

## Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*)

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Juvenile steelhead trout (*Salmo gairdneri*) and starry flounders (*Platichthys stellatus*) were reared 64–76 days under various experimental feeding regimes to determine if feeding periodicity influenced the production of daily growth increments on the otoliths. Both species produced daily increments when fed thrice daily, daily, or once every 3 days, as well as through 26–32 days of starvation. Daily growth increments were also deposited in vateritic ("crystalline") otoliths, which constituted 27% of the trout sagittae sampled. Feeding frequency affected increment appearance and the incidence of subdaily increments in trout, but not in flounders. The difference in effect was probably due to the higher metabolic rate of trout. Increment deposition in all flounders was far more variable than in trout, and some flounders apparently ceased increment formation altogether.

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Des individus immatures de la truite arc-en-ciel (*Salmo gairdneri*) et de la plie *Platichthys stellatus* ont été gardées à des régimes alimentaires expérimentaux durant 64–76 jours dans le but de vérifier si la périodicité influence la croissance journalière des otolithes. Les otolithes des deux espèces subissent une croissance journalière lorsque les poissons sont nourris trois fois par jour, une fois par jour ou une fois tous les 3 jours et même s'ils sont soumis à un jeûne de 26–32 jours. Des anneaux de croissance journaliers apparaissent également sur les otolithes à cristaux de vaterite, soit sur 27% des sagittas de truites examinées. La fréquence de l'alimentation affecte l'apparence des anneaux et produit des dépôts secondaires chez la truite, mais pas chez la plie, probablement à cause du taux de métabolisme plus élevé de la truite. La croissance des otolithes est beaucoup plus variable chez les plies que chez les truites et certaines plies ont apparemment même subi un arrêt complet de croissance de leurs otolithes au cours de l'expérience.

[Traduit par le journal]

Since Pannella (1971) first described daily growth increments in the otoliths of some fishes, numerous investigations have confirmed his observations on other species (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Wilson and Larkin 1980; and others). The apparent universality of daily increments in young fish has led to their application in many fisheries problems. Daily increments are now being used to age larval fishes (Townsend and Graham 1981; Kendall and Gordon 1981), determine daily growth rates (Methot 1981), and assess life history changes in individual fish (Pannella 1980; Brothers and McFarland 1981).

Little is known of the factors that influence daily increment production, and consequently, their reliability. Taubert and Coble (1977) suggested that the deposition of daily growth increments was regulated by an internal circadian rhythm, entrained by a 24-h light–dark cycle. Studies supporting (Tanaka et al.

1981) and rejecting (Campana and Neilson 1982; Neilson and Geen 1982) the role of photoperiod as a zeitgeber indicate that age or species effects may be important. Diel temperature fluctuation has also been implicated as a factor behind increment periodicity (Brothers 1981).

The role of feeding periodicity in otolith deposition has only recently been examined. Fish given multiple daily feedings have been reported to produce more increments than would be expected of daily production (Pannella 1980; Neilson and Geen 1982), although Marshall and Parker (1982) reported continued daily increment production under conditions of starvation. Time of feeding apparently does not influence the timing of increment deposition (Tanaka et al. 1981). None of the studies cited subjected fish to more than one nondaily feeding regime.

The objective of this study was to examine the role of feeding periodicity and starvation in the production of daily growth increments in otoliths. Both steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*) were studied to test for any influence of widely different metabolic rates. In addition, the consistency of increment deposition was compared in the two species.

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## Materials and methods

### Trout

Young-of-the-year steelhead trout were obtained from a hatchery on 19 October 1981 and held in flow-through tanks for 7 days. On 26 October 1981, 111 trout (standard length = 7.58 cm SD = 0.66 cm) were injected i.p. with 0.05 mL of 20 mg/mL oxytetracycline hydrochloride. Tetracycline is known to be incorporated into flounder otoliths within a day of injection (Campana and Neilson 1982). A similar response to injection has been noted in trout (S. E. Campana, unpublished). Since the incorporated compound fluoresces under ultraviolet (UV) light, the resultant band can be used as a temporal mark on the otolith, with the medial aspect of the band corresponding to the daily growth increment deposited on the day of injection.

The injected trout were divided into four 200-L tanks (30 fish in each of tanks 2 to 4 and 18 in tank 1). A seminatural photoperiod was maintained through the use of an outside photocell, and initial water temperature was 10°C. By the end of the experiment, water temperature had dropped to 4.5°C. Rations consisted of a commercial trout food.

Each aquarium was maintained under a different feeding regime as follows. Tank 1: once daily for 13 days, followed by starvation for up to 32 days more; tank 2: once every 3 days for 64 days; tank 3: once daily for 64 days; tank 4: thrice daily (at 8-h intervals) for 64 days. Feeding was carried out at 1400 for tanks 1 to 3, and at 0800, 1600, and 2400 for tank 4 (via an automatic feeder). Excess food was removed 4 h after each feeding (once daily in the case of tank 4). The quantity of food given to each tank through the course of the experiment was roughly equal.

Fish from tank 1 were sampled at 6-day intervals; fish from the other tanks were sampled 64 days after tetracycline injection. Sagittal otoliths were removed and prepared as described below.

### Flounders

Young-of-the-year starry flounders were collected from Bellingham Bay, Washington on 12 September 1981 and held in laboratory aquaria for 6 or 7 days. Age of these fish was roughly 7 months and their mean standard length was 5.36 cm (SD = 0.79 cm). Daily meals of live tubificid worms were provided.

On 18 September 1981, 90 flounders were injected i.p. with 20 mg/mL of oxytetracycline hydrochloride at a titre of 0.025 mL/5 g fish. Experimental design was similar to that of the trout: 30 fish in each of three 50-L aquaria (tanks 2 to 4). A further 25 flounders were injected and placed in tank 1 on 19 September 1981.

All aquaria were maintained under a 14 h light : 10 h dark photoperiod at a temperature of 16°C. By the end of the experiment, water temperature in all aquaria had gradually decreased to 10°C, although no diel fluctuations were observed. Salinity was <5‰, as per the collection site.

All fish from tanks 2 to 4 were killed after 74–76 days. Fish from tank 1 were sampled sequentially at 4- to 10-day intervals once starvation had started.

### Otolith preparation

After removal, left and right sagittal otoliths were brushed

free of tissue and embedded separately, sulcus side down, in Krazy Glue on a microscope slide. Metallurgical lapping film (grit size 30 µm to 0.3 µm) and a grinding jig (Neilson and Geen 1981) were used to grind and polish the otolith to the midplane, or until the daily growth increments on the postrostrum were most visible. Increment counts were made on the postrostral tip (flounders) or the lateral aspect of the postrostrum (trout) since increments were most distinct in this region of the otolith. Visual counts were made from the medial aspect of the fluorescent tetracycline band (Campana and Neilson 1982) at 1250× on a Leitz Orthoplan fluorescence microscope. Counts were repeated at a later date.

Scanning electron microscope (SEM) photographs were made of some otoliths, particularly when higher resolution was required. Flounder otoliths for SEM were prepared by etching with 0.1 M EDTA (ethylenedinitrilo tetraacetic acid) for 10 min or with 2% HCl for 16 min. Trout otoliths were etched in either 0.1 M EDTA for 4 min or in 2% HCl for 2 min. Etched otoliths were coated with gold and viewed at 10 kV on a Cambridge Stereoscan 250 scanning electron microscope.

As a check for visual counting accuracy, paired UV and bright light micrographs were prepared of some visually counted regions, and counts were made from the projected image (Campana and Neilson 1982). Visual, photographic, and SEM counts were then compared. In well-prepared sagittae, increment counts did not differ significantly among the techniques ( $P > 0.05$ ). However, regions of narrow increments were difficult to resolve visually; optimal etching for SEM was impossible when otolith curvature was present (especially in flounders), and photographs introduced daily or subdaily confusion owing to the fixed focal length.

The mean of the left and right sagittal increment counts from each fish was used in the data analysis. Left and right sagittal counts do not differ systematically in flounders (Campana and Neilson 1982) or trout (S. E. Campana, unpublished). In instances where one otolith had a substantially lower increment count than its paired counterpart (> 30% difference), the lower value was assumed to be anomalous and excluded from further analysis. Anomalous values were uncommon in trout, but occurred more frequently in flounders where increment deposition is variable (Campana and Neilson 1982).

## Results

### Trout

Daily growth patterns in trout otoliths were regular in contrast, with declining widths apparently due to decreasing temperatures. Increment counts did not differ significantly among the various feeding regimes, suggesting that feeding periodicity did not influence the daily production of growth increments ( $P > 0.05$ ) (Table 1). However, fish fed once every 3 days (tank 2) deposited significantly fewer increments than would be expected of daily production. Since the difference was minimal (< 6%), the "lost" increments were likely due to poor resolution rather than absence. Increments in the otoliths of fish fed once every 3 days tended to be narrower than those of fish fed more frequently (i.e., as

TABLE 1. Mean number of daily growth increments produced under various experimental feeding regimes

Feeding regime		Increment count	SE	Days elapsed	N
Flounder	Tank 2 (once per 3 days)	73.5	3.7	76	20
	Tank 3 (once daily)	72.2	2.1	75	27
	Tank 4 (thrice daily)	67.6	6.5	74	11
Trout	Tank 2 (once per 3 days)	60.6	1.1	64	29
	Tank 3 (once daily)	62.8	0.6	64	28
	Tank 4 (thrice daily)	62.8	1.0	64	28

narrow as  $0.85\ \mu\text{m}$ ); since otolith growth often reflects fish growth (Wilson and Larkin 1982), a significantly slower growth rate was probably responsible (Scheffé's test,  $P < 0.05$ ).

Fish starved for periods of up to 32 days did not cease production of daily increments (Fig. 1). Subdaily increments were not counted, but visual observations suggested that their frequency increased with the feeding frequency of the fish; such increments were not observed in fish that had been starved.

Although starvation and feeding periodicity had no effect on increment number, otolith microstructure differed among the experimental treatments. Increments deposited in starved fish were narrower than those produced before the start of the starvation period. The change was gradual but generally became noticeable 0–4 days after starvation started. Associated with the reduction in increment width was a decrease in the visual contrast of adjacent increments (i.e., increments became fainter). In addition, I observed a subtle 3-day pattern in many of the otoliths of fish fed once every 3 days. The pattern consisted of a dark increment followed by two fainter increments, but did not become evident until 15–30 days after the experiment began. Increment width did not vary within the pattern.

Twenty seven percent of the sagittae removed from the trout were vateritic ("crystalline"), as opposed to aragonitic (vaterite is an alternate mineral form of calcium carbonate; aragonite is the mineral that generally makes up an otolith). Despite the altered structure and glasslike appearance, daily increments were present (Fig. 2). In sagittae which were partially aragonitic and partially vateritic, increment counts were similar in the two mineral forms. Both regions had an otolith check associated with the tetracycline band. However, light transmitted through vaterite was highly refracted, resulting in a high proportion of visual artifacts associated with the incremental structure. It was not difficult to distinguish daily increments from visual artifacts, but counts of subdaily increments were unreliable.

### Flounders

Daily growth increments in flounders were far more difficult to count than were those of trout. Increment sequences were often interrupted by one or more otolith checks (discontinuities). Increments associated with checks were difficult to read, since their identity as daily, subdaily, or visual artifact was generally confused. Increment width was often irregular, particularly in the proximity of checks. Standard errors of mean increment counts were much higher in the flounder experiments than in the trout experiments (Table 1), demonstrating the greater irregularity of the flounder otolith microstructure. Subdaily increments contributed to the flounder data variance much more than was the case with the trout.

Feeding frequency had no effect on the mean number of increments produced in experimental flounders. Daily increments were produced in fish fed three times per day, daily, or once every 3 days (Table 1). Nor did starvation for periods up to 26 days result in cessation of increment deposition (Fig. 1). However, one to six fish from all feeding regimes deposited far less than one increment per day on one or both of their sagittae (Fig. 3). These instances, though infrequent, could not be attributed to counting error or otolith curvature.

Although subdaily increments on flounder otoliths were not counted, qualitative assessments indicated that they were more frequent on flounders than on steelhead, with no apparent correlation to feeding frequency. The ability to discern subdaily patterns was related to the width of the growth zone; resolution of very narrow increments was difficult.

Feeding periodicity had no observable effect on the otolith microstructure of flounders. Although some of the starved flounders produced narrow increments, other individuals were not so affected. Poststarvation increments did not appear to be fainter than those deposited previously. No 3-day pattern was observed in fish fed once every 3 days. If a pattern as subtle as that described in tank 2 trout sagittae had been present, it may have

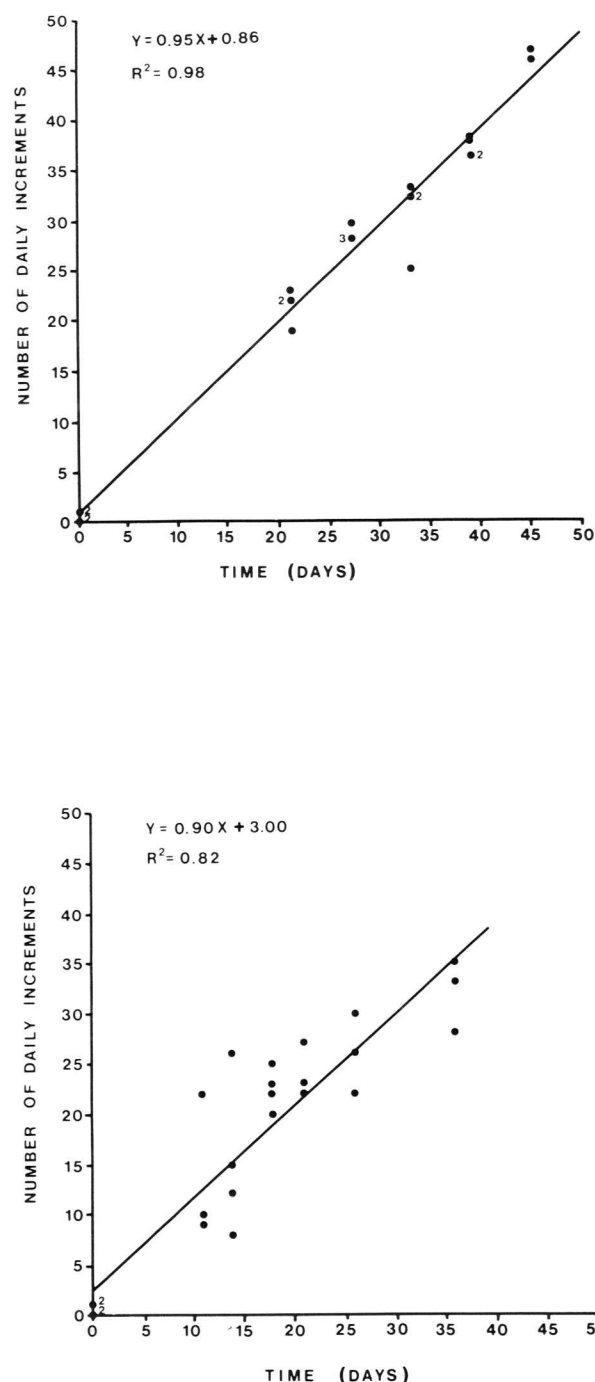


FIG. 1. Otolith increment counts as a function of time for starved steelhead trout (top) and starry flounder (bottom). Starvation began on day 10 for flounders and day 13 for trout. Neither regression slope is significantly different from 1.0 at the 95% confidence level. Numbers beside data points refer to coincident values.

been obscured by the general irregularity of flounder deposition.

### Discussion

Daily growth increments were deposited on the otoliths of steelhead trout and starry flounder under both daily and nondaily feeding regimes. In trout, there was some indication that the number of subdaily increments increased with feeding periodicity. No such relationship was evident in the flounder otoliths. These results are consistent with those of Taubert and Coble (1977), who reported that young mouthbrooders (*Tilapia mossambica*), given multiple daily feedings under a 15 h light : 9 h dark photoperiod, continued to produce daily growth zones. In contrast, Neilson and Geen (1982) found that fish fed four times per day produced a higher number of narrow increments than those fish fed daily, although increment number was not directly proportional to the number of meals provided. My results and those of Neilson and Geen (1982) are not necessarily contradictory if one assumes that the incidence of subdaily increments is related to feeding frequency. Such a relationship was suggested by this study; what appear to be broad daily and numerous intervening subdaily increments were also visible in the otoliths of chinook salmon (*Oncorhynchus tshawytscha*) fed four times per day (Neilson and Geen 1982, Fig. 2).

Trout and flounders starved for periods of 32 and 26 days, respectively, continued to deposit daily growth increments on their otoliths. Similar results have been reported for sockeye salmon (*Oncorhynchus nerka*) (Marshall and Parker 1982). The body fat reserves present in most fishes may provide sufficient energy for limited skeletal and otolith growth during periods of starvation (Buckley 1980; Jobling 1980; Marshall and Parker 1982). Therefore, daily increment deposition during starvation is plausible. However, first-feeding fish larvae would not have such a reserve and may cease increment deposition as a result. Examination of the otoliths of starved anchovy (*Engraulis mordax*) larvae support this suggestion (Methot and Kramer 1979); thus, the age determination of starved early stage larvae by means of daily growth increments may be unreliable.

Although flounders were not so affected, the otolith microstructure of trout was influenced by feeding periodicity. Many starved trout deposited narrow increments, while a subtle tridaily pattern was produced in fish fed once every 3 days. The absence of these characters in flounders is probably related to the different metabolic rates of the two species. Salmonids such as the sockeye salmon have a standard metabolic rate of approximately  $75 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$  at  $10^\circ\text{C}$  (Brett and Glass 1973), while pleuronectids such as the flounder



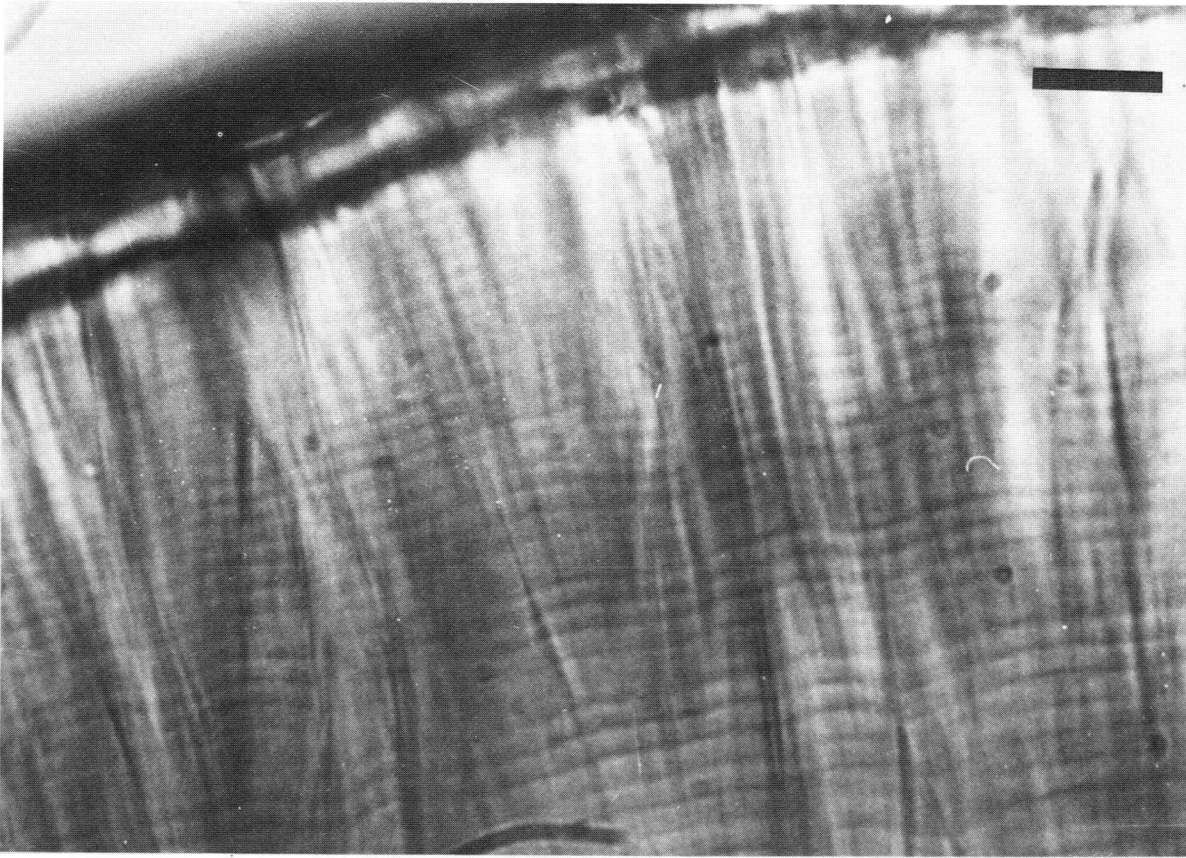


FIG. 2. Ground and polished vateritic sagitta from a steelhead trout showing daily growth increments. Bar = 10  $\mu\text{m}$ .

*Platichthys flesus* are closer to  $23 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$  at  $10^\circ\text{C}$  (Jorgensen and Mustafa 1980). (Metabolic rates have not been published for the species and (or) weights of fish used in my study, but the values mentioned are representative of the taxa; see Altman and Dittmer 1974.) Consequently, food is assimilated far more quickly in trout than in flounders; a rapid response to food availability or feeding would therefore be expected in trout and is apparently reflected in the pattern and width of daily growth zones, as well as the incidence of subdaily increments in the otoliths. Metabolic response to food intake in flounders may be too slow to affect the appearance of daily increments. Trout and flounders were reared at different temperatures in this study. However, the lower temperature at which the trout were reared would tend to mask, not enhance, short-term metabolic responses.

Few fishes feed only once per day. Rainbow trout (*Salmo gairdneri*) often feed several times a day (Grove

et al. 1978), while young flounders feed intertidally once or twice per day, depending on the tides (Thijssen et al. 1974; S. E. Campana, unpublished). Periods of starvation probably occur in most individuals at one time or another. If increment number was proportional to feeding frequency, otolith growth increments could not be used reliably in age or growth studies of wild fish. This study demonstrates that such concern is probably unwarranted, although the results cannot be extrapolated to early stage larval fishes. Tanaka et al. (1981) also reported that feeding did not entrain the production of daily increments.

To my knowledge, daily growth increments have not been previously reported in vateritic otoliths. Vateritic otoliths are uncommon among most wild fishes, but appear frequently in hatchery-reared salmonids (S. E. Campana, unpublished). Although vaterite is a different mineral form than aragonite, the fact that daily growth increments are present in the former implies that the

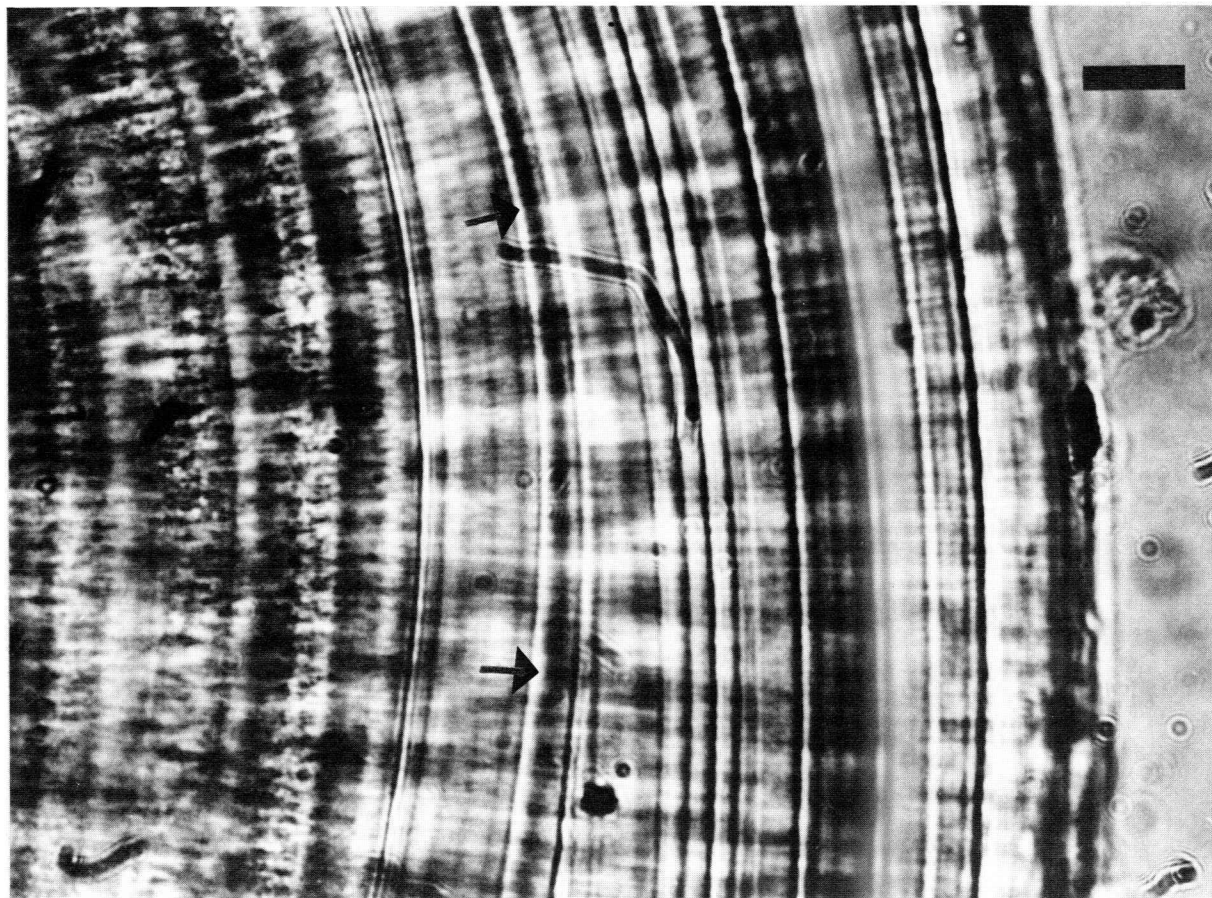


FIG. 3. Sagitta of a starry flounder fed once daily for 76 days. Far fewer than 76 growth increments are visible, suggesting cessation of sagittal growth at some point during the experiment. Bar = 10  $\mu\text{m}$ . Arrows indicate increment produced on date of injection.

depositional processes are similar in the two cases. Tetracycline incorporation did not differ appreciably between the two minerals.

A small number of flounders possessed otoliths that had apparently ceased increment deposition at various times after tetracycline injection. SEM observation of representative otoliths indicated that increments too narrow to be viewed by light microscopy were not responsible for the low increment counts. Curvature of the otolith periphery accounted for some "lost" increments, as was demonstrated when otoliths were ground from both sides to a thin section. However, I can only conclude that increment production ceased in a number of individuals, and in some fish, on only one of the sagittal pair. These anomalies remain unexplained, although they have been noted previously in both juvenile (Campana and Neilson 1982) and larval (Laroche et al. 1982) pleuronectids.

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