the total wet weight-time curve for unfed alevins at 10 °C is an artifact of the sampling method. This sampling error could account for the simultaneous occurrence of MAWW and MTW, and the significantly different k_D at MTW at 10 °C.

The tissue, yolk, and alevin (tissue plus yolk) parameters of fed fish varied significantly with time following initial food presentation. To simplify presentation of these results, fed alevins are classified according to the timing of their initial feeding relative to events observed for unfed alevins. For example, fed alevins are categorized as those first fed before, at, and after MAWW was reached; the acronyms MAWW and MTW refer to those maxima described for unfed alevins. The specific treatments in each category can be determined

Figure 11. Initial wet weight (●) of chinook alevins in treatments 1-9 at 6, 8, 10, and 12 °C. Sample dispersion is shown as $\pm$ 1 SD. Solid curves represent changes in wet weight of alevins in treatment 10; maxima of these curves represent maximum alevin wet weight (MAWW). Timing of maximum tissue weight (MTW) (↓) and complete yolk absorption (↑) also is indicated.

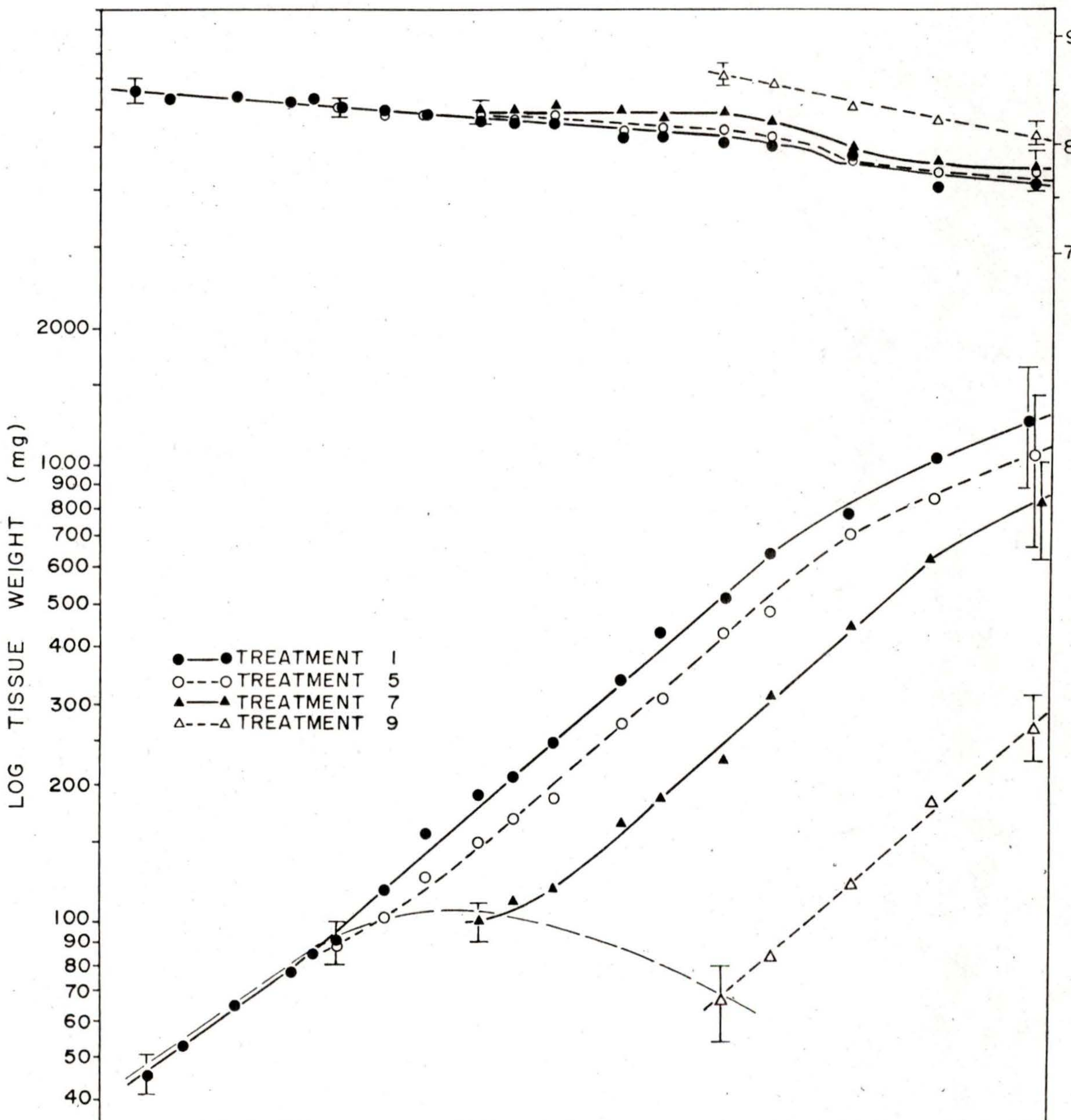

12°C
10°C
8°C
6°C
LOG WET WEIGHT (mg)
TIME AFTER FERTILIZATION (d)

by reference to Figure 11. Results at each temperature followed similar trends, and those from the 8 °C group were selected randomly for graphic illustration. For clarity, only data for treatments 1, 5, 7, and 9 are presented graphically.

1. <u>Tissue Weight and Water Content of Fed Alevins</u> Tissue weight (wet and dry) of actively feeding alevins did not differ significantly from that of unfed fish until about 40 tu before MAWW was reached. However, prior to MAWW tissue weight of actively feeding alevins was consistently less than that of unfed fish. Still, by the time MAWW was attained, tissue weight of alevins first fed before MAWW was about 120% of that of unfed fish. Throughout the study, tissue weight of alevins first fed before MAWW remained significantly greater than that of fish first fed at or after MAWW (Fig, 12).

Specific growth rates were calculated from the time tissue dry weight first differed significantly from that of unfed alevins until the final sampling period when cumulative mortality in treatment 10 surpassed 50%, or until a mean tissue dry weight of 700 mg was reached. At each temperature, these rates did not differ significantly among treatments 1-9 (Table IX). Thus, the specific growth rate of actively feeding alevins was unaffected by the timing of initial food presentation. On that basis, growth rates of treatments 1-9 were pooled at each temperature. These pooled rates (Table IX) varied significantly between the temperature groups and were correlated with temperature ($F = 377.53^{**}$, df = 3, 328; $r = 0.986^{*}$, df = 2). That is, the growth rate of actively feeding fish increased with increased temperature.

Figure 12. Tissue dry weight and water content of chinook alevins initially fed at various times at 8 °C. Tissue dry weight is presented in the lower portion of the figure, where the broken curve (— — —) represents changes in tissue dry weight of unfed alevins. Sample dispersion is shown as ± 1 SD. Curves fitted by eye.



90
80
70
WATER CONTENT (%)
2000
1000
900
800
700
600
500
400
300
200
100
90
80
70
60
50
40
LOG TISSUE WEIGHT (mg)
TREATMENT 1
TREATMENT 5
TREATMENT 7
TREATMENT 9
90
110
130
150
170
190
210
230
TIME AFTER FERTILIZATION (d)

Table IX. Specific growth rate ($\pm$ 95% confidence limits) of chinook alevins initially fed at various times at 6, 8, 10, and 12 °C. F-values and degrees of freedom from comparisons of rates between treatments, and pooled growth rates for the nine treatments are presented below each column.

	Growth rate (% d^{-1})			
	Temperature group (°C)			
Treatment	6	8	10	12
1	2.14 ± 0.24	2.97 ± 0.18	3.06 ± 0.29	4.11 ± 0.36
2	2.20 ± 0.24	2.66 ± 0.17	2.92 ± 0.24	3.81 ± 0.37
3	2.23 ± 0.14	2.73 ± 0.14	3.14 ± 0.20	4.00 ± 0.22
4	2.06 ± 0.26	2.75 ± 0.16	3.00 ± 0.20	3.82 ± 0.30
5	2.15 ± 0.15	2.76 ± 0.18	3.13 ± 0.27	4.01 ± 0.25
6	2.11 ± 0.21	2.90 ± 0.14	3.07 ± 0.18	3.83 ± 0.26
7	1.91 ± 0.28	2.83 ± 0.32	3.17 ± 0.28	4.03 ± 0.43
8	2.15 ± 0.26	2.68 ± 0.37	3.58 ± 0.81	4.09 ± 0.45
9	2.49 ± 2.11	3.02 ± 0.47	3.71 ± 0.95	3.61 ± 1.43
F(df)	1.29(8, 52)	1.62(8, 61)	1.94(8, 75)	1.28(8, 76)
pooled rate	2.12 ± 0.06	2.79 ± 0.06	3.10 ± 0.08	3.94 ± 0.10

The growth rate slowed after tissue dry weight surpassed a mean of about 700 mg (approximately 3200 mg wet weight), regardless of the timing of initial food presentation or temperature (Fig. 12). Insufficient data were collected after this point to enable calculation of the reduced growth rate. As all alevins completed yolk absorption before the final sampling period, final tissue weight was identical to final total (tissue plus yolk) weight (Section III(D.3)).

In all treatments, tissue water content decreased significantly with time following initial food presentation (Duncan's test) (Fig. 12). At each sampling period, tissue water content did not vary significantly among treatments where feeding was initiated before or at MTW (Fig. 11) (Duncan's test). Averaged over the four temperatures, the final tissue water content of fish first fed before or at MTW was 77.8 $\pm$ 0.4 % (n = 22). In treatments where food presentation was delayed until after MTW was attained, tissue water content increased significantly in relation to the period of food deprivation (Duncan's test); the greater the period, the greater the tissue water content. The final tissue water content of alevins in treatment 9 averaged 81.0 $\pm$ 0.7 % (n = 4).

In summary, exogenous feeding had no significant effect on tissue growth until shortly before MAWW was attained. Still, tissue weights of alevins first fed before MAWW remained greater than those of fish first fed at or after MAWW. Regardless of the specific timing of first feeding, a stanza or interval of rapid growth was evident once the tissue weight of actively feeding alevins differed from that of unfed fish. The growth rate during this stanza was unaffected by the timing of initial food presentation, but increased with increased temperature. In all treatments, tissue water content declined following initial feeding.

2. Yolk Weight and Water Content of Fed Alevins The yolk reserve of alevins, when first fed, varied from 64.7 ± 3.7 % of that at fertilization (dry weight) in treatment 1, to 0.3 ± 0.3 % in treatment 9 (n = 4). Regardless of the timing of first feeding, yolk weight (wet and dry) declined with time following initial food presentation (Fig. 13). The yolk utilization rate of actively feeding alevins was constant to a mean of about 20 mg dry weight (approximately 40 mg yolk wet weight) (Fig. 13). In treatment 1, this utilization rate (Table X) varied significantly among the temperature groups and was correlated with temperature (mean wet weight -- $F = 33.25^{**}$, df = 3, 25; $r = 0.997^{**}$, df = 2; mean dry weight -- $F = 28.91^{**}$, df = 3, 25; $r = 0.981$, df = 2). That is, the utilization rate increased with increased temperature.

Fish in treatment 1, the earliest fed alevins, were assumed the most likely to exhibit a possible interaction between exogenous feeding and yolk absorption. However, the yolk utilization rate in treatment 1 did not differ significantly from that of unfed alevins (wet weight basis -- $t_6 = 0.001$, df = 18; $t_8 = 0.482$, df = 18; $t_{10} = 0.364$, df = 14; $t_{12} = 0.356$, df = 18; dry weight basis -- $t_6 = 0.105$, df = 18; $t_8 = 0.508$, df = 18; $t_{10} = 0.163$, df = 14; $t_{12} = 0.802$, df = 18). As well, at each temperature yolk absorption was completed at the same time in all treatments (1-10). Additionally, at each sampling period neither yolk weight (wet and dry) nor yolk water content varied

Figure 13. Yolk dry weight and water content of chinook alevins initially fed at various times at 8 °C. Yolk dry weight is presented in the lower portion of the figure. Sample dispersion is shown as ± 1 SD. Curves fitted by eye. Where some alevins (n = 30) had completed yolk absorption, the number of alevins with yolk remaining is indicated.

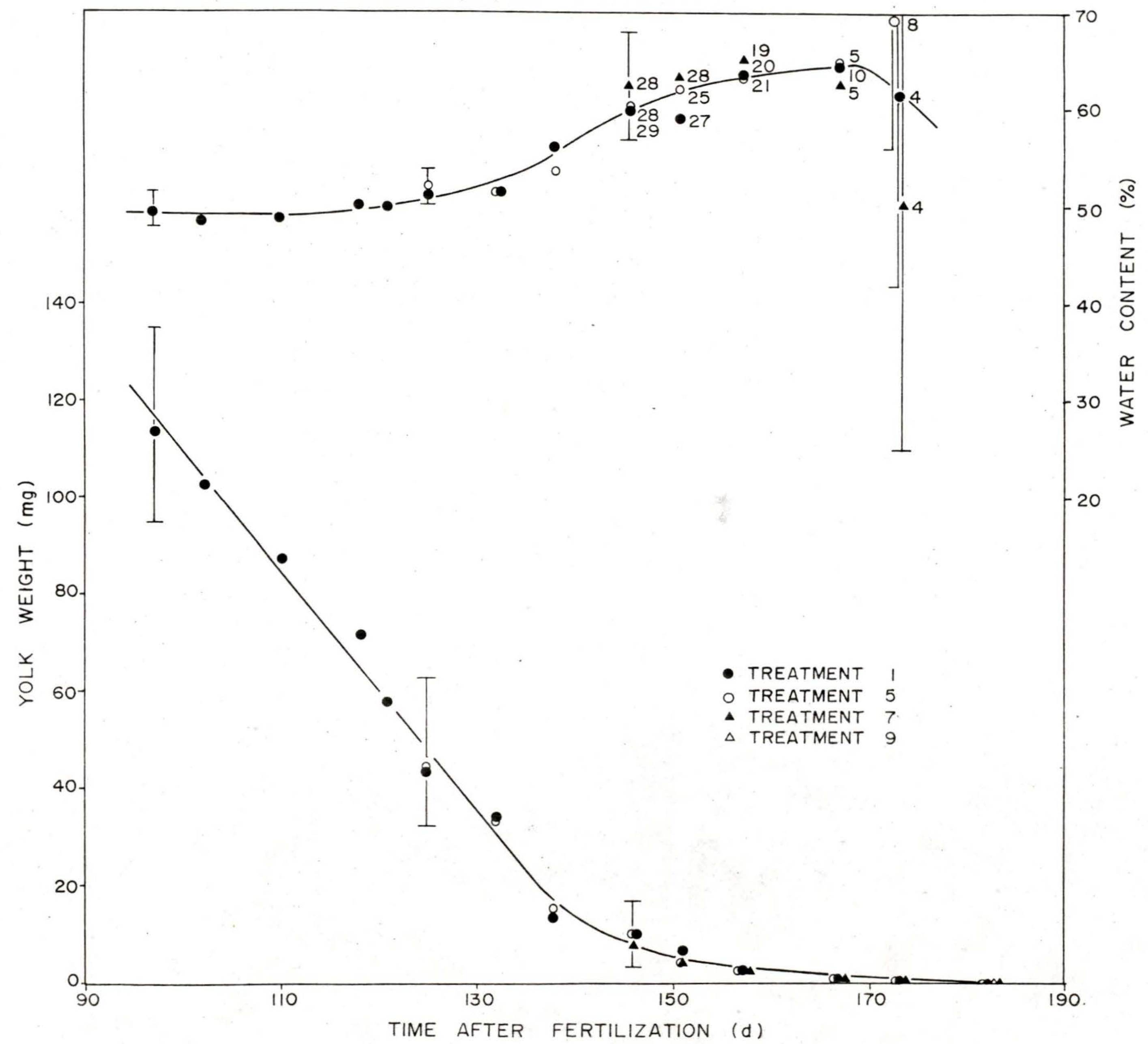

YOLK WEIGHT (mg)
WATER CONTENT (%)
TIME AFTER FERTILIZATION (d)
0
20
40
60
80
100
120
140
20
30
40
50
60
70
90
110
130
150
170
190
● TREATMENT 1
○ TREATMENT 5
▲ TREATMENT 7
△ TREATMENT 9

Table X. Yolk utilization rate (± 95% confidence limits) for fed chinook alevins (treatment 1) at 6, 8, 10, and 12 °C.

Temperature group (°C)	Yolk utilization rate (mg d^{-1})	
	Wet weight basis	Dry weight basis
6	3.18 ± 0.33	1.60 ± 0.17
8	4.41 ± 0.50	2.28 ± 0.21
10	5.10 ± 0.45	2.60 ± 0.20
12	6.14 ± 0.54	2.90 ± 0.29

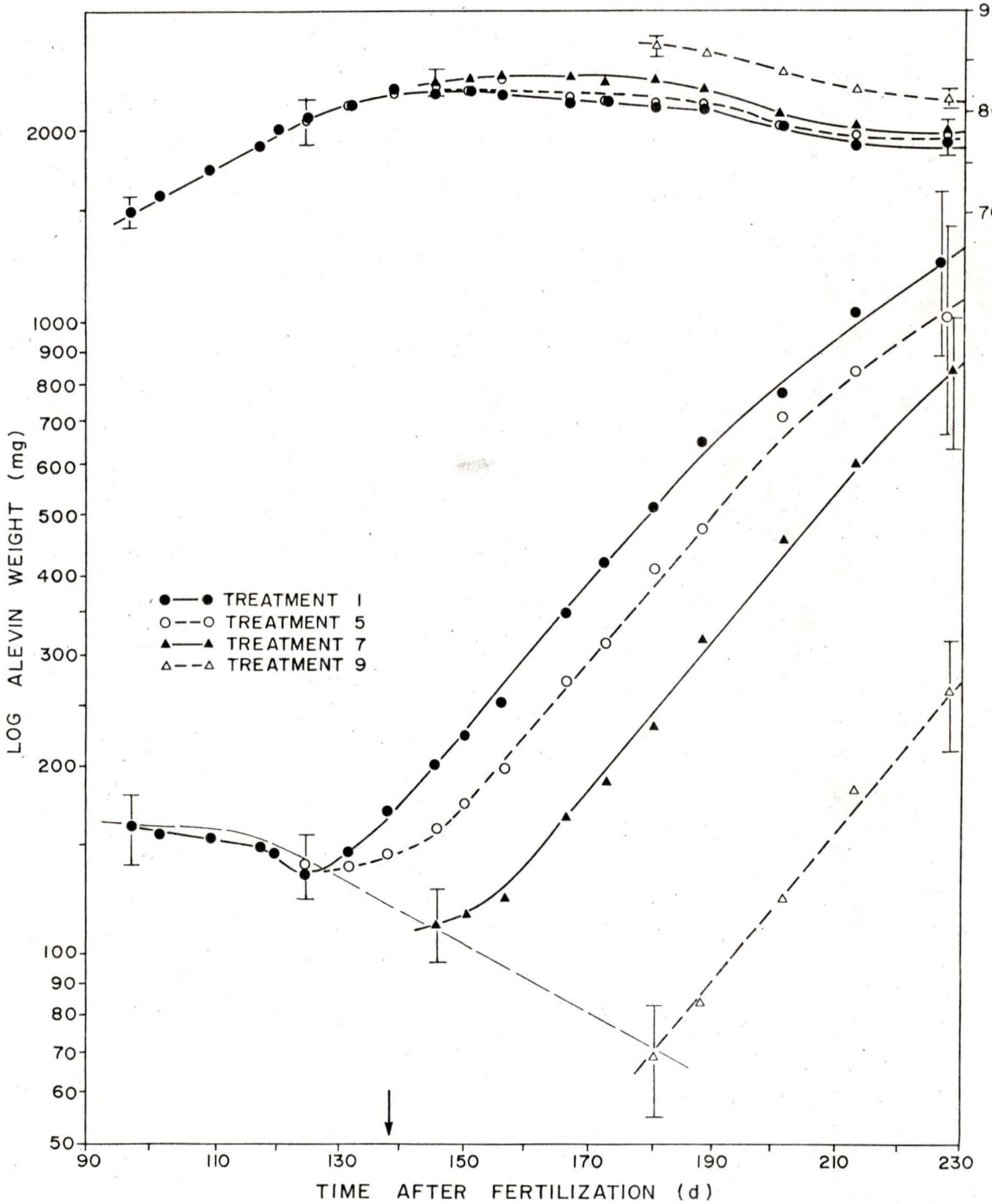
significantly between treatments 1-10. Thus, overall trends in yolk weight and water content of fed alevins were not distinguishable from those of unfed alevins (Section III(C.2)).

In summary, regardless of the timing of initial feeding, exogenous feeding had no effect on yolk absorption. At each temperature, all alevins (unfed and fed) utilized their yolk at the same rate, and completed yolk absorption at the same time.

3. Tissue-yolk-water Interactions of Fed Alevins Since exogenous feeding had no affect on yolk absorption, total wet and dry weights (tissue plus yolk) of actively feeding alevins reflected changes in tissue weights of feeding fish. Hence, total weight of actively feeding fish did not differ significantly from that of unfed alevins until about 40 tu before MAWW was attained (Fig. 14). However, throughout the study total weights of alevins first fed before MAWW remained significantly greater than those of fish first fed at or after MAWW.

Total weight at the final sampling period (Table XI) did not vary significantly among treatments where feeding was initiated before MAWW was attained (Fig. 11, treatments 1-6 at 6 and 8 °C, and treatments 1-5 at 10 and 12 °C) (Duncan's test). However, in treatments where first feeding commenced at or after MAWW, final total weight decreased significantly in relation to the period of food deprivation (Duncan's test); the greater the deprivation period, the less the final weight. The final total weight of alevins first fed at or after MAWW was achieved was related directly to the total weight when feeding was initiated (mean

Figure 14. Total dry weight and water content of chinook alevins initially fed at various times at 8 °C. Time of maximum alevin wet weight (MAWW) (↓) is indicated. Total dry weight is presented in the lower portion of the figure, where the broken curve (— — —) represents changes in total dry weight of unfed alevins. Sample dispersion is shown as ± 1 SD. Curves fitted by eye.



90
80
70
WATER CONTENT (%)
2000
1000
900
800
700
600
500
400
300
200
100
90
80
70
60
50
LOG ALEVIN WEIGHT (mg)
TREATMENT 1
TREATMENT 5
TREATMENT 7
TREATMENT 9
90
110
130
150
170
190
210
230
TIME AFTER FERTILIZATION (d)

Table XI. Final geometric mean total weight (± 95% confidence limits) of chinook alevins initially fed at various times at 6, 8, 10, and 12 °C. F-values (df = 8, 261) from comparison of means between treatments are given below each column. Part a -- Final wet weight, Part b -- Final dry weight.

Part a.

	Wet weight (mg)			
	Temperature group (°C)			
Treatment	6	8	10	12
1	3678(3283, 4120)	4943(4482, 5450)	4026(3640, 4453)	3439(3086, 3831)
2	4181(3714, 4707)	4670(4162, 5240)	3765(3327, 4260)	3267(2941, 3629)
3	4176(3623, 4814)	4482(3907, 5068)	3635(3212, 4113)	3442(3109, 3812)
4	3644(3308, 4014)	4739(4329, 5189)	4118(3618, 4687)	3008(2708, 3341)
5	3624(3321, 3955)	4474(3957, 5081)	3679(3326, 4070)	3124(2812, 3470)
6	3715(3413, 4044)	4575(4112, 5091)	3105(2855, 3377)	2602(2342, 2890)
7	3066(2867, 3279)	3672(3418, 3945)	2606(2396, 2835)	2140(1927, 2377)
8	2372(2246, 2505)	2522(2319, 2743)	1852(1703, 2014)	1496(1347, 1662)
9	1008(938, 1088)	1360(1279, 1446)	1352(1243, 1471)	847(804, 893)
F	81.59**	69.20**	50.34**	80.16**

Table XI (cont'd)

Part b.

Treatment	Dry weight (mg)			
	Temperature group (°C)			
	6	8	10	12
1	739(675, 809)	1101(983, 1233)	855(736, 992)	702(607, 809)
2	887(767, 1025)	1009(876, 1164)	793(682, 923)	675(605, 754)
3	878(739, 1044)	964(872, 1066)	730(626, 853)	699(622, 784)
4	748(678, 826)	1014(909, 1132)	855(759, 964)	592(513, 684)
5	768(688, 857)	957(870, 1052)	740(664, 826)	638(571, 713)
6	791(711, 880)	1001(883, 1151)	660(602, 724)	548(479, 620)
7	622(577, 670)	789(718, 867)	556(506, 610)	402(350, 461)
8	481(451, 513)	513(463, 569)	336(305, 370)	277(241, 317)
9	171(157, 185)	258(240, 277)	235(213, 259)	139(127, 152)
F	80.91**	63.28**	55.73**	80.85**

total wet weight -- r_6 = 0.997*, df = 1; r_8 = 0.998*, df = 1; r_{10} = 0.998**, df = 2; r_{12} = 0.989*, df = 2; mean total dry weight -- r_6 = 0.997*, df = 1; r_8 = 0.997*, df = 1; r_{10} = 0.996**, df = 2; r_{12} = 0.994**, df = 2). Final total weights (Table XI) cannot be compared directly between temperature groups because timing of the final sampling period, when cumulative mortality in treatment 10 surpassed 50%, varied between temperature groups. Accumulated tu to the final sampling period were 1724.1 tu at 6 °C, 1811.1 tu at 8 °C, 1758.3 tu at 10 °C, and 1635.9 tu at 12 °C. After similar accumulated tu (1634.0 $\pm$ 4.5 tu, n = 4) at each temperature, total weight of fed alevins (Table XII) followed trends identical to those described for final weights; at each temperature total weights of alevins first fed before MAWW were not significantly different, while weights of alevins first fed at or after MAWW were significantly less (Duncan's test). At 1634 tu, total weights of alevins first fed before MAWW did not differ between temperature groups (mean wet weight -- F = 1.34, df = 3, 716; mean dry weight -- F = 1.19, df = 3, 716). Averaged over the four temperatures, total wet weight of alevins first fed before MAWW was 3266 $\pm$ 145 mg (666 $\pm$ 32 mg total dry weight) at 1634 tu.

Total water content (tissue plus yolk) of fish first fed before MAWW increased to a maximum, and then declined (Fig. 14). This maximum water content was reached at the same time MAWW was achieved and averaged 81.1 $\pm$ 1.9 % over the four temperatures. In treatments where initial feeding was delayed until at or after MAWW, total water content decreased with time and tended to be greater than that of earlier-fed fish. Final total water content was identical to that of tissue (Section III(D.1)).

Table XII. Geometric mean total weight ($\pm$ 95% confidence limits) of chinook alevins initially fed at various times at 6, 8, 10, and 12 °C, at 1634 tu after fertilization. Part a -- Total wet weight, Part b -- Total dry weight.

Part a.

	Wet weight (mg)			
	Temperature group (°C)			
Treatment	6	8	10	12
1	3115(2794, 3499)	3403(3093, 3802)	3454(3112, 3855)	3439(3086, 3831)
2	3452(3136, 3800)	3312(3014, 3623)	3239(2930, 3597)	3267(2941, 3629)
3	3360(2985, 3731)	3171(2853, 3436)	3132(2839, 3480)	3442(3109, 3812)
4	3152(2905, 3407)	3347(3028, 3639)	3540(3199, 3987)	3008(2708, 3341)
5	3199(2882, 3470)	3152(2841, 3424)	3153(2854, 3493)	3124(2812, 3470)
6	3195(2899, 3547)	3224(2923, 3591)	2660(2506, 2845)	2602(2342, 2890)
7	2542(2336, 2775)	2388(2249, 2508)	2231(2106, 2365)	2140(1927, 2377)
8	1900(1753, 2064)	1775(1628, 1939)	1587(1447, 1562)	1496(1347, 1662)
9	859(811, 903)	951(901, 1012)	958(910, 1001)	847(804, 893)

Table XII (cont'd).

Part b.

Treatment	Dry weight (mg)			
	Temperature group (°C)			
	6	8	10	12
1	636(589, 709)	695(625, 790)	705(620, 799)	702(607, 809)
2	705(617, 805)	678(607, 755)	661(593, 754)	675(605, 754)
3	686(619, 774)	645(583, 722)	639(575, 718)	699(622, 784)
4	643(578, 716)	685(616, 767)	724(612, 820)	592(513, 684)
5	640(578, 725)	643(589, 720)	645(590, 722)	638(571, 713)
6	655(585, 764)	658(590, 759)	531(465, 615)	548(479, 620)
7	529(451, 600)	477(407, 532)	435(368, 498)	402(350, 461)
8	369(341, 417)	344(301, 392)	294(263, 340)	277(241, 317)
9	146(128, 155)	153(125, 172)	156(123, 173)	139(127, 152)

In summary, availability of external food had no significant effect on total weight and water content of chinook alevins until shortly before MAWW was reached. Alevins first fed before MAWW attained a similar final weight at each temperature. Final weights of alevins first fed at or after MAWW decreased in relation to the period of food deprivation, and were related directly to their total weight when first fed. At 1634 tu, total weight of fish fed before MAWW averaged 3266 mg (wet weight, 666 mg dry weight) over the four temperatures. Total water content of alevins first fed before MAWW increased to 81.1%, and then declined. Total water content of alevins first fed at or after MAWW decreased following initial food presentation, but tended to be greater than that of earlier-fed fish.

4. Length of Fed Alevins Alevin length at the final sampling period (Table XIII) varied in relation to the timing of initial food presentation with respect to MAWW. Lengths of fish first fed before MAWW was attained did not vary significantly (Duncan's test). However, final lengths of fish first fed at or after MAWW decreased significantly in relation to the period of food deprivation (Duncan's test); the greater the deprivation period, the less the final length achieved. Final lengths of representative alevins from each treatment at 8 °C are shown in Figure 15. As before, final treatment means cannot be compared directly between temperature groups.

E. Mortality of Unfed and Fed Alevins

Experimental work at each temperature was terminated when the

Table XIII. Final geometric mean length (± 95% confidence limits) of chinook alevins initially fed at various times at 6, 8, 10, and 12 °C. F-values (df = 8, 261) from comparison of means between treatments are given below each column.

	Final length (mm)			
	Temperature group (°C)			
Treatment	6	8	10	12
1	68.5(66.8, 71.2)	76.7(74.2, 79.4)	69.3(66.7, 72.1)	65.5(63.0, 68.0)
2	71.9(69.2, 74.8)	74.0(71.2, 76.8)	67.8(65.1, 70.5)	63.4(61.3, 65.5)
3	71.4(68.3, 74.7)	72.8(70.1, 75.6)	67.1(64.2, 70.1)	63.8(61.8, 65.9)
4	69.3(67.2, 71.5)	74.1(72.1, 76.3)	69.2(66.9, 71.5)	61.8(59.5, 64.2)
5	68.7(66.8, 70.6)	72.3(69.4, 75.3)	67.5(65.5, 69.6)	62.7(60.9, 64.5)
6	69.5(67.3, 71.7)	72.8(70.3, 75.4)	64.2(62.2, 66.2)	58.5(56.4, 60.7)
7	65.2(63.7, 66.7)	67.5(65.7, 69.4)	62.1(60.4, 63.8)	55.1(53.0, 57.2)
8	59.6(58.6, 60.6)	60.7(59.0, 62.4)	54.7(53.3, 56.2)	50.2(48.7, 51.8)
9	45.6(44.9, 46.3)	50.5(49.6, 51.3)	49.4(48.3, 50.6)	42.9(42.3, 43.7)
F	90.26**	69.17**	50.48**	75.33**

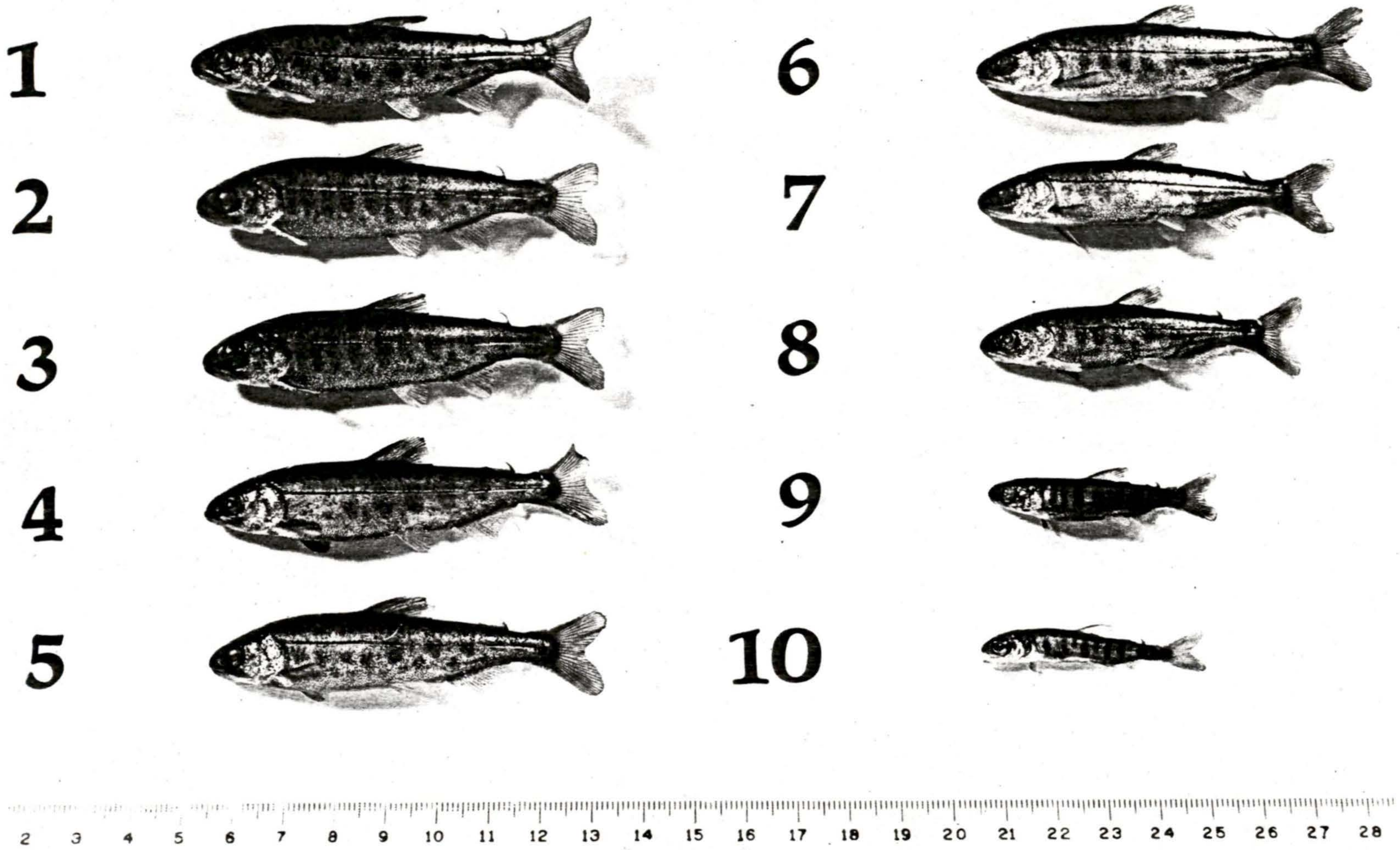


Figure 15. Representative chinook alevins from treatments 1-10 at the final sampling period at 8 °C. Scale in figure measures cm.

cumulative mortality in treatment 10 surpassed 50%. Elapsed time to the final sampling period (Table XIV) was correlated with temperature ($r = -0.997^*$, df = 2). That is, 50% cumulative mortality in treatment 10 was reached more rapidly at high temperatures. Accumulated tu to the final sampling period (Table XIV) showed no significant relationship with temperature ($r = -0.557$, df = 2). Yet, fewer thermal units were accumulated to 50% cumulative mortality at 12 °C.

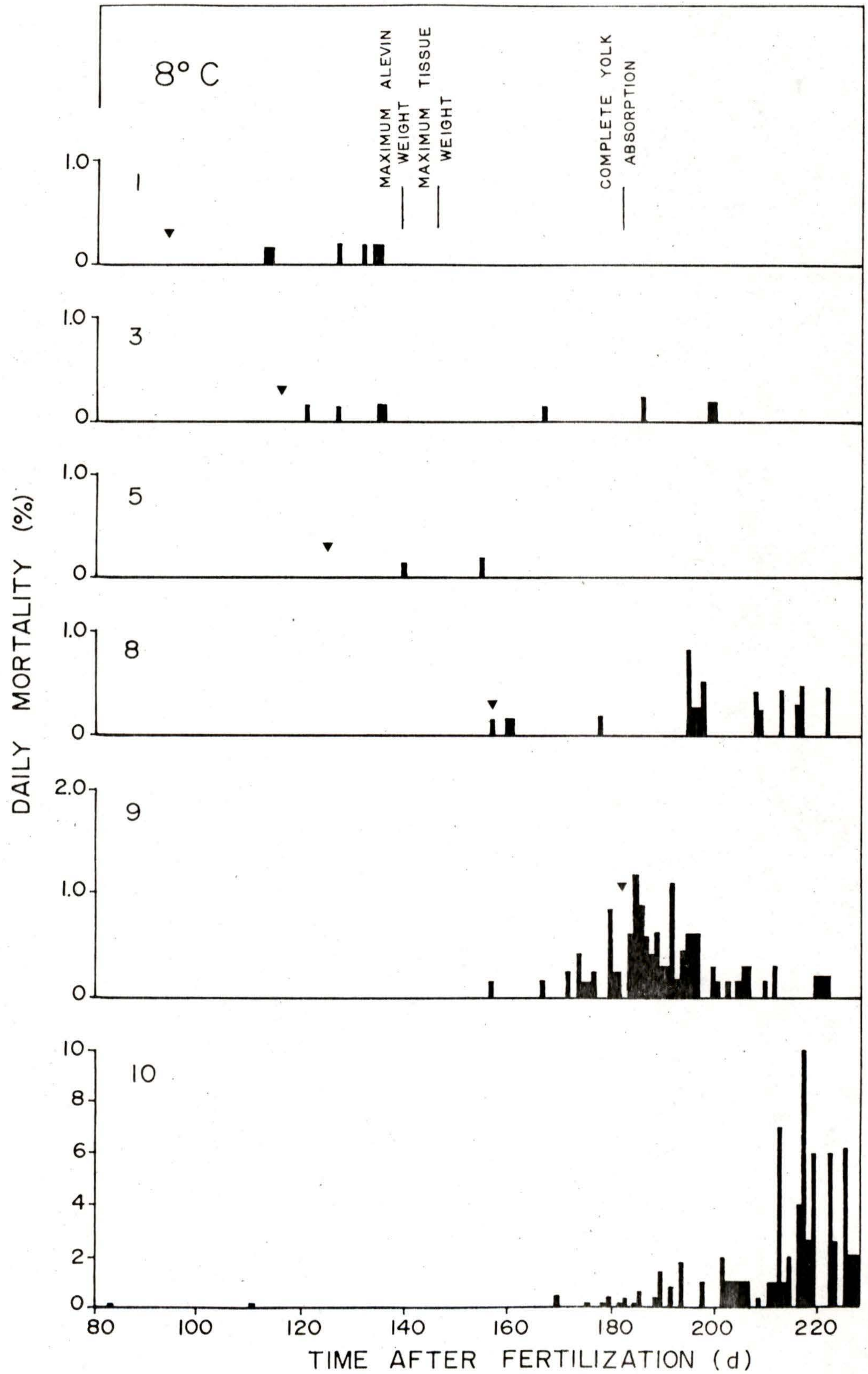
Cumulative mortality at the final sampling period (Table XIV) varied in relation to the timing of initial food presentation with respect to MTW. Cumulative mortality in treatments where feeding was initiated before or at MTW did not vary significantly at each temperature (Duncan's test). Most daily mortality in these treatments occurred after initial food presentation (Fig. 16), and was associated with embryonic hydrocoel (also termed "blue-sac"), coagulated yolk, structural anomalies, and/or a fungus-like material covering the gill filaments. Cumulative mortality was pooled for these treatments. These pooled levels averaged 1.0 ± 0.4 % at 6 °C (n = 7), 1.2 ± 1.0 % at 8 °C (n = 7), 2.1 ± 1.3 % at 10 °C (n = 6), and 10.8 ± 2.5 % at 12 °C (n = 7), and differed among the temperature groups ($F = 92.79^{**}$, df = 3, 50). This difference was attributable to significantly greater pooled mortality at 12 °C; pooled levels at 6, 8, and 10 °C did not differ significantly (Duncan's test).

In treatments where feeding was delayed until after MTW, cumulative mortality increased significantly in relation to the period of food deprivation; the greater the deprivation period, the greater the mortality. Most daily mortality in these treatments occurred after

Table XIV. Total mortality (± 1 SD) during the feeding experiments with chinook alevins at 6, 8, 10, and 12 °C. F-values (df = 9, 19) from comparison of means between treatments, and time of the final sample are given below each column.

	Total mortality (%)			
	Temperature group (°C)			
Treatment	6	8	10	12
1	1.0 ± 0.1	1.2 ± 0.5	2.9 ± 3.4	12.0 ± 0.8
2	1.2 ± 0.5	1.4 ± 0.6	3.6 ± 0.1	9.7 ± 2.8
3	0.6 ± 0.2	1.5 ± 1.7	0.9 ± 1.2	10.3 ± 0.1
4	1.3 ± 0.6	0.9 ± 0.8	0.4 ± 0.5	10.0 ± 0.1
5	0.7 ± 0.5	0.4 ± 0.6	1.6 ± 0.8	10.4 ± 1.5
6	1.1 ± 0.5	2.7 ± 0.8	3.0 ± 2.0	9.1 ± 5.8
7	1.6 ± 0.1	3.4 ± 0.1	5.6 ± 0.4	14.3 ± 0.8
8	3.7 ± 0.8	5.9 ± 2.4	9.7 ± 0.4	24.1 ± 9.6
9	18.7 ± 0.4	13.9 ± 3.2	26.7 ± 2.8	30.3 ± 0.1
10	51.1 ± 0.4	56.6 ± 6.5	50.8 ± 0.1	55.3 ± 4.2
F	1515.76**	77.17**	201.23**	28.05**
Time of Final Sample				
Elapsed time (d)	285.0	228.0	177.1	137.8
Thermal units (tu)	1724.1	1811.1	1758.3	1635.9

Figure 16. Daily mortality of chinook alevins initially fed at various times at 8 °C. Treatment number and timing of initial food presentation (▼) are indicated.



8° C
MAXIMUM ALEVIN WEIGHT
MAXIMUM TISSUE WEIGHT
COMPLETE YOLK ABSORPTION
1
3
5
8
9
10
DAILY MORTALITY (%)
TIME AFTER FERTILIZATION (d)

yolk absorption was complete (Fig. 16), and was associated with severe emaciation.

In treatment 10, daily mortality increased just prior to complete yolk absorption (Fig. 16). Mortality in this treatment also was associated with severe emaciation.

F. Unfed Alevins in Incubation Trays

Results for unfed alevins in Heath incubation trays, while not as extensively analysed, were very similar to those described for unfed alevins in growth tanks (Section III(C)). Data for alevins in trays are summarized in Figure 17.

Total wet weight of alevins in trays increased with time to a maximum, and then declined (Fig. 17). The maximum alevin wet weight attained (Table XV) did not differ significantly from that achieved in growth tanks ($t_6 = 1.449$, $t_8 = 1.146$, $t_{10} = 1.748$, $t_{12} = 0.915$; df = 58), and was reached within 16.7 ± 23.0 tu ($n = 4$) of that in growth tanks. The decline in total wet weight after this maximum, however, was greater in incubation trays than in growth tanks. From maximum alevin wet weight until complete yolk absorption, total wet weight of alevins in incubation trays declined 41.5 ± 5.4 % ($n = 4$).

At each temperature, alevins in incubation trays attained maximum tissue weight after maximum alevin wet weight was reached (Fig. 17). This maximum tissue weight (Table XV) did not differ significantly from that achieved in growth tanks (mean tissue wet weight -- $t_6 = 0.997$, $t_8 = 1.216$, $t_{10} = 0.867$, $t_{12} = 1.850$; df = 58; mean tissue dry weight -- $t_6 = 0.985$, $t_8 = 0.895$, $t_{10} = 0.933$, $t_{12} = 1.554$; df = 58), and was

Figure 17. Total wet weight of unfed chinook alevins in incubation trays at 6, 8, 10, and 12 °C. Timing of maximum tissue weight (↓) and complete yolk absorption (↑) are indicated. Sample dispersion is shown as $\pm$ 1 SD. Curves fitted by eye.

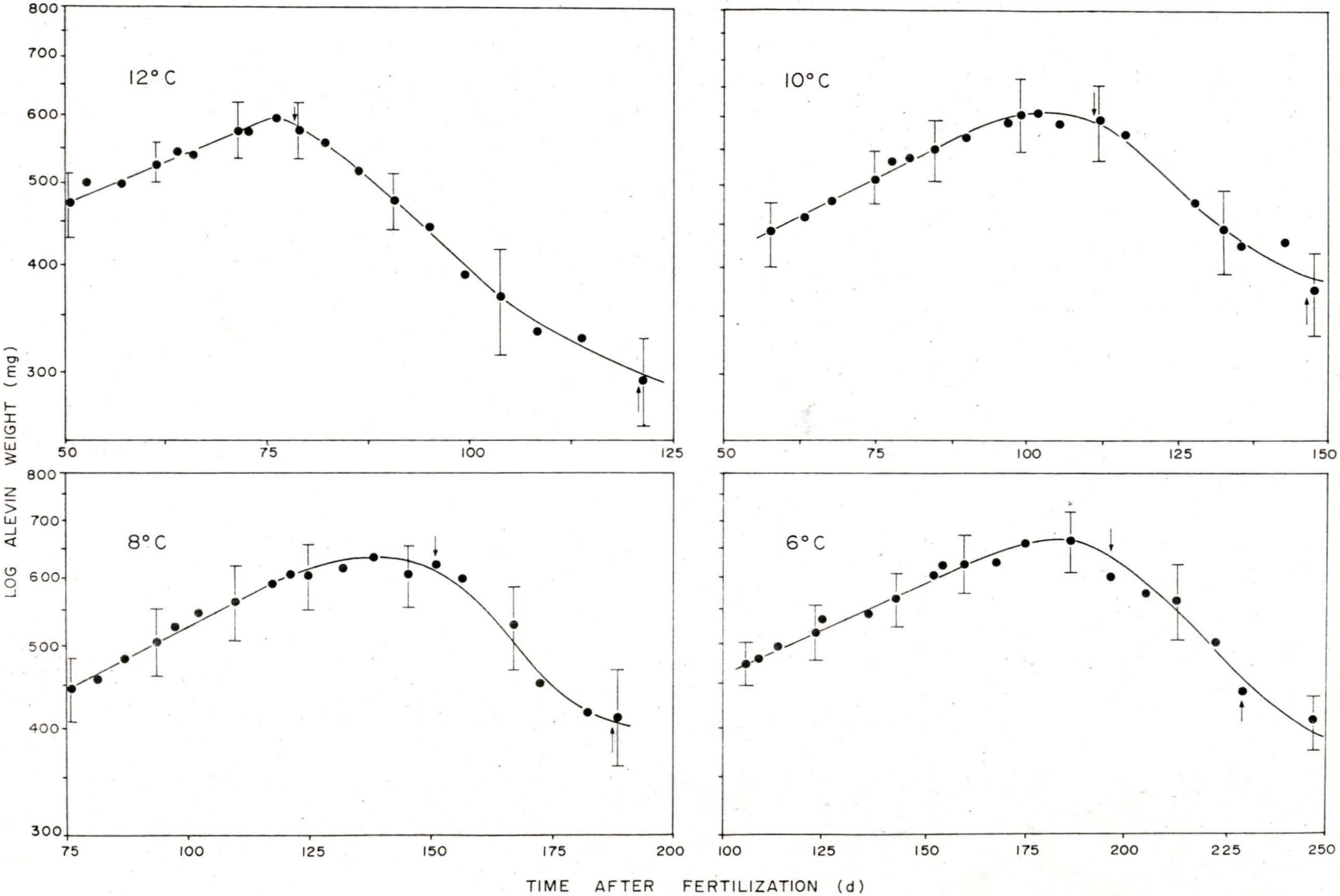

12° C
10° C
8° C
6° C
LOG ALEVIN WEIGHT (mg)
TIME AFTER FERTILIZATION (d)
800
700
600
500
400
300
50
75
100
125
150
175
200
225
250

Table XV. Geometric mean maximum alevin wet weight, maximum tissue weight, and maximum length achieved by unfed chinook alevins in incubation trays at 6, 8, 10, and 12 °C. Means are shown with their 95% confidence limits.

Temperature group (°C)	Maximum alevin wet weight (mg)	Maximum tissue weight		Maximum length (mm)
		Wet weight (mg)	Dry weight (mg)	
6	663(630, 697)	628(582, 678)	112(102, 123)	42.0(41.5, 42.6)
8	642(599, 688)	616(575, 660)	104(96, 113)	40.9(40.5, 41.3)
10	616(578, 656)	584(541, 630)	98(89, 108)	39.9(39.5, 40.4)
12	594(574, 615)	498(452, 549)	80(72, 89)	39.4(39.0, 39.9)

reached within 11.6 $\pm$ 27.2 tu (n = 4) of that in the growth tanks.

Alevins achieved a maximum length at the same time as maximum tissue weight was attained. This maximum length (Table XV) did not vary significantly from that attained in growth tanks ($t_6 = 0.961$, $t_8 = 1.849$, $t_{10} = 1.031$, $t_{12} = 0.127$; df = 58). Alevin length did not vary significantly with continued food deprivation after the maximum length was reached (Duncan's test). Alevins completed yolk absorption in the incubation trays within 4.6 $\pm$ 29.3 tu (n = 4) of alevins in the growth tanks.

Few differences in morphological development were evident between alevins from incubation trays and growth tanks. The Vernier (1969) stages of fish in trays did not differ significantly from those in growth tanks (see Fig. 6). This was especially evident during stages 35-37.

G. Emergence of Alevins from Gravel

Timing of 50% emergence, both as elapsed time and accumulated tu (Table XVI), was negatively correlated with temperature (r = -0.973*, r = -0.979*, respectively; df = 2). That is, 50% emergence was reached more rapidly and after accumulation of fewer thermal units at higher temperatures. Over the four temperatures, 50% emergence was reached within 26.8 $\pm$ 12.2 tu of attainment of MAWW by fish in growth tanks. Hence, emergence from the simulated redds occurred after fish in growth tanks had inflated their air bladders.

Percent mortality in the simulated redds (Table XVI) was not correlated with temperature (r = -0.942, df = 2). Mortality at 6 and

Table XVI. Timing of 50% emergence (± 95% confidence limits) for chinook alevins in simulated redds at 6, 8, 10, and 12 °C. Also shown is total mortality of alevins prior to emergence.

Temperature group (°C)	Timing of 50% emergence: Elapsed time (d)	Timing of 50% emergence: Thermal units (tu)	Mortality (%)
6	191.5 ± 1.0	1148.8 ± 6.1	1.5
8	135.8 ± 1.5	1087.8 ± 12.2	1.3
10	103.5 ± 1.4	1022.4 ± 14.1	4.0
12	85.0 ± 1.2	1002.7 ± 14.5	11.7

8 °C varied only slightly, while mortality increased substantially at 10 and 12 °C.

IV. DISCUSSION

The results establish that chinook salmon (*Oncorhynchus tshawytscha*) can and will ingest external food before yolk absorption is complete. Chinook began exogenous feeding while retaining 51% of their yolk reserve (dry weight basis, from fertilization). However, initial utilization of external food did not coincide with initial food ingestion. Feeding had no statistically significant effect on growth until shortly before maximum alevin wet weight (MAWW) was attained, and had no effect on survival until after maximum tissue weight (MTW) was reached. Yolk reserves when MAWW was reached increased with temperature from 9% at 6 °C to 29% at 12 °C (from fertilization). When MTW was achieved at the four temperatures, yolk reserves averaged 6%. Hence, while exogenous feeding before MAWW had no effect on growth and survival, feeding before complete yolk absorption increased growth and survival. Thus, chinook are capable of utilizing external food to supplement their endogenous yolk reserves.

Precocious feeding, involving ingestion of food not utilized for growth, also has been documented in sockeye salmon (*O. nerka*) (Harvey 1966, Hurley and Brannon 1969). Hurley and Brannon (op. cit.) concluded that precocious feeding was an experimental artifact, resulting from food presentation under "abnormal" circumstances. Nevertheless, they suggested that precocious feeding may have positive implications for subsequent feeding behaviour. However, Twongo and MacCrimmon (1976) found no relationship between timing of initial food presentation and feeding behaviour in rainbow trout (*Salmo gairdneri*). In this study, chinook alevins fed initially before MAWW was attained, achieved a similar ultimate size regardless of the specific timing of initial food presentation and, thus, the duration of precocious feeding. Hence, no evidence of a relationship between precocious feeding and subsequent growth was found for chinook. Prior to MAWW, precociously feeding alevins were consistently smaller than unfed alevins. Hence, the metabolic demands associated with precocious feeding appeared to reduce the resources available for growth. Thus, chinook salmon probably derived no benefit from precocious feeding.

Hurley and Brannon (1969) reported that precocious feeding increased mortality in sockeye salmon. Early feeding also has been associated with increased mortality in brook trout (*Salvelinus fontinalis*), Atlantic salmon (*Salmo salar*), and coho salmon (*Oncorhynchus kisutch*) (Atkins 1905). Neither of those studies examined causes of such mortality. However, Ochiai et al. (1977) found that erroneous swallowing of food through the pneumatic duct resulted in early mortality in cultured Ayu (*Plecoglossus altivelis*) larvae. Since salmonids initiate air bladder inflation at the water surface by swallowing air through the pneumatic duct into the air bladder (Tait 1960, Bams 1969), it is conceivable that erroneous swallowing of food through the pneumatic duct could occur during air bladder inflation (swim-up). Still, the current evidence does not support this inference for chinook salmon. Precocious feeding did not increase alevin mortality, regardless of whether feeding was initiated before or after swim-up.

Chinook alevins in this study were capable of ingesting external food before inflating their air bladders. Hence, exogenous feeding was not dependent on attainment of neutral buoyancy. Rather, it is possible that initial feeding was related to disappearance of a tissue plug in the alimentary tract, as found for rainbow trout (Twongo and MacCrimmon 1977). Occlusion of the upper alimentary tract by a tissue plug has been documented at hatching in Atlantic salmon (Battle 1942) and rainbow trout (Prakash 1961). Possible occlusion of the alimentary tract of Oncorhynchus sp. at hatching or during subsequent development has not been explored, and invites further study.

Under the current experimental conditions, chinook in growth tanks swam up about the same time as they began consuming external food. Yet, at each temperature alevins exposed to external food and light inflated their air bladders somewhat earlier than fish kept unfed and in darkness. Swim-up was accelerated in fed alevins, probably as a result of their early exposure to light (Disler 1953, Kolgaev 1963, Brannon 1965). As well, swim-up in growth tanks occurred before emergence and swim-up took place in simulated redds. Hence, swim-up behaviour of chinook alevins was influenced by substrate type. Thus, swim-up was a poorly defined stage with respect to development. Evidence of feeding with respect to swim-up in wild salmonids may not be directly comparable to feeding in gravel-free cultural situations.

As 50% emergence from the simulated redds occurred within 37 tu of attainment of MAWW, most alevins were capable of ingesting and utilizing external food before emerging. It is probable, therefore, that wild chinook salmon feed exogenously while in the gravel. Thomas and Shelton (1968) reported that 70-100% of the chinook alevins in the Abernathy incubation channel had fed on plankton before emerging. They suggested that this early feeding may explain the increased survival of wild migrating alevins compared with unfed hatchery releases.

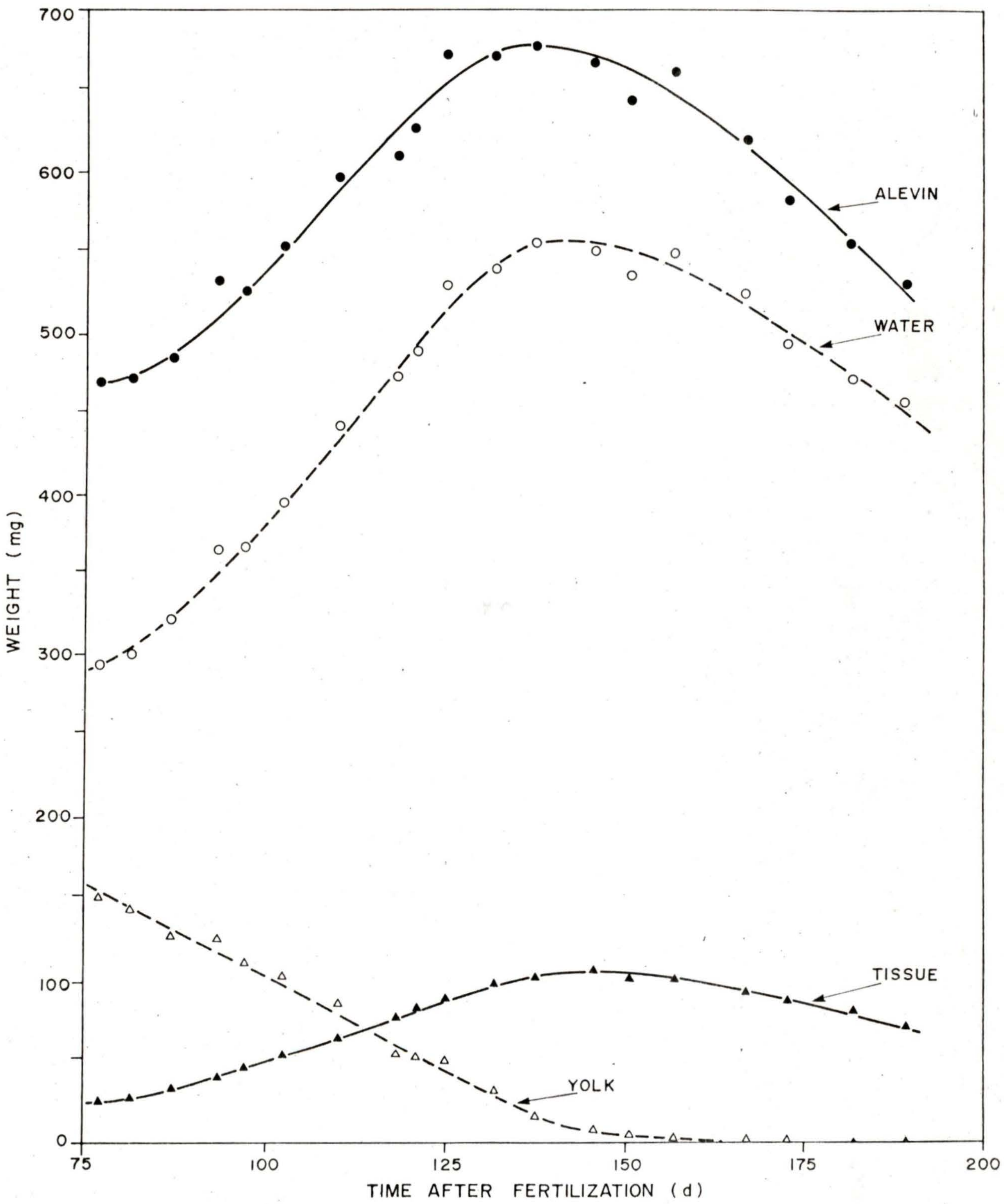
Before commencement of exogenous feeding, fish are dependent entirely on utilization of their yolk reserves to meet the demands of metabolism and growth (tissue synthesis) (Gray 1926, 1928a, Hayes 1949, Brannon 1965). The yolk reserves of chinook alevins at hatching constituted 68.7-73.8% of total alevin wet weight. These yolk/alevin ratios at hatching are slightly less than those reported for chinook from Soviet rivers (74-79%) (Smirnov 1975), but are within the range documented for salmonids in general (50-82%) (Gray 1926, Hayes 1949, Harvey 1966, Yastrebkov 1966, Smirnov 1975).

The rate of yolk utilization is important as it determines the length of time available to fish to complete the transition to exogenous feeding. Presumable, in food-limited environments fish with a longer period of time to encounter prey might have an advantage over those with a shorter time interval before incurring a metabolic deficit (Laurence 1973). Yolk utilization in chinook was dependent on temperature. This most likely reflects the dependence of metabolic rate on temperature (Winberg 1956, Brown 1957, Blaxter 1969, Brett 1979). Hayes and Pelluet (1945) and Hayes et al. (1953) reported that the yolk utilization rate of Atlantic salmon increased linearly with temperature. The current results (Table VI) illustrate a similar relationship between the yolk utilization rate of chinook and temperature, from 6 to 12 °C. Hopley (1975) found that the yolk utilization rate (wet weight basis) of unfed chinook alevins at 11.2 °C was 6.08 mg d^{-1}. The utilization rate predicted by linear interpolation of the current data at 11.2 °C is 5.94 mg d^{-1}. The close agreement between the measured and predicted rates supports a linear relationship between utilization rate and temperature.

At a given temperature, yolk utilization rate is reported to be independent of variations in metabolic demand (Brannon 1965, Bams 1969). That is, variations in the demands of maintenance and activity do not change the rate of yolk utilization. Rather, these variations alter the resources available for growth. The independence of yolk absorption and exogenous feeding in chinook salmon supports this finding. Unfed and fed alevins completed yolk absorption simultaneously. However, this may not be true for all fishes. Actively feeding larvae of the grunion (<u>Leuresthes tenuis</u>) (May 1971), <u>Tilapia</u> (<u>Tilapia sparmanni</u>) (Ishibashi 1974), and Kuben inconnu (<u>Stenodus leucichthys nelma</u>) (Bogdanova 1977) are reported to absorb their yolk more slowly than unfed larvae.

The yolk utilization rate of chinook salmon slowed during terminal yolk absorption (Fig. 18). This decrease in utilization rate followed an increase in yolk water content from 50.0 to 61.2% of wet weight. Both events likely are attributable to changes in the chemical composition of the yolk reserve. The relative composition of the yolk reserve is known to change markly during yolk absorption (Hayes 1949, Toetz 1966, Blaxter 1969, Nakagawa and Tsuchiya 1972, 1974). Smith (1957, 1958) reported that the triglyceride and carbohydrate constituents of yolk were selectively retained until near the end of yolk absorption.

Figure 18. Relationship between dry tissue, dry yolk, and water in unfed chinook alevins at 8 °C. Also shown is the total alevin wet weight (tissue plus yolk plus water).


700
600
500
400
300
200
100
0
WEIGHT (mg)
75
100
125
150
175
200
TIME AFTER FERTILIZATION (d)
ALEVIN
WATER
TISSUE
YOLK

He related utilization of these constituents to avoidance of ketosis, a preliminary symptom of starvation.

The specific rate of tissue growth in unfed chinook alevins was related directly to temperature and to the rate of yolk utilization. This is analogous to the increased growth rate of actively feeding chinook at increased temperatures, presumably as a result of increased food consumption (Brown 1957, Wurtsbaugh and Davis 1977, Brett 1979). Hence, the ultimate size achieved by unfed and fed chinook during any given time period (days) was greatest at 12 °C. However, the ultimate size achieved by alevins initially fed before MAWW did not differ between temperatures after similar accumulated thermal units (1634 tu after fertilization). Thus, no optimal temperature for growth of chinook was evident from 6 to 12 °C. However, an optimal temperature for growth is characteristic of many fishes (Brown 1957, Brett 1979) and it is possible that the optimal temperature for growth of chinook is outside the range examined. Banks et al. (1971) reported that the optimal temperature for growth of actively feeding chinook alevins was 15.6 °C. However, in this study fish at 12 °C experienced substantially greater mortality than alevins at lower temperatures. This suggests that 12 °C is above the optimal temperature for embryonic and early post-hatching development of Campbell River chinook salmon.

Unfed chinook alevins attained maximum tissue weight (MTW) and maximum length simultaneously. Hurley and Brannom (1969) reported a similar finding for sockeye salmon. Hence, measurement of alevin length could be used to determine occurrence of MTW. Both maximum length and MTW achieved decreased at higher temperatures. This probably is related to a decrease in the efficiency of yolk utilization, resulting from increased costs of maintenance at higher temperatures (Gray 1928b, Brown 1957, Hamor and Garside 1977, Brett 1979). However, gross utilization efficiencies from fertilization to MTW cannot be directly compared between temperatures, since a comparison of alevins at MTW does not ensure that "equivalent" developmental stages are being examined (Marr 1966). Still, gross efficiencies calculated for chinook (58.6-67.1%) are within the range reported for salmonids in general (41-70%) (Gray 1926, 1928a, Hayes and Pelluet 1945, Hayes 1949, Hayes et al. 1953, Smith 1957, Marr 1966, Hamor and Garside 1977).

At hatching, length and tissue weight of chinook alevins decreased at higher temperatures. Other authors report reduced size in fish hatched at high temperatures (Gray 1928b, Braum 1967, Alderdice and Forrester 1971, Alderdice and Velsen 1971, Peterson et al. 1977). The current results (Table 4) suggest that size differences at hatching primarily were due to reductions in the efficiency of yolk utilization during egg incubation; less growth resulted from yolk utilization at higher temperatures. Size reductions in other salmonids hatched at high temperatures have been related to increased costs of maintenance at higher temperatures (Gray 1928b, Hamor and Garside 1977). However, size at hatching at 12 °C also was influenced by the effect of temperature on time to hatch. That is, length and tissue weight at hatching were reduced in part because 12 °C fish hatched precociously. Peterson et al. (1977) attributed reductions in the length of Atlantic salmon hatched at higher temperatures to precocious hatching. Precocious hatching has been associated with the influence of temperature on the production and action of the hatching enzyme (Gray 1928b).

In addition to chinook salmon, many fishes have been found to attain maximum tissue weight and then exhibit negative growth, prior to complete yolk absorption (Smith 1947, Blaxter and Hempel 1963, Marr 1966, Toetz 1966, Blaxter 1969, Laurence 1969, 1973, Ishibashi 1974). Negative growth, a characteristic of starvation (Brown 1957), indicates that tissues are being catabolized. Hence, a potential metabolic deficit exists prior to complete yolk absorption in chinook salmon. However, as all alevins examined were capable of supplementing their endogenous yolk reserves with external food, the biological significance of this deficit is questionable. Nevertheless, the possibility exists that chinook at temperatures outside the range examined could experience a metabolic deficit before developing the capability of exogenous feeding. Laurence (1973) reported that tautog (Tautoga onitis) larvae at 22 °C experienced a metabolic deficit before developing the ability to feed exogenously, whereas larvae at 19 °C did not.

In most cases, there was no decrease in length of chinook alevins with continued starvation after maximum length was reached. Similar results are reported for unfed sockeye salmon (Hurley and Brannon 1969) and rainbow trout (Twongo and MacCrimmon 1976). However, reductions in length during starvation have been documented in many fishes (Farris 1959, Lasker 1964, Paine 1971, Bilton and Robins 1973). Bilton and Robins (op. cit.) suggest that these decreases in length may result from resorption of the cartilaginous material of the skeletal system.

An increase in tissue water content accompanied tissue catabolism. Such an increase has been documented during starvation in many fishes

(Love 1970), and can be attributed to replacement of catabolized body fats by imbided water (Phillips et al. 1966, MacLeod 1977). As well, starvation results in increased extracellular space and decreased cell size (Templeman and Andrews 1956, Love et al. 1968), both of which increase tissue water content. After commencement of exogenous feeding, tissue water content declined. This is a general phenomenon of growth, attributable to deposition of body fats (Phillips 1969) and a decrease in extracellular space (Love 1970).

Actively feeding chinook alevins exhibited an interval, or stanza, of rapid growth once they were capable of utilizing external food. Stanzas of growth are characteristic of many fishes (Brown 1957, Brett 1979), and are attributed to changes in shape (Ricker 1975) and in metabolic rate (Guma'a 1978). The growth rate of feeding chinook was unaffected by the timing of initial food presentation. Hence, there was no indication that short periods of starvation increased subsequent food utilization efficiency, as found in other salmonids (Atkins 1906, Bilton and Robins 1973, Twongo and MacCrimmon 1976). On the other hand, there was no indication that starvation until complete yolk absorption decreased subsequent food utilization efficiency. Hence, evidence that starvation during the transition to exogenous feeding retarded development of the alimentary tract (Kostomarova 1962, Bogdanova 1977), or resulted in substantial degeneration of the alimentary tract (Ehrlich et al. 1976, O'Connell 1976, Theilacker 1978) was not found in chinook salmon.

For most of the study, total wet weight (tissue plus yolk) of unfed chinook alevins increased as water was imbided and combined with yolk to form tissue (Fig. 18); wet weight of tissue synthesized was greater than that of yolk utilized. Water content of chinook yolk (50.0-61.2%) and tissue (82.6-85.4%) are within the range of values reported for the yolk and tissue of salmonids in general (50-60% and 80-90% respectively) (Gray 1926, Hayes 1949, Harvey 1966). Thus, salmonid yolk can be regarded as a concentrated nutrient requiring absorption of water for its conversion to tissue (Gray 1926, Blaxter 1969). However, the continual decrease in total dry weight of unfed alevins illustrates that not all yolk utilized was converted to tissue. As previously discussed, tissue synthesis competes with maintenance and activity for the resources provided by yolk utilization. The demands of maintenance are related directly to the amount of tissue present, and these demands increase as growth proceeds (Gray 1928a, Smith 1958, Blaxter 1969). As well, activity levels of fish increase with time following hatching (White 1915, Dill 1977), and the associated metabolic demands can be expected to increase. Hence, the efficiency of yolk utilization decreases with time (Gray 1928a, Marr 1966), and as a consequence, a point is reached eventually where the wet weight of tissue synthesized is less than that of yolk utilized. Thus, total wet weight will decline despite continued tissue synthesis. In this study, both tissue weight and alevin length continued to increase after total wet weight began to decline. This suggests that measurement of total wet weight is a poor indication of growth. Continued growth after maximum total wet weight is achieved also has been reported in brown trout (Gray 1928b) and Atlantic salmon (Marr 1965).

Gray (1928b) empirically predicted the occurrence of MAWW before MTW. He related the yolk reserve remaining at MAWW to the demands of maintenance, and the water content of yolk and tissue. As the demands of maintenance increase with increased temperature (Gray 1928b, Winberg 1956), Gray (op. cit.) predicted that the yolk reserve remaining at MAWW would increase at higher temperatures. The current results (Table VII) support this finding. In addition to an increase in the yolk reserve remaining at MAWW, the maximum weight attained decreased at higher temperatures. As well, alevins at higher temperatures reached MAWW more rapidly, after accumulation of fewer thermal units, and at a greater developmental index (k_D) than fish at lower temperatures. This suggests that alevins at higher temperatures attained MAWW earlier in development. Hence, temperature influences the developmental stage when alevins reach MAWW, and the alevin size and yolk reserve remaining at MAWW. The size advantage of chinook when MAWW was attained at lower temperatures may be an important determinant of early survival. Larger fish are more resistant to the effects of starvation (Adelman et al. 1955, Blaxter and Hempel 1963, MacLeod 1977), and presumably, would have a higher survival potential in food-limited environments.

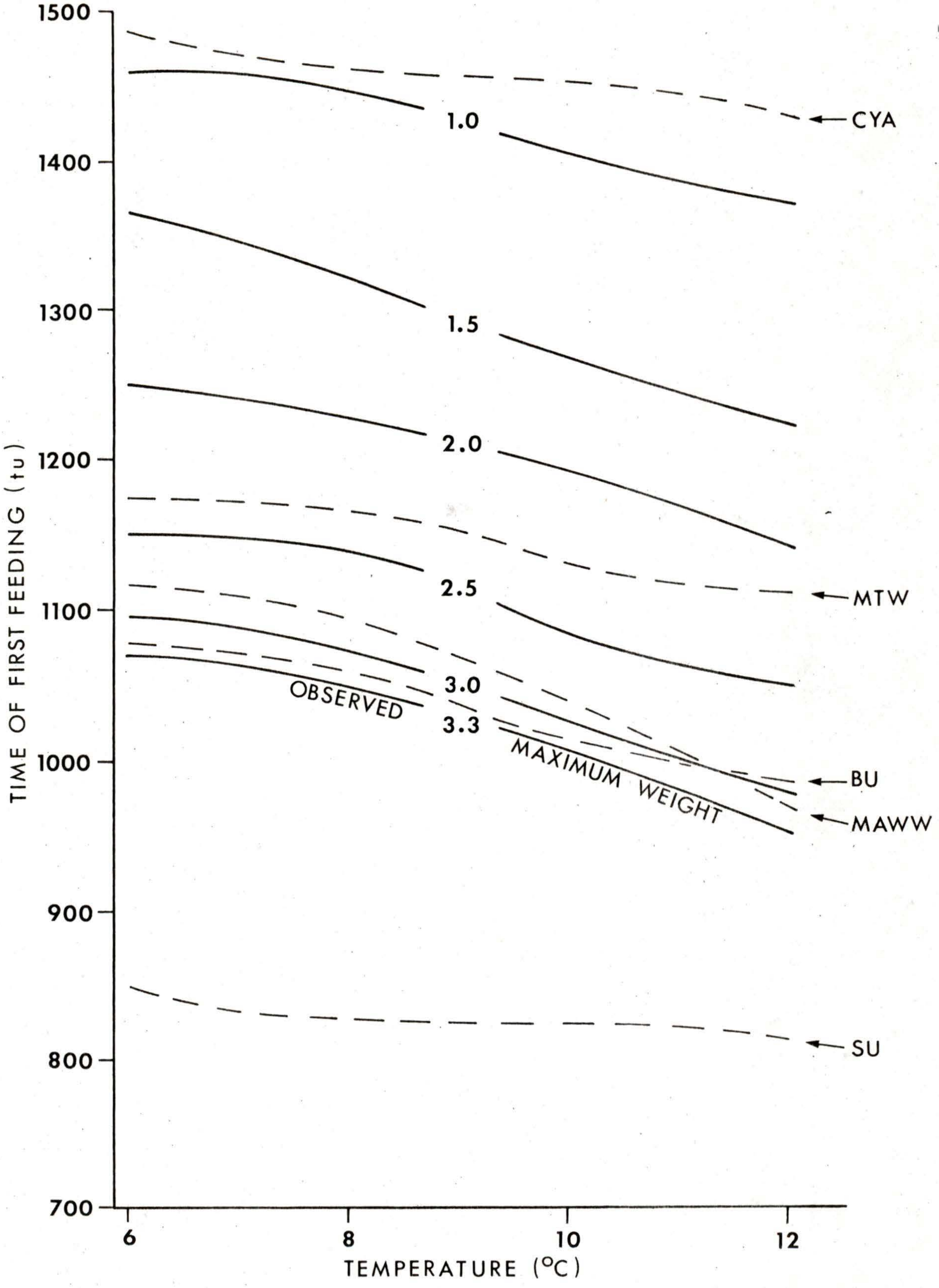
<u>Optimal Timing of Initial Feeding</u> Both the ultimate size achieved and total survival were maximized when feeding commenced before alevins attained maximum alevin wet weight (MAWW). The ultimate size achieved was reduced when feeding was delayed until at or after MAWW was reached, and survival was reduced when feeding was delayed until after maximum tissue weight (MTW) was reached. The severity of these reductions was related directly to the period of food deprivation; the longer alevins were deprived of external food, the greater the reductions

in growth and survival. Hence, the optimal time to commence feeding of chinook salmon is before alevins attain MAWW. Such optimally fed alevins did not reach a maximum wet weight; their total wet weight continued to increase while that of unfed fish reached a maximum and then declined. Thus, occurrence of MAWW can be regarded as a preliminary symptom of starvation, indicating that alevins could have achieved a greater ultimate size if feeding had commenced earlier in their development.

The existence of a relationship between MAWW and the optimal time to commence feeding is supported by findings of other studies. Marr (1965) reported that survival of Atlantic salmon was maximized by initiating feeding when alevins reached MAWW. Reinterpretation of Palmer and colleagues' (1951) data indicate that growth and survival of chinook alevins was maximized when feeding commenced before MAWW. Similarly, reinterpretation of Harvey's (1966) findings indicate that the optimal time to commence feeding sockeye was at or shortly before alevins attained MAWW. Thus, in many fishes the optimal time to commence exogenous feeding appears to be at or shortly before MAWW is reached.

The total wet weight achieved by chinook salmon after similar accumulated thermal units at each temperature (1634 tu after fertilization, Table XII) is presented (Fig. 19) in relation to the timing of initial food presentation (Table III) and temperature from 6 to 12 °C. At 1634 tu, total wet weight of alevins first fed before MAWW did not differ significantly between treatments or between temperature groups, and averaged 3.3 g. Hence, regardless of the specific timing of initial feeding, alevins fed initially at or before occurrence

Figure 19. Contours of total wet weight (g) at 1634 tu after fertilization, in relation to time of first feeding (tu), for chinook salmon at 6, 8, 10, and 12 °C. Broken lines indicate timing of associated developmental events: SU -- swim-up, MAWW -- maximum alevin wet weight(unfed), BU -- button-up, MTW -- maximum tissue weight(unfed), CYA -- complete yolk absorption. Contours fitted by eye.


1500
1400
1300
1200
1100
1000
900
800
700
TIME OF FIRST FEEDING (tu)
6
8
10
12
TEMPERATURE (°C)
1.0
1.5
2.0
2.5
3.0
3.3
OBSERVED
MAXIMUM WEIGHT
CYA
MTW
BU
MAWW
SU

of the "observed maximum weight" contour in Figure 19 achieved a weight of 3.3 g by 1634 tu after fertilization. As chinook derived no benefit from precocious feeding, feeding need not be commenced until that observed maximum weight contour is reached, to maximize growth.

In this study, no easily distinguishable feature or developmental stage of chinook alevins was correlated with occurrence of the observed maximum weight contour (Fig. 19). As previously discussed, swim-up was influenced by substrate type and lighting conditions, and as a consequence, was poorly defined with respect to development. Hence, swim-up should not be used as a definitive criterion for commencement of external feeding. Attainment of Vernier's (1969) stage 37 (buttoning-up) occurred after the maximum weight contour (Fig. 19). Hence, the ultimate size achieved by chinook would be reduced if feeding was delayed until button-up. Similarly, delaying initial food presentation until MAWW, MTW, or complete yolk absorption occurred would reduce total wet weight achieved by 1634 tu (Fig. 19).

The effects of delaying initial food presentation until after alevins attain MAWW may be more severe for fish reared in Heath trays than Figure 19 suggests. While MAWW and complete yolk absorption were reached at about the same times both in incubation trays and growth tanks, the decline in total wet weight from MAWW to complete yolk absorption was greater for chinook salmon in trays (41.5% of MAWW) than in tanks (26.5%). Hence, unfed alevins in incubation trays lost weight more rapidly than fish in growth tanks.

Conservative estimates of the optimal time (tu) to commence feeding of chinook, and yolk reserve remaining at that time are presented in Table XVII. Initiating feeding of chinook alevins at or before those times should maximize subsequent growth and survival. In order to appreciate the relationship between growth and survival of optimally fed alevins over the four temperatures, expected biomass at 1634 tu is presented (Table XVII). The biomass expected at 1634 tu from 1000 chinook eggs, with optimal feeding of resulting alevins, decreased at higher temperatures. This decrease in expected biomass resulted from a decrease in total survival of chinook, from fertilization to 1634 tu, at higher temperatures (Table XVII). This suggests that the optimal temperature for embryonic development and early post-hatching development of Campbell River chinook is at or below 6 °C.

Table XVII. Optimal time (tu after fertilization) to commence feeding and yolk reserve remaining at that time (percentage of yolk dry weight at fertilization), for chinook salmon at 6, 8, 10, and 12 °C. Also shown is the expected survival and biomass from 1000 chinook eggs, for optimally fed alevins at 1634 tu after fertilization.

Temperature group (°C)	Optimal time of first feeding		Survival (%)	Biomass (kg)
	Thermal units (tu)	Yolk reserve (%)		
6	1070	22	91.9	3.00
8	1050	25	90.5	2.96
10	1005	30	88.7	2.90
12	950	32	78.5	2.56

SUMMARY AND CONCLUSIONS

The initial feeding strategy of chinook salmon was examined from 6 to 12 °C. Importance of the timing of initial food presentation for subsequent growth and survival was determined. As well, emergence of alevins from simulated redds was examined. The experimental results afforded the following conclusions;

1. Chinook salmon were capable of ingesting and utilizing exogenous food to supplement their endogenous reserves. This "mixed feeding" primarily determined subsequent growth and survival.
2. Alevins consumed food while retaining 51% of their yolk reserve (at fertilization, dry weight basis). However, under the current experimental conditions growth was not significantly affected by food ingestion until shortly before unfed alevins attained their maximum alevin wet weight (MAWW). The yolk reserve remaining at MAWW increased with temperature from 9% at 6 °C to 29% at 12 °C.
3. Precocious feeding, involving ingestion of food not utilized for growth, offered no significant advantage or disadvantage to subsequent growth and survival of chinook.
4. Exogenous feeding was not dependent on attainment of neutral buoyancy (swim-up). As 50% emergence occurred within 37 tu of attainment of MAWW, chinook alevins probably are capable of ingesting and utilizing exogenous food before emerging from the gravel.
5. Averaged over the four temperatures, unfed alevins attained maximum tissue weight (MTW) at 1125.1 tu. Yolk reserve

remaining at MTW averaged 6% of that at fertilization. Tissue weight declined after MTW was reached. Thus, unfed alevins began tissue catabolism before yolk absorption was complete. Total survival was reduced when initial food presentation was delayed until after alevins attained MTW. Measurement of alevin length probably is adequate to determine attainment of MTW; maximum length and MTW occurred simultaneously.

6. No optimal temperature for growth of unfed and fed alevins was found from 6 to 12 °C. However, the optimal temperature for embryonic and early post-hatching development appeared to be at or below 6 °C. Growth rate of actively feeding fish was unaffected by the timing of initial food presentation.

7. Yolk absorption was unaffected by exogenous feeding. Yolk utilization rate increased linearly with increased temperature from 6 to 12 °C. Averaged over the four temperatures, unfed and fed alevins completed yolk absorption at 1456.1 tu. The developmental index (k_D) of unfed alevins at complete yolk absorption averaged 1.96.

8. Total wet weight of unfed chinook alevins increased with time as a result of an increase in imbided water. Total wet weight reached a maximum (MAWW) and began to decline before alevins attained MTW and maximum length. Thus, measurement of total wet weight was a poor indication of growth. Temperature influenced the developmental stage when MAWW was reached, and alevin size and yolk reserve reamining at MAWW. The ultimate size achieved by chinook was reduced when initial food presentation

was delayed until at or after MAWW.

9. Growth and survival of chinook salmon were maximized when feeding commenced before alevins attained MAWW, regardless of the specific timing of initial food presentation. Optimally fed fish did not exhibit a MAWW, and thus occurrence of MAWW can be regarded as a preliminary symptom of starvation. No distinguishable feature or developmental stage of chinook salmon was correlated with the optimal time to commence feeding. Timing of swim-up was influenced by substrate type and exposure to light, and as consequence, swim-up was poorly defined with respect to development. Button-up, MAWW, MTW, and complete yolk absorption occurred after the optimal time of initial feeding. Thus, delaying initial food presentation until these developmental events occurred would result in decreased growth and survival. Estimates of the optimal time (tu) to commence feeding of chinook salmon varied from 1070 tu after fertilization at 6 °C, to 950 tu at 12 °C.

REFERENCES CITED

Adelman, H.M., J.L. Bingham, and J.L. Maatch. 1955. The effect of starvation upon brook trout of three sizes. Prog. Fish-Cult., 17: 110-112.

Alderdice, D.F., and G.R. Forrester. 1971. Effects of salinity, temperature and dissolved oxygen on early development of the Pacific cod (Gadus macrocephalus). J. Fish. Res. Board Can., 28: 883-902.

__________, and F.P.J. Velsen. 1971. Some effects of salinity and temperature on early development of Pacific herring (Clupea pallasi). J. Fish. Res. Board Can., 28: 1545-1562.

__________, and F.P.J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (Oncorhynchus tshawytscha). J. Fish. Res. Board Can., 35: 69-75.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1971. Standard methods for the examination of water and wastewater. 13th ed. Amer. Public Health Assoc. Inc., Washington, D.C. 874 pp.

Amosov, V.A. 1960. Changes in weight and length of fish after fixation in formalin followed by soaking in water. Voprosy Ikhtiologii, 16: 187-190. Fish. Res. Board Can., Transl. Series No. 452.

Atkins, C.E. 1905. The early feeding of salmonoid fry. Trans. Amer. Fish. Soc., 34: 75-81.

__________. 1906. Experiments in fasting of fry. Trans. Amer. Fish. Soc., 35: 123-129.

Bams, R.A. 1969. Adaptions of sockeye salmon associated with incubation in stream gravels. Pages 71-87 in T.G. Northcote, ed. Symposium on salmon and trout in streams. The University of British Columbia, Vancouver.

__________. 1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can., 27: 1429-1452.

__________, and K.S. Simpson. 1977. Substrate incubators workshop -- 1976. Report on current state-of-the-art. Fish. Mar. Service, Environ. Can. Tech. Report No. 689. 68 pp.

Banks, J.L., L.G. Fowler, and J.W. Elliot. 1971. Effects of rearing temperature on growth, body form and hematology of fall chinook fingerlings. Prog. Fish-Cult., 33: 20-26.

Battle, H.I. 1942. Hepatogenesis of the Atlantic salmon, Salmo salar L. Can. J. Res., D, 20: 79-97.

Bell, G.R. 1964. A guide to the properties, characteristics, and uses of some general anaesthetics for fish. Fish. Res. Board Can., Bull. No. 148. 4 pp.

Bilton, H.T., and G.L. Robins. 1973. The effect of starvation and subsequent feeding on survival and growth of Fulton Channel sockeye salmon, Oncorhynchus nerka. J. Fish. Res. Board Can., 30: 1-5.

Blaxter, J.H.S. 1969. Development: eggs and larvae. Pages 178-252 in W.S. Hoar and D.J. Randall, ed. Fish physiology, Vol. III, Reproduction and growth, bioluminescence, pigments, and poisons. Academic Press, New York.

__________, and K.F. Ehrlich. 1974. Changes in behaviour during starvation of herring and plaice larvae. Pages 575-588 in J.H.S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

__________, and G. Hempel. 1963. The influence of egg size on herring larvae (Clupea harengus L.). J. Conseil Perm. Intern. Explor. Mer, 28: 211-240.

Bogdanova, L.S. 1977. The growth and development of the larvae of the Kuben inconnu, Stenodus leucichthys nelma, under conditions of varying temperatures and feeding regimes. J. Ichth., 17: 582-590.

Brannon, E.L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. Intern. Pac. Salmon Fish. Comm., Prog. Report No. 12. 26 pp.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behaviour and the food supply. Pages 113-131 in S.D. Gerking, ed. The biological basis of freshwater fish production. Blackwell Scientific Publ., Oxford.

Brett, J.R. 1979. Environmental factors and growth. Pages 599-677 in W.S. Hoar, D.J. Randall, and J.R. Brett, eds. Fish physiology, Vol. VIII, Bioenergetics and growth. Academic Press, New York.

__________, and C. Groot. 1963. Some aspects of olfactory and visual responses in Pacific salmon. J. Fish. Res. Board Can., 20: 287-303.

Brown, C.J.D. 1938. The feeding habits of the Montana grayling. J. Wildl. Management, 2: 135-145.

__________, and C. Buck, Jr. 1939. When do trout and grayling fry begin to take food? J. Wildl. Management, 3: 134-140.

Brown, M.E. 1957. Experimental studies on growth. Pages 361-400 in M.E. Brown, ed. The physiology of fishes, Vol. I, Metabolism. Academic Press, New York.

Brown, R.I., and H.H. Buck. 1977. Brown's nautical almanac. Daily tide tables for 1977. Brown, Son and Ferguson, Ltd., Glasgow, U.K. 959 pp.

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

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Board Can., 32: 2295-2332.

Dill, L.M. 1967. Studies on the early feeding of sockeye salmon alevins. Can. Fish Cult., 39: 23-34.

Dill, P.A. 1970. On the development of diel activity rhythms in Atlantic salmon and rainbow trout. Ph.D. Thesis, University of Western Ontario, London. 90 pp.

__________. 1977. Development of behaviour in alevins of Atlantic salmon, *Salmo salar*, and rainbow trout, *S. gairdneri*. Animal Behaviour, 25: 116-121.

Disler, N.N. 1953. Ecological and morphological characteristics of the development of the Amur autumn chum salmon, *Oncorhynchus keta* (Walb.). Pages 33-41 *in* Pacific salmon (selected articles from Soviet periodicals). Israel Program for Scientific Translation, Jerusalem, 1961. Office Tech. Serv., U.S. Dept. Comm., Washington.

Ehrlich, K.F. 1974. Chemical changes during growth and starvation of herring larvae. Pages 301-323 *in* J.H.S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

__________, J.H.S. Blaxter, and R. Pemberton. 1976. Morphological and histological changes during the growth and starvation of herring and plaice larvae. Marine Biology, 35: 105-118.

Elliot, J.M. 1973. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc., Sci. Publ. No. 25. 148 pp.

Farris, D.A. 1959. A change in the early growth rates of four larval marine fishes. Limnol. Oceanogr., 4: 29-36.

Godin, J.-G.J. 1979. Diel rhthms of behaviour in juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum). Ph.D. Thesis, The Unviersity of British Columbia, Vancouver. 294 pp.

Gray, J. 1926. The growth of fish. I. The relationship between embryo and yolk in Salmo fario. Brit. J. Exp. Biol., 4: 215-225.

__________. 1928a. The growth of fish. II. The growth-rate of the embryo of Salmo fario. Brit. J. Exp. Biol., 6: 110-124.

__________. 1928b. The growth of fish. III. The effect of temperature on the development of the eggs of Salmo fario. Brit. J. Exp. Biol., 6: 125-130.

Guma'a, S.A. 1978. On the early growth of 0^+ perch, Perca fluviatilis, in Windermere. Freshwater Biol., 8: 213-220.

Gunnes, K. 1979. Survival and development of Atlantic salmon eggs and fry at three different temperatures. Aquaculture, 16: 211-218.

Hamor, T., and E.T. Garside. 1976. Developmental rates of embryos of Atlantic salmon, Salmo salar L., in response to various levels of temperature, dissolved oxygen, and water exchange. Can. J. Zool., 54: 1912-1917.

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

Harvey, H.H. 1966. Commencement of feeding in the sockeye salmon (Oncorhynchus nerka). Verh. Internat. Verein. Limnol., 16: 1044-1055.

Hayes, F.R. 1949. The growth, general chemistry, and temperature relations of salmonid eggs. Quart. Rev. Biol., 24: 281-308.

__________, and D. Pelleut. 1945. The effect of temperature on the growth and efficiency of yolk conversion in the salmon embryo. Can. J. Res., D, 23: 7-15.

__________, D. Pelleut, and E. Gorham. 1953. Some effects of temperature on the embryonic development of the salmon (Salmo salar). Can. J. Zool., 31: 42-51.

Hempel, G. 1965. On the importance of larval survival for the population dynamics of marine food fish. California Coop. Oceanic Fish. Invest., Report X: 13-23.

Henshall, J.A. 1904. Experiments in feeding fry. Trans. Amer. Fish. Soc., 33: 76-78.

__________. 1907. Culture of Montana grayling. U.S. Bur. Fish. Doc. No. 628. 7 pp.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapport Process-Verbauz Reunions Conseil Perm. Intern. Explor. Mer, 20: 1-228.

_________. 1926. Fluctuations in the year classes of important food fishes. J. Conseil Intern. Explor. Mer, 1: 5-38.

Hopley, C.W., Jr. 1974. Feeding of chinook salmon alevins. Pages 24-25 in Proceedings of the Northwest Fish Culture Conference (1974). University of Washington, Seattle.

_________. 1975. The effect of early feeding on the rate of yolk absorption in chinook salmon (Oncorhynchus tshawytscha) alevins. Pages 121-125 in Proceedings of the Northwest Fish Culture Conference (1975). University of Washington, Seattle.

Hubbs, C.L. 1943. Terminology of early stages of fishes. Copeia, 1943: 260.

Hublou, W.F. 1963. Oregon pellets. Prog. Fish-Cult., 25: 175-180.

Hurley, D.A., and E.L. Brannon. 1969. Effect of feeding before and after yolk absorption on the growth of sockeye salmon. Intern. Pac. Salmon Fish. Comm., Prog. Report No. 21. 19 pp.

Ishibashi, N. 1974. Feeding, starvation and weight changes of early fish larvae. Pages 339-344 in J.H.S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

Jones, B.C., and G.H. Geen. 1977. Morphometric changes in an elasmobranch (Squalus acanthias) after preservation. Can. J. Zool., 55: 1060-1062.

Kolgaev, A.M. 1963. On the premature assumption of active swimming by young chum salmon, Oncorhynchus keta infraspecies autumnalis Berg, and the consequences of this phenomenon as studied under hatchery conditions. Voprosy Ikhtiologii, tom 3, vyp 3(28): 561-562. Fish. Res. Board Can., Transl. Series No. 545.

Kostomarova, A.A. 1962. Effect of starvation on the development of the larvae of bony fishes. Tr. Inst. Morfol. Zhivotn. Akad. Nauk. SSSR, 40: 4-77.

Lasker, R. 1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia, 2: 399-405.

Latta, W.C. 1969. Some factors affecting survival of young-of-the-year brook trout, Salvelinus fontinalis (Mitchill), in streams. Pages 229-240 in T.G. Northcote, ed. Symposium on salmon and trout in streams. The Univeristy of British Columbia, Vancouver.

Laurence, G.C. 1969. The energy expenditure of largemouth bass larvae, *Micropterus salmoides*, during yolk absorption. Trans. Amer. Fish. Soc., 99: 398-405.

_________. 1973. Influence of temperature on energy utilization of embryonic and prolarval tautog, *Tautoga onitis*. J. Fish. Res. Board Can., 30: 435-442.

Leach, G.C. 1923. Artificial propagation of brook trout and rainbow trout, with notes on three other species. U.S. Bur. Fish., Document No. 955. 74 pp.

Liao, P.B. 1971. Water requirements of salmonids. Prog. Fish-Cult., 33: 210-215.

Litchfield, J.T., Jr. 1949. A method for rapid graphic solution of time-percent effect curves. J. Pharm. Exp. Therapeutics, 96: 399-408.

Love, R.M. 1970. The chemical biology of fishes. Academic Press, New York. 547 pp.

_________, I. Robertson, and I. Strachan. 1968. Studies on the North Sea cod. VI. Effects of starvation. 4. Sodium and potassium. J. Sci. Food Agr., 19: 415-422.

MacLeod, M.G. 1977. Effects of salinity on fasted rainbow trout, *Salmo gairdneri*. Mar. Biol., 43: 103-107.

Marr, D.H.A. 1965. Factors affecting the growth of salmon alevins and their survival and growth during the fry stage. Yearb. Assoc. River Auth., 1965: 133-141.

_________. 1966. Influence of temperature on the efficiency of growth of salmonid embryos. Nature, 212(5065): 957-959.

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

May, R.C. 1971. Effects of delayed initial feeding on larvae of the grunion, *Leuresthes tenuis* (Ayres). Fish. Bull., 69: 411-425.

_________. 1974. Larval mortality in marine fishes and the critical period concept. Pages 3-19 *in* J.H.S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

Nakagawa, H., and Y. Tsuchiya. 1972. Studies on rainbow trout eggs (Salmo gairdneri irideus). IV. Changes in yolk content during embryogenesis. J. Fac. Fish. Anim. Husb., 11: 111-118.

__________, and Y. Tsuchiya. 1974. Studies on rainbow trout eggs (Salmo gairdneri irideus). V. Further studies on the yolk protein during embryogenesis. J. Fac. Fish. Anim. Husb., 13: 15-27.

Ochiai, T., K. Kodera, T. Kon, T. Miyazaki, and S.S. Kubota. 1977. Studies on disease owing to erroneous-swallowing in Ayu fry. Fish. Path., 12: 135-139. English Abst.

O'Connell, C.P. 1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, Engraulis mordax Girard. J. Exp. Mar. Biol. Ecol., 25: 285-312.

Paine, J.R. 1971. Fulton River fry quality and ecology program. Report of 1970 studies. Can. Dept. Fish. For., Can. Fish. Serv. Tech. Report No. 1. 38 pp.

Palmer, D.D., H.E. Johnson, L.A. Robinson, and R.E. Burrows. 1951. The effect of retardation of the initial feeding on the growth and survival of salmon fingerlings. Prog. Fish-Cult., 13: 55-62.

Parker, R.R. 1963. Effects of fromalin on length and weight of fishes. J. Fish. Res. Board Can., 20: 1441-1455.

Peterson, R.H., H.C.E. Spinney, and A. Sreedharan. 1977. Development of Atlantic salmon (Salmo salar) eggs and alevins under varied temperature regimes. J. Fish. Res. Board Can., 34: 31-43.

Phillips, A.M. 1969. Nutrition, digestion, and energy utilization. Pages 391-432 in W.S. Hoar and D.J. Randall, eds. Fish physiology, Vol. 1, Excretion, ionic regulation and metabolism. Academic Press, New York.

__________, D.L. Livingston, and H.A. Poston. 1966. The effect of changes in protein quality, calorie sources and calorie levels upon the growth and chemical composition of brook trout. N.Y. State Dept. Conserv. Fish. Res. Bull., 29: 6-7.

Prakash, A. 1961. Distribution and differentiation of alkaline phosphatase in the gastrointestinal tract of steelhead trout. Exp. Zool., 146: 237-251.

Ricker, W.E. 1975. Computations and interpretations of biological statistics of fish populations. Bull. Fish. Res. Board Can., No. 191. 382 pp.

Roley, D.D. 1974. Feeding of hatchery-reared coho salmon alevins. Pages 26-28 in Proceedings of the Northwest Fish Culture Conference (1974). University of Washington, Seattle.

Rosenthal, H., D. Kuhlmann, and O. Fukuhara. 1978. Shrinkage of newly hatched larvae of the Red Sea bream (Chryophrys major Temminck and Schlegel) preserved in formalin. Arch. Fisch Wess., 29(1/2): 59-63.

Salo, E.O., and W.H. Baycliff. 1958. Artificial and natural production of silver salmon, Oncorhynchus kisutch, at Minter Creek, Washington. Wash. State Dept. Fish. Res. Bull., 4. 76 pp.

Silver, S.J., C.E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Trans. Amer. Fish. Soc., 92: 327-343.

Simonova, N.A. 1972. The feeding of sockeye fry in spawning-grounds and their food supply. Izv. Tikhookean Nanchno-Issled Inct. Rybn Khoz Okeanogr, 82: 179-189. Fish. Res. Board Can., Transl. Series No. 2911.

Smirnov, A.I. 1975. The biology, reproduction and development of the Pacific salmon. Izd Mosk. Univ: 1-335. Fish. Mar. Serv., Transl. Series No. 3861.

Smith, S. 1947. Studies in the development of the rainbow trout (Salmo irideus). I. The heat production and nitrogenous excretion. J. Exp. Biol., 23: 357-373.

__________. 1957. Early development and hatching. Pages 323-359 in M.E. Brown, ed. The physiology of fishes. Vol. I. Metabolism. Academic Press, New York.

__________. 1958. Yolk utilization in fishes. Pages 33-53 in D. Rudnick, ed. Embryonic nutrition. The University of Chicago Press, Chicago.

Snedecor, G.W., amd W.G. Cochran. 1967. Statistical methods. The Iowa State University Press, Ames, Iowa. 593 pp.

Sokal, R.R., and F.L. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco. 776 pp.

Sprague, J.B. 1973. The ABC's of pollutant bioassay using fish. Pages 6-10 in Biological methods for the assessment of water quality, ASTM STP 528, Amer. Soc. Testing Materials.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill Book Co., Ltd., New York. 481 pp.

Stuart, T.A. 1953. Spawning migration, reproduction and young stages of loch trout (Salmo trutta L.). Scottish Home Dept., Freshwater Salmon Fish. Res., 5: 1-39.

Tait, J.S. 1960. The first filling of the swim bladder in salmonids. Can. J. Zool., 38: 179-187.

Templeman, W., and G. Andrews. 1956. Jellied condition in the American plaice, Hippoglossoides platessoides. J. Fish. Res. Board Can., 13: 147-182.

Theilacker, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, Trachurus symmetricus, larvae. Fish. Bull., 76: 403-414.

Thomas, A.E., and J.M. Shelton. 1968. Operation of Abernathy channel for incubation of salmon eggs. U.S. Fish Wildl. Serv., Bureau Sport Fish., Tech. Paper No. 23. 19 pp.

Toetz, D.W. 1966. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. Invest. Indiana Lakes and Streams, VII(4): 115-146.

Twongo, T.K., and H.R. MacCrimmon. 1976. Significance of the timing of initial feeding in hatchery rainbow trout, Salmo gairdneri. J. Fish. Res. Board Can., 33: 1914-1921.

__________, and H.R. MacCrimmon. 1977. Histogenesis of the oropharyngeal and oesophageal mucosa as related to early feeding in rainbow trout, Salmo gairdneri Richardson. Can. J. Zool., 55: 116-128.

Vernier, J.-M. 1969. Chronological table of the embryonic development of rainbow trout. Annales d'Embryologie et de Morphogenese, 2: 495-520. Fish. Mar. Serv., Transl. Series No. 3913.

White, G.M. 1915. The behaviour of brook trout embryos from the time of hatching to the absorption of the yolk sac. J. Anim. Behav., 5: 44-60.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berl.), 33: 71-86.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Nauch. Tr. Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina, Minsk. Fish. Res. Board Can., Transl. Series No. 194. 251 pp.

Wurtsbaugh, W.A., and G.E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. J. Fish. Biol., 11: 87-98.

Yastrebkov, A.A. 1966. Effects of egg size upon size and growth rate of pink salmon larvae. Trudy Murmanskogo Morskogo Biologocheskogo Instituta, 12(16): 45-53. Fish. Res. Board Can., Transl. Ser. No. 1822.

Appendix Table I. Temperature variation ($\bar{x} \pm 1$ SD) between growth tanks housing chinook alevins at 6, 8, 10, and 12 °C.

Temperature group (°C)	Variation between tanks (°C)
6	0.08 ± 0.03
8	0.06 ± 0.04
10	0.08 ± 0.04
12	0.04 ± 0.01

Appendix Table II. Morphological features used to characterize Vernier's (1969) stages 31-37.

Vernier stage	Principle characteristics
31	appearance of first rays in anal and dorsal fins
32	evidence of primordial adipose fin
33	appearance of dermal pelvic fin rays
34	adipose fin well defined, edge of anal fin projects beyond embryonic fin fold
35	pectoral fins rounded with serrated edge
36	yolk sac almost entirely (> 1/2) covered with chromatophores
37	yolk sac entirely covered with chromatophores (button-up)

Appendix Table III. Estimates of the relationship between characteristics of chinook alevins at 6, 8, 10, and 12 °C, and time (t) (days after fertilization).

Temperature group (°C)	Treatment	Equation		n
a.	Tissue dry weight (td) before maximum tissue weight			
6	10	$\log_e$ td = 0.0206t	+ 1.1750	9
8	10	0.0296	0.9627	7
10	10	0.0384	0.9024	8
12	10	0.0510	0.4628	8
b.	Yolk wet weight (yw) to 40 mg			
6	10	yw = 632.94	- 3.18t	14
8	10	642.43	- 4.34	13
10	10	607.63	5.25	10
12	10	624.34	6.35	14
c.	Yolk dry weight (yd) to 20 mg			
6	10	yd = 314.85	- 1.59t	14
8	10	320.64	2.17	13
10	10	313.36	2.73	10
12	10	303.07	3.07	14
d.	Tissue dry weight (td) to 700 mg			
6	1	$\log_e$ td = 0.0214t	+ 0.9998	9
	2	0.0220	0.9261	8
	3	0.0223	0.7967	9
	4	0.0206	1.0884	9

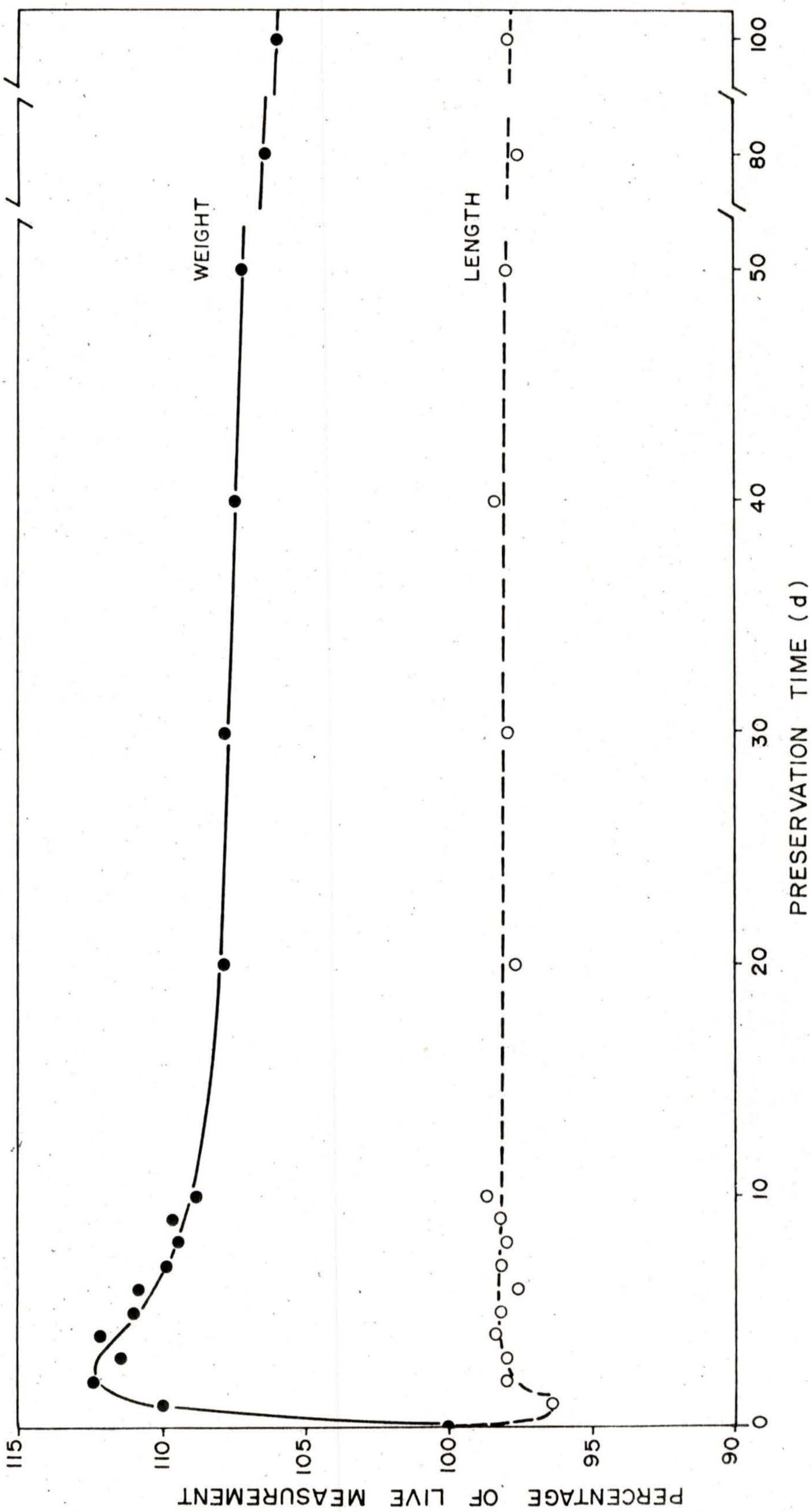
Appendix Table III (cont'd).

Temperature group (°C)	Treatment	Equation	n
d(cont'd).			
6	5	0.0215 0.8982	9
	6	0.0211 0.9132	9
	7	0.0191 1.1488	8
	8	0.0215 0.1061	6
	9	0.0249 - 1.8909	3
8	1	$\log_e$ td = 0.0297t + 0.8614	10
	2	0.0266 1.2544	10
	3	0.0273 1.0755	10
	4	0.0275 1.0788	10
	5	0.0276 0.9860	10
	6	0.0290 0.6491	9
	7	0.0283 0.3698	8
	8	0.0268 0.2692	8
	9	0.0302 - 1.2724	5
10	1	$\log_e$ td = 0.0306t + 1.5169	12
	2	0.0292 1.6263	13
	3	0.0314 1.3083	12
	4	0.0300 1.4785	12
	5	0.0313 1.2356	11
	6	0.0307 1.1435	12
	7	0.0317 0.7617	10
	8	0.0358 - 0.4050	7
	9	0.0371 - 1.1704	6

Appendix Table III(cont'd).

Temperature group (°C)	Treatment	Equation		n
d(cont'd).				
12	1	$\log_e td = 0.0411t$	+ 1.1904	12
	2	0.0381	1.4667	12
	3	0.0400	1.2042	12
	4	0.0382	1.3502	11
	5	0.0401	1.1045	12
	6	0.0383	1.1269	11
	7	0.0403	0.5591	9
	8	0.0409	0.1025	8
	9	0.0361	0.0161	7
e. Yolk wet weight (yw) to 40 mg				
6	1	yw = 627.54	- 3.18t	8
8	1	614.02	4.41	9
10	1	606.03	5.10	8
12	1	639.18	6.14	8
f. Yolk dry weight (yd) to 20 mg				
6	1	yd = 314.33	- 1.60t	8
8	1	335.50	2.28	9
10	1	296.25	2.60	8
12	1	292.54	2.90	8

Appendix Figure 1. Changes in total wet weight and length of chinook alevins (live weight -- 409.6 $\pm$ 35.0 mg, live length -- 25.0 $\pm$ 0.5 mm; n = 15) preserved in 5% neutral formalin for a 100-day period. Curves fitted by eye.


WEIGHT
LENGTH
PERCENTAGE OF LIVE MEASUREMENT
PRESERVATION TIME (d)
90
95
100
105
110
115
0
10
20
30
40
50
80
100

VITA

Surname: HEMING   Given Names: THOMAS ARTHUR

Place of Birth: GUELPH, ONT.   Date of Birth: June 3, 1953

Educational Institutions Attended, with Date of Entering and Leaving:

UNIVERSITY OF GUELPH, ONT.   1972 to 1976

UNIVERSITY OF VICTORIA, B.C.   1976 to 1979

Degrees Awarded, with Dates and Names of Institutions:

B.Sc. (Honours)   1976   University of Guelph, Ont.

Honours and Awards:

McArthur-Humphries Scholarship, 1972/73

N.R.C. Postgraduate Scholarship, 1976/77 and 1977/78

Publications:

Sprague, J.B., D.W. Rowe, G.F. Westlake, T.A. Heming, and I.T. Brown. 1978. Sublethal effects of treated liquid effluent from a petroleum refinery on freshwater organisms. Fisheries and Environment Canada, and Petroleum Association for Conservation of the Canadian Environment. October 1978.