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Daily growth patterns in otoliths of larval and juvenile plaice (*Pleuronectes platessa* L.): influence of temperature, salinity, and light conditions

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Daily growth increments were studied in otoliths of larval and juvenile plaice reared in the laboratory. The influence of temperature, salinity, and light cycle on increment deposition was investigated. Otolith growth was related to somatic plaice growth under all environmental conditions examined. Various constant temperature and salinity conditions influenced somatic growth rate and increment widths in otoliths. At 10°C, wide clear increments were deposited in the otoliths. At 5°C, slow growth rates were observed associated with deposition of narrow otolith increments. Low salinity (20 ppt) negatively affected somatic and otolith growth of larvae when combined with low temperature. Low salinity when combined with optimal temperature negatively affected otolith increment width of juveniles. Abrupt changes in the rearing conditions also invoked a direct response of increment widths in otoliths. Temperature increase led to growth acceleration and deposition of wide increments in the otoliths. On the other hand, temperature and salinity decrease led respectively to growth retardation and narrow increment deposition. Light cycle had a less pronounced effect on the increment width.

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Introduction

Analyses of otolith microstructure in various fish species have been carried out in recent years and daily increments in fish otoliths have helped in ageing of cold, temperate, and tropical species (Pannella, 1971; Ralston, 1976; Taubert and Coble, 1977; Victor and Brothers, 1982). Moreover, in growth studies mainly of early life history stages, daily increment analyses in otoliths were employed for examining the effects of feeding and temperature on experimental fish (Radtke and Dean, 1982; Campana 1984; Neilson and Geen, 1985; Gutierrez and Morales-Nin, 1986; Eckmann and Rey, 1987). However, in order to avoid the problem of measuring extremely narrow increments, some of these studies were based on otolith radius or diameter measurements or other crude parameters (Struhsaker and Uchiyama, 1976; Wilson and Larkin, 1982; Methot, 1981; Volk *et al.*, 1984). A more detailed study of the biotic and abiotic factors affecting increment deposition in fish otoliths and their relation to somatic daily growth would help to assess the potential use of otolith microstructure analysis in growth studies. This has already been pointed out in a recent review work on otolith studies by Campana and Nielson (1985).

For plaice (*Pleuronectes platessa* L.), a common and commercially important flatfish species of the North Sea, limited information is available on otolith growth. Usually macrostructural aspects have been considered in plaice ageing (Reibisch, 1899; Rauck, 1974) and little attention has been given to microstructural analysis of plaice otoliths (Blacker, 1975; Berghahn, 1985).

In the present study, daily growth increments were analysed in otoliths of laboratory-reared larval and juvenile plaice. The main objectives of the study were: (1) to investigate the relation between otolith and somatic growth of early-stage plaice under various environmental conditions; (2) to reveal the influence of various constant environmental conditions (temperature, salinity, light cycle) on otolith growth of young plaice; and (3) to check the effects of abrupt environmental changes during early life stages on plaice otolith microstructure.

Material and methods

Plaice eggs were collected during egg surveys in the southern North Sea and incubated in the laboratory. Newly-hatched larvae, segregated by date of hatching, were reared up to early juvenile stage (25–28 mm TL)

in 1 l glass containers (20 larvae/container) and fed *ad libitum* on freshly hatched *Artemia* nauplii. Water was exchanged and food remnants and dead *Artemia* nauplii were removed on a daily basis. The effects of temperature, salinity, and light cycle were tested. The following experimental treatments were carried out with four replicates each: at 5°C: (a) 20 ppt salinity, 12L/12D light cycle; (b) 30 ppt salinity, 12L/12D light cycle, (c) 30 ppt salinity, 10L/14D light cycle; at 10°C: (a) 20 ppt salinity, 12L/12D light cycle; (b–e) 30 ppt salinity and 12L/12D, 10L/14D, 24L, 16L/8D light cycle respectively.

In addition to the treatments listed above, where the rearing conditions were kept constant over 60 d, the effects of abrupt changes in rearing conditions were investigated in another series of treatments. For this purpose, 30 d after hatching, one of the factors under investigation was changed as follows: (a) temperature increase from 2 to 5°C and from 5 to 10°C (at 30 ppt salinity, 12L/12D light cycle), (b) temperature decrease from 10 to 5°C (at 30 ppt salinity, 12L/12D light cycle), (c) salinity decrease from 30 to 20 ppt salinity (at 10°C, 12L/12D light cycle), and (d) photoperiod change from 8L/16D to 16L/8D at 10°C and 30 ppt salinity.

In order to estimate as closely as possible the relation between otolith microstructure and somatic daily growth, sampling was carried out at 10-d intervals. Five plaice were sampled randomly from each treatment, anaesthetized with 1% MS-222 (tricaine methanesulfonate) and measured immediately to the nearest mm TL.

After dissecting the post-opercular area, sagittal otoliths were extracted and stored in 80% ethanol until the final preparation. Otoliths were analysed by light microscopy and SEM. After cleaning, otoliths were attached with the sulcus upwards on SEM stubs and ground to the midplane on a rotating glass plate using silicon carbide as abrasive (for details, see Karakiri and von Westernhagen, 1988). Before coating with gold for SEM observation, specimens were etched using a 0.1 M EDTA solution (Karakiri, 1989). Daily increment counts, measurements of the longest axis of the sagittae, and increment widths were carried out from SEM photographs.

Analysis of covariance (ANCOVA) was employed to check on the differences between the various experimental sets in the slopes of the linear regressions of increment width at age (Sokal and Rohlf, 1969; Sachs, 1984).

Results

General observations

Otoliths of early-stage plaice showed the typical flatfish pattern. The size of the primordium (the calcification nucleus formed during the late embryonal stages) ranged from 20 to 22 μm in diameter. The first increment was formed 5–7 d prior to hatching. Once started, increment formation displayed a daily pattern. The first increments, embryonic and yolk-sac larval, deposited around the primordium were extremely narrow, varying from 0.3 to 0.8 μm, while depositions during the larval stage were usually wider (up to 1.8 μm).

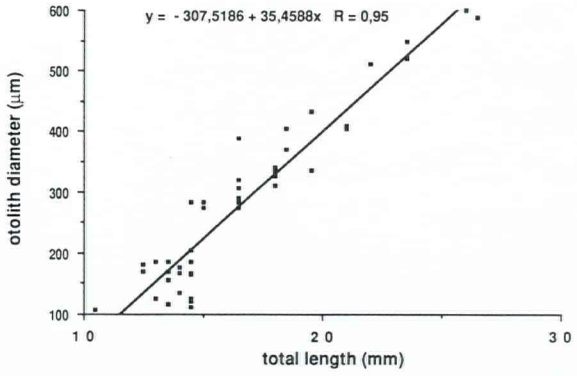

Figure 1. Otolith growth measured as longer diameter of sagitta (μm) related to fish total length (mm) for laboratory-reared plaice larvae up to 60 d old, n = 50.

Among the factors tested, temperature had the strongest influence on growth rate, survival, and otolith increment width in larval (6.5–14 mm TL) and juvenile (14.1–28 mm TL) plaice. The larval stage lasted over 100 d for plaice reared at 5°C and between 40 and 50 d for animals reared at 10°C. At 5°C only 10–15% of the larvae survived over 100 d up to the early juvenile stages (12–15 mm TL). At 10°C survival rates ranged between 90 and 100% for larvae and 70 and 80% for juvenile plaice.

Otolith growth, measured as the longest axis of the sagitta, was positively related to somatic growth measured as total length for all treatments pooled ($r = 0.95$, Fig. 1).

Temperature effects

Daily increment width in larvae varied according to growth rate. For the first 70 d of life (i.e. over the whole experimental period) a tendency of increasing increment width with age was detected. In fast-growing larvae at 10°C, increment width ranged from 0.7 to 1.8 μm (Fig. 2a) and from 1.8 to 3 μm in juveniles (14.1–28 mm TL). On the other hand, in slow-growing individuals at 5°C larval increment widths ranged from 0.3 to 0.8 μm (Fig. 2b).

For each experimental set individual mean increment width was plotted against age. Highly significant differences could be detected by analysis of covariance between the linear regressions of increment width on age at 5°C and 10°C (Fig. 3a, $F = 6.20$, $p < 0.001$).

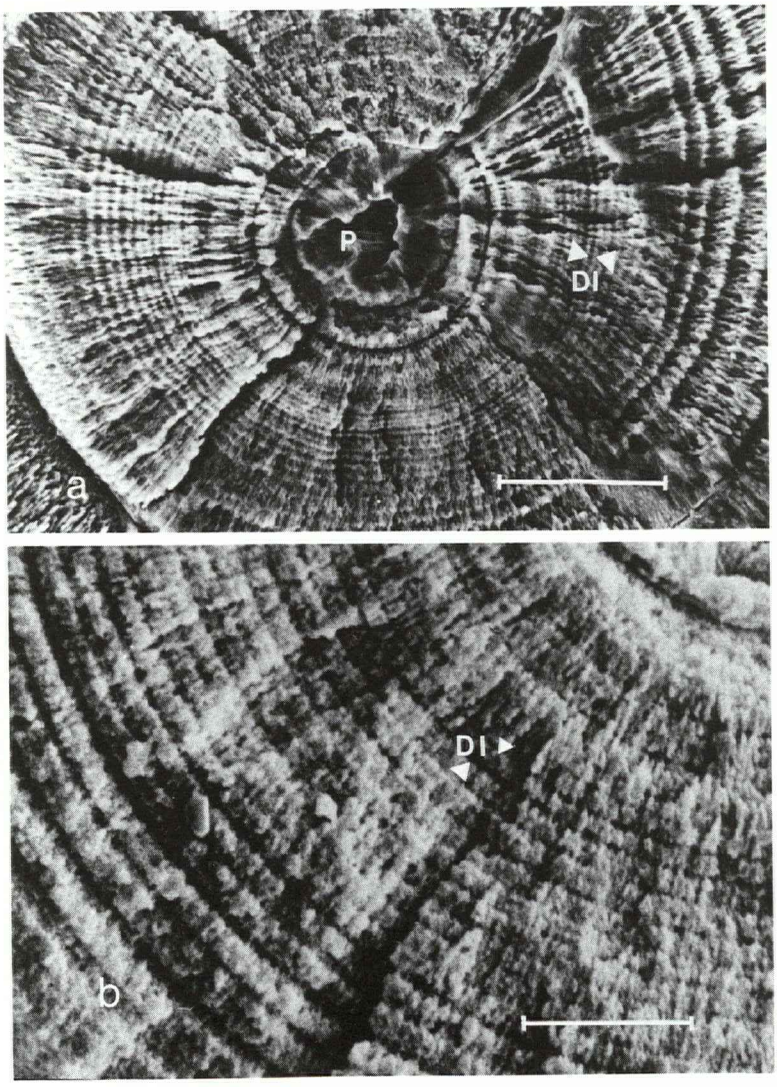

Figure 2. Plaice otoliths viewed by SEM. a: Part of the sagitta of a fast-growing individual, reared at 10°C, with increment widths ranging between 0.9 and 1.8 μm, P: primordium, DI: daily increment, bar = 20 μm. b: Part of the sagitta of a slow-growing individual, reared at 5°C, with increment widths ranging from 0.3 to 0.7 μm, DI: daily increment, bar = 3 μm.

Abrupt changes of temperature (increase or decrease), 30 d post-hatch, invoked a drastic response in otolith increment width. Plaice larvae reared for 30 d at 2°C showed stunted growth and extremely narrow increments (0.2–0.4 μm). After transfer to 5°C, they continued to deposit only narrow increments. However, plaice larvae reared at 5°C for 30 d and then moved to 10°C showed a significant increase in increment width immediately after transfer (Fig. 3b, $F = 4.97$, $p < 0.001$). Plaice larvae reared for 30 d at 10°C and then moved to 5°C showed narrower increments after the transfer to lower temperature and the transition phase to the bottom-dwelling mode of life was prolonged (Fig. 3c). Highly significant differences in otolith growth were revealed in plaice reared at 10°C and in the individuals subjected to an abrupt temperature decrease from 10°C to 5°C ($F = 2.49$, $p < 0.001$).

Salinity effects

Salinity also influenced somatic growth rate and increment widths of plaice larvae and juveniles. At 5°C, a salinity of 20 ppt caused lower growth rate and deposition of narrower increments in otoliths than a salinity of 30 ppt during the first 6 weeks of life (Fig. 4a). For the first 40 d, significant differences were detected employing ANCOVA ($F = 2.49$, $0.01 < p < 0.025$). After 40 d post-hatch, salinity did not affect either somatic or otolith growth of larvae reared at low temperature.

At 10°C, plaice larvae showed no significant differences in growth when reared at 30 ppt or at 20 ppt. In contrast, plaice at the age of 40–50 d (during and shortly after the transition to the bottom-living stage), showed a negative response of somatic growth to low

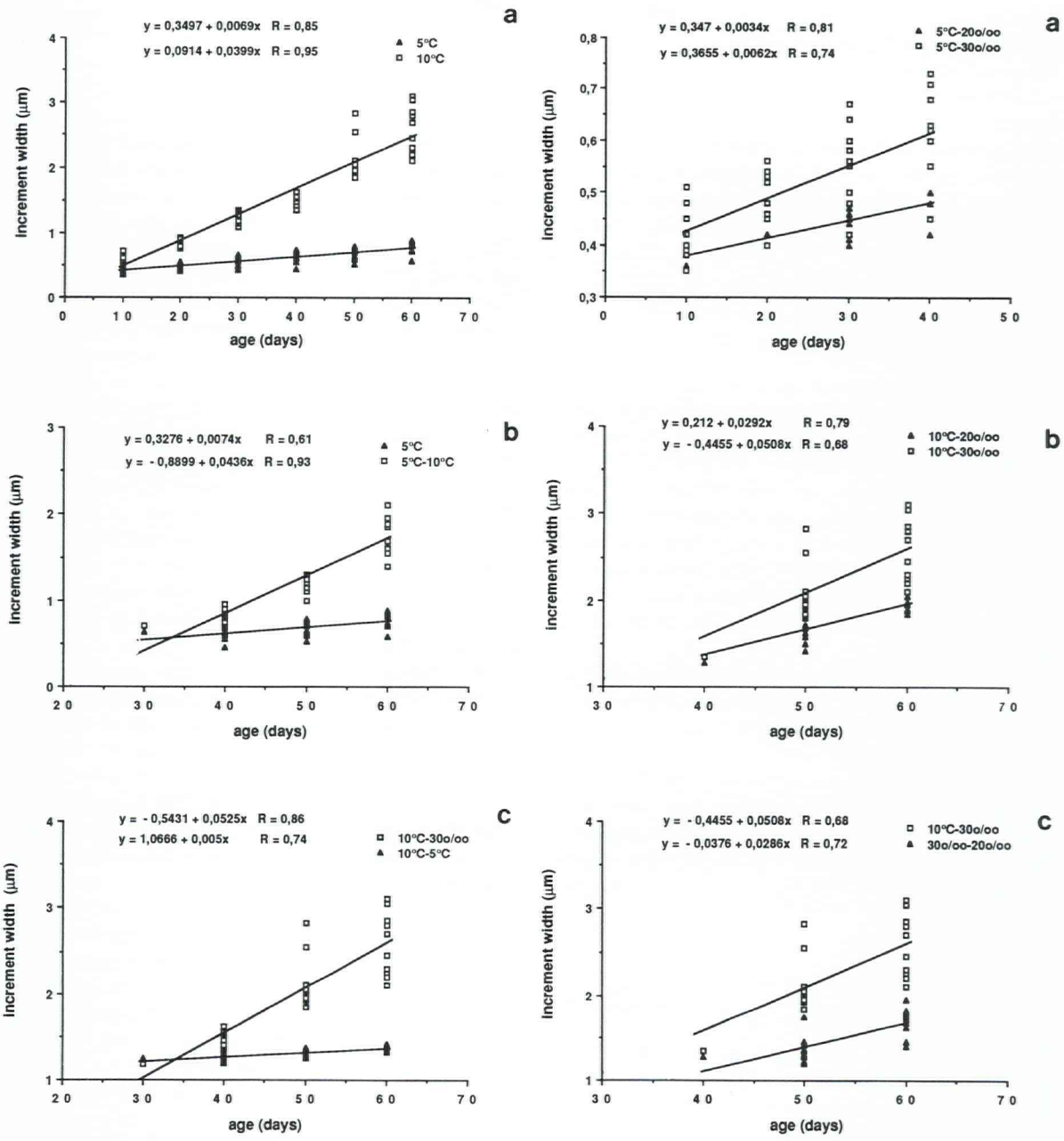

Figure 3. Influence of temperature conditions on increment width during early development: all experiments at 30 ppt salinity. Each point on the graph represents the mean increment width at the respective age for each analysed specimen. a: Plaice reared at 5°C and plaice reared at 10°C constant temperature, n = 20. b: Plaice reared at 5°C constant temperature and plaice subjected to a temperature increase from 5°C to 10°C at 30 d post-hatch, n = 20. c: Plaice reared at 10°C constant temperature and plaice subjected to a temperature decrease from 10°C to 5°C at 30 d post-hatch, n = 20.

Figure 4. Influence of salinity conditions on increment width during early development. Each point on the graph represents the mean increment width at the respective age for each analysed specimen. a: Salinity effects for plaice reared at low constant temperature (5°C), 20 ppt and 30 ppt, n = 20. b: Salinity effects for plaice reared at 10°C constant temperature, 20 ppt and 30 ppt, n = 20. c: Effects of salinity changes at 10°C, plaice reared at 30 ppt constant salinity and plaice subjected to salinity change from 30 ppt to 20 ppt at 30 d post-hatch, n = 20.

salinity (20 ppt) that was reflected in reduced increment widths (Fig. 4b). Significant differences were detected by ANCOVA between day 40 and day 60 in juvenile plaice reared at 20 ppt and juvenile plaice reared at 30 ppt salinity ($F = 2.49$, $0.01 < p < 0.025$).

Likewise, a transfer to low salinity 20 ppt during the transitional phase to the bottom-living stage caused a slightly negative response in growth rate and otolith increment width (Fig. 4c). In addition, a prolongation of almost 10 d of the transitional phase was observed. However, no significant differences were detected in increment width after day 30 between these groups ($F = 1.81$, $0.075 < p < 0.1$).

Light cycle effects

The effects of day length on somatic and otolith growth of plaice larvae were less pronounced than the effects of temperature and salinity shown above. At low temperature (5°C), no effects of light cycle (12L/12D, 10L/14D) could be detected on either somatic or otolith growth. At 10°C only slight differences were observed among larval groups reared under various light cycles (12L/12D, 14L/10D, 16L/8D, 24L). Growth rates were only slightly higher for plaice larvae reared at 24L or 16L/8D cycles, than for plaice larvae reared under 12L/12D.

A slight increase in otolith increment widths was observed in a group of plaice larvae reared for 30 d at 10°C under a light cycle of 8L/16D and then moved to a light cycle of 16L/8D.

Another group of plaice larvae was reared for 30 d at 10°C and 16L/8D light cycle before they were moved to 8L/16D light cycle (Fig. 5). In this case, significant negative effects of a short day length were detected ($F = 2.51$, $0.01 < p < 0.025$).

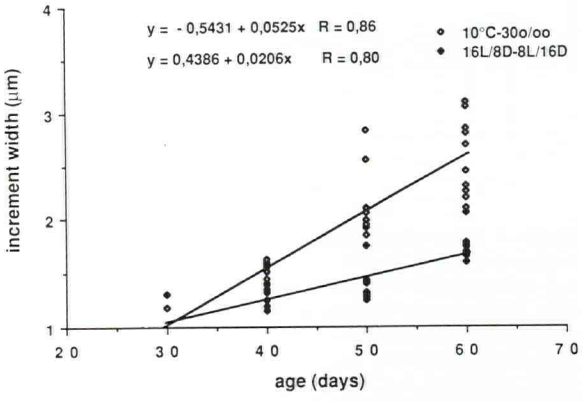

Figure 5. Effects of day length on increment width during development at 10°C and 30 ppt: plaice reared under constant day length cycle of 12L/12D and plaice subjected to a change of light cycle from 16L/8D to 8L/16D at 30 d post-hatch. Each point on the graph represents the mean increment width at the respective age for each analysed specimen, n = 20.

Discussion

The otoliths of larval and juvenile plaice showed the typical flatfish otolith pattern as described for English sole *Parophrys vetulus* (Rosenberg, 1982) and starry flounder *Platichthys stellatus* (Campana, 1984). Narrow larval increments surround the primordium, while accessory primordia are formed at settlement and wider increments are deposited during the bottom-living stage. Increment deposition before hatching was also reported for Atlantic silverside *Menidia menidia* (Barkman, 1978), chinook salmon *Oncorhynchus tshawytscha* (Neilson and Geen, 1982), mummichog *Fundulus heteroclitus* (Radtke and Dean, 1982), winter flounder *Pseudopleuronectes americanus* (Radtke and Scherer, 1982) and tilapia *Oreochromis aureus* (Karakiri and Hammer, 1989). Deposition of the first increment may relate to the duration of embryonic development so that species with a short embryonic period may lay down the first increments only after hatching. Thus, for two flounder species, *Rhombosolea tapirina* and *Ammotretis rostratus*, the deposition of the first increment was reported to coincide with the day of complete yolk absorption, about 5 d post-hatch (Jenkins, 1987). However, these results were obtained employing light microscopy and resolution difficulties may have occurred.

In otoliths of early-stage plaice, deposition of growth increments followed a daily pattern, being strictly related to chronological age and independent of growth rate and environmental conditions. This result is contradictory to that reported for otoliths of turbot larvae *Scophthalmus maximus* (Geffen, 1982) examined by light microscope where increment deposition was interpreted as being growth-dependent. More probably this result is based on a misinterpretation due to inadequate preparative and microscopical evaluation techniques.

Among the parameters examined, temperature was found to be the main factor influencing growth rate of larval and juvenile plaice. Consequently, increment widths were strongly affected by temperature conditions. High otolith growth rate was caused by a constant temperature of 10°C. The deposition of wider daily increments at higher temperatures has also been shown experimentally in otoliths of chinook salmon *Oncorhynchus tshawytscha* by Neilson and Geen (1982) and starry flounder *Platichthys stellatus* by Campana (1984).

A constant rearing temperature of 5°C caused stunted growth, low survival rates, and a delay of the transition to the bottom-dwelling mode of life of almost 50 d compared with 10°C. Moreover, cessation of growth at 2°C indicated that constant temperatures below 5–6°C cannot sustain growth of larval plaice under laboratory conditions. In contrast, a diel temperature cycle (10°C/6°C) allowed intermediate somatic and otolith growth rates with the formation of high-contrast increments in otoliths when viewed by light microscope, or wider

incremental zones when viewed by SEM (Karakiri, 1989). It thus appears that temperatures around 5°C are the lower limits that allow growth in juvenile plaice and consequently easily visible increments in otoliths. This finding contrasts with information gathered from the field where plaice larvae occur through February/March in waters with temperatures between 4 and 6°C (Ehrenbaum, 1910). It is unlikely that a "no growth" situation prevails in the field under normal conditions and we must conclude that growth under field conditions at these temperatures must be better than in the laboratory for various reasons, such as food quality or feeding stimuli (von Westernhagen and Rosenthal, 1981).

It has been shown that abrupt increase or decrease of rearing temperature caused a direct response of otolith growth, with growth acceleration after transfer of plaice larvae from lower to higher temperature and growth retardation and delay of the transition to the bottom-dwelling mode of life with the reverse procedure. In this context, it is important to note that increments continue to be deposited daily even under stressful conditions (like extremely low temperature) and no otolith resorption takes place even when no somatic growth occurs (Campana and Neilson, 1985). The mechanism through which temperature influences otolith microstructure is uncertain. It is known that otoliths are formed by the deposition of calcium carbonate (aragonite crystals) in a protein matrix (Degens *et al.*, 1969). It has been shown experimentally that calcium for subsequent deposition on the otoliths is derived from the ambient water, through a regulated branchial pathway and not from dietary sources (Simkiss, 1974; Mugiya *et al.*, 1981; Campana, 1983). Recent investigations have shown that neuroproteins, secreted in the macula, control the rate of aragonite crystal growth (Gauldie and Nelson, 1988). According to the same investigation, neuroprotein secretion is continuously modulated so that narrow, mineral-deficient bands and wider, mineral-dense bands alternate to constitute daily increments. This secretion is subjected to temperature effects and to the supply of physiological calcium ions.

Moreover, these findings may explain the negative effects, such as those of salinity on increment width. The reduced calcium content in low salinity water may have caused the observed reduction in increment deposition. At low temperature this effect was enhanced compared with the reaction of plaice larvae reared at higher temperatures (10°C). Fast-growing plaice juveniles were affected more strongly than larvae by lower concentration of dissolved calcium ions, which may reflect the generally higher calcium-demand in more advanced developmental stages.

The detected variations in increment widths, caused by salinity, support the hypothesis that variations in calcium uptake and deposition in otoliths are also responsible for the variations in appearance and width of daily increments (Mugiya *et al.*, 1981; Tanaka *et al.*, 1981; Campana, 1983). This makes the daily increment readings in otoliths a suitable tool for tracing rhythmic and migratory patterns of juvenile fish in fluctuating environments such as the coastal waters of most seas.

Photoperiod proved to be of secondary importance to increment formation of larval and juvenile plaice, as also reported for other species (Brothers, 1981). A light cycle of 8–10 h day length might be enough to promote maximum growth of plaice under normal physiological conditions. A slight decrease in somatic and otolith growth of larvae moved to shorter day length might be due to the fact that plaice larvae, known to be "visual" feeders, had less time to feed.

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