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DAILY GROWTH INCREMENTS IN THE OTOLITHS OF EUROPEAN SMELT, *Osmerus eperlanus* L., LARVAE.

by

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Abstract

Fish larvae and juveniles of European smelt, *Osmerus eperlanus* L., were collected in the lower Elbe River and aged using daily growth increments in the otoliths. The otolith microstructure in the sagittae and lapilli of larvae sampled was examined and the daily pattern in increment formation was validated using the marginal increment technique. This technique consists of catching fish larvae within a 24-hour period and then, the time of completion of an increment is determined following the width of the last formed increment. The formation of the first daily growth increment corresponds to the onset of exogenous feeding. Measurements which were performed with the assistance of an image analysis system correspond to the width of daily growth increments, perimeters and areas of the otolith microstructures. A potential function was fitted between otolith radius and standard length. Integrated somatic growth rate was estimated as 0.556 $mm \cdot day^{-1}$ from the linear relationship between standard length and the number of daily growth increments enumerated from the sagittae. Back-calculated hatching dates showed two main hatching batches during April 1993 and the time span of the hatching was not longer than 16 days. Some otolith-based back-calculation methods were improved to relate otolith growth to somatic growth.

Introduction

European smelt, *Osmerus eperlanus* L., is the most abundant fish species in the lower Elbe River (Möller 1988, Thiel *et al.* in press). The anadromous smelt has a relatively high fecundity and spawns in the lower Elbe, upstream and downstream of the city of Hamburg mainly along southern shores and within tributaries. The early life history of the Elbe smelt has been described by Ehrenbaum (1894) and Lillelund (1961). The egg, which has a diameter ranging from 0.75 to 0.90 mm is spawned between March and April, depending on the water temperature. The fish hatch as larvae approximately at 4.8 mm total length after 17 days at 12 °C (Borchardt 1986). The yolk sac is fully absorbed at a total length of 8 mm, 9 days after hatching at 17.7 °C (Lillelund 1961). Yolk sac larvae are transported from the spawning grounds to the head of the estuary, and afterwards develop in the marginal areas of the river (Sepúlveda *et al.* 1993). In May, high amounts of smelt larvae can be found in marginal areas immediately downstream of Hamburg. Oxygen depletion occurs in the retention areas and probably causes high mortalities of smelt larvae. An early onset of oxygen depletion can lead to an extinction of an entire fish population in the Elbe estuary (Möller and Scholz 1991). Since 1990 the extension and frequency of this phenomenon has become less conspicuous, and is probably due to reduced pollution (Reincke *et al.* 1992).

In this sense, environmental factors can be structuring forces of the recruitment and larval growth in the anadromous smelt of the Elbe estuary. The effects of these environmental factors i.e. temperature, pH, food availability, oxygen concentrations on otolith and fish growth have been pointed out by different authors (Brothers and McFarland 1981, Karakiri and von Westenhagen 1989). Otoliths are a powerfull tool to recognize transitions and growth patterns (Campana 1992).

Age determination through otolith microstructures can give the age of fish larvae in days, hatching date distributions and approximations about daily growth rate (Moksness 1992). However this kind of analysis require the validation of temporal patterns of deposition of the increments. Validation techniques include monitoring reared larvae of known age (Rice *et al.* 1987; Moksness 1992), marking otoliths with tetracycline or other fluorescent compounds (Tsukamoto *et al.* 1989), observing early life history features that can offer a statistical inference in the counting of increments (Karakiri *et al.* 1991) or marginal increment analysis (Ré 1984, 1993).

Timola (1977) showed the growth pattern in otoliths of Bothnian smelt using scanning electron microscopy and described the fast growth zones (summer ring) consisting of approximately 170 daily growth increments. Lardeaux (1986a) recognised also microstructures in sagittae of the smelt from the Loire River. Garnås (1982) performed investigations upon determination of age and growth comparisons for different year classes of mature smelts (age 1+ to age 6+).

The main purpose of the present study was to investigate the growth pattern of early life stages of European smelt in the lower Elbe River. The formation of growth microincrements and their daily nature were verified; and then, estimates of specific growth rate in the nursery and in the maximal retention zone of smelt larvae were made.

Material and Methods

European smelt larvae were caught from 21 May to 17 April 1993, every two days in a fixed station (53°32'50" N; 9°51'21" E) indicated in Figure 1 as station 1 and located at the upper part of the estuary. Fish larvae were collected also during a 24 hour period in the station 2 (53°32'42" N; 9°48'10"E) and station 3 (53°33'20" N; 9°41'50" E, Figure 1). The mean depths at these stations are 2.90, 2.44 and 3.91 m, respectively. Water temperature and salinity at the water surface were estimated using a portable conductivity meter (LF 196, WTW). Dissolved oxygen was taken using a portable OXI-meter (OXI 196, WTW).

Plankton samples were taken with two different framed ring trawls with mesh size of 300 µm (0.5 m diameter) and 1000 µm mesh size (0.9 m diameter), both provided with digital flow meters (General Oceanics). The sampling was carried out with R/V Ratibor. At each site, the gear was positioned against the current; however alternative oblique hauls, moving in a circle, were performed with an outboard motor boot when the stream velocities were lower than $0.3\ m \cdot s^{-1}$. The duration of the hauls was on the average 1.45 min. A total of 39 samples were taken for otolith microstructure analysis. All samples were fixed immediately after collection in 5 % formaldehyde solution in filtered water and buffered with sodium borate (pH 8.5-9).

Smelt larvae were sorted and counted in laboratory. Larval standard length was measured to the nearest 0.01 mm using an electronic drawing board. Each pair of sagittae and some lapilli were dissected using fine needles, washed with distilled water and 95% alcohol, and mounted using the mounting media DePeX (SERVA) to analyse otolith microstructures. The method used for dissecting, mounting and observing the otoliths was described earlier by Ré (1983). The otoliths were mounted with their plane face (internal face) downwards. Otolith measurements were performed using an image analysis system based on a CCD video camera fitted to a compound optical microscope and connected to a multiscan monitor obtaining a maximal magnification of 3700 times. The video camera was attached to a digitizer board (PC VISION VS-100-AT, Imaging Technology Inc.) installed in a personal computer. Otolith images obtained with this system were analysed with an image analysis software (OPTIMAS v. 4.0, BIOSCAN). Four kinds of measurements were taken in the otoliths: widths of growth increments (µm) and radius (µm), perimeters (µm) and areas (μm^2) of each otolith. Radius were measured from the central focus to the postrostrum in the sagittae. Area and perimeter measurements were obtained with the use of an autotracing function around the otoliths.

To verify the daily nature in the formation of the microincrements, the marginal increment technique was applied. This technique consists of catching fish larvae within a 24-hour period and then, the time of completion of an increment is determined following the width of the last growth increment in relation to the one immediately anterior along the time (Ré 1984). The percentage of marginal increment completion (c), can be estimated as (Morales-Nin 1992) :

$$c = 100 \cdot \left(\frac{l_n}{l_{n-1}}\right) \qquad (1)$$

where (l_n) represents the width of the increment in process of formation and l_{n-1} correspond to the measure of the last formatted increment.

To determine the integrated growth rate, the relationship between daily growth increments and standard length was linearly correlated. Length frequency analysis and length-wet weight relationship established for smelt larvae allow the estimation of the daily length increment (DLI) and the specific growth rate (SGR), respectively. Length-wet weight relationship for 265 fresh smelt larvae was estimated (a = 7.683 E-07, b = 3.476, R^2 = 0.993).

Specific Growth Rate (SGR) was calculated according to the following formula (Houde and Scheckter 1981):

$$SGR = \left(\exp\left(\frac{\ln(Wt_2) - \ln(Wt_1)}{(t_2 - t_1)}\right) - 1\right) \cdot 100 \qquad (2)$$

where, SGR is in percentage per day and, Wti's are, in this study, average wet weights of larvae (in mg) at days 1 and 2.

Daily length increment (DLI in $mm \cdot d^{-1}$) was estimated according to:

$$DLI = \frac{(SL_2 - SL_1)}{(t_2 - t_1)} \qquad (3)$$

where SL_1 and SL_2 are the average standard length of the larvae (in mm) at days t_1 and t_2.

Results

Validation of daily growth increments

A total of 219 sagittae were considered for this analysis. Otoliths were selected from larvae between 7.84 and 21.60 mm standard length (mean SL=16.92 mm). However, few otoliths from fish larvae smaller than 9.0 mm could not be analysed due to difficulties in discerning increments near the otolith margin and the narrow widths in the last increment. The percentage of completion index of the marginal increment during the 24 hour period is shown in Figure 2. Complete deposition of the marginal increment (discontinuous zone) was observed around sunrise (05.45 and 08.45 h, local time) with the incremental zones being deposited in an oscillatory trend during the rest of the 24 hour cycle (Figure 2). In 21 cases, the completed increment was up to approximately 5 % wider than the previouly formed increment and hence, represented daily growth in the otolith.

Otolith growth and microstructure

Yolk-sac larvae (SL < 8.0 mm approximately) were analysed for the occurrence of growth increments, but obvious evidence of deposition of growth zones during the endogenous feeding stage did not exist. Smelt larvae with functional mouths and remaining yolk-sac are already capable of performing exogenous feeding. In this sense, we can assume that the first discontinuous zone correspond to the first feeding check. Measurements in 164 sagittae confirm that the mean radius of the first feeding check was 10.93 ± 1.22 µm (Figure 3). The mean size of the daily growth increments in the sagittae varied from 2.16 µm for the first deposited rings (n = 162) to 11.4 µm for the wider increments (n = 13); whereas the mean size in the lapilli varied from 1.25 µm to 4.11 µm, for the first (n = 26) and the last (n = 1) daily growth increments, respectively.

Statistical comparisons between different otolith size measurements performed with the use of the image analysis system were made. There were no significant differences between the radius, area and perimeter of both sagittae (Wilcoxon test, $p > 0.05$, n = 74). The comparison between the number of increments enumerated in the right and left sagittae anyhow the lapilli showed no significant differences (Wilcoxon test, $p > 0.05$, n = 22). However, counting in the lapilli otoliths was more laborious due to smaller size and increment width. Significant differences were found between the mean size of the sagittae and the lapilli (Wilcoxon test, $p < 0.01$, n = 22).

The statistical intercept of the fitted curve between daily growth increments and standard length (Figure 4) was 6.191 mm and the integrated growth rate (slope) correspond to 0.556 mm·day^{-1} ($r = 0.955$, $n = 164$). Length frequency distributions are shown in Figure 5. Results of daily length increment (DLI) and the specific growth rate (SGR) estimations are shown in Table I.

TABLE I: Summary of the mean length estimates for the smelt larvae between 21 April and 17 May 1993.

	Date	Mean Length (mm)	Mean Wt (mg)	DLI (mm·d^{-1})	SGR (%·d^{-1})
April	21	5.93	0.373	0.590	32.43
	26	8.88	1.521	0.315	12.66
	28	9.51	1.930	0.359	13.48
	30	10.23	2.485	0.663	23.60
May	02	11.55	3.797	0.581	18.14
	04	12.71	5.299	0.625	17.71
	06	13.96	7.342	0.356	9.04
	08	14.68	8.730	0.386	9.32
	10	15.45	10.433	0.157	3.55
	12	15.74	11.188	0.679	15.43
	14	17.12	14.908	0.176	3.60
	16	17.47	16.001	0.431	8.84
	17	17.91	17.415		
mean		13.17	7.802	0.443	13.98
sd		3.59	5.611	0.174	7.94

To compare the relationship between different measurements of the sagittae (radius OR, areas AR and perimeter PE) and fish length, potential curves were fitted (Figure 6) and the parameters of the non-linear regressions are summarised in Table II. All three fitted curves are significant ($p<0.001$). The relationship between standard length and the area of the otolith showed the best fit ($R^2 = 0.942$).

TABLE II: Exponential model of the form $SL = a X^b$ fitted between different measurements in the sagittae and fish larvae length. SL= standard length in mm, X =independent variable (radius, OR; area, AR and perimeter, PE).

Independent variable	intercept a	slope b	R^2	Standard error of the estimate
Radius	2.7878	0.37863	0.9311	0.07799
Area	2.1081	0.19746	0.9424	0.07129
Perimeter	1.4755	0.38899	0.9378	0.07410

The relationship between the number of daily growth increments and otolith size (i.e. radius, area and perimeter) was evaluated by fitting exponential curves (Figure 7). In all cases, the curves showed a good fit for counts lower than 22 daily growth increments. Points to the right (i.e. bigger fish larvae) deviate more from the fitted curve, suggesting a decreasing otolith growth rate.

Hatching date distributions

The average temperature in the sampling stations during the period 21 April to 17 May 1993 was 17.8 °C (sd = 0.59 and n = 39). Smelt larvae deposit the first increment on their otoliths near the end of the yolk-sac stage. According to Lillelund's (1961) experimental observations regarding the span of survival of smelt yolk-sac larvae, the post-hatching age is estimated by adding 9 days to the number of increments counted in the otoliths. Back-calculated hatching date distributions for smelt larvae for 1993 are summarized in Figure 8. The hatching dates showed a bimodal distribution with a first peak centered on 12 April and a secondary peak on 18 April. Hatching duration is thus assumed to last approximately 16 days.

The hatching date distributions given in Figure 8 were evaluated for possible temporal variations in otolith growth taking into consideration the fluctuations on increment size of sagittae. Three age groups were considered: smelt larvae which hatched between 7 to 15 April, between 16 to 19 April, and between 20 to 29 April. The mean cumulative width of the daily microincrements for three hatching groups of smelt larvae in relation to back-calculated age of larvae are shown in Figure 9. There were no significant differences between the slopes of the fitted curves (ANCOVA, $F = 0.541$, $p > 0.05$). However, the slight curvilinearity of the growth trajectories in Figure 9, suggests that the mean cumulative widths of the microincrements at age were best fitted with a one-cycle Gompertz function (Zweifel and Lasker 1976). The final model is summarized in the following equation:

$$L = L_0 \left[\frac{G}{\alpha} (1 - \exp(-\alpha T)) \right] \qquad (4)$$

where L is the mean width of daily growth increments, L_0 is the radius size at hatching (6.715 µm, cv = 0.133), G is the otolith growth rate at hatching (65.127 d^{-1}, cv = 0.019), α is the rate of exponential decay of G (0.063 d^{-1}, cv = 0.071) and T is the back-calculated age from the hatched date (adjusted $R^2 = 0.996$, $n = 28$, $p < 0.001$).

Discussion

Marginal increment analysis is very often used as a standard technique to follow the annual increment formation in adult fish. Given the difficulties in discerning the increments near the larval otolith margin, determination of the completion of the last (marginal) increment is not always conclusive (Geffen 1992). This study confirms the daily nature of otolith growth increments in European smelt larvae using the marginal increment technique described for fish larvae by Ré (1984). Smelt otoliths allow the use of this technique due to their clear microstructure and relatively wider increments (ca. 4 µm), at least in fish larvae bigger than 8 mm. Ré (1984) emphasized that this method is only applicable to fish larvae which remain in the same area and do not migrate vertically during the day.

These conditions are meet for the stations sampled in this study. Firstly, the sampling sites are located in shallow marginal areas of the lower Elbe estuary where current velocities are about 10 % lower than those observed in the main stream (Thiel *et al.* 1993) leading to lower drift effects of smelt larvae in the marginal areas. Sepúlveda *et al.* (1993) found that smelt larvae achieve maximal retention in the study area, whereby maximal larval densities of 600 $ind \cdot m^{-3}$ were found for the same sampling period. Möller (1988) suggested that the main spawning ground for the species are probably located in this area of the southern shore line of the lower Elbe River. Secondly, in these stations the mean depth is 2.4 m, therefore smelt larvae do not make significant vertical migrations through the water column.

Earlier studies in this area, emphasized the importance of zooplankton, particularly the larval stages of the copepod *Eurytemora affinis* as well as cladocerans, in the feeding ecology of 0-group smelt (Ladiges 1935, Fiedler 1990). It is claimed that smelt larvae considered in this study have optimal nutritional conditions during the sampling period. High integrated growth rate estimates (0.556 $mm \cdot d^{-1}$) in waters with a mean temperature of 17.8 °C were found and substantiate this presumption. No information in the literature exist about the growth of European smelt larvae that permit comparisons of these results. Similar daily length increments for larvae between 5 and 20 mm can only be inferred from Ehrenbaum's (1894) investigations. The growth rate of rainbow smelt larvae from the Lake Michigan during the period May and June 1979 was approximately 0.30 to 0.37 $mm \cdot d^{-1}$ (Tin and Jude 1983).

Hatching date distribution analysis is considered as one of the most promising tools for the study of recruitment processes (Campana and Jones 1992). This method could only be used when the samples are collected over a long period of time through which a better approximation of the real dates of production of the newly-hatched larvae can be obtained. In this study the entire hatching duration on 1993 was practically covered.

The back-calculated hatching date distributions of smelt larvae collected in April - May 1993 showed two peaks within the main hatching season. This bimodality is reflected to a certain extent in the length-frequency data. Hatching duration is estimated to be approximately 16 days for 1993. Lillelund (1961) reported a mean hatching span in an average of 14 days for the years 1954-1969. This author emphased the advantages of this, in that smaller larval age and length differences should be found. However, a short hatching span results in a more limited dependence of the age-group of the year to the environmental and feeding conditions. In field experiments done by Borchardt (1986), smelt eggs hatched at 12 °C approximately after 17 days. Considering these determinations, one can estimate that for the year 1993, smelt spawned between 22 March and 7 April with a maximum on 29 March. These results match the earlier field investigations done in this study.

Growth rates estimated for three previously defined hatching groups were not statistically different during the studied period. The Gompertz growth model fitted for larval age versus the cumulative widths along otolith radius, and the relationship fitted for the number of daily growth increments versus different otolith measurements (Figure 7), give evidence of the start of an oscillatory growth trend for larvae over 33 days old. Strong seasonal oscillations of the linear growth of the smelt population of the Loire estuary, excluding fish larvae were found by Lardeaux (1986b).

Image analysis appears to be reliable method for semi-automatic counting of daily growth increments and otolith measurements. Measurements of areas and perimeters are very simple to perform around the otoliths with use of auto- and manual tracing functions, because they are more reliable and accurate. This fact was confirmed for the estimations presented in the relationships between different otolith measurements and larval length (Figure 6). The method avoids subjective decision making about which axis should be measured (Michaud *et al.* 1988) and in some cases, where one should define the centre for each primordia. Moreover otolith areas are two-dimensional variables that are expected to be closer to somatic growth and could give more realistical explanations for growth effects, discussed for example by Secor and Dean (1992) based on otolith diameter - standard length relationships, where in slower growing larvae relatively larger otoliths were found. Area measures would be considered in future analysis to test the accuracy of different growth back-calculation methods.

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Literature cited

Borchardt, D. 1986. Untersuchungen über dir Stinte der 0-Gruppe in Abhängigkeit von den Umweltbedingungen in der Elbe 1985. M. Sc. thesis, University of Hamburg: 103 pp.

Brothers, E. B. and McFarland, W. N. 1981. Correlations between otoliths microstructure, growth, and life history transitions in newly recruted french grunts (*Haemulon flavolineatum*). Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 369-374.

Campana, S. E. 1992. Measurement and Interpretation of the Microstructure of Fish Otoliths, p. 59-71. In Stevenson, D. K. and Campana S. E. [ed.] Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences, 117.

Campana, S. E. and Jones, C. 1992. Analysis of otolith microstructure data, p. 73-100. In Stevenson, D. K. and Campana S. E. [ed.] Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences, 117.

Ehrembaum, E. 1894. Beiträge zur Naturgeschichte einiger Elbefische. Wissenschaftlichen Meeresuntersuchungen Abt. Helgoland, N. F., 1: 37-82.

Fiedler, M. 1990. Die Bedeutung von Makrozoobenthos und Zooplankton der Unterelbe als Fischnahrung. Dissertation, math.-nat. Fac., University of Kiel, 266 pp.

Garnås, E. 1982. Growth of different year classes of smelt *Osmerus eperlanus* L., in Lake Tyrifjorden, Norway. Fauna norv. Ser., A3: 1-6.

Geffen, A. J. 1992. Validation of otolith increment deposition rate, p. 101-113. In D. K. Stevenson and Campana S. E. [ed.] Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences, 117.

Houde, D. E. and Scheckter, R. C. 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 441-453.

Karakiri, M., R. Berghahn, and van der Veer H. W. 1991. Variations in settlement and growth of 0-group plaice (*Pleuronectes platessa* L.) in the Dutch Wadden Sea as determined by otoliths microstructure analysis. Netherland Journal of Sea Research, 27: 345-351.

Karakiri, M. and v. Westernhagen, H. 1989. Daily growth patterns in otoliths of larval and juvenile plaice (*Pleuronectes platessa*): Influence of temperature, salinity and light conditions. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 376-382.

Ladiges, W. 1935. Über die Bedeutung der Copepoden als Fischnahrung im Unterelbegebiet. Zeitschrift für Fischerei, 33: 1-84.

Lardeaux, F. 1986a. Biologie, ecologie et dynamique de population de l'eperlan (*Osmerus eperlanus*, L.) (Poisson, Clupéiforme, Osméridé) dans l'Estaire de la Loire (France). These de Doctorat presèntée à l'Universite de Bretagne occidentale et préparée au Laboratoire de biologie marine de l'Universite de Nantes, France, 614 p.

Lardeaux, F. 1986b. Elements de dynamique de population de l'eperlan (*Osmerus eperlanus*) dans l'estuaire de la Loire. Journal de Recherche Océanographique. 11: 25-28.

Lillelund, K. 1961. Untersuchungen über die Biologie und Populationsdynamik des Stintes *Osmerus eperlanus* (Linnaeus, 1758), der Elbe. Archiv für Fischereiwissenschaft, 12: 1-128.

Michaud, M., Dutil, D. D. and Dodson, J. J. 1988. Determination of the age of young American eels, *Anguilla anguilla*, in freshwater, based on otolith surface area and microstructure. Journal of Fish Biology, 32: 179-189.

Moksness, E. 1992. Validation of daily increments in the otolith microstructure of Norwegian spring-spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 49: 231-235.

Möller, H. 1988. Fischbestände und Fischkrankheiten in der Unterelbe 1984 - 1986. Möller Verlag 344 p.

Möller, H. and Scholz, U. 1991. Avoidance of oxygen-poor zones by fish in the Elbe River. Journal of Applied Ichthyology, 7: 176-182.

Morales-Nin, B. 1992. Determination of growth in bony fishes from otolith microstructure. FAO Fisheries Technical Paper No. 322. Rome, FAO. 51 p.

Ré, P. 1983. Daily growth increments in the sagitta of pilchard larvae *Sardina pilchardus* (Walbaum, 1792), (Pisces: Clupeidae). Cybium, 7: 9-15.

Ré, P. 1984. Evidence of daily growth in pilchard larvae based on otolith growth increments, *Sardina pilchardus* (Walbaum, 1792). Cybium, 8: 33-38.

Ré, P. and Gonçalves, E. 1993. Growth of sprat (*Sprattus sprattus*) larvae in the German Bight (North sea) as inferred by otolith microstructure. Marine Ecology Progress Series, 96: 139-145.

Reincke, H., Lischke, P. and Schindler, J. 1992. Vorstellung der Ergebnisse der Arbeitsgruppe "Meß- und Untersuchungsprogramme" der Internationalen Kommission zum Schutz der Elbe. Proceeding of the 4. Magdeburger Gewässerschutzseminars zur Situation der Elbe, 275-282.

Rice, J. A., Crowder, L. B. and Holey M. E. 1987 Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society, 116: 703-718.

Secor, D. H. and Dean J. M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Canadian Journal of Fisheries and Aquatic Sciences 47: 2219-2227.

Sepúlveda, A., Thiel, R. and Nellen, W. 1993. Distribution patterns and production of early life stages of European smelt, *Osmerus eperlanus* L., from the Elbe River. ICES C.M. 1993 / M: 52.

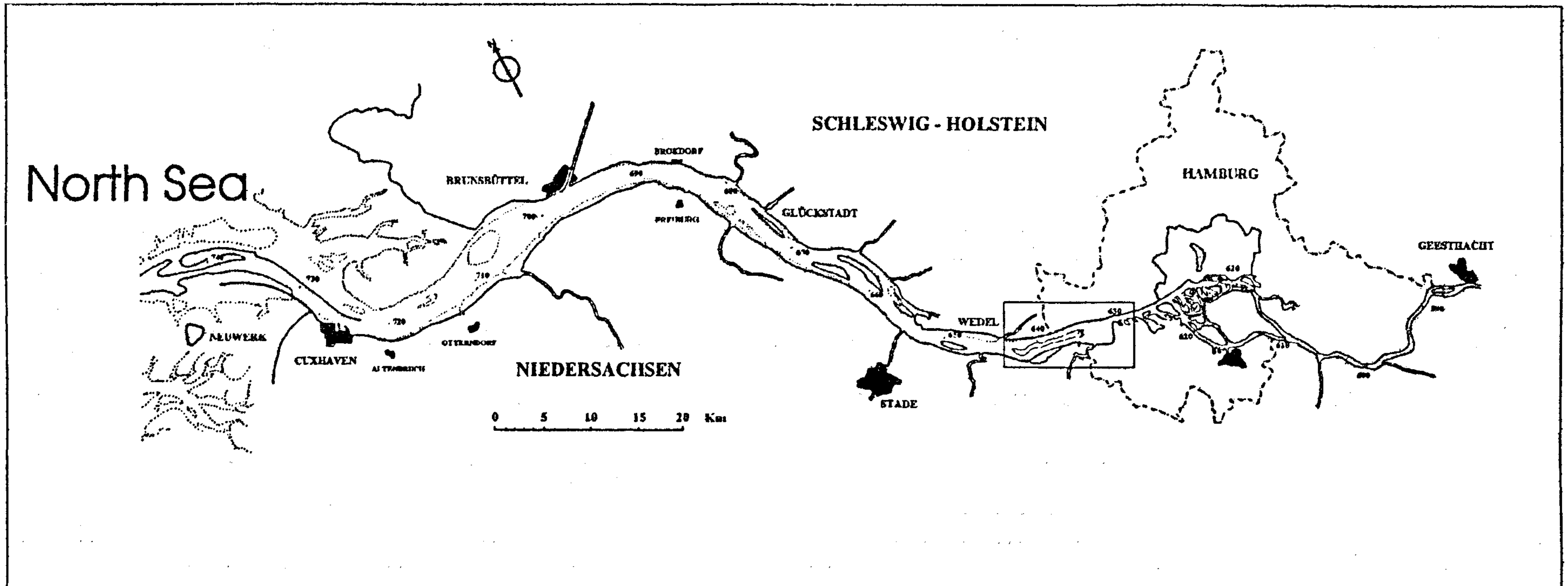
Thiel, R., Sepúlveda, A., Kafemann, R. and Nellen, W. (in prep). Environmental factors as forces structuring the fish community of the lower Elbe River. 27 pp.

Timola, O. 1977. Scanning electron microscope studies on the growth patterns of smelt, *Osmerus eperlanus* (L.), otoliths. Aquilo, Ser. Zool. 17: 57-60.

Tin, H. T. and Jude, D. J. 1983. Distribution and Growth of Larval Rainbow Smelt in Eastern Lake Michigan, 1978-1981. Transactions of the American Fisheries Society, 112: 517-524.

Tsukamoto, K., Kuwada, H., Hirokawa, J., Oya, M., Sekiya S., Fujimoto, H. and Imaizumi, K. 1989. Size dependent mortality of red sea bream, *Pagrus major*, juveniles released with fluorescent otoliths-tags in News Bay, Japan. Journal of Fish Biology 35 (Suppl. A): 59-69.

Zweifel, J. R. and Lasker, R. 1976. Prehatch and posthatch growth of fishes -a general model. U. S. Fishery Bulletin 74: 609-621.



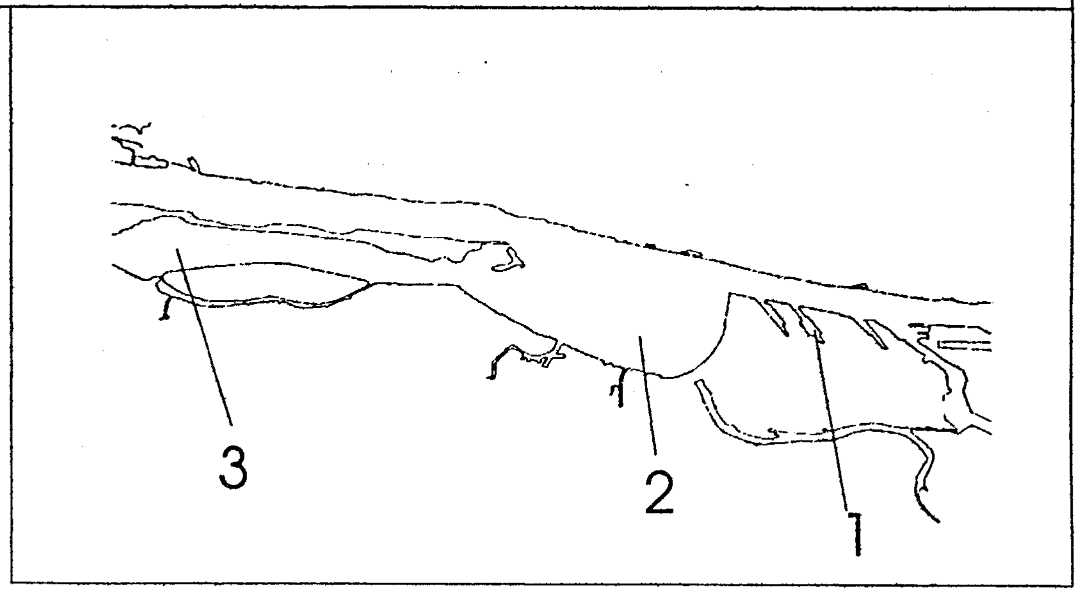


Figure 1. Study area with sampling sites (enlarged).

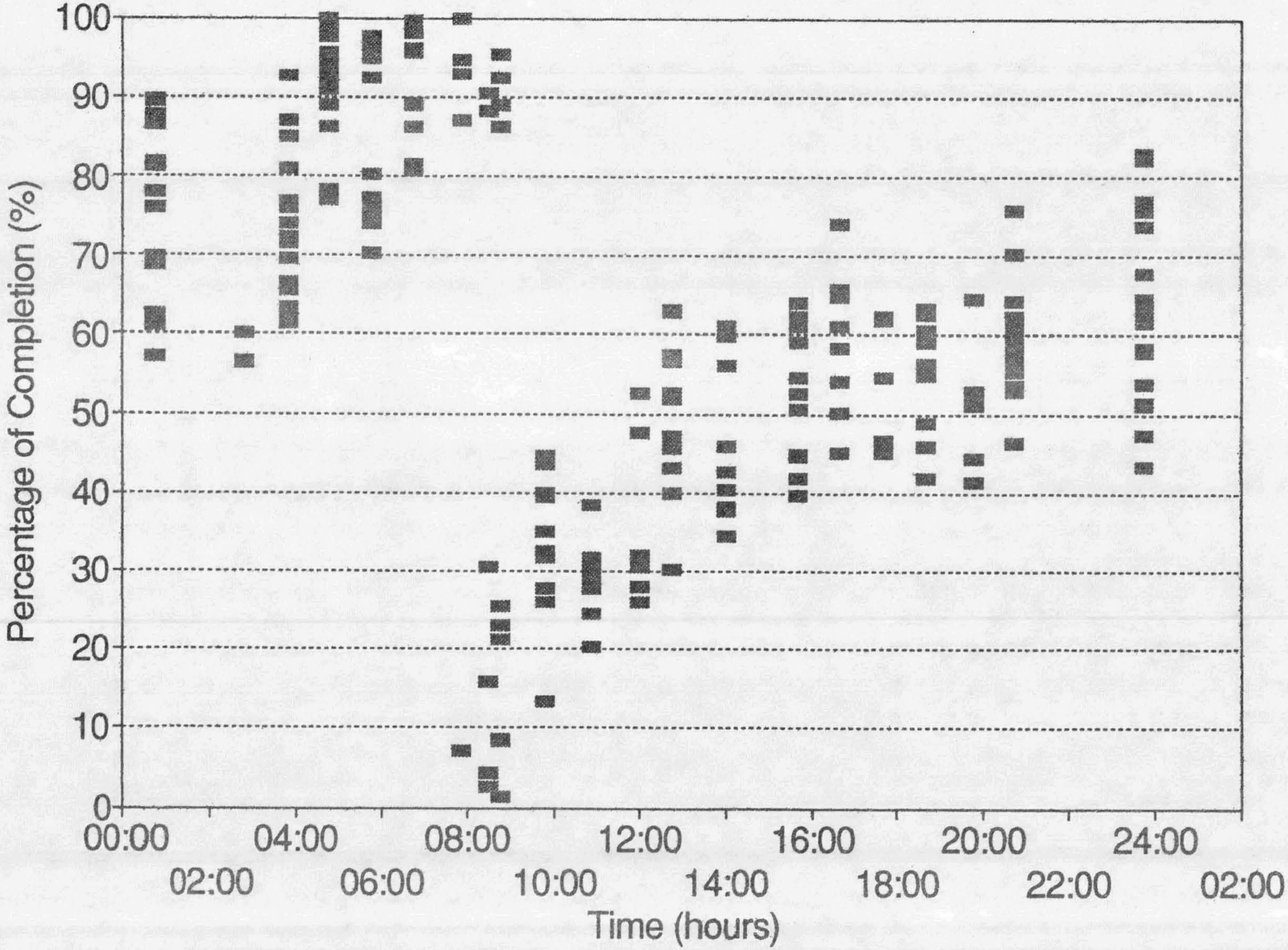


Figure 2. Diel changes in the index of completion (in percentage) of the marginal increment in the sagittae of smelt larvae (219 otoliths) sampled in stations 2 and 3.

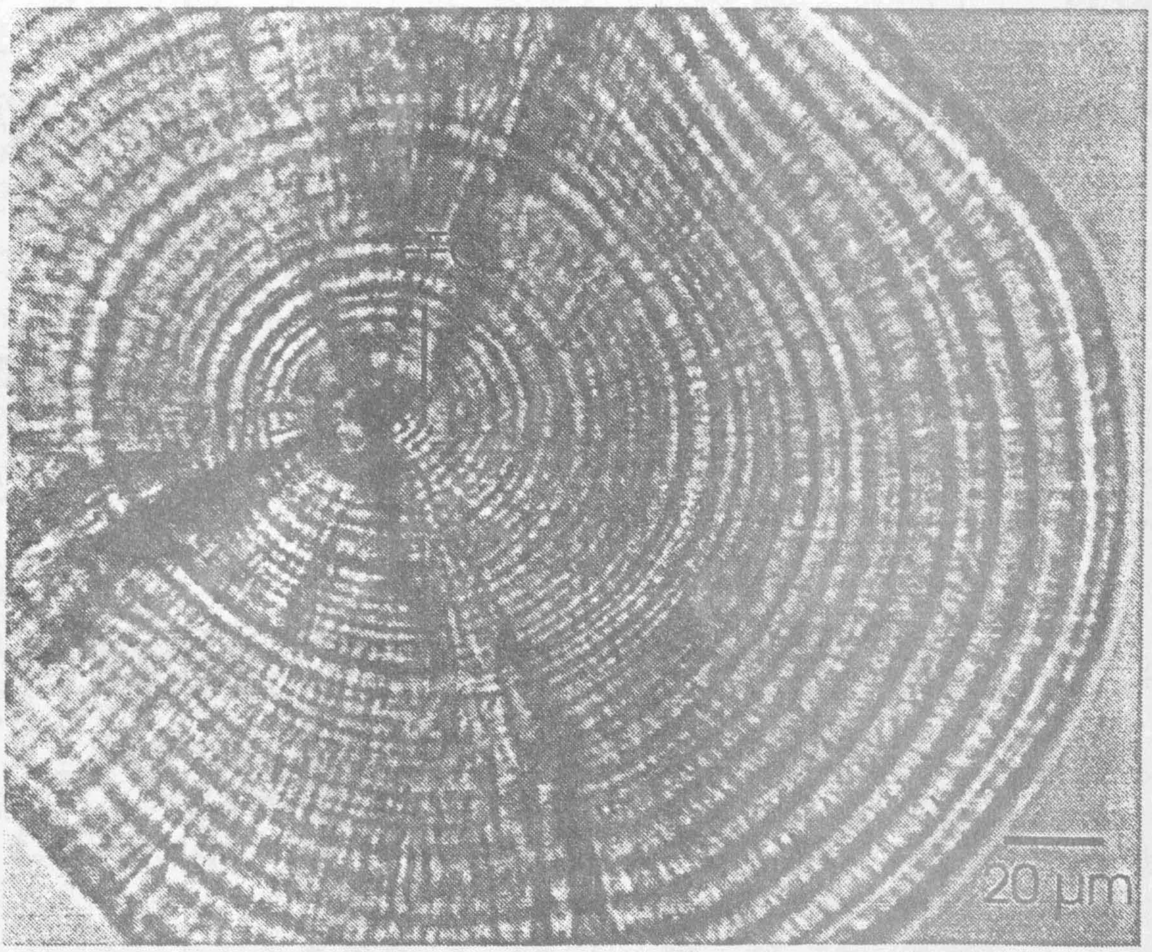


Figure 3. Processed image print of smelt larval sagittae with a standard length of 19.8 mm. The first feeding check increment is showed as FFC.

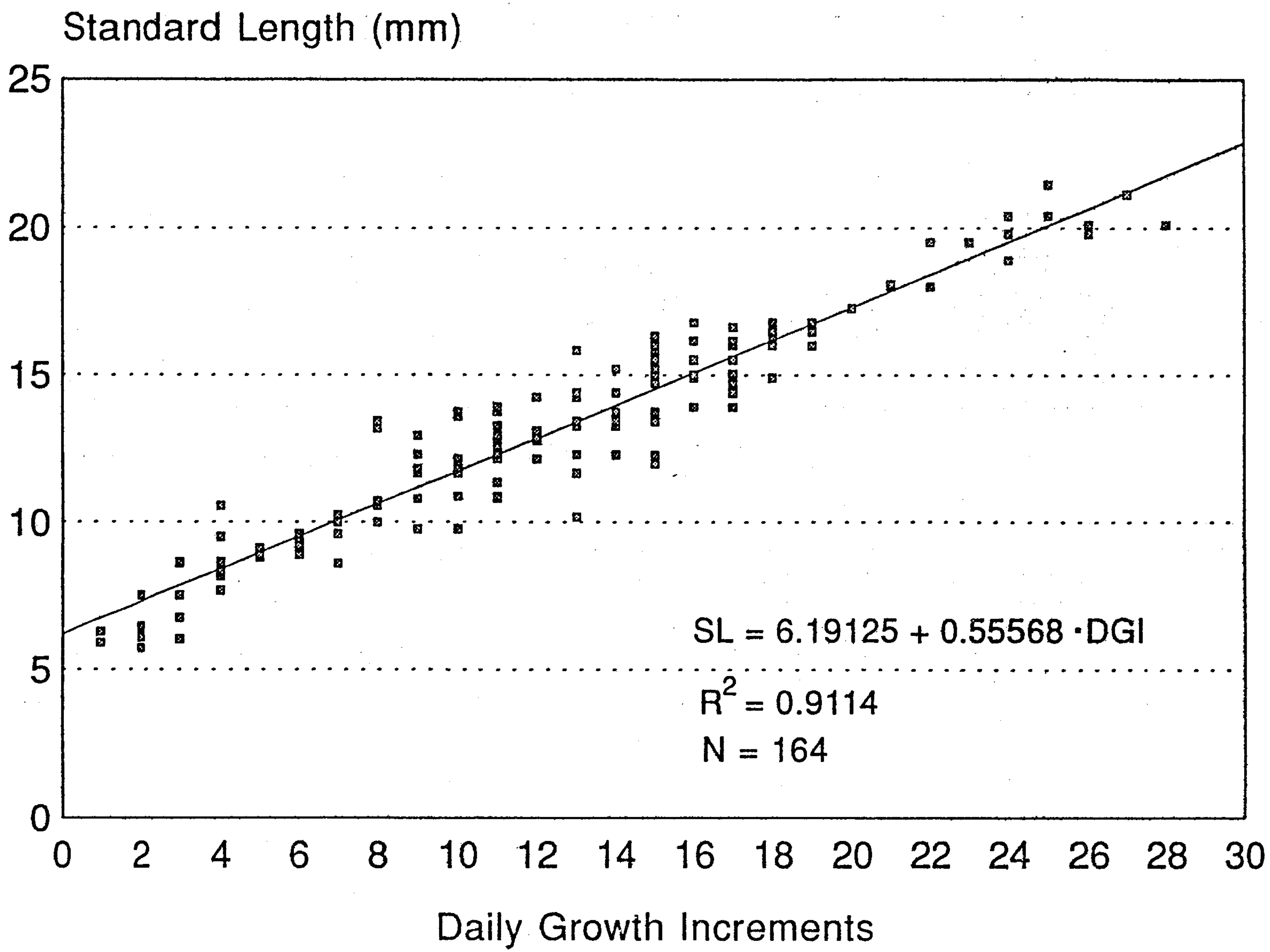


Figure 4. Estimated relationship between the number of daily growth increments (DGI) versus standard length (SL) for larvae of European smelt collected every two days at Station 1 from 21 May to 17 April 1993.

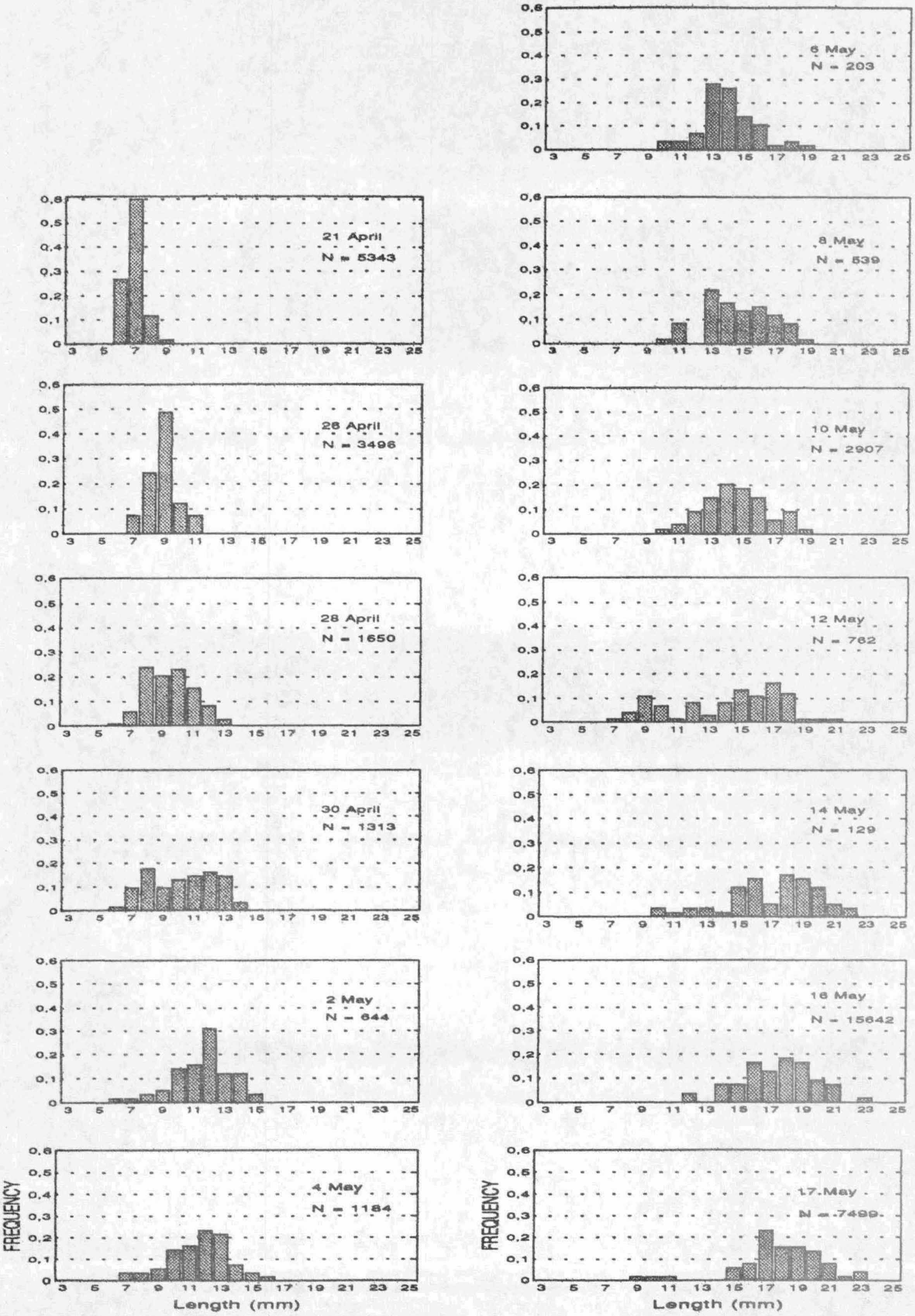
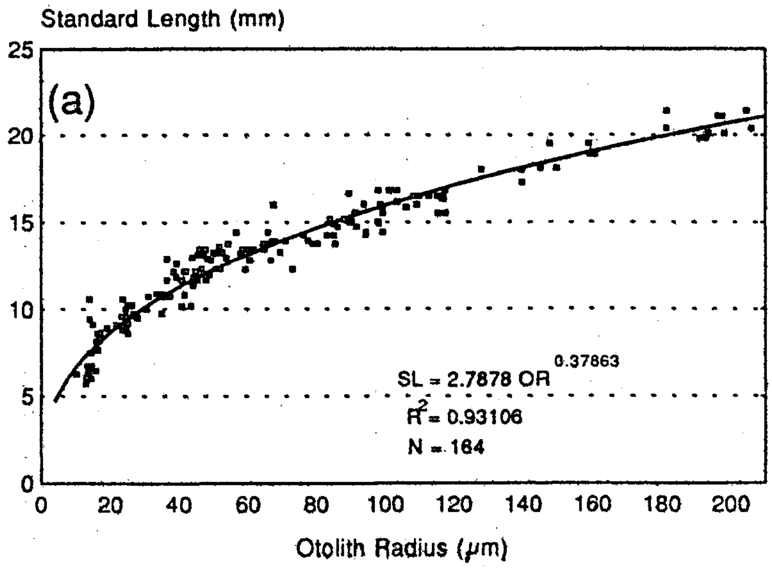
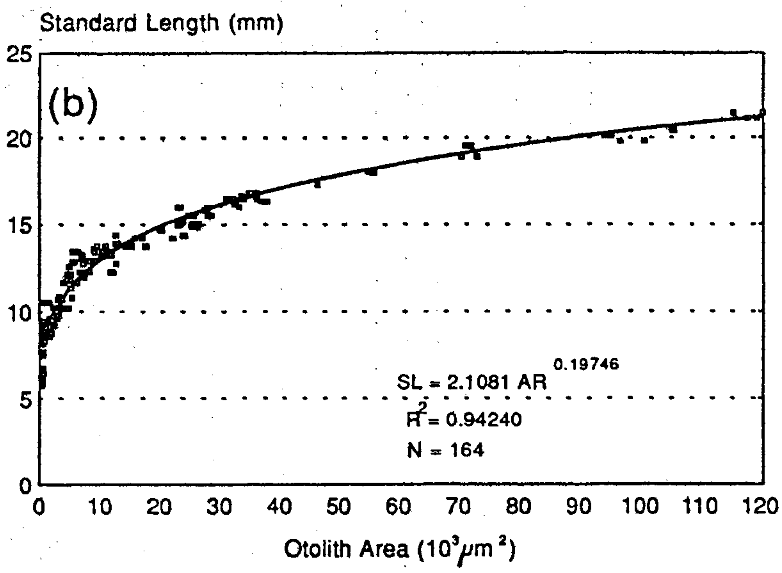


Figure 5. Length frequency distributions of smelt larvae. (N) is number of individuals per 100 m^3.





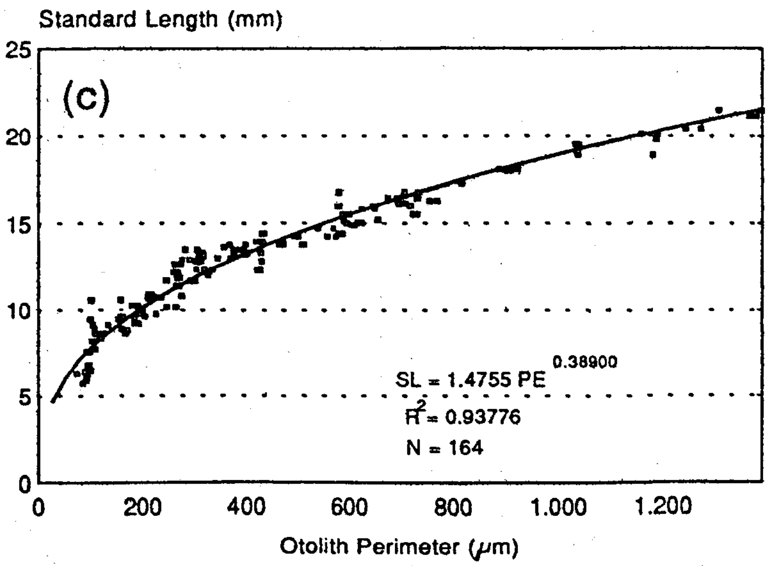


Figure 6. Relationship between different otolith measurements and standard length (SL). (a) Potential regression for otolith radius (OR) versus SL. (b) for otolith area (AR) versus SL. and (c) for otolith perimeter (PE) versus SL.

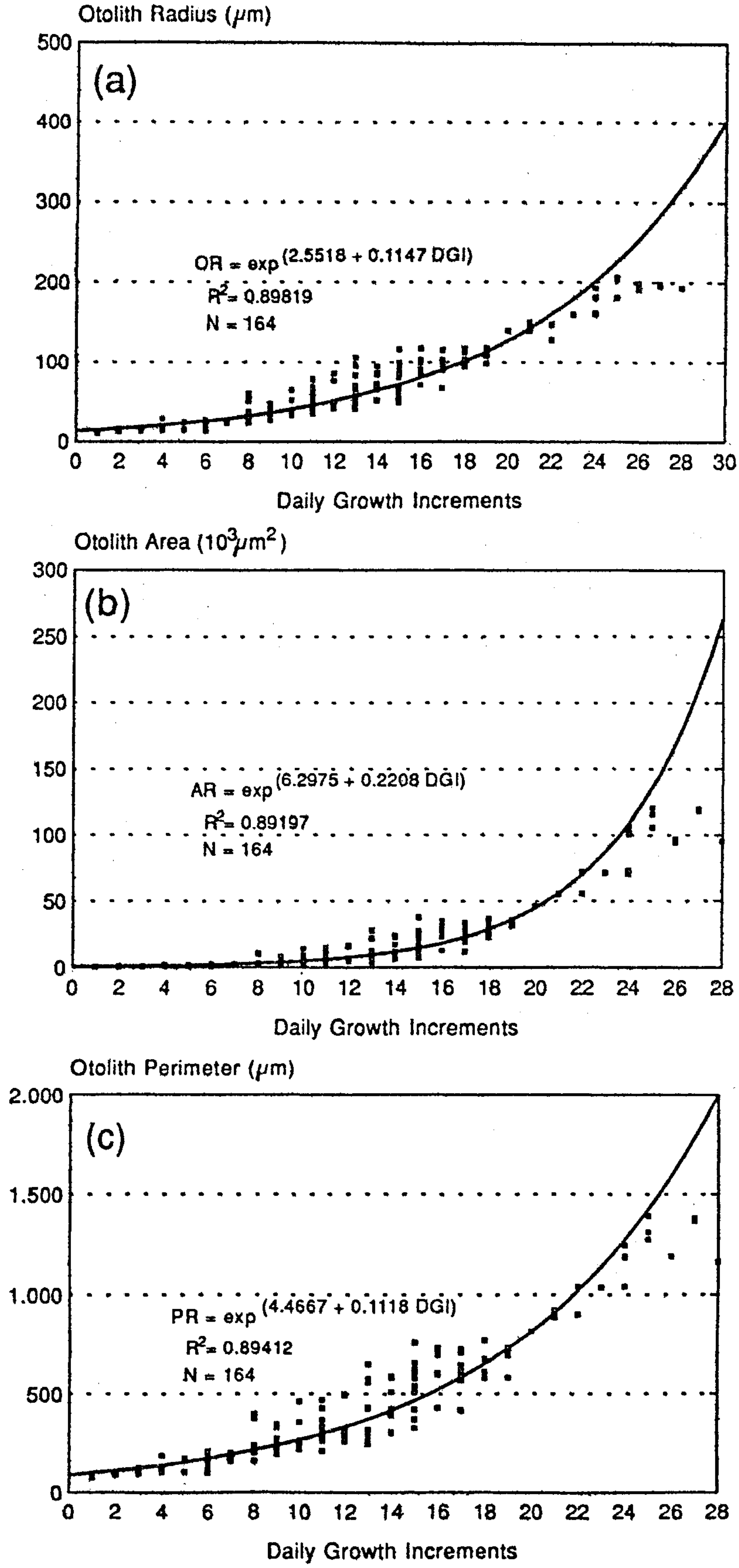


Figure 7. Relationship between number of daily growth increments (DGI) and different otolith measurements. **(a)** Exponential regression for DGI versus otolith radius (OR) in µm. **(b)** DGI and otolith area measured in μm^2. **(c)** and DGI versus otolith perimeter (µm).

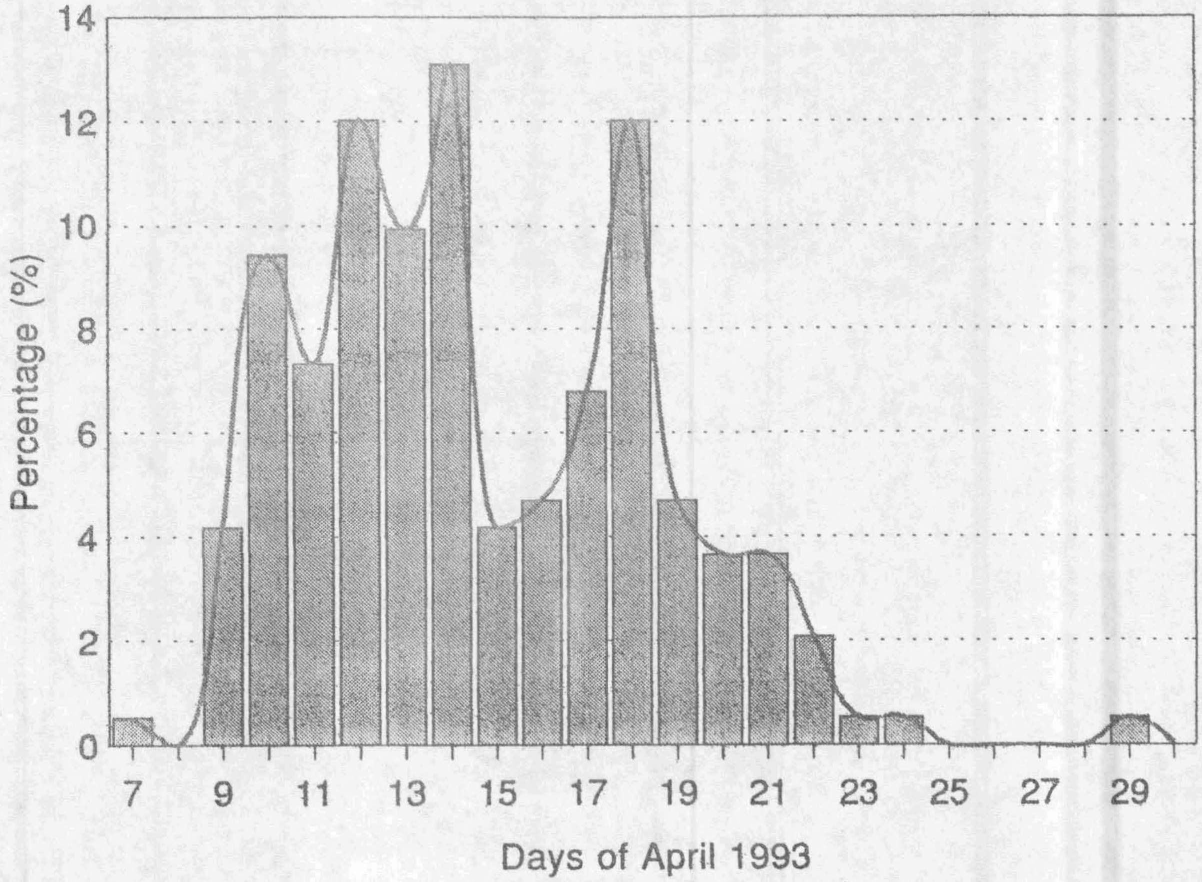


Figure 8. Hatching date distribution of smelt larvae sampled in April - May 1993 back-calculated from 219 larvae.

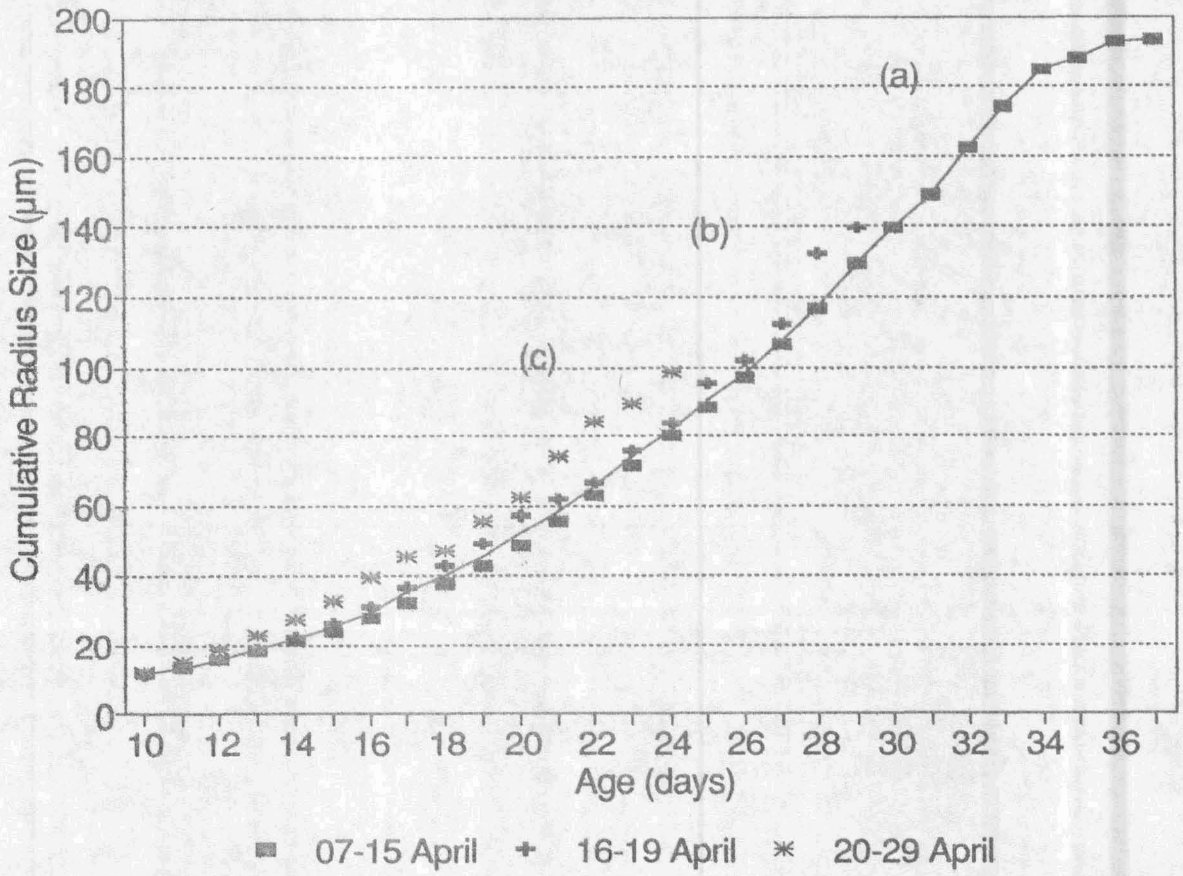


Figure 9. Relationship between the back-calculated age (in days) and the cumulative mean size (width of the increments) measured along the otolith radius of 219 smelt larvae. (a) for larvae hatched between 7 and 15 April. (b) for larvae hatched between 16-19 April. (c) for larvae hatched between 20-29 April.