RING DEPOSITION IN THE OTOLITHS OF LARVAL PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

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ABSTRACT

The first normal ring in the sagittae of Pacific herring, *Clupea harengus pallasi*, larvae is deposited at the age of complete yolk absorption. The rates of deposition of subsequent rings in four groups of larvae that were fed daily ranged from 0.12 to 0.96 rings per day, and only two of the four groups had a daily pattern. Larvae that were starved from hatch deposited one normal ring on day 6 posthatch, but all ring deposition stopped thereafter. The starvation of subgroups of larvae after 7 days of feeding and after 25 days of feeding produced deposition rates that were not significantly different from those of the parent feeding groups. The average rates of normal ring deposition were positively correlated with the average rates of growth in length. Daily ring deposition in herring larvae <20 mm long occurs in populations with an average growth rate equal to or higher than 0.36 mm per day.

Rings or increments in the otoliths of fishes have been used to age wild larvae of several species (Ralston 1976; Kendall and Gordon 1978; Methot and Kramer 1979; Townsend and Graham 1981; Lough et al. 1982; Victor 1982). This method has two assumptions: 1) The first ring is deposited at a fixed age in each species, and 2) the rate of ring deposition is constant at 1 ring/d. Evidence from studies of ring deposition in enclosure-reared larvae of the Atlantic herring, *Clupea harengus harengus*, (Geffen 1982; Lough et al. 1982); northern anchovy, *Engraulis mordax*, (Brothers et al. 1976); and English sole, *Parophrys vetulus*, (Laroche et al. 1982) indicates that these two assumptions may not be true in first-feeding larvae that are starving or growing slowly. The deposition of subsequent rings may be significantly <1 ring/d. This paper reports that the first ring is deposited at a fixed age in herring larvae and that this age is coincidental with the age at complete yolk absorption. It also confirms that the subsequent rate of deposition is not always daily but that it is positively correlated with the rate of growth in body length.

MATERIALS AND METHODS

Experimental Groups

The batch experiments reported here were part of a research program on culturing Pacific herring larvae. Several different container sizes, temperatures, and prey types were employed (Table 1). Six groups of Pacific herring larvae were reared from the egg: Four were fed daily from hatch, one was starved from hatch, and one was terminated 3 d after hatch before food was offered. Two additional starving groups were formed from subgroups that were removed from feeding tanks after 7 d of feeding and after 25 d of feeding and then starved to death.

TABLE 1.—The experimental groups of Pacific herring larvae and their rearing conditions.

Group	Tank volume (l)	Rearing Temperature (°C)	Feeding treatment	Food organisms
1980A	50	12.1	fed from day 2	*Artemia*
1980B	50	12.1	starved from day 7	none
1980C	50	12.1	starved from hatch	none
1980D	50	7	starved from hatch	none
1981A	1,000	8-9	fed from hatch	*Artemia*, plankton
1981B	2,000	9-10	fed from hatch	plankton
1982A	25	8-9	fed from hatch	*Artemia*
1982B	25	8-9	starved from day 30	none

Rearing Conditions

Three groups, 1980A, 1980C, and 1980D, were raised from eggs in 50 l circular aquaria in April-June 1980. The eggs were laid on the walls of a holding tank by adult herring that had been captured in the Strait of Georgia by personnel of the Pacific Biological Station, Nanaimo, B.C. Therefore, the eggs came from the lower east coast stock (Taylor 1964). After 14 d incubation at 7°C, the eggs were hatched and the larvae of 1980A and 1980C were transferred to the rearing aquaria. The mean (±1 SD) temperature of these tanks during the rearing period was 12.1° ± 0.9°C. The 1980A group was fed from hatch to the

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end of the experiment, and the 1980C group was starved from hatch to death. The 1980D group was reared at 7°C for 3 d, before it was accidentally destroyed. A fourth group, 1980B, was formed from a 1980A subsample and was placed in its own 50 l aquarium after 7 d of feeding and then starved for 5 d.

Two groups, 1981A and 1981B, were reared in April-May of 1981 at the Bamfield Marine Station, Bamfield, B.C. The eggs came from spawn laid on *Fucus* spp. in the intertidal zone of Toquart Bay, Barkley Sound, B.C. Therefore, the eggs came from the lower west coast stock. The first population, 1981A, was raised in a 1,000 l circular, flow-through aquarium. The water temperature rose gradually from 8° to 9°C over the rearing period. Food was added daily. Group 1981B was reared in a culture chamber suspended in Bamfield Inlet. The chamber, a 2,000 l circular tank (Marliave 1981), floated at the surface of the Inlet. Wild plankton was swept through louvres on one side of the chamber by tidal currents and was trapped in the chamber where it served as food for the larvae. During the first 3 wk , no herring larvae was in the plankton from the Bamfield Inlet, so the tank population was not contaminated with wild herring. The surface water temperature of the Inlet over the rearing season was 9°-10°C.

One group, 1982A, was reared from eggs in the laboratory at the Bamfield Marine Station, April-May 1982. The group grew in a 25 l rectangular aquaria cooled to 8°-9°C. The eggs came from spawn laid on eelgrass, *Zostera marinus*, in the intertidal zone at the head of Bamfield Inlet and, therefore, came from the lower west coast stock. The fish were fed from hatch to age 30 d, and then the survivors were moved to another tank of the same size where they were starved for 8 d. This subgroup was named 1982B.

The lighting for all the laboratory groups was fluorescent and was on a 10-h light: 14-h dark cycle. This cycle was cued to the natural photoperiod with light sensors. Water in all of the tanks, except 1981A and 1981B, was gently aerated with an airstone, and about one-third of the volume was replaced daily with fresh seawater. Dead organisms and feces were daily siphoned off the floor in all tanks, except 1981B which did not accumulate wastes because its floor, drilled with over 1,000 small holes, was self-cleaning.

Hatching

All larvae in any single group were hatched within 24 h of each other. In 1980, hatching was stimulated by scraping the eggs off the wall of a holding tank. In 1981 and 1982, hatching was stimulated by exposing late-stage eggs to air for 15 min. The exposure caused an explosive hatch when the eggs were returned to seawater. The egg masses were removed from the tanks <24 h after hatching began.

Food

Food for three of the four fed populations consisted of freshly hatched *Artemia* nauplii. One of the feeding groups, 1981B, fed exclusively on wild plankton swept into the chamber by tidal currents. Another group, 1981A, was raised on a diet of *Artemia* nauplii supplemented with wild plankton captured with a plankton net from the surface of Bamfield Inlet. In all feeding groups, food was first supplied either at hatch or before the second day after hatch, the day when Pacific herring larvae first begin to exhibit feeding behavior. Both the *Artemia* nauplii and the wild zooplankters were attracted to the overhead light, and they tended to cluster in a patch at the surface of the water. Enough food organisms were added each day to the feeding groups to maintain the patches at all times so that the larvae of these groups had the opportunity to feed at will at any time. It is not known whether the 1981B larvae in the culture chamber had a similar opportunity, but the relatively high growth rate of this group indicates that food was abundant.

Absence of food organisms in the water of starving groups was ensured by filtering seawater through a layer of glass wool before it was added to a tank. Samples of filtered water were examined under a microscope to verify the absence of food organisms.

Samples

Samples of 10-18 larvae were taken from each of the groups at intervals of 2-20 d. In 1980 the fish were frozen at −10°C, and in 1981 and 1982 they were preserved in 37% isopropyl alcohol. The standard length was measured from the tip of the snout to the end of the notochord with the vernier scale of a compound microscope. Some of the larvae were measured live before preservation, stored individually, and then measured again 1-6 mo later. Freezing caused a mean (±1 SD) percent shrinkage of 6.3 ± 3.5 ($n = 26$), and isopropyl alcohol caused a mean (±1 SD) percent shrinkage of 0.04 ± 3.2 ($n = 97$) which was not significantly different from 0% shrinkage ($t = 0.0124$, df = 96, $P > 0.9$). An examination of the individual percent shrinkages showed no trend with live standard length. Frozen lengths were corrected to live lengths by multiplying by the factor

1.063. Alcohol-preserved lengths did not require correction.

Ring Counting

After extraction from the skull the sagittae were placed on a glass slide under immersion oil; their diameters were measured with an ocular micrometer. Sagittae are slightly flattened spheroids in young larvae and tend to become more oval in shape as the fish grows. The diameter measured was always the longest axis of the otolith. The sagittae were photographed at 400-1,000×, the developed film was projected on a screen, and the rings were counted. A single ring consisted of a dark band and an adjacent light band. All rings, no matter how faint, were counted in order to avoid observer bias towards a daily ring pattern. Two classes of rings were observed: 1) A group of 1-5 thin, faint rings clustered about the nucleus surrounded by 2) wider, darker rings that composed the majority of the rings in most larvae. In some sagittae the second class of rings were separated from the first by a distinct ring which may have been a check deposited in response to the exhaustion of the yolk. The two classes could not always be clearly distinguished, particularly in slow-growing fish. The first class corresponds to Geffen's (1982) "yolk sac" rings and the second to her "normal" or "regular" rings. In this paper the first class will be unnamed for two reasons: 1) Most of the rings were found in the larvae that had completely absorbed their yolk, so they were not exclusively yolk-sac rings, and 2) it has not been established that the two classes of rings are fundamentally different from each other, so the introduction of new terminology is premature. Geffen (1982) defined a "first heavy ring" that was found between the outer margin of the nucleus and the first normal ring. This term has not been used because the first normal ring was not always distinguishable from subsequent normal rings on the basis of width or darkness.

Each sagitta was counted three times, and the mean of the three counts was taken as the final count of that sagitta. The ring count of a fish was the mean of the final counts of its two sagittae. The mean (±1 SD) difference in final counts between sagittae from the same fish was 1.3 ± 1.4 which was not significantly different from zero ($t = 0.9028$, df = 148, $0.4 > P > 0.2$). The sagittae of 21 large larvae (live length range = 14-29 mm, age range = 20-54 d posthatch) selected at random from several groups were photographed and then fixed to a glass slide with cyanoacrylate glue and ground to the midplane with metallic lapping paper. They were rephotographed and recounted. The mean (±1 SD) difference was 1.1 ± 2.0 which was not significantly different from zero ($t = 0.5273$, df = 20, $0.5 > P > 0.9$). Inspection of the data revealed no trend of the difference with age or with the ring count of the nonground sagittae.

Data Analysis

The average rates of ring deposition and of growth in length were calculated as the slopes of linear predictive regressions of mean ring number and mean length on age posthatch. The homogeneity of the variances of the means of a group was tested with Bartlett's test (Sokal and Rohlf 1969), and, if they were found to be heterogenous, each mean was weighted with its sample size divided by its variance. *T*-tests were used to test the significance of differences between the slope of a regression of mean ring number on age and 1 ring/d and 0 ring/d. *F*-tests were used in covariance analyses to test for significant differences between two slopes.

RESULTS

Growth in live standard length was positive in all groups except 1980C and 1980B, in which the starving larvae shrank (Fig. 1). There are indications that growth was curvilinear, especially in 1980A and 1981B where the growth rates between the two last sampling dates in each group were much less than the previous growth rates. However, linear growth was assumed for the purpose of obtaining average growth rates to compare with the average ring deposition rates (Table 2). Growth rate was highest in the 2,000 l culture chamber and lowest in the 25 l aquarium, and there was a positive but nonsignificant correlation between growth rate and container size in the four fed groups ($n = 4$, $r = 0.90$, $0.05 > P > 0.10$).

Thin, faint rings of the first class were found in the otoliths of most of the 1980 fish that were <14 mm long, but were not found in the otoliths of any 1981 and 1982 fish (Fig. 2). These rings may have been deposited at any time between the late embryo and the postyolk-sac stage. The only sample of otoliths

TABLE 2.—Linear regressions of mean standard length on age in 7 groups of Pacific herring larvae.

Group	y-intercept (mm)	Slope (mm/d)	SE of slope	r	No. of means	n	df
1980A	10.4	0.180	0.030	0.97	4	36	1,2
1980B	13.1	−0.004	0.019	0.19	3	20	1,1
1980C	11.2	−0.107	0.031	0.90	5	50	1,3
1981A	8.2	0.231	0.011	0.99	6	57	1,4
1981B	8.4	0.290	0.049	0.96	5	60	1,3
1982A	10.6	0.090	0.047	0.89	3	38	1,1
1982B	11.4	0.100	0.035	0.89	4	39	1,2

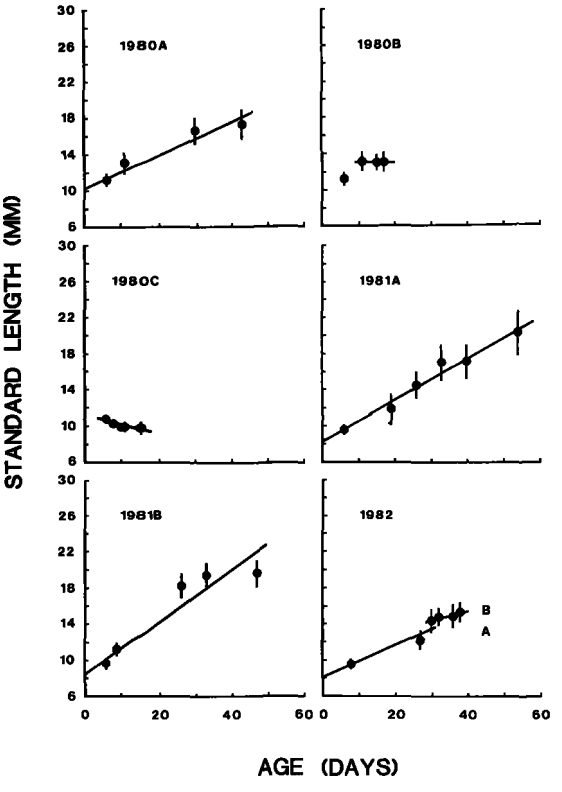

FIGURE 1.—Mean (±1 SD) live standard length at age posthatch for seven groups of Pacific herring larvae. See Table 2 for the regression equations.

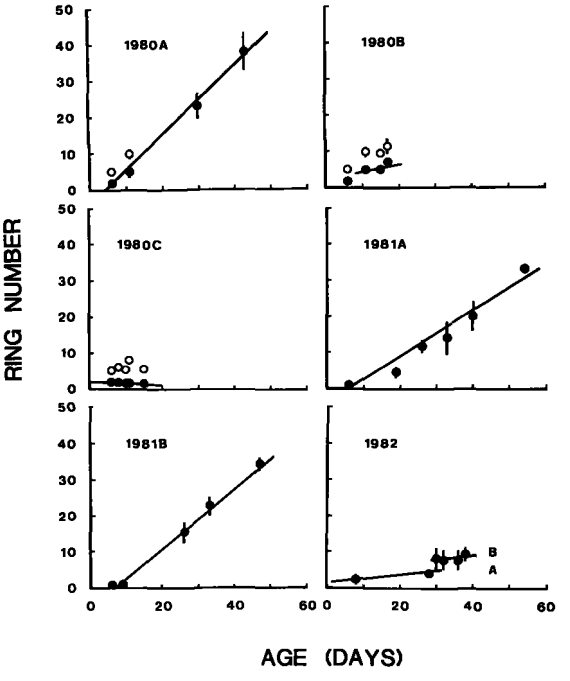

FIGURE 2.—Mean (±1 SD) ring count at age posthatch for seven groups of Pacific herring larvae. Open circles are total rings and closed circles are normal rings only. See Table 3 for the regression equations.

from yolk-sac larvae was a single sample from 1980D that had a mean (±1 SD) ring count of 5.2 ± 0.8 (n = 9) on day 1 posthatch. The rings were not observed in older, larger larvae; they may have been present but obscured by overburden over the nucleus. This phenomenon has been observed in the otoliths of larval largemouth bass, *Micropterus salmoides*, (Miller and Storck 1982). A group of 7-8 "prolarval rings" that were clustered about the nucleus at swim-up were visible for only 10-15 d afterward, because the nucleus became more opaque with age.

The first normal ring was deposited in all groups including 1980C by day 6 posthatch, the day after complete yolk absorption. This agrees well with the age at first increment of 4.5 (range = 0-9 d) found for Atlantic herring by Lough et al. (1982) and with the age of 6 d found for the same species by Geffen (1982). This indicates that herring larvae of both species do have a fixed age at first increment deposition and that it coincides with the age at complete yolk absorption.

Rates of subsequent ring deposition for the four fed groups were not all daily, and they ranged from 0.12 to 0.96 rings/d (Table 3); only two groups, 1980A and 1981B, had rates that were not significantly different from 1 ring/d ($t = 0.5772$, df = 3, $0.5 > P > 0.9$ and $t = 2.0142$, df = 4, $0.10 > P > 0.20$, respectively). The 1981A group had a rate that was significantly <1 ring/d ($t = 6.3465$, df = 5, $0.01 > P > 0.001$) but also significantly > 0 ($t = 10.8062$, df = 5, $P < 0.001$) and the 1982A group had a rate that was significantly <1 ring/d ($t = 10.0228$, df = 2, $0.01 > P > 0.001$) and not significantly >0 ($t = 1.3667$, df = 2, $0.20 > P > 0.40$).

The rate of ring deposition in 1980C, the group that was starved from hatch, was −0.05 ring/d, which was

TABLE 3.—Linear regressions of mean normal ring number on age in 7 groups of Pacific herring larvae.

Group	y-intercept (mm)	Slope (ring/d)	SE of slope	r	No. of means	n	df
1980A	−4.12	0.96	0.06	0.99	4	36	1,2
1980B	2.06	0.23	0.28	0.63	3	20	1,1
1980C	2.12	−0.05	0.02	0.83	5	50	1,3
1981A	−9.31	0.63	0.05	0.99	6	57	1,4
1981B	−5.60	0.83	0.08	0.99	5	60	1,3
1982A	1.45	0.12	0.08	0.83	3	38	1,1
1982B	4.90	0.10	0.11	0.53	4	39	1,2

not significantly different from 0 ($t = 2.2831$, df = 4, $0.10 > P > 0.20$). This indicates that the starvation of first-feeding larvae stopped ring production. The 1980B group had a rate which was not significantly different from one of 1 ring/d ($t = 2.3397$, df = 2, $0.10 > P > 0.20$) and not significantly different from a rate of 0 ($t = 0.6989$, df = 2, $0.50 > P > 0.90$) or from the rate of its parent feeding group, 1980A ($F = 5.9185$, df = 1.3, $0.25 > P > 0.50$). One reason for these results is that the 1980B group had only three data points for the regression, and the standard error of the slope was therefore relatively high: 122% of the value of the slope (Table 3). I conclude that starvation for 5 d after a feeding period of 6-7 d has no effect on the rate of ring deposition. The 1982B group had a ring depoistion rate that was not significantly different from 0 ($t = 0.7843$, df = 3, $0.40 > P > 0.50$) and which was not significantly different from the rate of its parent feeding group, 1982A ($F = 0.1352$, df = 1, 3, $P > 0.75$). I conclude that starvation for 8 d after a feeding period of about 25 d has no effect on the rate of ring deposition, at least not in 25 l enclosures.

The average ring deposition rates were significantly positively correlated with the average growth rates ($n = 7$, $r = 0.83$, $0.01 > P > 0.05$) (Fig. 3). The regression of ring rate on growth rate was:

$$\text{Ring rate} = 0.14 + 2.40\ (\text{growth rate}).$$

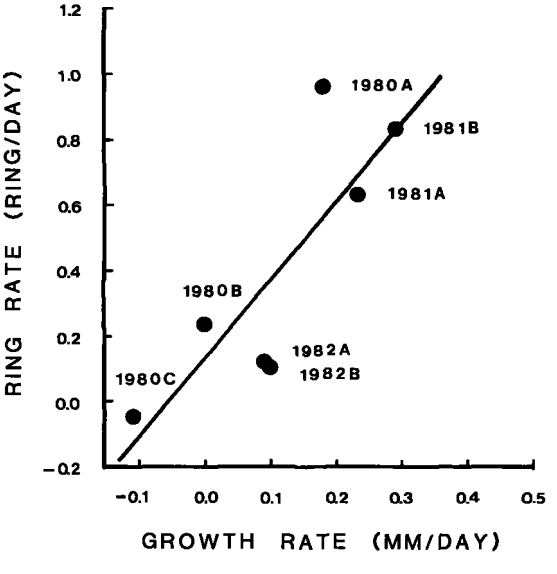

FIGURE 3.—Relationship between the average ring deposition rates and the average growth rates of seven groups of Pacific herring larvae. See text for regression equation.

The residuals of this regression were not correlated with container size, and there was no obvious relationship with prey type. However, there was a significiant positive correlation between the residuals and the mean rearing temperature ($n = 7$, $r = 0.83$, $0.01 > P > 0.02$). The midpoints of the temperature range were used as an estimate of the mean temperature (Table 1). A regression of ring deposition rate on growth rate and temperature increase the multiple r to 0.99:

$$\text{Ring rate} = -1.39 + 3.36\ (\text{growth rate}) + 0.14\ (\text{temperature}).$$

These results confirm the correlation between ring deposition rate and growth rate found for Atlantic herring larvae by Geffen (1982), who interpreted the relationship as being curvilinear and linearized it by transforming both variables with logarithms. In order to compare the two sets of data the relationship between ring deposition rate and growth rate was assumed to be linear. A covariance analysis of the slopes of the two linear regressions indicated that there was no significant difference between them at the 0.05 probability level. Data from this study and from Geffen's were pooled and a single linear regression was calculated ($n = 12$, $r = 0.85$, $P < 0.001$):

$$\text{Ring rate} = 0.17 + 2.12\ (\text{growth rate}).$$

The influence of temperature on ring deposition rate could not be compared between the two data sets because the rearing temperature for Geffen's fish was not constant over the rearing period.

Plots of fish length on otolith diameter for the seven populations were curvilinear, and the rate of growth of fish length decreased with increasing otolith diameter. Transforming otolith diameter with logarithms best linearized the data, transforming both variable with logarithms produced lower correlation coefficients in all groups. Thus length was regressed on log (otolith diameter) (Table 4, Fig. 4). An analysis of covariance that included all seven groups indicated that the slopes of the regressions were significantly different from each other at the 0.05 probability level. Inspection of the slopes and their standard errors indicated that the fed groups and 1980B had slopes of a similar value and that 1980C and 1982B had slopes of a similar value but that they were much lower than those of the fed groups. The two groups were subjected to separate covariance analyses, and in each group the slopes were found to be not significantly different from each other at the 0.05 probability level. The

TABLE 4.—Linear regressions of fish length on log (otolith diameter).

Group	y-intercept (mm)	Slope (mm/μm)	SE of slope	r	n	df
1980A	−5.76	11.57	0.49	0.97	36	1,34
1980B	−4.54	10.77	3.17	0.73	12	1,10
1980C	2.73	4.40	2.10	0.28	52	1,50
1981A	−7.50	13.36	0.43	0.97	57	1,55
1981B	−5.50	12.14	0.46	0.96	60	1,58
1982A	−7.24	12.73	1.45	0.83	38	1,36
1982B	4.82	5.94	1.65	0.59	27	1,25

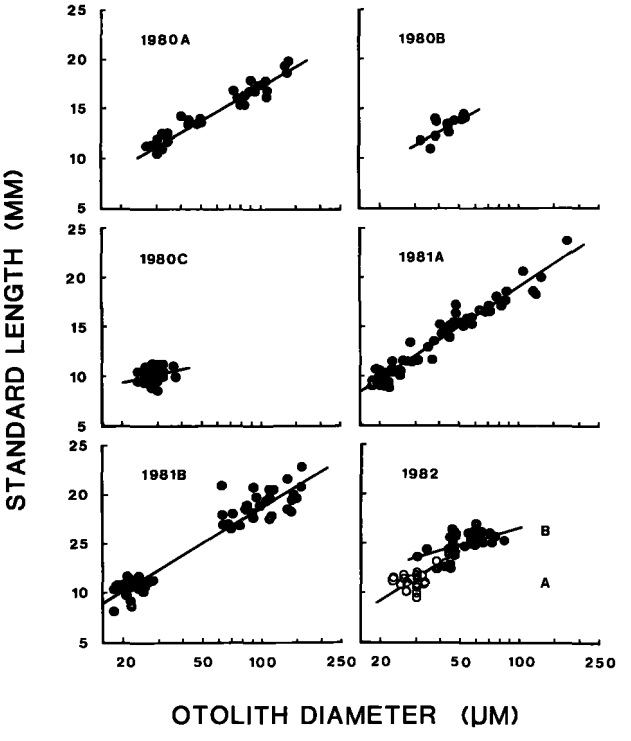

FIGURE 4.—Relationship of fish length to log (otolith diameter) for seven groups of Pacific herring larvae. Open circles in 1982 are 1982A and solid circles are 1982B. See Table 4 for the regression equations.

slope of the 1980B group was not significantly different from either the feeding groups or the starving groups because of its high standard error. The four fed groups were pooled to give a single regression ($n = 191, r = 0.95, P < 0.001$):

$$\text{Fish length} = 30.90 + 12.49 \log (\text{otolith diameter}).$$

The three starved groups could not be pooled because of the different growth and feeding histories of each group.

DISCUSSION

The first class of thin rings was found in the otoliths of Atlantic herring larvae by Geffen (1982) and by Lough et al. (1982); they have also been described in the otoliths of larval turbot, *Scopthalmus maximus*, (Geffen 1982) and Arcto-Norwegian cod, *Gadus morhua*, (Gjøsaeter and Tilseth 1982). Increments have also been found inside the nucleus in Atlantic herring (Lough et al. 1982), in three species of the genus *Lepomis*, and in the Mozambique mouthbreeder, *Tilapia mossambica*, (Taubert and Coble 1977). In at least one species of fish, the mummichog, *Fundulus heteroclitus*, these nonregular rings are regular daily rings that are deposited before hatching (Radtke and Dean 1982). The relationship between the number of nonregular rings, the age and size of the fish, and rearing conditions can only be determined with more experimental work, particularly on the sagittae of embryo and yolk-sac herring.

Presence of the thin rings in the 1980 fish and their absence in the 1981-82 fish was not the result of genetic differences between the eggs of the lower east coast stock and the eggs of the lower west coast stock. The sagittae of many small (length range = 9-20 mm) wild herring larvae captured from Bamfield Inlet in 1981 and 1982 were found to have several thin, faint rings around the nucleus (McGurk unpubl. data). It seems more reasonable to hypothesize that

the difference arose from factors that have already been reported to affect the rate of deposition of normal rings. These factors include temperature (Taubert and Coble 1977; Marshall and Parker 1982), short-term temperature fluctuations (Brothers 1978), and feeding activity (Uchiyama and Struhsaker 1981; Neilson and Geen 1982). Lough et al. (1982) suggested that the first class of thin rings were related to the inability of first-feeding larvae to meet their metabolic energy demands during the transition from yolk to exogenous food. This argument implies that the 1980 herring larvae were less able to capture sufficient food during first feeding than the 1981-82 larvae. However, this hypothesis does not explain the presence of the faint rings in the 1980C larvae that were starved from hatch.

Results of this study confirm the observations of Geffen (1982) that the rate of normal ring production is not always daily in young herring larvae and that it is positively correlated with the rate of growth in body size. The correlation means that normal rings cannot be used with confidence to age wild herring larvae less than about 20 mm long, unless the average growth rate of the population is known to be higher than about 0.36 mm/d (calculated from the regression of ring deposition rate on growth rate for Pacific herring only). Growth of larval fishes is influenced by several factors: temperature (Kramer and Zweifel 1970), food density (Haegele and Outram 1978), and container size (Theilacker 1980). The tendency for larger containers to support higher growth rates in the four fed groups of this study may explain why only two of the four had a daily ring pattern. The correlation implies that, if the rate of growth is slowed or stopped by starvation after a period of feeding, then the rate of ring deposition should also slow or stop. The two experimental groups that were treated in this manner did not produce rings at rates that were significantly different from those of their parent feeding groups. This suggests that a starvation period >5-8 d is necessary in order to demonstrate a statistically significant effect. Larger rearing containers are also recommended to produce greater contrast in growth rates between feeding and starving fishes.

Container size, temperature, or prey size may possibly have additional effects on the rate of ring deposition apart from that which is explained by growth rate. Temperature does explain some of the residual variance of the ring deposition rate-growth rate regression. However, published evidence on effect of constant temperature on ring deposition does not support the hypothesis that higher temperatures produce more increments. For example, Neilson and Geen (1982) found no difference between the number of increments produced by juvenile chinook salmon, *Oncorhynchus tshawytscha*, reared at 5.2°C and at 11.0°C. The effects of such environmental factors as light, temperature, and prey type on the ring pattern of herring sagittae can only be determined with a well-controlled experimental study.

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