

Patterns of growth in the early life history of the round herring *Etrumeus teres*

G. PLAZA*, H. HONDA‡, H. SAKAJI*† AND K. NASHIDA*

*Kochi Kuroshio Research Laboratory, National Research Institute of Fisheries Science (NRIFS), Fisheries Research Agency (FRA), Sanbashi-dori 6-1-21, Kochi 780-8010, Japan and ‡Research Promotion and Development Department, FRA, Minato-Mirai 2-3-3, Nishi-Ku, Yokohama 220-6115, Japan

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Early life history traits of young-of-the-year (YOY) round herring *Etrumeus teres*, caught in Tosa Bay (south-western Japan), were studied using otolith microstructure analysis for the 2000–2003 year classes. Hatch dates ranged from October to March, and were restricted to either autumn or winter within each year class. YOY ranged from 50 to 123 mm total length (L_T) and from 57 to 192 days in age. The relationship of L_T to otolith radius was linear. Individual growth rates (G_I) were backcalculated between the 70th and 150th days (the size range of most YOY caught) using the biological intercept method. G_I ranged from 0.3 to 1.4 mm day⁻¹ and decreased in most cases as season progressed irrespective of year class, although G_I in winter cohorts were significantly higher than in autumn cohorts. Otolith growth rates (G_O) ranged from 2.13 to 12.25 $\mu\text{m day}^{-1}$ for autumn spawned YOY and from 3.12 to 12.41 $\mu\text{m day}^{-1}$ for YOY spawned in winter. The G_O trajectories followed three consistent patterns: (1) an increase in increment widths after first feeding through the second week of larval life, then (2) a plateau in increment spacing before increment widths increased again until reaching the maximum growth rate, followed by (3) a gradual decrease in increment widths until the end of the fifth month. The three stages occurred irrespective of spawning season, although YOY spawned in October and December had higher G_O during stages (1) and (2) than YOY spawned in February and March, whereas higher G_O was observed for late-winter cohorts in stage (3). Otolith growth from YOY spawned in December and January showed an intermediate pattern between YOY hatched in the early autumn (October to December) and late winter (February to March). The G_O trajectories were cross-matched to the calendar date to estimate time series of otolith growth rates (G_{OTS}) for each year. A parabolic trend was found with maximum G_{OTS} in autumn and spring and minimum values in winter. This trend was significantly correlated to daily sea surface temperature variations. The differences in otolith growth trajectories suggest that the otolith microstructure of *E. teres* may be used as a natural tag for identifying autumn and winter spawned cohorts.

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Key words: ARIMA; cross-correlation; growth rate; hatch date; otolith increment width; sagittae.

†Author to whom correspondence should be addressed. Tel.: +81 88 8325146; fax: +81 88 8313103; email: hidekun@fra.affrc.go.jp

INTRODUCTION

Growth during the early life of clupeoids can be divided into three stages: the egg and yolk sac stage, larval feeding stage and juvenile growth. The duration of the egg and yolk sack stage is closely related to water temperature, whereas the length of the larval feeding stage seems to be a function of both temperature and abundance of food (Blaxter & Hunter, 1982). Growth during the early juvenile stage, particularly during the metamorphosis from larva to juvenile, is asymptotic in most species (Blaxter & Hunter, 1982; Thorrold, 1989; Watanabe & Saito, 1998; Takahashi *et al.*, 2001). Asymptotic growth suggests that a marked decline in growth occurs during metamorphosis, a stage that encompasses substantial changes in morphology, physiology and ecology, and as a consequence is a potentially vulnerable time for fish survival (Watanabe & Saito, 1998; Webb, 1999). It remains uncertain, however, whether the decrease in growth occurs irrespective of the environmental conditions affecting growth (*e.g.* food and water temperature) or merely as a result of ontogenetic changes that occur during metamorphosis. Likewise, growth patterns after metamorphosis during the late juvenile stages for clupeoids are poorly known.

Growth rates can be reconstructed for individual fishes by measuring the width of the daily otolith increments due to the proportionality between fish length and otolith length. Backcalculations from young-of-the-year (YOY) fishes to larvae cannot be made if the otolith and fish length relationship for the entire early life history period is not known (Campana & Jones, 1992; Hare & Cowen, 1995; Folkvord & Mosegaard, 2002). When this information is not available individual growth rates can only be estimated for the range of length of the YOY collected. An alternative approach, however, is to use the increment alone as a proxy of fish growth. Moreover, the increment width of a group of YOY can be cross-matched to the calendar date and combined to estimate daily time series of otolith growth rates (G_{OTS}). Consequently, if daily data of oceanographic local conditions are available potential modifiers of growth success can be identified.

The round herring *Etrumeus teres* (DeKay) is distributed worldwide, with several separate populations in the Red Sea, eastern Africa, Japan, southern Australia, eastern Pacific and western Atlantic Oceans. Despite its commercial importance, there is little knowledge of its early life history traits, particularly during the early and late juvenile stages. In this study the otolith growth patterns of YOY of this commercially important clupeoid were examined. Once the relationship between otolith growth and fish growth was established, the individual growth rates were estimated for the size range of YOY collected. Then, the otolith growth trajectories were reconstructed from first feeding through the first 5 months of YOY life for monthly-hatched cohorts. Finally, the relationships between daily time series of increment width and surface water temperature (SST) using cross-correlation analysis were examined.

MATERIALS AND METHODS

Young-of-the-year *E. teres* were caught by commercial set nets in spring and summer in 2000, 2001, 2002 and 2003 in two locations (Iburi 32° 48' N; 133° 59' E and Komam 32° 47' N; 132° 42' E) in Tosa Bay, southern Japan (Table I). The fish were analysed

TABLE I. Summary statistics of young-of-the-year (YOY) *Etrumeus teres* collected (n) in commercial set nets in the nearshore zone in Tosa Bay, southern Japan. n corresponds to the number of fish collected and also to fish used for otolith microstructure analysis, except for dates with subscripts

Year	Date	n	Mean \pm s.d. L_T (mm)	Range (mm)
2000	5-Apr	3	89.77 \pm 2.66	87–91
	17-Apr	6	118.85 \pm 4.37	112–123
	18-Apr	23	96.68 \pm 15.08	72–121
2001	17-Apr	80 ^a	61.12 \pm 5.38	50–73
	14-May	17	84.10 \pm 7.35	66–100
	27-May	5	107.20 \pm 7.12	98–113
	17-Jun	6	87.54 \pm 9.36	76–99
	19-Jun	10	87.51 \pm 7.91	77–102
	24-Dec	21	162.76 \pm 8.46	140–179
2002	14-Apr	2	88.50 \pm 2.12	87–90
	5-May	1	113.00	113–113
	29-May	11	101.00 \pm 11.82	74–114
2003	29-Mar	150 ^b	93.09 \pm 6.69	75–107
	31-Mar	32	78.26 \pm 13.49	60–105
	5-May	3	96.09 \pm 4.03	92–99

^{a,b} Subsample from 100 and 196 YOY, respectively

fresh or frozen at -15°C so that analyses could be made later. Total lengths (L_T) were measured to the nearest 0.01 mm, and then the left and right sagittae were removed, cleaned of adhering tissue, dried and stored in clean envelopes. Sagittae were prepared using the slide-glass embed method (Plaza *et al.*, 2005). After polishing, counts of the daily increments were made twice across the area of distinctive increments. Otolith radii (R_O) and increment widths were measured through a linear axis from the core along the postrostrum of the sagittae, consistently the best axis for increment counting and measurement. The increment widths were standardized to the maximum radius to minimize any possible variation from the linear trajectory of measurement.

The fish collected in the four year classes ranged from 50 to 123 mm L_T and from 57 to 192 days in age, but within years the L_T and ranges were restricted (Table I). In addition, the set net sampling did not provide a complete random design on a temporal and spatial scale. For these reasons, comparisons of mean L_T and age as well as mean daily growth rates (*i.e.* the slopes of the L_T and age relationship) between hatched cohorts and years were not carried out in this study. Conversely, the study focused on estimating the otolith growth pattern by monthly cohort and G_{OTS} . For this purpose, samples from 2001 and 2003 were sufficient to apply the statistical tests needed. Samples available for otolith analysis were smaller for 2000 and 2003; nevertheless, these samples could be used to assess the annual otolith growth patterns for these years.

Otolith increments are deposited on a daily basis for this species on the second day after hatching (Hayashi & Kawaguchi, 1994). The relationship between L_T and R_O for the juveniles analysed from Tosa Bay was described by a linear regression. Consequently, backcalculations of previous L_T were possible. Backcalculations were made using the biological intercept method (BIM) (Campana, 1990) given by: $L_T = L_c + (R_i - R_c) / (L_c - L_{T2d}) (R_c - R_{2d})^{-1}$, where L_T is the biological intercept (*i.e.* 6.5 mm L_T) at first feeding, R_{2d} is the otolith radius at the first daily ring, L_c is the size of the fish at capture, R_i is the otolith radius at a previous age and R_c is the otolith radius at the time of capture. The daily mean individual growth rates (G_I) were averaged for each 10 day period from the 70th

day through to the 150th day by the formula $G_i = 0.1(L_{T_i} - L_{T_{i-10}})$, where L_{T_i} is total length at age i . Differences in G_i and increment widths among cohort and over time (*i.e.* age) were tested using a repeated measure (RM) ANOVA (Sokal & Rohlf, 1995). The analysis was a mixed two-factor design, with cohort as an independent factor [*i.e.* between-subject factor (a) with cases arranged in rows], and age as a repeated factor [*i.e.* within-subjects factor (b) with numbers of levels arranged in columns]. G_i and increment widths were averaged every 10 days before applying RM ANOVA. To facilitate statistical comparison and based on the growth patterns the data from all years were combined to examine the progression of G_i and increment width of YOY hatched in each month. All RM ANOVA were achieved on a balanced set of observations [*i.e.* 'n' the smaller sampling size in the comparison between cohorts (a)] and a balanced set of levels over age [given by the level (b) with the younger age]. Degrees of freedom were $a - 1$ for between-subjects factor, $a \times (n - 1)$ for between subjects-error term, $b - 1$ for within-subjects factor and $a \times (b - 1)(n - 1)$ for within-subjects error term. Four RM ANOVAs were set: (1) an overall analysis among the six monthly cohorts [*i.e.* overall-between cohorts, $a = 6$ (December, October, December, January, February, March CL), $n = (26)$] and over age [*i.e.* overall age with $b = 6$ (70, 80, ..., 120) for G_i and $b = 12$ (10, 20, ..., 120) for increment width]; (2) between October and November cohorts (*i.e.* cohorts_{Oct-Nov}, $a = 2$, $n = 37$) and over age (*i.e.* age_{Oct-Nov} with $b = 9$ (70, 80, ..., 150) for IGR and $b = 15$ (10, 20, ..., 150) for increment width); (3) between December and January cohorts (*i.e.* cohorts_{Dec-Jan}, $a = 2$, $n = 29$) and over age [*i.e.* age_{Dec-Jan} with $b = 6$ (70, 80, ..., 120) for G_i and $b = 12$ (10, 20, ..., 120) for increment width]; (4) between February and March (*i.e.* cohorts_{Feb-Mar}, $a = 2$, $n = 26$) and over age [*i.e.* age_{Feb-Mar} with $b = 6$ (70, 80, ..., 120) for G_i and $b = 12$ (10, 20, ..., 120) for increment width].

Birth dates (BD) of YOY were backcalculated by subtracting the total age in days from the calendar day of sampling plus 2-days. Birth date distributions were not corrected for mortality effects, because survival rates during the larval stage are unknown for *E. teres*. Hence, BD were only used to describe the spawning characteristics of adults.

TIME SERIES OF OTOLITH GROWTH (G_{OTS})

The daily increments for an individual fish can be cross-matched to the day it was formed using the total age and day of capture to estimate G_{OTS} . Each YOY otolith, however, has its own biological growth curve, which can influence the population growth series. Hence, growth-rate effect must be removed to make increment width of individual series comparable within a group of fish. To remove the age effect, least square means of G_{OTS} were estimated by using ANOVA as follows: $\ln(O_{gr} + 0.5) = \mu + \alpha_i + \beta_j + \epsilon_{ijk}$, where O_{gr} is the otolith growth rate, μ is the overall mean growth rate, α is the effect of the calendar-date i , β is the effect of the specimen age j , and ϵ_{ijk} is the error term (Ralston, 1995).

Hourly data of sea surface water temperature (SST) were obtained from two monitoring buoys located in Tosa Bay (buoy number 10: 33° 01' N; 134° 07' E; buoy number 12: 33° 07' N; 133° 37' E) belonging to the Kochi Prefectural Fisheries Experimental Station. The temperature profile covered the spatial range to which larvae and YOY were exposed. Hence, the daily average (from the 24 hourly observations and the two stations) was used as an index of daily SST variation. The relationship between G_{OTS} and SST were examined using cross-correlation analysis. For this purpose, the series were firstly examined using autoregressive (AR), moving averages (MA), and autoregressive integrated moving average (ARIMA) (Box & Jenkins, 1976). The order of an ARIMA model is usually denoted by the notation (ARIMA) (p, d, q), where p is the order of the autoregressive part, d is the order of the differencing and q is the order of the moving-average process. Given a dependent time series ($Y_t; 1 \leq t \leq n$), mathematically the ARIMA model is written as: $\phi B(1 - B)^d Y_t = \mu + \theta(B)a_t$, where t is a time index, μ is the mean term, B is the backshift operator, that is, $BX_t = X_{t-1}$; $\phi(B)$ is the autoregressive operator, represented as a polynomial in the back shift operator:

$\phi(B) = 1 - \phi_1 B - \dots - \phi_p B^p$, $\theta(B)$ is the moving-average operator, represented as a polynomial in the back shift operator: $\theta(B) = 1 - \theta_1 B - \dots - \theta_q B^q$ and a_t is the random error. At first, univariate models for the independent variable were used to filter both the SST and G_{OTS} before estimating their cross-correlation functions. This process, termed 'prewhitening', is used to eliminate the spurious high correlation due the autocorrelation. The identification was based in the examination of the autocorrelation (ACF) and partial autocorrelation functions (PACF) as implemented in SYSTAT and SAS Inc. softwares.

RESULTS

OTOLITH MORPHOLOGY AND MICROSTRUCTURE

Whole sagittae of juvenile round herring were very thin (mean \pm s.d. thickness = 0.31 ± 0.09 mm, range: $0.22 - 0.43$ mm), long and slightly concave. The whole sagittae of all juveniles had a translucent core visible under induced light without polishing. All sagittae had a distinctive check surrounding the otolith core [mean \pm s.d. radius 6.7 ± 1.25 μ m; range: $4-10$; Fig. 1(a)], and the first distinctive increment surrounded a diffuse zone after the first check at a mean \pm s.d. radius of 11.49 ± 2.26 μ m [range: $7-17$ μ m; Fig. 1(a)]. No increments were observed between the two checks, even in double polished sagittae. The first daily increment forms 2 days after hatching for *E. teres* (Hayashi & Kawaguchi, 1994), although the radius of the sagittae at the first increment deposition is unknown. Hence, the first increment after the diffuse zone was

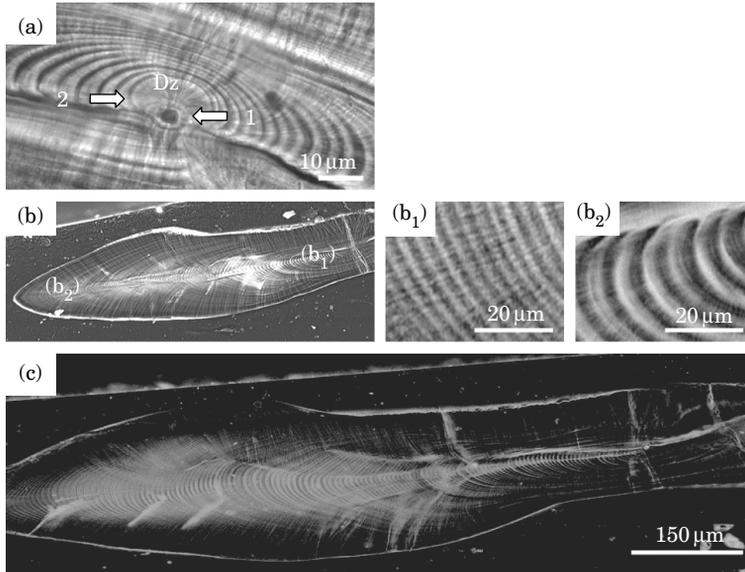


FIG. 1. Light microscope images of (a) the frontal plane of a sagitta from a young-of-the-year (YOY) *Etrumeus teres* collected in Tosa Bay, northern Japan in winter 2001 (1, first check surrounding the dark primordium; 2, second check surrounding the diffuse zone (Dz)). (b) Inverted image of a sagittae from 95 mm L_S YOY spawned in autumn 2000. (b₁) Increment widths at the onset of the increment deposition. (b₂) Increment widths at the otolith edge. (c) Inverted image of a sagittae from 110 mm L_T YOY spawned in winter 2001.

considered as the beginning of daily deposition in this study. Otolith increments of YOY up to 150 days could be read clearly [Fig. 1(b), (c)], but most increments became unreadable thereafter, especially when a decrease in spacing and resolution accompanied the onset of the deposition of the first hyaline zone. These otoliths, collected on 24 December 2001 (Table I), were only used for fitting the L_T and R_O relationship.

LIFE HISTORY TRAITS

Backcalculated birth dates of the collected YOY ranged from early October to late March, although birth dates were restricted to autumn [Fig. 2(a), (d)] or winter [Fig. 2(b), (c)] within year classes. The relationships between L_T and R_O were fitted using the combined data by year and cohorts to increase both the sampling size and the range of the analysis. The relationship of L_T to R_O was well described by a linear regression with no apparent heteroscedasticity in the residuals (Fig. 3). Consequently, the BIM was used to backcalculate fish growth trajectories through the size range of the YOY analysed. Individual growth rates averaged each 10 day period from the 70th to the 150th day ranged from 0.31 to 1.24 mm day⁻¹. G_I varied over fish age (overall-within ages: $F_{5,150}$, $P < 0.001$) and between monthly cohorts (RM ANOVA, overall-between cohorts: $F_{5,750}$, $P < 0.001$), showing a decreasing trend for October and November cohorts [Fig. 4(a), (b); cohorts Oct–Nov: $F_{1,72}$, $P = 0.18$; age Oct–Nov: $F_{8,576}$, $P < 0.001$], low variability for December and January over time [Fig. 4(c), (d); cohorts Dec–Jan: $F_{1,56}$, $P < 0.001$; age Dec–Jan: $F_{5,280}$, $P = 0.022$], and a parabolic tendency for February and March cohorts [Fig. 4(e), (f); cohorts Feb–Mar: $F_{1,50}$, $P = 0.084$; age Feb–Mar: $F_{5,250}$, $P < 0.001$].

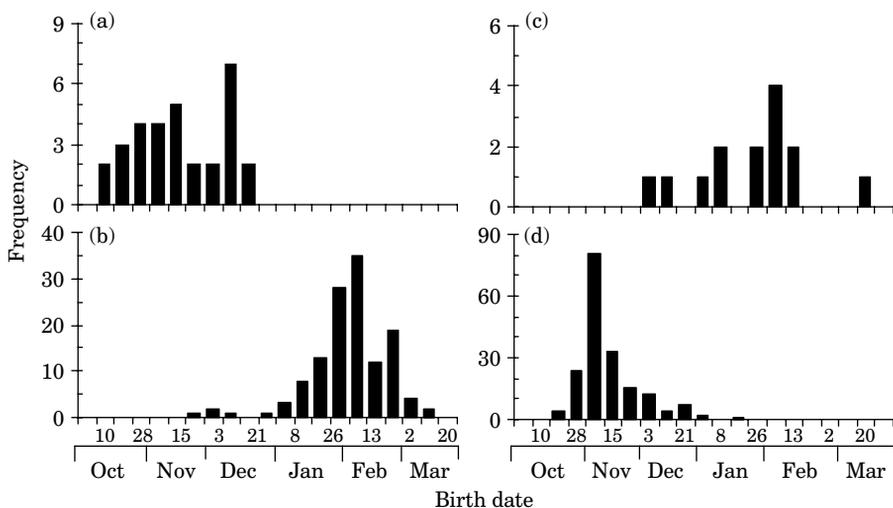


FIG. 2. Hatch date distributions for four year-classes of the young-of-the-year *Etrumeus teres* collected from spring to summer: (a) 2000 [$n = 31$, mean \pm s.d. age (A_M) = 152 \pm 25 days], (b) 2001 ($n = 129$, $A_M = 64 \pm 32$ days), (c) 2002 ($n = 14$, $A_M = 122 \pm 17$ days) and (d) 2003 ($n = 185$, $A_M = 130 \pm 13$ days) in Tosa Bay, southern Japan.

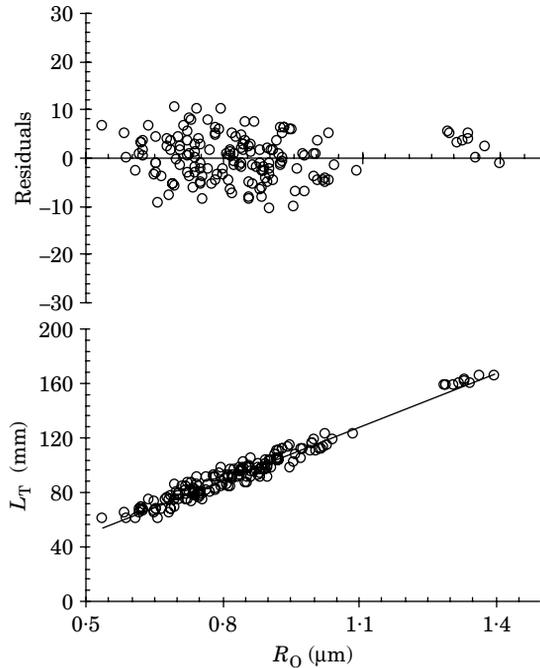


FIG. 3. Least square regressions of total length and otolith radius for juvenile *Etrumeus teres* collected in Tosa Bay, southern Japan, from 2000 to 2003. The curve was fitted by: $y = 131.27 (2.19) x - 16.60 (1.88)$ (S.E. are given in parenthesis) ($r^2 = 0.98$). Residuals (observed-predicted) of the linear fit are also shown.

OTOLITH GROWTH TRAJECTORIES AND SEASONALITY IN WATER TEMPERATURES

The G_O ranged from 2.05 to 12.43 $\mu\text{m day}^{-1}$ for autumn spawned YOY and from 3.18 to 12.54 $\mu\text{m day}^{-1}$ for YOY spawned in winter. Hence, G_O were also combined across years to examine the otolith growth trajectories by monthly cohorts. In general, three consistent patterns in otolith growth occurred: (1) increased growth after first feeding through to the second week of larval life, then (2) a plateau in increment spacing before growth increased again until the maximum growth rate was reached, and finally (3) a progressive decrease in increment width throughout the late juvenile life (until the fifth month). The three stages occurred irrespective of spawning season, although the trajectories over age (overall-within ages: $F_{11,1650}$, $P < 0.001$) differed between spawning cohorts (overall-between cohorts: $F_{5,150}$, $P < 0.001$); YOY spawned in October and November had higher G_O during the larval and early juvenile stages [Figs 1(b) and 4(g), (h); RM ANOVA, cohorts $_{\text{Oct-Nov}}$: $F_{1,72}$, $P = 0.47$; $\text{age}_{\text{Oct-Nov}}$: $F_{14,1008}$, $P < 0.001$] than YOY spawned in February and March [Figs 1(c) and 4(k), (l); cohorts $_{\text{Feb-Mar}}$: $F_{1,50}$, $P = 0.79$; $\text{age}_{\text{Feb-Mar}}$: $F_{11,550}$, $P < 0.001$] but the opposite occurred after the second month of YOY life. G_O of December and January cohorts showed an intermediate pattern between the early autumn and late winter hatched YOY [Fig. 4(i), (j); cohorts $_{\text{Dec-Jan}}$: $F_{1,56}$,

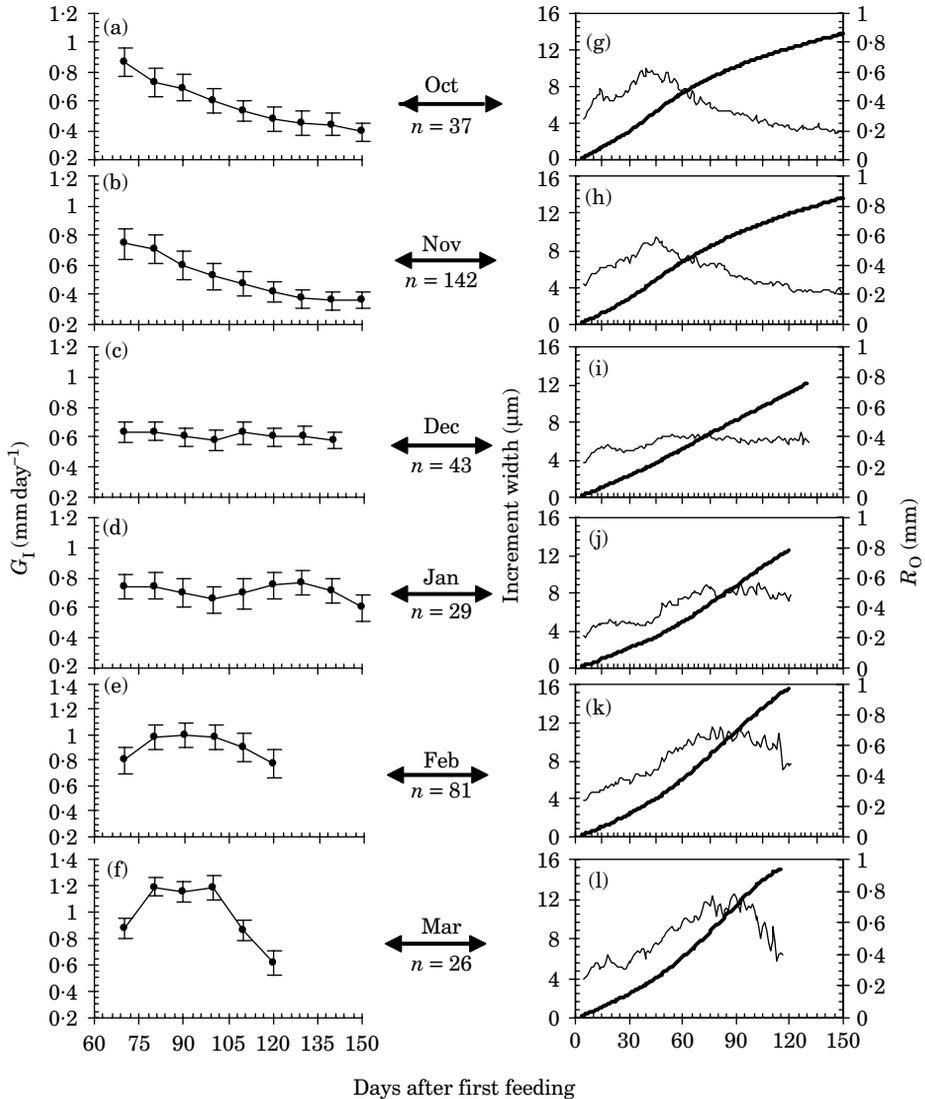


FIG. 4. (a)–(f) Mean \pm s.d. individual growth rates (G_1) and (g)–(l) mean increment width profiles (—), and mean otolith radius (R_O ; - - -) for monthly hatched cohorts of young-of-the-year *Etrumeus teres* caught in Tosa Bay, southern Japan.

$P < 0.001$; age_{Dec–Jan}: $F_{11,616}$, $P = 0.043$]. Different trajectories between autumn and winter cohorts were also found in the otolith radius (Fig. 4(g)–(l)).

The inverse pattern found between autumn and winter cohorts in the individual otolith growth trajectories were also found in G_{OTS} (Fig. 5). Likewise, daily SST series showed parabolic trends from autumn to the subsequent spring for the four-year-classes, with the minimum values and period of fast oscillation from January to April [Fig. 6(a)–(d)]. SST series were first differenced at lag 1 to remove the linear trend, and IMA models were used to filter G_{OTS} (Table II).

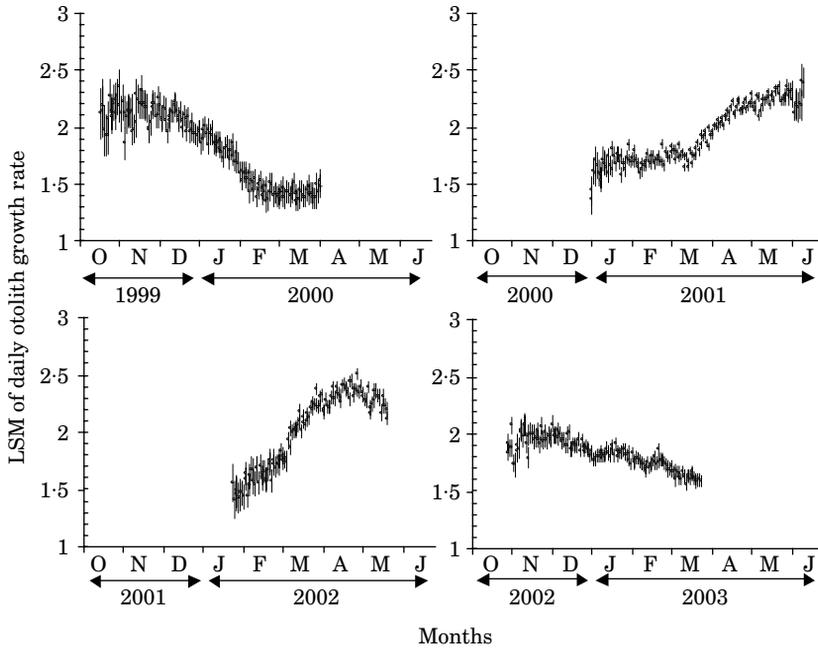


FIG. 5. Least square mean (LSM) \pm s.e. of daily time series of otolith growth rates for autumn and winter cohorts of young-of-the-year *Etrumeus teres* caught in Tosa Bay, southern Japan.

Cross-correlation analysis showed a positive cross-correlation from lags -3 to 3 between SST and G_{OTS} for the four-year classes [Fig. 7 (a)–(d)].

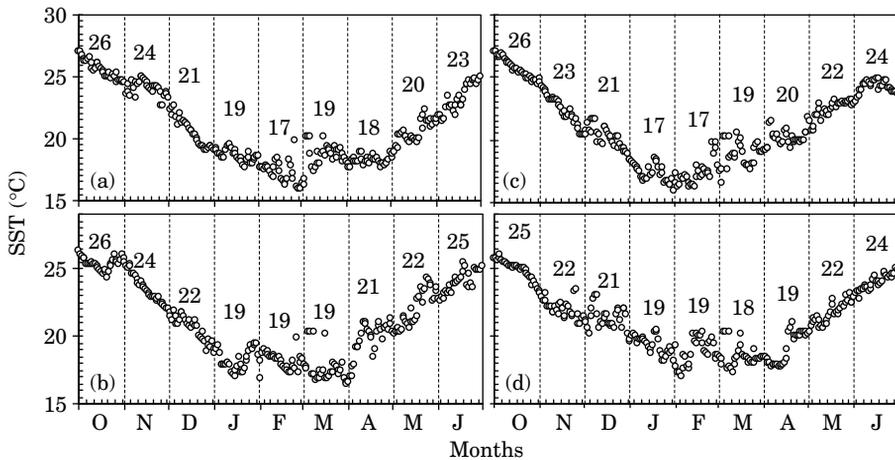


FIG. 6. Scatter plots illustrating the seasonal parabolic trend of daily sea surface temperature (SST) recorded from early October in (a) 1999, (b) 2000, (c) 2001 and (d) 2002 to late June of the subsequent year in Tosa Bay, southern Japan. IMA models for SST shown in Table II were only fitted over the range of occurrence of daily time series of otolith growth rates. Numbers within the vertical grid lines are monthly mean SST.

TABLE II. Summary statistics of IMA models estimated for daily SST over the range of daily time series of otolith growth rates in each cohort. All parameters are significant at $P < 0.001$. SSTs were ln-transformed before fitting the models

Cohort	Model notation	Estimated model	R _v	r ²
Autumn 1999	(0,1,1)	$(1 - B)Y_t = (1 - 0.39B)a_t$	0.527	0.68
Winter 2001	(0,1,1)	$(1 - B)Y_t = 1 - 0.514B a_t$	0.534	0.86
Winter 2002	(0,1,2)	$(1 - B)Y_t = 0.003 + (1 - 0.45B - 0.34B) a_t$	0.492	0.88
Autumn 2002	(0,1,1)	$(1 - B)Y_t = (1 - 0.234B) a_t$	0.521	0.77

R_v, residual variance.

DISCUSSION

OTOLITH MICROSTRUCTURE

Daily increments of YOY round herring were very distinctive from the core to the edge for almost all sagittae. The core was delimited by a distinctive check, after which a diffuse zone appeared delimited by a less distinctive second check. These observations closely agree with the results reported by Hayashi & Kawaguchi (1994). Under captive rearing conditions, they found that *E. teres* deposited the first increment 2 days after hatching, which coincided closely with the first feeding. Hence, the first check and second check found in otoliths of YOY in the present study might correspond to the hatch check and first feeding check, respectively.

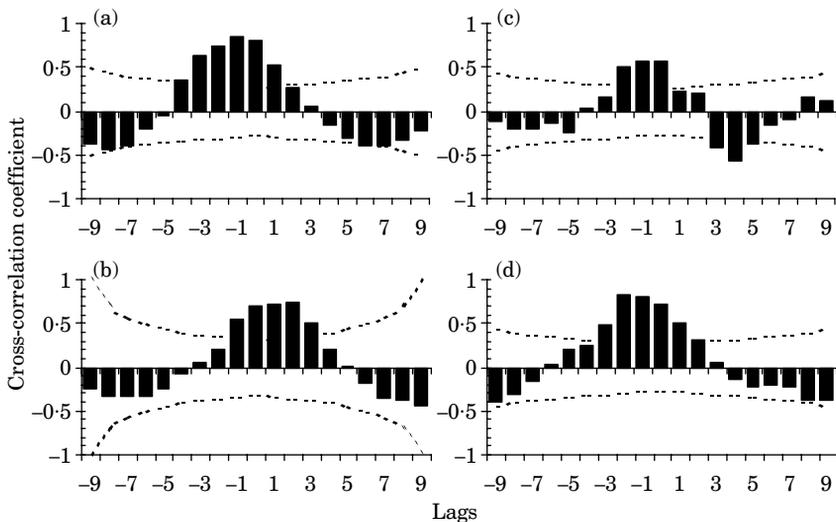


FIG. 7. Estimated cross-correlation coefficients between daily SST and least square mean of daily time series of otolith growth rates (G_{OTS}) for (a), (b) autumn and (c), (d) winter cohorts of the round herring *Etrumeus teres*. Correlation for a negative lag indicates G_{OTS} series lagged over SST, the correlation at lag 0 is the Pearson correlation, and a correlation at positive lags denotes SST series lagged over O_{GRTS} ---, 2S.E.

Given a close correlation between the otolith size and fish size, otolith growth trajectories can be used as a proxy of fish growth, particularly when the assumptions for applying backcalculation procedures are not successfully met. A curvilinear L_T and R_O relationship is typical for many species during the larval stage (Campana & Neilson, 1985; Thorrold & Williams, 1989; Jenkins & Davis, 1990; Otterlei *et al.*, 2002), and this is also true of clupeoid larvae (Moksness & Fossum, 1992; Watanabe & Kuroki, 1997; Takahashi *et al.*, 2001). In contrast, an isometric relationship is more common for juveniles (Campana & Neilson, 1985). In the current study, relationships between L_T and R_O were linear, suggesting that fish growth and otolith growth variations followed the same direction. For the period corresponding to sizes lower than the size range of YOY collected, the relationship between L_T and R_O is unknown, but is presumably allometric as in other clupeoids. Changes in otolith growth, however, should at least reflect the direction of changes in somatic growth during the larval and early juvenile stages for *E. teres*.

EARLY LIFE HISTORY TRAITS

A first caveat to discuss the extent of the finding of this study is the different pattern in occurrence of autumn and winter cohort between years. This species, has a protracted spawning season all year round with two maxima in reproductive activity (a minor peak in autumn and a major peak in winter and spring) and a resting period in August and September (Honda *et al.*, 2002). Hence, the co-occurrence of autumn and winter cohorts within a year is the expected pattern. In the present study, hatch dates were not corrected by differential cumulative mortality, and the set net sampling did not provide a complete random design on a temporal and spatial scale. These factors suggest that differential occurrence of autumn and winter cohorts between years could be purely coincidental. Conversely, a link between hatch date occurrence and differential survival of YOY between autumn and winter cohorts across years cannot be discarded, because hatch date distribution backcalculated from juveniles are less biased by differential cumulative mortality during the larval stage (Campana & Jones, 1992). A further analysis incorporating information of year-class strength of the adult stock in the study area (*i.e.* once YOY from each year have recruited to the adult population) could provide additional insight into the feasible link between the different spawning times and survival during the larval and early juvenile stages for this species.

Otolith growth rate differed in magnitude and trajectory between early autumn and late winter cohorts, *i.e.* higher growth rate were found for the October–November cohorts during the larval and early juvenile stages, conversely, growth rates were higher for the late juvenile period for February and March cohorts. In addition, December and January cohorts showed an intermediate pattern. These facts suggest that both the growth trajectory and the changes in growth magnitude seem to be ontogenetically and environmentally triggered, respectively. The main two environmental variables affecting larval growth rate during the early larval stages of fishes are food availability (Shepherd & Cushing, 1980; Jenkins, 1987) and water temperature (Miller *et al.*, 1988; Houde & Zastrow, 1993). In Tosa Bay, temperature variations were found

to follow a consistent seasonal trend from early autumn through winter and spring in the 4 years of the study. In addition, a significant correlation between SST and G_{OTS} , was also found and the parabolic seasonal pattern in G_{OTS} for the 4 years studied was also very evident. Consequently, seasonal changes in water temperature seem to account for a significant fraction of the variation in otolith growth between autumn and winter cohorts for *E. teres*.

The increase in width spacing during the larval stage suggests rapid growth after first feeding. During this stage there is a continuous development of morphological characteristics and sensory apparatus that increase both the motility and ability of larval fishes to catch prey (O'Connell, 1981; Thorrold & Williams, 1989). Consequently an increase in growth would be expected. The present results indicate that growth during the larval stage is an ontogenetic event for *E. teres* owing to the consistent increase in width spacing between spawning cohorts. Similar patterns in otolith growth or larval growth have been reported in other clupeoids during the larval feeding stage (Thorrold & Williams, 1989; Ohshimo *et al.*, 1997).

The asymptotic shape in the increment width profile was the preponderant feature at the onset of the second stage after which increment width seemed to increase without an evident transition in growth. This plateau in width spacing is probably linked to a reduction in growth at the onset of metamorphosis, as has been documented in other clupeoids (Youson, 1988; Oozeki & Zenitani, 1996; Watanabe & Kuroki, 1997). Metamorphosis in clupeoids can produce reduction in growth by changes in allometry as the body deepens and the larvae put on extra mass (Blaxter & Hunter, 1982), and allometric changes can also affect consequently otolith growth. Likewise, the plateaus and posterior increase in increment width found during the second stage suggest that growth resumes after metamorphosis, such as suggested for other clupeoids (Youson, 1988; Oozeki & Zenitani, 1996; Watanabe & Kuroki, 1997).

In the third stage, YOY spawned in winter had higher G_1 than autumn spawned YOY, probably due to the higher temperatures which YOY spawned in winter were exposed to in spring. Therefore, the delay in spawning, which was associated with lower growth rates during the larval and early juvenile stages, seems to be compensated for by the parabolic trend in water temperature. Based on variations in water temperatures, growth rates should increase again during the subsequent spring for YOY spawned in autumn. Conversely, the observed tendency for growth to decrease in winter spawned YOY as water temperature increases suggests that high temperatures may limit growth in summer. Both the increase and decrease in otolith growth after the third stage for autumn and winter cohorts, respectively, were also found for the few older YOY aged. In addition, the fact that the readability of daily increments decreased with the onset of deposition of the hyaline zone is further evidence that slow growth occurs during the late summer months.

TIME SERIES OF OTOLITH GROWTH AND SST

In the present study, least square means (Ralston, 1995) were used to account for the size-effects in G_{OTS} . After the standardization, the otolith growth rates of the round herring and SST were found to be positively correlated at lag -3 to -3 in the 4 years, with positive correlation at lag 0 as the consistent pattern. Such

correlations suggest that otolith growth of round herring respond quickly to local SST. Correlations at negative lags indicate a lagged effect of SST on otolith growth and suggest a conservative response of otolith growth to SST variations. Further, correlations at positive lags suggest that SST continues affecting the otolith growth for 1–2 days. Certainly, the inertia between growth process and the exogenous influence (Secor & Dean, 1992; Ralston, 1995) can trigger a lagged response of growth to the environmental perturbation. In the case of SST, time lags from 1–7 days have been reported in other species (Gutiérrez & Morales-Nin, 1986; May & Jenkins, 1992). Likewise, SST can also influence other growth controllers (*i.e.* plankton productivity), and consequently extend its effect on fishes and otolith growth.

An inherent assumption when examining the SST and G_{OTS} relationship is that most YOY caught were retained in Tosa Bay after spawning. Although neither the spawning origin nor the drift path during the egg and larval stage can be ascertained, three general sources of larval supply into Tosa Bay can be recognized based on published oceanographic information for the Kuroshio region (Nakata *et al.*, 1995; Zenitani *et al.*, 1996): 1) a local origin provided by larval retention, 2) exogenous origin from southern spawning grounds with larvae transported into Tosa Bay by an offshore-onshore shift of the Kuroshio axis and 3) returned larvae previously dispersed to the offshore side of the Kuroshio Current. In the present study, a significant correlation was found between local SST and otolith growth of YOY despite the potential variability generated by differential spawning origins. This evidence suggests that retention mechanisms are playing a key role in the adaptive strategy that the round herring has developed to use preferred coastal areas as spawning and nursery grounds.

In summary, growth rates of autumn and winter spawned cohorts of *E. teres* were found to closely match seasonal trends in SST. As a consequence, the otolith growth trajectories differed significantly between autumn and winter spawned juveniles, suggesting that otolith microstructure may provide a natural tag with a great potential for discriminating fish with unknown spawning origin. If YOY collected over the same season are available, discriminant analysis could be applied, and once discriminant algorithms have been generated the otolith growth trajectories from adult fish (once otoliths have been polished) may be used for estimating the proportion of spawning cohorts recruited into the adult population.

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