EFFECTS OF FEEDING REGIMES AND DIEL TEMPERATURE CYCLES ON OTOLITH INCREMENT FORMATION IN JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

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ABSTRACT

The effects of constant and diel cyclic water temperature regimes, feeding frequency, fish activity, and ration level on growth increment formation in juvenile chinook salmon, *Oncorhynchus tshawytscha*, are described. Of the variables examined, any event which recurred more than once every 24 hours increased the rate of increment production above 1 increment per 24 hours. The results were consistent with the hypothesis that environmental variables modify the rate of increment formation by altering the periodicity of fish activity. Both water temperature and ration level interacting with water temperature affected otolith increment width, a measure of fish growth, although ration level did not.

To realize the potential of otolith microstructure in detailed age and growth studies of fishes, knowledge of factors influencing otolith growth is required. The principle features of otoliths likely to be used in such studies are the growth increments which are deposited in a concentric fashion around the otolith nucleus. The frequency of deposition (often 1 increment/24 h) and the width of the increments are both affected by environmental conditions (Neilson and Geen 1982).

The growth increments result from accretion of $CaCO^3$ and to a lesser extent, protein (Simkiss 1974). The daily nature of their deposition observed by many workers (Pannella 1971; Brothers et al. 1976; Wilson and Larkin 1982; and others) appears related to a daily rhythm in the relative rates of calcium carbonate and protein deposition (Mugiya et al. 1981). The cyclic deposition of calcium and protein over a 24-h period results in the formation of the bipartite features now referred to as daily growth increments.

The effects of environmental variables on otolith increment formation have been the subject of some controversy. Taubert and Coble (1977) concluded that a 12:12 LD photoperiod was responsible for entraining diel rhythms in the growth of juvenile *Lepomis* and *Tilapia* sp. otoliths. However, juvenile starry flounder, *Platichthys stel-* *latus*, and chinook salmon, *Oncorhynchus tshawytscha*, continued to produce daily growth increments when exposed to constant light (Campana and Neilson 1982; Neilson and Geen 1982). The latter authors presented evidence that feeding frequency affected both increment number and width in *O. tshawytscha*. They also suggested that feeding frequency (or any other environmental variable) was probably not the ultimate factor determining the frequency of otolith increment production. Environmental modulation of endocrine rhythms (Menaker and Binkley 1981) may ultimately control otolith increment periodicity.

Diel cycles in water temperature have received little consideration as an environmental variable potentially affecting increment formation. Brothers (1978) suggested that diel temperature variations were responsible for otolith increment formation in temperate stream-dwelling fish although no data were presented. This gap in our understanding of factors influencing otolith increment production is significant since diel changes in water temperature are a common feature of aquatic environments. In this study we examined the effects of diel water-temperature regimes on formation of otolith growth increments in *O. tshawytscha* alevins and fry. We also present data on the effects of interactions of water-temperature regimes, feeding frequency, and ration level on otolith increment formation in *O. tshawytscha* fry. Finally, we tested the suggestion made earlier (Neilson and Geen 1982) that feeding periodicity (or any other periodic event affecting fish activity) modifies the rate of otolith increment production through changes in fish activity.

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METHODS

Alevins

Fish used in the experiments described below originated from the 1981 brood of the Canada Department of Fisheries and Oceans Capilano Hatchery. Eggs were transferred to incubation facilities at Simon Fraser University at the "eyed" stage of development, corresponding to 347 Celsius degree-days. Prior to transfer, the eggs were held under a 12:12 LD photoperiod and at a constant 8°C water temperature. The eggs were held for 5 d in our laboratory at 8.5°C before exposure to diel water-temperature regimes.

Two lots of 100 fish were exposed as eggs and later, as alevins, over a 69-d period to a water-temperature regime whose diel amplitude averaged 2° and 4°C (range 1.8°-2.4° and 3.0°-4.5°C) above a daily average minimum temperature of 8.5°C. These temperatures were similar to those observed in May-June 1981 in the Deadman River, B.C., a stream supporting an *O. tshawytscha* population. All eggs hatched by day 29. Eggs or alevins ($n = 10$) were sampled at days 19, 40, 55, and 69. On day 39, 20 alevins were transferred from a temperature regime with a 4°C amplitude and 24-h period to a regime with the same temperature amplitude but a 12-h period. A fourth group was held at a constant 8.5°C. The constant water temperature corresponded to that of the cool period of the diel water-temperature regimes.

Sagittal otoliths were removed from preserved fish and prepared following the methods of Neilson

and Geen (1981). Otolith sections were examined using a light microscope or scanning electron microscope (SEM) as described in Neilson and Geen (1982).

Fry

Fry used in these experiments were about 90-d-old posthatch and originated from Capilano River hatchery stock. Prior to transfer to 25 l aquaria at Simon Fraser University, fish were held under natural light at a constant 8°C and fed once every 24 h. After transfer to our laboratory, fry were held for 2 wk in flow-through aquaria supplied with aerated and dechlorinated water at 6°C before experiments commenced. During this period the 50 fish in each aquarium were fed to satiation with Oregon Moist Pellets once per 24 h and exposed to a 12:12 LD photoperiod.

Experimental feeding and temperature regimes to which fry were exposed are summarized in Table 1. Amplitude of daily temperature fluctuations was 4°C (range 3.6°-4.4°C) above the average minimum of 6°C. The diel temperature cycle in relation to photoperiod and feeding events is shown in Figure 1. The activity of one group of fish was artificially increased to examine the effects of activity on otolith increment formation. These fish were forced to evade a slowly moving aquarium net for 10-min beginning at 1900 h daily. The induced activity level appeared similar to that associated with feeding. Ration provided to experimental lots of fish was maintained as a constant proportion (4% or 8%) of average fish dry weight by
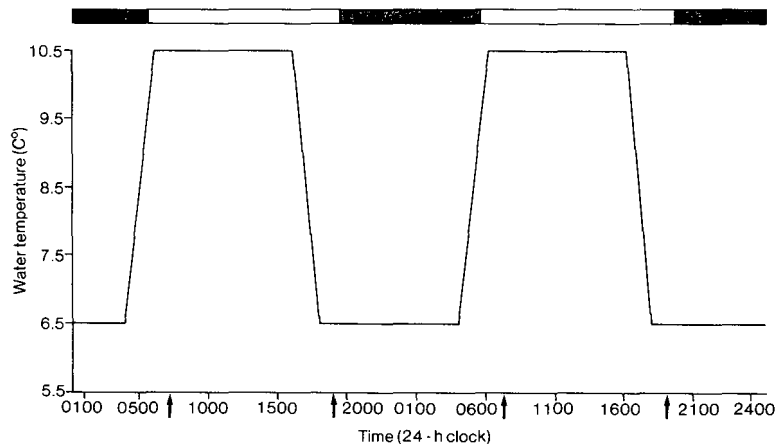

FIGURE 1.—Diel water-temperature cycle in relation to photoperiod and feeding events (↑) for *Oncorhynchus tshawytscha* fry. Light and dark periods are indicated by the open and solid bars respectively.

TABLE 1.—List of abbreviations denoting experimental regimes to which *Oncorhynchus tshawytscha* fry were exposed in 1982. Percent ration (% of body weight offered every 24 h) is given and the water temperature at time of feeding during the diel cycle, if applicable, is indicated in parentheses. Refer to Figure 1 for details of feeding, temperature, and photoperiod regimes.

Treatment	Time of feeding (h)
8% (warm)	0700
8% (cool)	1900
8% (constant)[1]	0700
4% (warm)	0700
4% (cool)	1900
4% (constant)[1]	0700
2 × 4%[2]	0700 and 1900
2 × 2%[2]	0700 and 1900
4% + activity[3]	0700
Starvation	n/a

[1] Fish in these treatments were held at constant temperature.
[2] Fish in these treatments were fed 2 times per 24 h.
[3] Fish in this treatment were held at a constant temperature and exposed to a 10-min bout of forced activity at 1900 h every day.

adjusting total food offered as fish grew or were sampled. Every third day, excess food was removed from the aquaria within 30 min of offering, weighed, and consumption estimated.

On day 26, we exposed fry for 30 min to a hypertonic solution of 1 g/l sodium chloride and 40 mg/l oxytetracycline hydrochloride. The tetracycline was incorporated into the otolith and provided a time marker which exhibited fluorescence when viewed with ultraviolet illumination. All fry were successfully marked by this method.

Originally, we had intended to sample 15 fish at days 10, 20, and 40. However, an accidental interruption of the dechlorinated water supply on day 19 resulted in the mortality of some fish in treatments 4% (cool), 4% (constant), 2 × 4%, and 4% + activity. Complete mortality of starved fish occurred at that time. To ensure an adequate ($N \geq$ 10) sample on experiment completion, no samples were taken at day 20 for the above four treatments. Even so, only five fish remained by day 40 in the 4% (cool) treatment.

Fork lengths were determined immediately after the fish were sacrificed. Fish were then dried to a constant weight (60°C for 48 h) in individual labeled containers, and weighed. Sagittal otoliths were then removed, weighed with an electrobalance, and prepared for examination with the SEM or a light microscope.

Increment counts were conducted as described by Neilson and Geen (1982). No attempt was made

to distinguish between the daily and subdaily increments as did Brothers (1978) and Campana (1983). Such distinctions are often based on subjective appraisals of increment continuity and appearance when viewed with a light microscope. We did not observe any such differences in growth increments of *O. tshawytscha*. Moreover, as the purpose of this study was to determine the periodicity of increment formation as a basis for detailed study of fish growth, the classification of increments as daily or subdaily was not necessary.

RESULTS

Eggs and Alevins

The formation of growth increments commenced before hatching under all experimental regimes. One increment/24 h was formed on average under all temperature regimes (Table 2). No significant departure from unity was noted (analysis of variance, $P > 0.05$). However, the appearance of the daily growth increments differed between treatments. Otoliths of fish subject to a cycle of temperature were characterized by more regular and easily observed growth increments than those held under constant temperatures (Fig. 2).

Examination with a SEM at 1,000× revealed that the bipartite nature of otolith growth increments differed between the temperature regimes. After etching with a weak acid (Neilson and Geen 1982), the relatively deeply etched portion of the bipartite growth increment (corresponding to the opaque portion of the bipartite structures when viewed with a transmitted light microscope) comprised a larger average fraction of the growth increments ($P < 0.01$) in otoliths of fish subjected to a diel cycle in temperature than those of fish held at constant water temperatures. The lightly etched portion of daily growth increments did not differ significantly between fish held in diel temperature regimes with 2°C and 4°C amplitude (analysis of

TABLE 2.—Summary of *Oncorhynchus tshawytscha* otolith increment counts for alevins held under various temperature regimes.

Experiment day	Increment count[1]		
	Constant temperature	2°C amplitude	4°C amplitude
19	17.8 ± 2.6	18.5 ± 1.2	17.4 ± 1.0
40	—	38.0 ± 2.4	39.5 ± 2.1
55	51.8 ± 2.8	54.1 ± 1.9	53.3 ± 3.0
69	68.4 ± 5.6	68.4 ± 4.1	70.2 ± 4.6

[1] ± 1 standard deviation indicated, n = 10.

FIGURE 2.—Comparison of *Oncorhynchus tshawytscha* alevin (length 30-31 mm) otolith microstructure in fish held for 60 d in diel water-temperature regimes of 4°C amplitude (right), 2°C amplitude (middle), and constant temperature (left).

variance and the Student-Newman-Keuls test, $P > 0.05$).

Oncorhynchus tshawytscha transferred from a 4°C diel temperature regime (24-h period) to a regime with a 12-h period and similar amplitude produced an average of 1.56 increments/24 h. The slope of the regression of mean increment count on experiment day differed significantly from unity ($P < 0.01$). An example of an otolith from a fish exposed to the 12-h period, cyclic temperature regime is shown in Figure 3 and illustrates the narrower increments associated with the 12-h cycle.

Fry

Otolith growth increments were formed at the rate of one every 24 h in fish fed once per day. No significant departures were noted (t-tests, $n \geq 20$, $P > 0.05$). Fish which received 2 feedings/24 h or 1 feeding and a 10-min bout of activity deposited significantly >1 increment/24 h (t-tests, $P < 0.01$). Arithmetic mean regressions of increment counts on experiment day for the latter treatments are given below:

Treatment	Regression equation	r^2
8% B.W. ration fed 2 times/24 h	$y = 1.45\,(x) + 1.58$	0.91
4% B.W. ration fed 2 times/24 h	$y = 1.76\,(x) - 1.40$	0.98
4% B.W. ration and forced activity	$y = 1.50\,(x) - 0.80$	0.93

Slopes of regressions in groups of fish producing >1 increment/d did not differ significantly from each other (analysis of covariance, $P > 0.10$).

The distributions of increment widths in fed groups of fish are presented in Figure 4. A summary of the comparisons of increment width data among treatments is provided in Figure 5. One-way analysis of variance and the Student-Newman-Keuls test indicated that mean increment widths in otoliths of fish receiving a ration of 8% B.W./24 h in one feeding differed significantly between groups ($P < 0.05$). Mean increment widths in otoliths of fish receiving a ration of 4% B.W./24 h in one feeding did not differ significantly in fish receiving the ration either during the cool or warm portion of the diel temperature cycle (Student-Newman-Keuls test, $P > 0.05$). However, fish receiving 4% B.W./24 h under constant water temperature produced growth increments whose mean width was significantly less than those of fish held in the diel water-
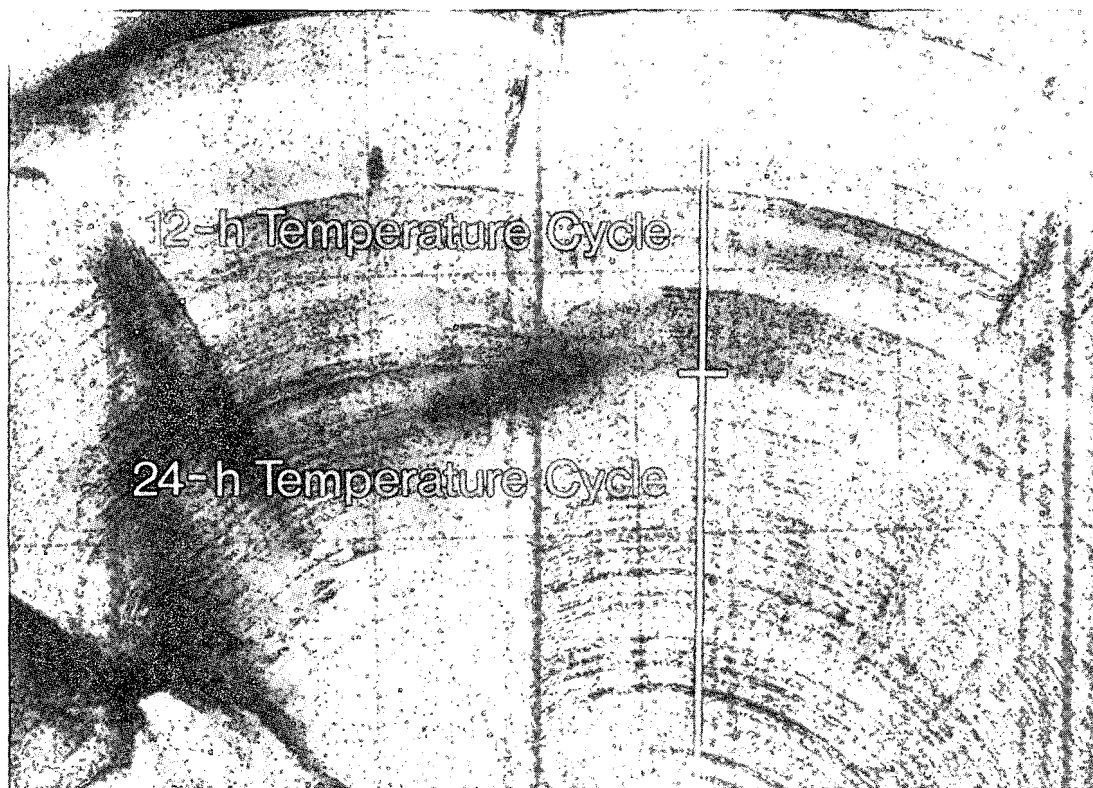
FIGURE 3.—Change in otolith microstructure in a *Oncorhynchus tshawytscha* alevin transferred from a 24-h period temperature cycle (4°C amplitude) to a 12-h period temperature cycle (4°C amplitude).

50 μm

temperature regimes ($P < 0.05$, Student-Newman-Keuls test).

The top two horizontal strata of Figure 4 constitute a 3×2 factorial design and were examined with a two-way analysis of variance. The effects of time of feeding with respect to the diel temperature cycle, ration level, and their interaction were examined in relation to mean otolith increment width. The effect of time of offering with respect to the diel temperature cycle on mean increment width was significant ($P < 0.001$), whereas ration level was not ($P > 0.05$). The interaction of time of offering in relation to the diel temperature cycle and ration level on otolith increment width was also significant ($P < 0.001$).

Fish in treatments receiving 2 feedings/24 h or fed once per 24 h and exposed to a 10-min bout of activity produced growth increments whose average widths were significantly less than those of fish in treatments fed the same ration once per 24 h. Treatments in which fish received either rations of 8% or 4% with 1 or 2 feedings/24 h comprise a 2×2 factorial design, and were analyzed with a two-way analysis of variance. Increased feeding frequency significantly reduced mean increment width ($P < 0.001$), although ration level did not ($P > 0.1$). The interaction of feeding frequency and ration level was not significant ($P > 0.1$).

Widths of otolith increments formed when fish were fed 4% B.W./24 h and subjected to a 10-min bout of activity were not significantly different from widths of increments in fish which received two feedings equivalent to the 4% B.W./24 h ration level (t-test, $P > 0.05$). However, fish fed a ration of 8% B.W./24 h with two feedings produced increments whose average width was significantly greater than the latter two treatments (analysis of variance and the Student-Newman-Keuls test, $P < 0.01$). Mean increment widths in fish fed 4% B.W./24 h and exposed to a constant water-temperature regime were compared with increment widths in fish receiving the same ration plus
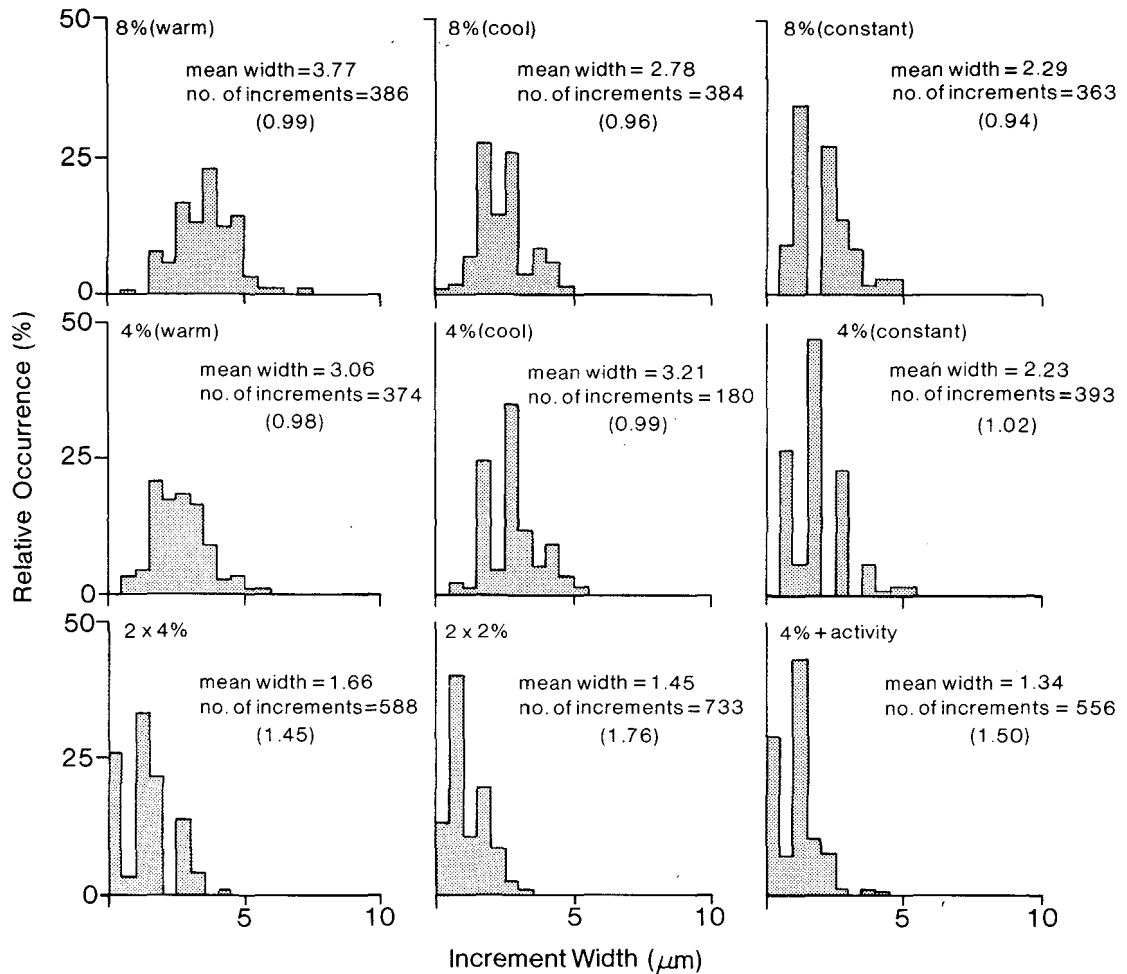
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FIGURE 4.—Distribution of otolith increment widths under the experimental regimes. Treatments are identified by numbers in the top-left corners of histograms and correspond to treatments listed in Table 1. The average rate of increment formation every 24 h is shown in brackets.
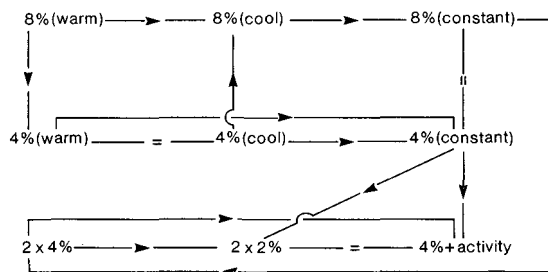

FIGURE 5.—Summary of Student-Newman-Keuls or t-test ($\alpha = 0.05$) comparisons of mean increment widths in *Oncorhynchus tshawytscha* fry held under the various experimental regimes. Arrow heads pointing left or right signify "less than" and "greater than" respectively.

a 10-min period of enforced activity. The mean increment width associated with the latter treatment was significantly less (t-test, $P < 0.01$).

Production of the narrower growth increments associated with 2 feedings/24 h or 1 feeding and induced activity did not occur immediately upon commencement of the experimental regimes. A period of transition in otolith microstructure was evident. Figure 6 shows the decrease in increment widths with time in fish previously provided a ration of 8% B.W./24 h in one feeding and then offered the same total ration in 2 feedings/d. For comparison, data on increment widths in fish fed 8% B.W./24 h are provided (Fig. 6). The slope of the regression of increment width on date in the latter
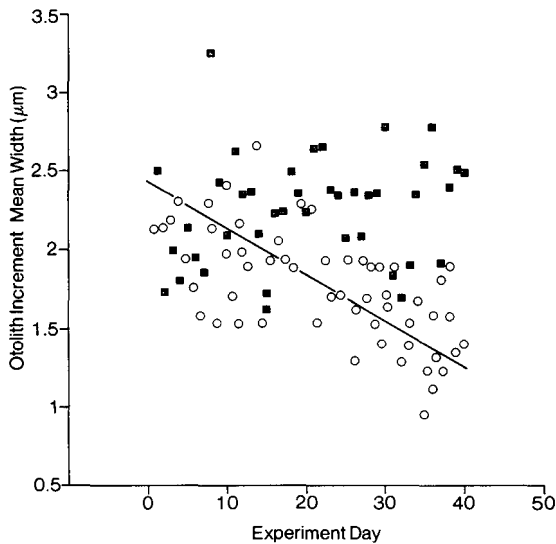
FIGURE 6.—Mean otolith increment widths (0) for *Oncorhynchus tshawytscha* fry from the 2 × 4% experimental feeding regime over days 1-40. Prior to day 1, fish were fed once every 24 h. Also shown are mean increment widths (■) of fish from the 8% (constant) feeding regime, where fish received one feeding only every 24 h.

treatment did not significantly differ from zero ($P > 0.10$), whereas the former did (t-test, $P < 0.01$).

Starved fry continued to produce one otolith increment every 24 h. However, the growth increments were faint when observed with a transmitted light microscope. That portion of otolith growth formed under starvation conditions was more transparent than the portion of otolith growth produced when fish were fed. Growth increment diel periodicity was also more pronounced during the portion of otolith growth corresponding to that period when fish were fed (Fig. 7).

To confirm that increment widths were proportional to fish growth, we plotted instantaneous growth in dry weight against average increment width for all treatments except the starved group (Fig. 8). The coefficient of determination (r^2) associated with those treatments in which fish formed 1 growth increment/24 h was 0.735 and the slope of the regression was significantly different from zero ($P < 0.01$). Note that points associated with treatments in which fish formed more than 1 increment/24 h lie considerably above the regression. The regression of these data differs signifi-
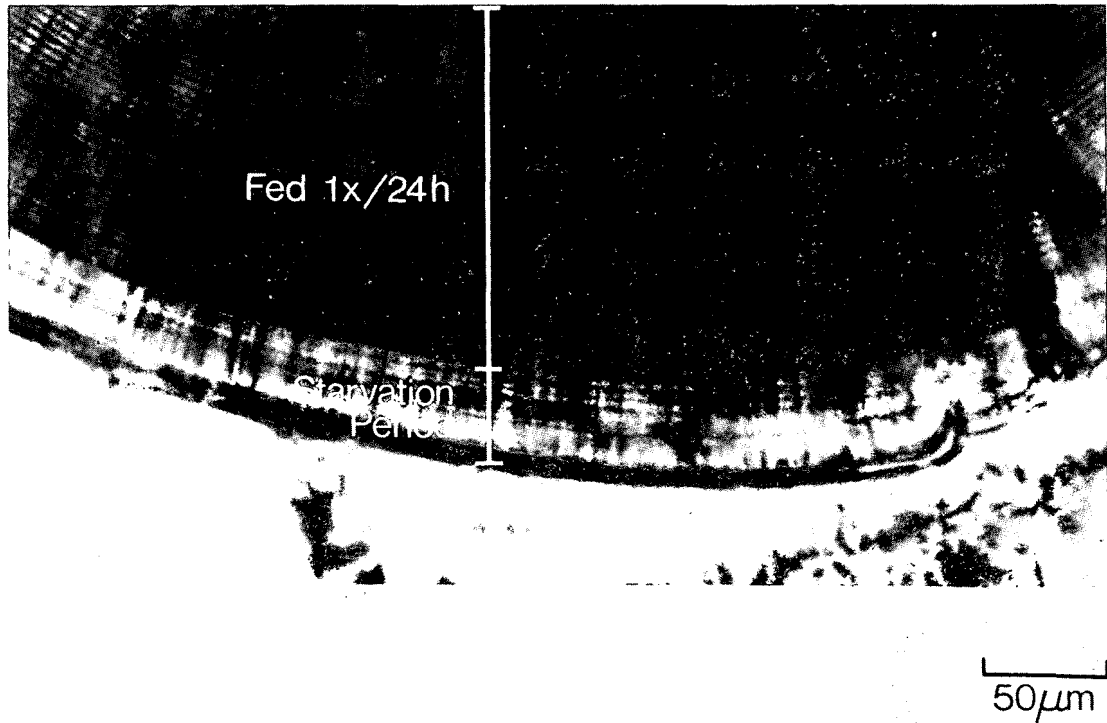

FIGURE 7.—Example of otolith microstructure from a starved *Oncorhynchus tshawytscha* salmon fry when viewed with transmitted light microscopy. The relatively transparent region near the otolith periphery corresponds to the starvation period.
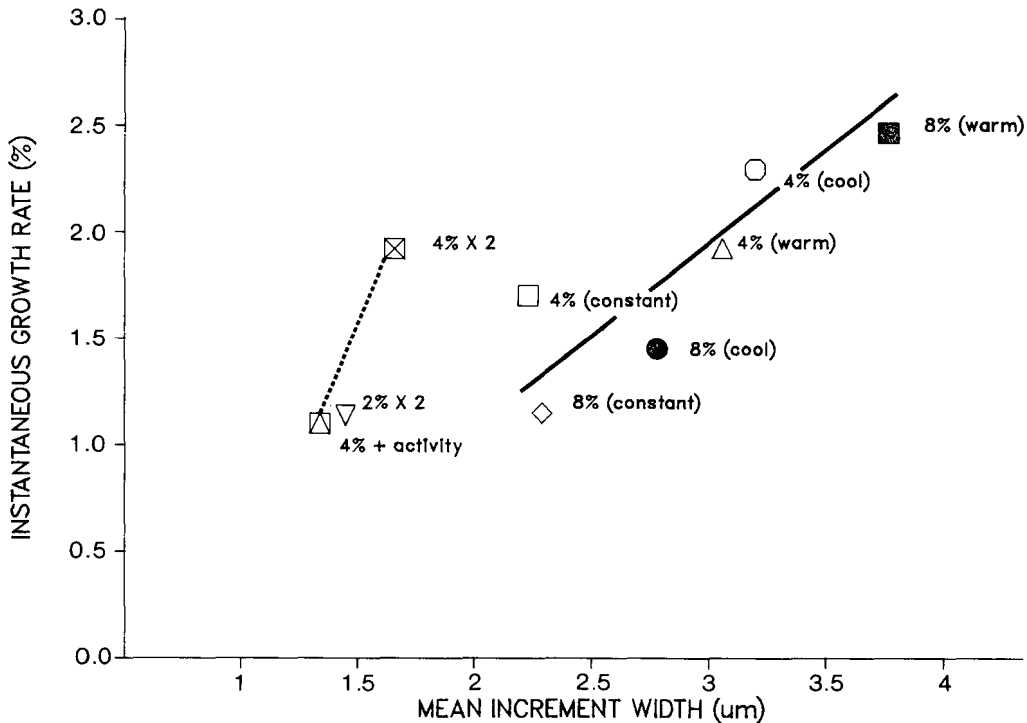
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FIGURE 8.—Regressions of mean otolith increment width versus instantaneous growth rate (dry weight) for the various experimental regimes. Solid line represents groups where fish produced one increment every 24 h on average; dashed line represents treatments where fish produced significantly more than one increment every 24 h.

cantly in both slope and y-intercept (analysis of covariance and t-test, $P < 0.01$) from that of fish fed once per day.

Slopes of arithmetic mean linear regressions of fish dry weight on experiment day indicated that the average rate of growth of fish fed 8% B.W./24 h at the beginning of the warm portion of the diel temperature cycle was significantly greater than that of fish fed at the beginning of the cool period of the diel temperature regime or at the constant water temperature (6°C) (analysis of covariance and the Student-Newman-Keuls test, $P < 0.01$). Similar analyses among treatments in which fish were fed 4% B.W./24 h [4% (warm), 4% (cool), 4% (constant)] or among fish that received two feedings or one feeding coupled with an additional bout of activity (2 × 4%, 2 × 2%, 4% + activity) indicated no significant differences in growth rate ($P > 0.05$).

To determine whether otolith growth-fish growth relationships were similar among treatments, we calculated otolith weight-fish dry weight regressions for data from all experimental regimes. Analysis of covariance indicated that the

slopes of the predictive regressions among groups of fish fed 8% B.W./24 h and exposed to different temperature regimes did not significantly differ from each other ($P > 0.1$). Nor were there significant differences among treatments in which fish were fed twice/24 h or fed once/24 h and exposed to an enforced 10-min bout of activity. The slope of the regression representing the otolith weight-fish weight relationship for those fish receiving a ration of 4% B.W./24 h on the cool portion of the diel cycle was significantly greater than the slopes of regressions representing fish fed 4% B.W./24 h (warm or constant) (analysis of covariance and the Student-Newman-Keuls test, $P < 0.05$). However, as mentioned earlier, the treatment where fish received a ration of 4% B.W./24 h on the cool portion of the diel temperature cycle was affected by an interruption in water supply. Only five fish survived to day 40 and may not have been representative of fish held under those conditions.

DISCUSSION

Under most environmental conditions consid-

ered during this study and reported by Neilson and Geen (1982), one otolith growth increment was formed each day. This supports the hypothesis that an endogenous rhythm influences growth increment formation. Earlier, Neilson and Geen (1982) reported that multiple feedings within a 24-h period resulted in the formation of >1 increment/24 h. We suggested that this resulted from the interaction of an endogenous diel rhythm of increment production and some regularly recurring environmental event. Data presented here are consistent with that view, as increased feeding frequency, exposure to a warm/cool temperature cycle twice in 24 h and an enforced increase in fish activity were all associated with an increased rate of increment formation. The effects of at least some of these environmental events on otolith microstructure may be mediated through activity-induced modification of fish metabolism, which often follows a circadian rhythm (Matty 1978). If otolith growth increment production follows a circadian rhythm that is sometimes overlain by environmental events, it seems reasonable to assume that fish may produce one or more growth increments but not less than one every 24 h. In our studies, *O. tshawytscha* alevins and fry produced one or more growth increments every 24 h, a result consistent with most earlier studies. Even when fish were exposed to light and temperature stimuli with periods >24 h, Campana and Neilson (1982) reported that only one increment was formed every 24 h.

Diel water-temperature fluctuations were not required for otolith increment production in *O. tshawytscha*. However, cyclic changes in temperature with a 24-h periodicity apparently result in differences in the appearance of otolith growth increments (Fig. 2). The deeply etched portion of the increments is significantly wider in otoliths of fish taken from a diel water-temperature regime than those from fish held in water of constant temperature. Mugiya et al. (1981) concluded that the deeply etched portions of goldfish, *Carassius auratus*, otoliths have a relatively high concentration of protein relative to calcium carbonate. Degens et al. (1969) suggested that the deposition of the organic matrix is not readily modified by environmental events. If these results are applicable to salmonids, the greater contrast in otoliths of fish reared under a diel temperature regime may result from changes in the rate of calcium carbonate deposition. However, the presumed change in composition and structure of daily growth increments produced under various en-

vironmental conditions does not affect the increment width-fish growth relationship illustrated in Figure 8.

Interactions between ration level and time of feeding with respect to the 24-h temperature cycle affected mean increment width. Ration level as a single factor influencing increment width was not significant. However, the interaction between temperature and ration on increment width was not significant suggesting higher calcium carbonate deposition on the otolith when temperatures were elevated at time of feeding. In a two-way comparison with ration level and feeding frequency (water temperature was constant), increment width was affected by feeding frequency but not by ration level. This agrees with the results of Neilson and Geen (1982) who showed that the rate of increment production is affected by feeding frequency.

Mean increment width reflected fish growth under a variety of water-temperature and ration regimes (Fig. 8). However, different equations described increment width-growth relationships under conditions that produced 1 increment/d or >1 increment/d (Fig. 8). The extent to which increment width data can be used to predict instantaneous growth rates in natural populations remains to be examined.

Increment widths can provide an indicator of environmental changes and consequent alteration of growth rates. However, such changes, at least under laboratory conditions, did not occur rapidly (Fig. 6). These data suggest that at least 3 wk would be required before the change in increment width would be statistically detectable.

Our data indicate that otolith weight-fish weight regressions are similar under a range of experimental conditions suggesting that otolith growth in salmon fry is closely coupled to fish growth. Marshall and Parker (1982) also reported that differences in ration and water temperature did not significantly affect slopes of otolith size-fish size regressions among fed sockeye salmon, *O. nerka*, fry. Exceptions to the isometric growth relation between fish size and otolith size have only been observed in recently hatched salmonid alevins (Neilson unpubl. data) and in starved *O. tshawytscha* fry. Fry deprived of food for 19 d continued to form daily growth increments. Assuming fish dry weight did not increase over this period, then the slope of the otolith weight-fish weight regression would probably be greater than for fed fish. Marshall and Parker (1982) also reported continued otolith growth in *O. nerka* fry

over a 2-wk starvation period. Evidently continued otolith growth in starved fish resulted from the metabolism of stored energy reserves.

Estimates of food consumption indicated that fish held under diel cyclic temperatures and fed 8% B.W./24 h consumed significantly more food per gram of fish when the food was offered during the warm period (t-test, $P < 0.01$). No differences in food consumption were noted in fish receiving a 4% B.W./24 h ration on either the warm or cool portion of the diel water-temperature regime (t-test, $P > 0.05$). It is likely that fish were not satiated at this ration under either water-temperature regime. Under the high ration, fish were satiated even when the food was offered during the cool period of the water-temperature cycle. Additional consumption occurred only if food was offered during the warm portion of the diel temperature cycle. The additional food consumption was associated with increased growth rates. It is not clear whether the increased growth was simply a response to differences in food consumption or also reflected enhanced efficiency of food utilization in fish exposed to cyclic temperatures similar to that described by Brett (1979) and Biette and Geen (1980). Differences in growth rate of fish fed 4% B.W./24 h strongly suggest more efficient food utilization in fish exposed to a cyclic temperature regime. Food consumption did not differ although growth rates (and increment widths) are significantly greater.

Given that water temperature and food consumption are considered the most important features of fishes' environment affecting their growth (Paloheimo and Dickie 1966), it is not surprising that water-temperature regimes and ration levels influence otolith growth increment production. Our findings and those of English (1981) suggest that interpretation of prey abundance and feeding success from otolith microstructure data may be masked by relatively small changes in water temperature. Workers attempting to quantify fish growth with respect to ration size through examination of otolith microstructure should be aware of the effects of water temperature documented here and design studies accordingly.

ACKNOWLEDGMENTS

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