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The Propagation of Cod *Gadus morhua* L.

A RELATIONSHIP BETWEEN THE NUMBER OF GROWTH INCREMENTS ON THE
OTOLITHS AND AGE OF LARVAL AND JUVENILE COD, *Gadus morhua* L.

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ABSTRACT

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A study of the relationship between the number of growth increments on the otoliths and age was based on larval and juvenile cod, *Gadus morhua* L., from laboratory and pond reared populations.

Lapilli were larger than sagittae at hatching and remained so for approximately 25 days. Sagittae became significantly larger than lapilli at the end of the larval period. Major growth trends of the otoliths corresponded to the growth in standard length reported for the populations. Marked elongation along the anteroposterior axis and formation of marginal lobes started immediately prior to metamorphosis.

Comparison of otolith diameter and the diameter of the first, usually very distinct, growth increment indicated that zone formation started somewhat before hatching. The diameter of the first increment was higher in lapilli than in sagittae.

The number of growth increments, as recorded using light microscopy, did not appear to be a constant function of larval age between hatching and metamorphosis at age 35-40 d. The larger of the otoliths at any given age, either the lapilli or the sagittae, showed higher increment numbers than the smaller. There was some indication that the rate of increment formation was related to the individual growth rate of the larva in this period.

In addition to the primary increments recognized in the larval otoliths, composite broader zones appeared after metamorphosis. These broader zones were on the average formed daily at least until 140 days after hatching. The frequency of deposi-

tion of these structures did not appear affected by individual growth rate variation.

INTRODUCTION

Studies of the early life history of cod, *Gadus morhua* L., and other species have always been limited by the lack of adequate methods for determining the exact age of individual larvae or juveniles. Knowledge of age forms an essential basis for studies of the recruitment mechanisms of natural fish stocks; it is required for estimating growth and mortality rates as well as for obtaining knowledge of the age structure of a cohort in its first year of life. Traditionally, morphological and morphometric data, known from experiments designed to study developmental rates under controlled conditions, have been used to estimate an approximate age. This approach may only seldomly give very reliable estimates, since it is highly dependent on knowledge of temperatures experienced by the larvae in the past and since precision is acceptable for most uses within a usually very narrow age range.

Observations indicate that otoliths of larval and juvenile fish contain a number of growth increments corresponding to the average age, measured as the number of days since an early stage in their life history (Pannella, 1971, 1974; Brothers et al., 1976; Taubert and Coble, 1977; Barkman, 1978; Schmidt and Fabrizio, 1980; Radtke and Dean, 1982; Victor and Brothers, 1982; and others). Counting growth increments should then form the basis for potentially very precise and reliable ageing in cases where other methods prove inadequate.

A routine application of increment counting for age determination rests on several assumptions, among others the following:

a) increment formation is initiated at approximately the same age in all larvae.

b) increment deposition rate following this age equals 1 increment per day ($\text{incr} \cdot \text{d}^{-1}$) in the age interval studied, is

independent of growth rate of the fishes within wide limits and is unaffected by the environmental variability likely to be found in the natural habitat.

Some studies have shown that these assumptions may not always be valid, and hence that for some species there may be a definite need for assessing the limitations inherent in the method. Thus, age at first increment formation may vary somewhat (Penny and Anderson, 1981; Laroche et al., 1982), deposition rate may deviate from $1 \text{ incr} \cdot \text{d}^{-1}$ even during periods of positive growth (Blacker, 1975; Pannella, 1980; Geffen, 1982; Neilson and Geen, 1982), and structural growth rate variation within normal levels may affect deposition rate (Geffen, 1982).

Previous studies of cod for the purpose of validating increment counting on otoliths as an ageing method covered the very early and the late parts of the larval period (Radtke and Waiwood, 1980; Gjørseter, 1981; Gjørseter and Tilseth, 1982). The first two studies were based on larvae of known age reared in the laboratory, in a large outdoor basin or a natural pond, whereas the third included wild larvae staged according to morphological criteria. The results indicated that increment formation proceeded at a general rate of $1 \text{ incr} \cdot \text{d}^{-1}$, thus supporting Pannella's (1971) suggestion that the observed ~ 360 primary units in otoliths (sagittae) of young cod represented daily growth increments.

The present study was meant as an attempt to test the hypothesis of daily increment formation over a wider age interval. Assessment of the magnitude of deviations from this pattern was made in order to evaluate how reliable increment counting can be expected to be for ageing larvae and juveniles from natural populations. I was able to relate the number of increments to real age through the supply of larvae from rearing experiments in a natural pond supplemented by groups kept in the laboratory.

MATERIALS AND METHODS

Samples of larval and juvenile (post-metamorphic) cod were

obtained from populations stocked in a 60.000 m³ natural pond at Austevoll, Western Norway in 1980 and 1981 (Øiestad and Kvenseth, 1981; Kvenseth, 1983; Kvenseth and Øiestad, 1984). The mean time of hatching was known in both years. In 1981 hatching occurred within a period of 5 days (70% of larvae within ± 1 day of the day of 50% hatching), and the samples contained larvae of mean age of 8-140 days after hatching. In 1980 the range in hatching time was wider (8-9 days) and the age-range and size of samples less adequate. Thus, most results are based on the 1981 samples.

Since yolk sac larvae were not included in the pond samples, eggs from stripped females were incubated at 5°C (± 1 °C) and a photoperiod of 12 h of light and 12 h of darkness (fluorescent lamps) in 2 l cylindrical beakers. Sorting at the onset of hatching provided groups of larvae hatched within a 24 h period for use in the otolith studies. Development with regard to yolk absorption, gut differentiation and body growth (standard length and myotome height) was as described by Ellertsen et al. (1980). No food was offered, and mass starvation occurred after 11-12 days.

70 - 95% ethanol (pH \sim 9 due to addition of NaOH) was used as the preservative for fish of all life stages. Prior to dissection, the larvae were immersed in a drop of distilled water on a clean glass slide. Extraction of larval otoliths was done with insect needles mounted on wooden rods working at 25-40 X magnification under a dissecting microscope (reflected light, black background). Juvenile otoliths were most easily found after a frontal section of the head just deep enough to expose the brain had been made.

The otoliths were identified as sagitta, lapillus and asteriscus according to their position in the otic organ. All six otoliths were extracted when possible, although most attention was focused on the two larger, the lapillus (utricle otolith) and the sagitta (sacculus otolith).

Larval otoliths were dried at 60°C for three or more hours, mounted in a clear synthetic mounting medium (EPON, Pro-Texx), covered with a coverslip and left to harden overnight (60°C for EPON, room temperature for Pro-Texx). Otoliths from

older larvae (SL > 7 - 8 mm) were mounted with their concave sides pointing upwards.

Sagittae from juveniles required grinding to expose increments in their central region. Sagittal, frontal and transverse sections, following Pannella (1980), were made of selected sagittae to facilitate comparison. Transverse sections at the focal level appeared to give the most complete picture of the total growth of the otolith and were chosen for routine use. Corresponding sections were described by Steffensen (1980).

Whole sagittae were embedded in rectangular blocks of EPON. A dentist's drill equipped with fine-grit finishing discs (3M Sof-Lex) was used for grinding, working under a dissecting microscope. Each otolith was ground from the anterior tip towards the plane of the focus and mounted with the ground surface against the slide. After hardening, a transverse section could be obtained by grinding from the posterior tip towards the plane of the glass slide. The ground sections were finally mounted in EPON and covered with a coverslip.

Making measurements on otoliths using light microscopy is difficult due to their shapes and structural properties. Larval lapilli and sagittae are almost hemispherical and thus appear circular. A simple measurement of their longest diameter was found acceptable for describing their growth prior to metamorphosis (SL ~ 12 mm). Juvenile sagittae were measured before grinding along their longest anteroposterior and dorsoventral axes.

A ring appearing close to the nucleus was usually markedly more prominent than those following and was chosen as the starting point when counting. The ring was classified as "distinct" or "indistinct", and measured as the longest diameter drawn through the nucleus.

Two kinds of increments were defined for larval and juvenile otoliths respectively. Larval otoliths contained increments consisting of a narrow dark band and a wide light band, similar and probably corresponding to "discontinuous" and "incremental" zones (Tanaka et al., 1981). Juvenile sagittae contained wider composite growth increments, each consisting of 1 - 5 of the narrower units seen in the larval otoliths.

The number of increments on larval otoliths was accepted as the maximum number of single concentric units (as defined above) from the first increment to the edge. In juvenile sagittae the maximum number of composite bands from the central region to the edge was registered. (The central region is not equivalent to the nucleus, rather to the part of the otolith formed prior to metamorphosis).

RESULTS AND DISCUSSION

Counting error, exclusion of otoliths

Initial tests demonstrated that a standardization of the counting procedures was necessary to obtain acceptable correspondence between different persons' counts of increments on the same otoliths (Bergstad, 1983). Defining increments according to the principles mentioned and restricting the choice of magnification to 400 X for all counts significantly reduced variation between counters. 170 larval otoliths were counted by two persons independently. The otoliths were presented in a random sequence (with respect to age) and larval age was not known to the counters. In 65% of the counts the deviation was less or equal to one increment, in 83% less or equal to two increments while 92% of the counts differed by three or less increments. A randomly selected group of otoliths was counted by a third person who obtained results agreeing well with those obtained by the main counters.

All sagittae from juveniles (sections) were counted by two persons independently. Deviations varied greatly around a mean of 9 - 10 increments (10 - 20% of the mean number of composite zones). Large deviations could usually be explained by less than optimal quality of the sections, ill-defined transition between larval increments (central region) and the first broad increments or obvious misinterpretations of structures in parts of the otoliths.

Otoliths having abnormal shape, those broken through handling at any point of the preparation and those in which poor

separation made increments visible in parts of the radius only or made deviation between independent counts exceed certain limits were excluded from further studies. Limits were set according to the number of increments estimated from two counts. Thus, when the estimated number was less than or equal to 15, maximum acceptable deviation was 1 increment, whereas when the estimated number was higher no more than a deviation of 2 increments was accepted. In cases where deviations exceeded these limits, the otoliths were counted again, this time allowing discussions between the counters.

Around 1.5% of the otoliths were classified as abnormal. Of otoliths from the pond larvae (1981) not excluded due to abnormality or breakage, 15% were excluded since their quality was too poor to allow any estimate of increment number to be made. In addition, 8% were omitted since deviations exceeded limits. (It should be noted, though, that exclusion of an otolith through this procedure did not necessarily mean exclusion of a larvae, since other otoliths of the same individual often showed acceptable quality).

It was found systematically that otoliths from laboratory kept larvae had less distinct increments than those from larvae from the pond, agreeing with observations made by others (Geffen, 1982; Bailey, 1982; Laroche et al., 1982). This, together with their smaller size often leading to fracture during handling, led to higher counting error and higher numbers of omitted otoliths from these groups.

Counts of composite zones in juvenile sagittae were made on the section having the best quality, thus only one otolith per fish (either the left or the right sagitta) was treated. The section was discussed when deviations between the counts by two persons exceeded 15 increments (4 out of 22 sections from fish older than 90 days). All sections were accepted after common treatment since obvious misinterpretations fully explained the extensive initial deviation.

Development and growth of otoliths

The embryogenesis of the otoliths of cod has been described

by Dale (1984). All larvae hatched with planoconvex lapilli and sagittae, whereas the asterisci were either very small or not formed at this stage. The lapilli were always larger than sagittae at hatching and until a standard length of approximately 6 mm was reached (age \sim 25 days in this case) (Table 1). In the later parts of the larval period, the sagitta became the larger and gradually became elongated along its anteroposterior axis. At metamorphosis the first marginal lobes appeared, and at age 90 days it already resembled the adult sagitta. The lapillus and the asteriscus similarly attained the shapes seen in adults following metamorphosis.

Both the larger otoliths grew slowly the first 15-20 days compared with the rates seen in the late larval period and after metamorphosis. This corresponded with the changes in body growth rate of the larvae as reported by Kvenseth (1983) and Øiestad and Kvenseth (1981).

Formation of first increment

A prominent increment close to the nucleus was present on almost all otoliths from the pond larvae (91 out of 98 larvae had this characteristic on at least 3 out of 4 otoliths). This may correspond to a distinct ring observed by transmission electron microscopy of otoliths from newly hatched larvae (Dale, 1984). Increments were found closer to the nucleus in only 2 - 3 cases which indicated that the heavy ring usually marked the initiation of increment formation.

The first increment was not always as well defined on the otoliths from the laboratory larvae. Only about 60% of the larvae showed this characteristic. This may reflect differences in rearing conditions.

In the laboratory larvae the fraction of larvae having a distinct increment did not increase with age from hatching towards the end of the yolk sac period, nor did its position relative to the focus show much variation. Also, otoliths with or without a distinct first ring showed the same number of increments at yolk absorption. The diameter of the otoliths at hatching, as indicated in Table 2 and as measured by Radtke and

TABLE 1

Mean diameter of otoliths related to mean age. s standard deviation, n - no. of larvae

a) Cod larvae from pond and laboratory groups

Age (days)	Group	Mean otolith diameter (μm)					
		Lapillus			Sagitta		
			s	n		s	n
0	Lab.	28.4	1.4	9	20.7	1.7	10
2	"	29.8	0.5	5	21.4	0.9	5
4	"	30.8	1.6	5	23.6	2.2	5
6	"	32.5	2.1	5	26.0	1.2	5
8	Pond(81)	33.4	1.7	11	24.6	1.8	11
10	"	32.7	2.0	14	24.3	2.6	14
12	"	33.5	1.6	8	25.9	1.6	8
15	"	36.5	3.1	14	27.9	3.3	14
18	"	38.7	1.0	15	32.5	1.2	14
20	"	42.8	1.9	12	38.8	3.3	12
24	"	50.5	-	4	54.0	-	4
26	"	59.2	-	3	62.5	-	4
31	"	63.3	7.6	13	99.8	13.9	12
33	"	69.0	-	2	127.0	-	2

b) Juveniles of cod from pond experiments, 1981

Age (days)	Mean diameter of sagitta (mm)					
	Anteroposterial	s	n	Dorsoventral	s	n
38	0.18	-	3	0.15	-	3
40	0.22	0.03	5	0.20	0.05	5
47	0.39	0.08	6	0.28	0.04	6
93	3.23	0.25	10	1.43	0.11	10
124	4.14	0.46	5	1.82	0.12	5
140	5.09	0.74	7	2.22	0.36	7

TABLE 2

a) The mean diameter of the first distinct increment on otoliths from cod larvae from pond and laboratory groups. \bar{D} - Mean diameter (μm , all ages), s - standard deviation, n - no. of otoliths

Group	Sagitta			Lapillus		
	\bar{D}	s	n	\bar{D}	s	n
Pond (1980)	16.1	1.9	29	20.9	2.2	29
Pond (1981)	16.1	2.1	167	21.1	2.3	171
Lab. (1)	18.3	2.0	15	21.9	2.1	25
Lab. (2)	16.9	2.3	26	23.5	1.8	23

b) The mean diameter of the otoliths at hatching. Cod larvae from laboratory groups. Symbols as in a)

Group	Sagitta			Lapillus		
	\bar{D}	s	n	\bar{D}	s	n
Lab. (1)	20.7	1.7	10	28.4	1.4	9
Lab. (2)	22.2	2.2	9	30.6	1.7	9

Waiwood (1980), appears always somewhat longer than the diameter of the first increment. This suggests that the first increment (be it distinct or not) is formed immediately prior to or at hatching as also found by Radtke and Waiwood (1980). It should be noted, though, that some lapilli showed a distinct increment followed by 2 - 3 increments at hatching, which probably means that the formation of the first ring is independent of the process of hatching.

The regular occurrence of a distinct structure corresponding to the end of yolk absorption, as suggested by Radtke and Waiwood (1980), was not supported by my observations of laboratory and pond larvae.

Increment number vs age - Larvae

No systematic difference between left and right otoliths of the same kind, with regard to size or the number of increments, was found (Bergstad, 1983). Thus, the mean of counts for the two was used as a basis for calculating the age-group averages shown in Fig. 3 and Table 3. From the laboratory larvae, only one otolith of each kind was examined (Fig. 1).

No direct correspondence between the mean number of increments and mean age was found. This was true in both the laboratory kept and pond reared groups. The only exception was the average number of increments on sagittae from 31 days old larvae.

A deviation from daily increment deposition in the laboratory larvae may not be surprising, at least not passed day six when most yolk reserves had been absorbed. Thus, most conclusions concerning increment deposition were based on the larvae from the pond.

For larvae younger than about 18 d, the number of increments was generally lower than what would correspond to a daily depo-

TABLE 3

Mean number of growth increments on sagitta (S) and lapillus (L) of cod larvae from pond (1981). Results of t - tests for paired comparisons within each age are shown

Age (days)	No. of incr.		t	d.f.	p	L vs. S
	S	L				
8	5.2	5.9	1.89	9	0.05 < p < 0.1	L > S
10	5.3	6.3	3.02	9	0.01 < p < 0.02	L > S
12	5.5	7.3	3.96	7	0.001 < p < 0.01	L > S
15	6.7	7.8	3.42	11	0.001 < p < 0.01	L > S
18	8.7	8.6	-0.26	12	0.5 < p < 0.9	L = S
20	9.8	10.3	1.05	10	0.2 < p < 0.4	L = S
31	30.0	22.0	-7.48	10	p < 0.001	L < S

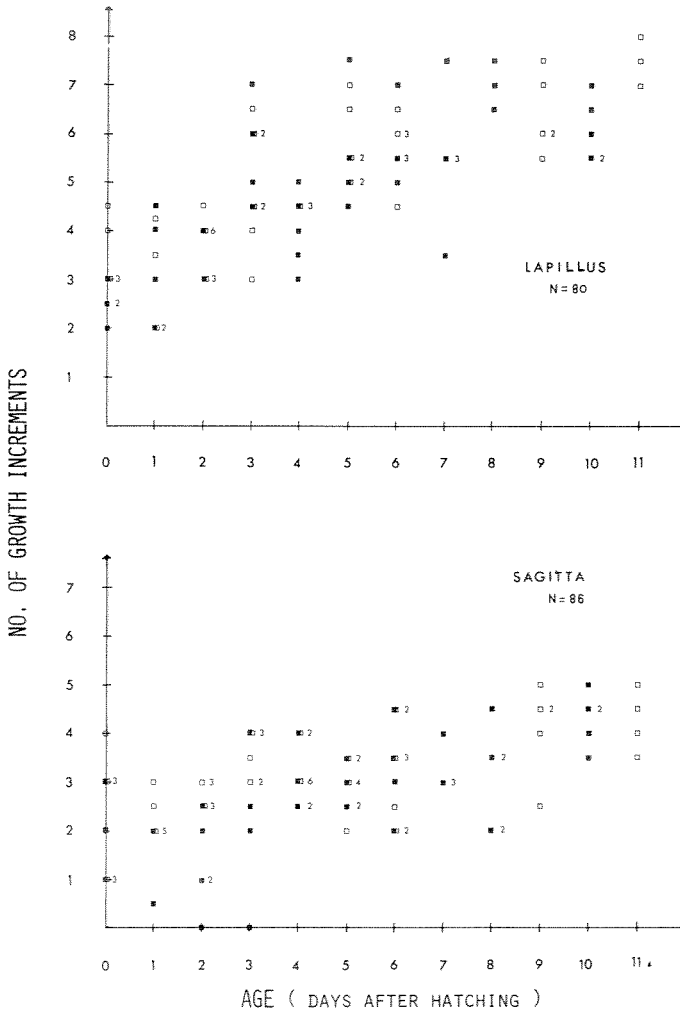


Fig. 1. The number of growth increments on the utricular (upper, lapillus) and saccular (lower, sagitta) otoliths vs age. Cod larvae from laboratory groups 1 and 2 (filled and open squares respectively). N - no. of larvae

sition rate since the time of 50% hatching. This could either be real; i.e. the otoliths indeed contained less increments than expected, or the counts were biased towards too low numbers. The last alternative could result from systematic inability to observe very faint increments. This may be a serious problem when the otoliths grow as slowly as indicated in Table 1; the daily increase in radius being no more than $.35 - .40 \mu\text{m}$. Since the resolving power of the microscope was in the range $.35 - .45 \mu\text{m}$, chances are that "daily" increments, if present, would not always be separable. Indeed, increasing the resolving power does give overall somewhat higher counts, although not high enough to make "increment count" equal to age. One problem is that in the process of increasing resolving power, contrast gets lower and optical artifacts tend to increase the possibility of misinterpretation. Nevertheless, it is probably not safe to conclude that the overall low counts were exclusively caused by low frequency of deposition. Unfortunately, I was not able to use scanning electron microscopy to clarify this problem any further.

Passed day 20, however, the otoliths grew fast enough per day to expect "daily" increments, if present, to be wide enough to be resolved. An average of 30 increments on sagittae from the larvae of mean age 31 d would seem to indicate a mean daily increments deposition since hatching. At the same age, the counts on lapilli seemed too low. Now, both these figures may be underestimates of the true number of increments since, if the arguments mentioned above are correct, counts in the innermost regions of the otoliths are too low. Thus, increment deposition rate appeared to increase after day 20, although probably not as much as suggested by the plot in Fig. 2.

On the sagittae, it appears that more than one increment was formed each day. No obvious grouping into "daily" and more diffuse "subdaily" units (sensu Taubert and Coble, 1977; Campana and Neilson, 1982; and others) seemed possible.

A comparison of independent counts on sagittae and lapilli from the same individual revealed significant differences (Table 3). Lapillus usually had slightly more increments than sagitta in the early larval stages, whereas the converse was

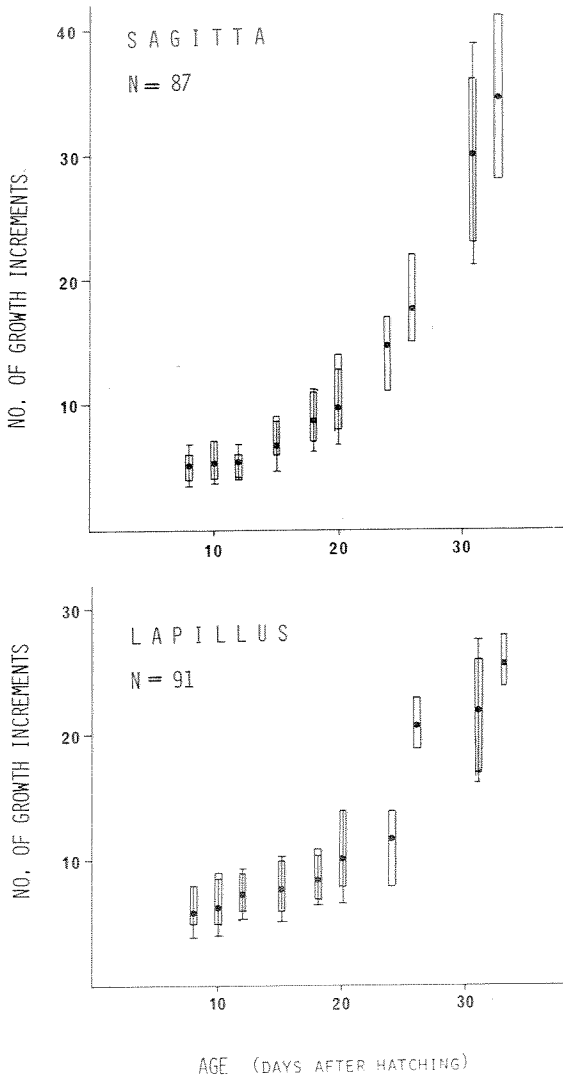


Fig. 2. The mean number of growth increments on sagitta and lapillus vs. age. Cod larvae from pond experiment (1981). Dots - age-group means, bars - range, vertical lines - ± 2 s (standard deviation), N - no. of larvae.

true at the end of the larval period. This corresponds with the size differences of the two otoliths as seen in Table 1a. Counting bias cannot be excluded as explanation for the slight differences in the early parts, while the differences at 31 d seem real.

The conclusions to be drawn from these studies depend strongly on the magnitude of counting bias during the period of slow growth; a factor which also makes age estimates less reliable for routine use. Counting bias can, however, hardly account for all the deviation seen. The average rate of increment formation appears lower than 1 incr d^{-1} the first 20 days, after which it increases. This contrasts somewhat with indications of an average daily increment formation found by others (Radtke and Waiwood, 1980; Gjørseter, 1981; Gjørseter and Tilseth, 1982). The discrepancy may not be very severe, though, since a comparison of the actual data reveals only slight differences (differences in conclusions can stem from the very narrow age intervals covered in the earlier studies).

Low rates of increment deposition during the early larval period were reported for herring, *Clupea harengus*, by Lough et al. (1982). Also, rates higher than 1 incr d^{-1} have been observed (Geffen 1982; Neilson and Geen, 1982).

In the study of cod larvae, general rates of increment formation, otolith growth (Table 1a) and body growth (Kvenseth, 1983) all increased from a low level the first 20 days to a higher level the rest of the larval period. This suggests that there is an overall positive correlation between otolith growth rate (and hence, larval growth rate) and increment deposition rate.

That otolith growth is correlated with body growth has been shown for several species (Taubert and Coble, 1977; Barkman, 1978; Methot, 1981; Radtke and Dean, 1982; Neilson and Geen, 1982; Laroche et al., 1982) and is thus not unexpected. A positive correlation between body growth rate and increment deposition rate was demonstrated by Geffen (1982) for herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae, while Taubert and Coble (1977), Barkman (1978) and Radtke and Dean (1982) found no such tendencies for green sunfish

(*Lepomis cyanellus*), Atlantic silversides (*Menidia menidia*) and the mummichog (*Fundulus heteroclitus*) respectively, as long as growth was not severely suppressed.

The results for cod larvae presented here give no firm basis for concluding that a correlation between otolith growth rate and ring deposition rate is the main explanation for the lack of linearity in the increment vs age relationship. In this case, working with a single population only, the range of counts between larvae of the same mean age have to be wider than what can reasonably be expected from random variation (counting error, age variation and variable age at first ring deposition) to be able to detect any such correlation.

The range of counts increased from 5 increments at age 15 days (lapillus) to 13 increments at age 31 days (sagitta). To test the consistency of counts, the two main counters repeated their counts of the 15 days lapilli and the 31 days sagittae after about 3 months. The counts were highly consistent, which clearly showed that the main source of variance within an age group was real differences in ring numbers between individual larvae (i.e. not counting error).

Maximum deviation from mean time of hatching was ± 2 days, and the age at first increment formation (although not determined exactly) appears to vary only slightly among larvae. Thus, these factors alone can hardly explain the extensive and increasing variation observed within age groups. This may indicate that real differences in ring numbers among larvae of the same age exist as a consequence of individual variation in formation rates.

As usual, a size hierarchy soon developed within the populations indicating some individual variation in growth rate (Øiestad and Kvenseth, 1981; Kvenseth, 1983). Table 4 shows within age group correlation coefficients between otolith size and the number of growth increments (r_2 is assumed to relate the growth of the otolith after hatching to increment number). Although sample sizes are small and within age group variation in otolith size is limited, the analysis suggests an overall positive correlation between the variables. Thus, this may strengthen the impression that there is an effect of individual

TABLE 4

Correlation between otolith diameter and number of increments within age-groups. Cod larvae from pond (1981).

r_1 - otolith diameter vs no. of increments

r_2 - (otolith diameter - diameter of first increment) vs no. of increments

* cases in which $H_0 : \rho = 0$ is rejected, $p < 0.05$

n - no. of larvae

Age (days)	Lapillus			Sagitta		
	r_1	r_2	n	r_1	r_2	n
8	0.426	0.730*	9	-0.191	0.637*	8
10	0.345	0.617	7	-0.314	0.743*	9
12	-0.411	-0.269	8	0.236	0.570	6
15	0.353	0.244	10	0.483	0.583	14
18	0.518	0.589*	12	0.096	0.345	12
20	0.587	0.732*	9	0.277	0.492	10
31	0.541	0.655*	11	0.656*	0.636*	11

growth rate leading to higher formation rates in fast-growing larvae (getting large otoliths) compared to slow-growing larvae. It does not, however, prove that a correlation between larval growth and ring deposition rate is always present in cod larvae, but clearly emphasizes the need for further testing of this hypothesis.

Increment number vs age - Juveniles

The means of two persons independent counts of broad, composite increments on sagittae from individual post-metamorphic cod are shown in Fig. 3. The increments counted are similar to those reported by Steffensen (1980) from 0-group East Baltic cod, by Campana and Neilson (1982) from juvenile starry flounder (*Platichthys stellatus*) and by Bailey (1982) from Pacific hake (*Merluccius productus*). The mean number of these structures appeared to correspond to the number of days past

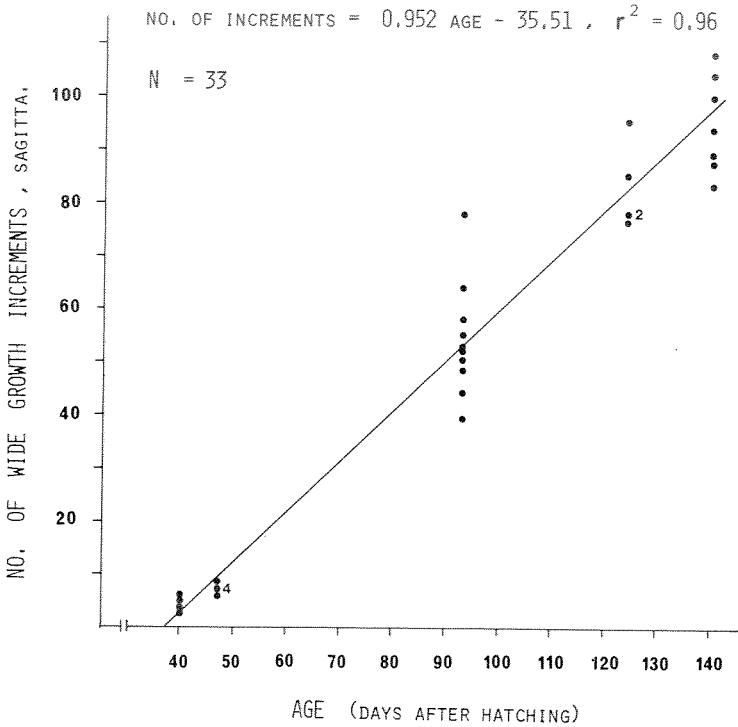


Fig. 3. The number of wide composite growth increments on sagitta vs. age. Juvenile cod from pond experiment (1981). Dots - means of counts from single fish, N - no. of juveniles.

the average age of metamorphosis. A straight line fitted to the data had a slope not significantly different from unity, and intersected the age axis at 37.5 days after hatching which is very close to the age of metamorphosis (Øiestad and Kvenseth, 1981; own observation). Thus, on average, one broad increment was deposited each day, and the structures recognized may be characterized as "daily" increments sometimes containing narrow "subdaily" increments.

The variation within age groups was considerable and was probably mainly caused by counting error. Defining the starting point was difficult and the increments were not always well

TABLE 5

Correlation between dorsoventral diameter of sagitta and the number of wide growth increments within age-groups. Juvenile cod from pond (1981). n - no. of larvae

Age (days)	r	n
40	- 0.395	4
47	- 0.087	6
93	- 0.132	10
124	0.422	5
140	- 0.333	7

separated. Some improvement of the preparation of sections may reduce counting error variability and importance.

Nevertheless, within age group variation seemed high to be accounted for by counting error alone (at least in the older groups). There could be room for some individual variation. This could not be related to variation in otolith size in this case (Table 5), even though a wide range of otolith sizes occurred (reflecting the range of lengths of the fish).

CONCLUSIONS

Studies of otoliths from two populations of cod larvae left to feed on natural food sources exposed to ambient light conditions in a large natural pond did not support the hypothesis of a constant daily deposition of growth increments throughout the larval period. This could, at least partly, be due to inability to resolve very narrow increments formed during a period of slow growth. The need for testing to which extent variation in body growth rate affects increment deposition rate was demonstrated. Compared with growth and developmental patterns seen in other large systems (Ellertsen et al., 1981; Gamble and Houde, 1984) the pond populations appeared rather

normal. On this basis it must be concluded that increment counts may not always give as unbiased age estimates as suggested by previous studies.

There seems to be some basis for determining the number of days after metamorphosis by counting wide composite increments on juvenile sagittae. The precision of an age estimate based on such counts may not be very high since, in addition to counting error, the age at metamorphosis may vary considerably between and within populations (Laurence, 1978; Ellertsen et al., 1981; Kvenseth, 1983).

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TABLE 5

Correlation between dorsoventral diameter of sagitta and the number of wide growth increments within age-groups. Juvenile cod from pond (1981). n - no. of larvae

Age (days)	r	n
40	- 0.395	4
47	- 0.087	6
93	- 0.132	10
124	0.422	5
140	- 0.333	7

separated. Some improvement of the preparation of sections may reduce counting error variability and importance.

Nevertheless, within age group variation seemed high to be accounted for by counting error alone (at least in the older groups). There could be room for some individual variation. This could not be related to variation in otolith size in this case (Table 5), even though a wide range of otolith sizes occurred (reflecting the range of lengths of the fish).

CONCLUSIONS

Studies of otoliths from two populations of cod larvae left to feed on natural food sources exposed to ambient light conditions in a large natural pond did not support the hypothesis of a constant daily deposition of growth increments throughout the larval period. This could, at least partly, be due to inability to resolve very narrow increments formed during a period of slow growth. The need for testing to which extent variation in body growth rate affects increment deposition rate was demonstrated. Compared with growth and developmental patterns seen in other large systems (Ellertsen et al., 1981; Gamble and Houde, 1984) the pond populations appeared rather

normal. On this basis it must be concluded that increment counts may not always give as unbiased age estimates as suggested by previous studies.

There seems to be some basis for determining the number of days after metamorphosis by counting wide composite increments on juvenile sagittae. The precision of an age estimate based on such counts may not be very high since, in addition to counting error, the age at metamorphosis may vary considerably between and within populations (Laurence, 1978; Ellertsen et al., 1981; Kvenseseth, 1983).

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