

The growth–mortality relationship in larval cohorts of *Sardinops melanostictus*, revealed by using two new approaches to analyse longitudinal data from otoliths

G. PLAZA*† AND M. ISHIDA‡

*School of Marine Science, Faculty of Natural Resources, Pontificia Universidad Católica de Valparaíso, Avenida Altamirano 1480, Casilla 1020, Valparaíso, Chile and ‡Kochi Kuroshio Research Laboratory, National Research Institute of Fisheries Science, 6-1-21 Sanbashi-dori, Kochi 780-8010, Japan

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The growth–mortality relationship was assessed for larval cohorts of the Japanese sardine *Sardinops melanostictus* using two new approaches: (1) repeat measures in general linear model (RM-GLMs) and (2) the autoregressive-individual method (AIM). Both methods were compared to the traditional approach in which repeat-measure ANOVA was used to compare the changes in increment width (W_1) at age and otolith radii (R_O) at age between individuals from an original population and survivors. In RM-GLMs, both the W_1 at age and R_O at age (*i.e.* at 5, 10, 15 and 20 days) were used as the dependent variables, and the standardized residuals of both regressions R_O and age and R_O and total length (L_T), age class, and day of the year as independent variables. A significant increase in W_1 at age and R_O at age from younger to older age classes was seen as indicative of growth-dependent selection. In AIM, the R_O -at-age relationship for each fish was fitted for the first 20 days, using autoregression, and then the growth traits (*i.e.* slopes) between the original cohorts and survivors were compared using ANOVA. In the traditional approach, the W_1 at age and R_O at age for the first 20 days of an original population were compared with those of survivors sampled in later stages. GLMs and traditional approaches supported the growth rate (*i.e.* the faster an individual grows, the higher its probability of survival) and bigger is better (*i.e.* larger individuals at any given age will have lower probability of mortality than smaller individuals of the same age) mechanisms. Furthermore, AIM showed that individuals from original cohorts had lower otolith growth rates than those from survivors, giving further support for the growth–mortality hypothesis for the larval stage of this clupeid.

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INTRODUCTION

Recently, it has been an increasing interest among fisheries biologists to test to what extent growth is critical for survival and subsequent recruitment of marine fish larvae. By growing faster individuals will reach larger sizes at any given age enhancing their probability of survival in comparison with

†Author to whom correspondence should be addressed. Tel.: +56 32 2274272; fax: +56 32 2274206; email: guido.plaza@ucv.cl

smaller individuals of the same age (*i.e.* 'the bigger-is-better mechanism'; Miller *et al.*, 1988; Leggett & DeBlois, 1994). Likewise, if mortality is size dependent, then higher growth rate will reduce the time over which individuals experience high mortality rates and thus, fast-growing larvae will have a lower probability of mortality compared to slower growing larvae (*i.e.* 'the growth-rate mechanism'; Shepherd & Cushing, 1980). Likewise, by growing faster individuals within a cohort move faster through those early vulnerable stages increasing their probability of survival (*i.e.* 'the growth-rate and stage-duration mechanisms'; Chambers & Leggett, 1987).

A traditional approach to test the growth–mortality hypothesis is by comparing the mean growth history in terms of mean daily growth rates (*i.e.* growth-rate mechanism) and mean backcalculated length (*i.e.* bigger-is-better mechanism) from larvae of an original population (*e.g.* daily or weekly) with the growth history of survivors of the same population sampled at later stages (Hovenkamp, 1992; Mosegaard *et al.*, 2002). Several studies, however, have suggested that faster growing fishes at a given size have smaller otoliths than slower growing fish (termed the growth-rate effect; Secor & Dean, 1989; Francis *et al.*, 1993; Hare & Cowen, 1995), which can affect the otolith radius (R_O) and total length (L_T) relationship based on cross-sectional data, and consequently limit the use of backcalculation methods to evaluate the extent to which selective mortality could be occurring in the field.

An alternative approach to test the growth-rate and bigger-is-better mechanisms is to compare increment width (W_1) at age and R_O at age between age classes of cohorts that have grown under similar environmental conditions (Hare & Cowen, 1997). A significant increase in the mean R_O at age with increasing age is seen as evidence of growth-dependent selection (Hare & Cowen, 1997; Folkvord & Mosegaard, 2002). Even in this approach, however, a fraction of the variability of W_1 at age and R_O at age could be accounted by the otolith growth-rate effect, and consequently reducing the capacity to use R_O as a proxy for fish growth.

Hare & Cowen (1995) proposed a method to reveal if faster growing fishes have a smaller otolith at a given size than a slower growing fishes (termed the growth-rate effect on the otolith size and fish size relationship). They stated that residuals from the R_O on body size provide a measure of large and small otoliths at a given size, whereas residuals from the age on body size provide a measure of fish growth. The growth-rate effect is then expressed as the strength of the correlation between residuals of R_O on body size *v.* residuals of body size on age. In contrast, the correlation between residuals of R_O on age *v.* body size on age provide a measure of the relationship between otolith growth and somatic growth (termed the age effect on the otolith size and fish size relationship) (Hare & Cowen, 1995; Folkvord & Mosegaard, 2002). Despite the importance that age and growth-rate effects could have for the otolith-size and fish-size relationship and consequently for any approach to study growth patterns in the early life stage of fishes, so far no study has attempted to test them in the field after Hare and Cowen's (1995) conclusions, although Folkvord *et al.* (2004) did so under experimental conditions.

The goal of this paper was to provide two new approaches as tools to analyse longitudinal data derived from otoliths to assess the growth–mortality

relationship in a given species. A first approach, in which age classes as well as age and growth-rate effects were used as independent variables to assess the variability in W_1 at age and R_O at age (*i.e.* dependent variables) in repeated-measures general linear models (RM-GLM); and a second approach termed the autoregressive-individual method (AIM) in which the radii-at-age relationship for each fish was fitted using autoregression (*i.e.* a regression analysis that corrects for serial autocorrelation). In RM-GLM, a significant increase in the least-square means of mean W_1 at age as age class increased was seen as indicative that older fish grew faster than younger fish. A similar approach was applied for radii at age to see if older fish were larger than younger fish at a given age. In AIM, the growth traits (*i.e.* slopes) between the original population and survivors were compared using analysis of variance. Both approaches were contrasted with the traditional approach in which repeated-measure ANOVA is used to compare the changes in W_1 at age and R_O at age between individuals from original population and survivors.

For the current study, the Japanese sardine *Sardinops melanostictus* (Temminck & Schlegel), a commercially important clupeoid that has undergone marked long-term fluctuations in population size reaching at current their historically lowest levels (Kuroda, 1991; Kawasaki, 1993; Watanabe *et al.*, 1995). As a result of the fluctuations in population size, this clupeid expanded its spawning area from coastal waters of south-western Japan during the period of low biomass in the 1960 and early 1970s (Kawai, 1994; Watanabe *et al.*, 1995) to oceanic waters around the Kuroshio Current when biomass increased to a maximum in 1988. After the decrease in biomass in the 1990s, the spawning area contracted again to the coastal area and is at present limited to coastal areas around Shikoku Island in Tosa Bay (Ishida, 2006).

MATERIALS AND METHODS

SAMPLING AND OTOLITH ANALYSIS

Larvae and early juvenile were obtained from commercial Shirasu seiners operating in Tosa Bay from November 2003 to March 2004 in five sites covering spatially and temporally the spawning of this species in the bay (Fig. 1). A seine used was 70–80 m in mouth aperture, 200–300 m in length and 2 mm in cod-end, and was towed by two boats at *c.* 1 m s^{-1} for 5 to 10 min several times in the first few hours after sunrise. After capture, the contents were preserved in 90% alcohol.

The Shirasu fishery corresponds to commercial catching of later stages of three main clupeoid larvae co-occurring in coastal waters, *S. melanostictus*, Japanese anchovy *Engraulis japonicus* Temminck & Schlegel and round herring *Etrumeus teres* (DeKay). Shirasu sub-samples were preserved in 95% ethanol as otoliths could be removed later. Once sardine specimens were identified, the L_T was measured to the nearest 0.1 mm. Each pair of sagittae were removed using fine needles, cleaned from adhering tissue and mounted on slide glass with a drop of transparent nail polish. Growth increments were clearly discernible and no further polishing was required. The R_O and W_1 were measured through a linear axis from the core along the post-rostrum of the sagittae, which was consistently the best axis for increment counting and measurement. All counting and measuring were carried out using an image analysis system (LATOC Co. Ltd, Tokyo, Japan) at magnifications of $\times 400$ –1000. Otolith increments for *S. melanostictus* are deposited on a daily basis from the third day after hatching, which corresponds to the first feeding (Hayashi *et al.*, 1989). Hence, the total daily age was

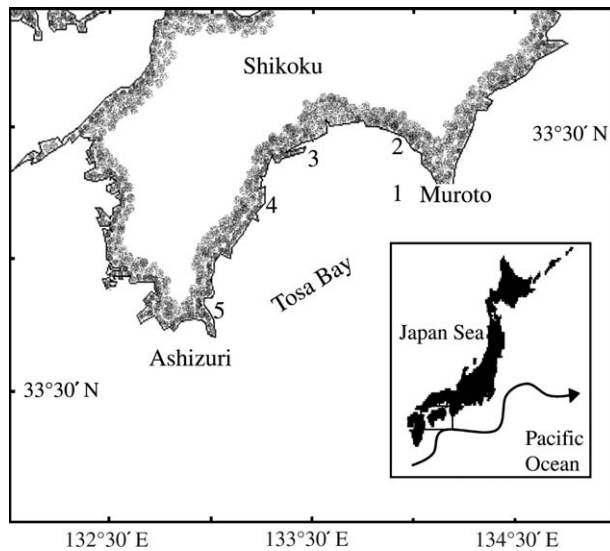



FIG. 1. Coastal locations (1–5) where larval *Sardinops melanostictus* were collected by Shirasu seiners in Tosa Bay, southern Japan. , the path of the Kuroshio Current.

estimated as the numbers of otolith increments +2 days. Hatch dates of larvae were backcalculated by subtracting the total age in days from the calendar day of sampling.

GENERAL LINEAR MODELS

In total 398 individuals including larvae and early juveniles hatched from November 2003 to February 2004 were available for this study. The overall database was separated in 10 day age classes, 11–20, 21–30, 31–40, 41–50, 51–60 and >61 days old (Table I). The aged fish covered the range from post-flexion larvae (10 days) to early juvenile (86 days). The relationship between L_T and R_O for the range of larvae was analysed together with the R_O hatch month interaction. To examine both the age and the growth-rate effects in the L_T and R_O size relationship, the approach described by Hare & Cowen (1995) was used.

TABLE I. Total length (L_T) and age of *Sardinops melanostictus* larvae collected in Tosa Bay southern Japan, from autumn 2003 to spring of 2004 used for general linear models

Age class (days)	<i>n</i>	L_T (mm)		Age (days)	
		Mean \pm s.d.	Range	Mean \pm s.d.	Range
11–20	63	16.7 \pm 2.8	11–22	16.8 \pm 3.0	9–20
21–30	147	22.5 \pm 3.1	15–30	25.5 \pm 2.8	21–30
31–40	105	28.9 \pm 3.6	20–39	34.6 \pm 2.7	31–40
41–50	32	31.5 \pm 5.2	23–43	44.2 \pm 2.7	41–50
51–60	18	40.8 \pm 5.9	29–50	55.7 \pm 3.3	51–60
>61	33	55.1 \pm 7.2	41–70	71.8 \pm 3.8	61–86
Total	398	16.7 \pm 10.5	11–70	33.2 \pm 15.2	9–86

n, number of fish.

Repeat measures in general linear models (RM-GLMs; McCullagh & Nelder, 1989), with age classes as independent variables, were used to assess the variability in W_I at age (*i.e.* dependent variable). The RM-GLMs require that the data for all individuals be available for exactly the same points to estimate the covariance matrix. Therefore, RM-GLMs were set at each 5, 10, 15 and 20 day intervals to avoid too much reduction in the data set, reaching a total of 336 larvae for this analysis. A \ln transformation was applied to R_O at age and W_I at age before the analyses to homogenize the variance. Hatch dates were incorporated in RM-GLMs if they differed among age classes. Hence, hatch dates were converted to day of year by subtracting hatch dates to 1 November (assigned day 1). Then, a Kolmogorov-Smirnov two-sample test was used to compare hatch distribution among size classes at a frequency interval of 10 days. The standardized residual of the age and R_O relationship (R_{SAOR}) and that of L_T and R_O relationship (R_{STLOR}) were also included in the RM-GLMs to deal with the influence of age and somatic growth-rate effects in the GLMs. The GLM had the following structure:

$$\ln G_i = a_o + a_c + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + a_c X_1 + a_c X_2 + a_c X_3 + e_i \quad (1)$$

where G is the W_I or R_O at age, a_o is the overall intercept, a_c is the age-class effect, β_1 - β_3 are the estimated coefficients for each numerical covariate, X_1 = day of year (D_Y), X_2 = R_{STLOR} , X_3 = R_{SAOR} and e_i is the error term. The model also includes the interactions between the fixed factor (a_c) and the covariates (*i.e.* D_Y , R_{STLOR} and R_{SAOR}).

A significant increase in the least-square means of mean W_I at age (*i.e.* at age 5, 10, 15 and 20 days) as age class increased (*i.e.* 11-20, 21-30, 31-40, 41-50, 51-60 and >61 days old) was seen as indicative that older fish grew faster than the younger ones, which constituted evidence that faster growing fish had a higher probability of survival (*i.e.* evidence for the growth-rate mechanism). A similar approach was applied for radii at age to see if older fish were larger than younger ones during the first 20 days of larval life (*i.e.* evidence for the bigger-is-better mechanism). The Tukey honest difference test was used for multiple comparisons in least-square means (LSM) between age-classes.

AUTOREGRESSIVE-INDIVIDUAL METHOD (AIM)

Larvae ($n = 173$) collected from early January to early February were regarded as the original population. To avoid the influence of temporal variation in environmental conditions, the larvae were grouped into four groups at interval of 10 hatching days (Table II). Likewise, 92 early juveniles corresponding to the same population, collected after *c.* 1 month later were regarded as the survivors. The radii-at-age relationship for each fish was analysed using autoregression models, *i.e.* a linear regression analysis that includes an autoregressive error term to correct for serial autocorrelation in AUTOREG module of SAS Inc. (Cary, NC, U.S.A.) software. Previous to AIM and to evaluate the extent of the autoregressive-error terms, radii-at-age series from larvae of the original population and survivors of cohort A (see Table II) were examined using the 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. The identification of ARIMA models was based on the examination of the autocorrelation (ACF) and partial autocorrelation (PACF) functions. Once the order of autoregressive error was identified the radii-at-age series were truncated at the 20th day and analysed using autoregression. The slope of the radii-at-age relationship was used as a measure of growth rate during the first 20 days of larval life. Then, the growth traits (*i.e.* slopes) between the original population and survivors were compared using ANOVA because assumptions of normality and homoscedasticity were met. It is necessary to underline that AIM could not be applied to W_I

TABLE II. Cohorts (A–D) of *Sardinops melanostictus* larvae and juveniles collected during the winter 2004 in Tosa Bay (southern Japan), which were used in the ‘traditional method’

Cohort	Hatch date	n	Original population				Survivors			
			L_T mean \pm s.d. (mm)	Age mean \pm s.d. (days)	CD	n	L_T mean \pm s.d. (mm)	Age mean \pm s.d. (days)	CD	
A	01–10 January	40	24.8 \pm 4.5	30 \pm 6.9	03 February	22	53.7 \pm 7.5	70 \pm 6.1	15 March	
B	11–20 January	46	20.2 \pm 3.4	25 \pm 5.1	07 February	24	49.1 \pm 7.6	63 \pm 6.9	17 March	
C	21–31 January	41	21.3 \pm 3.8	23 \pm 4.6	19 February	25	42.2 \pm 5.7	55 \pm 5.6	17 March	
D	01–10 February	46	21.7 \pm 3.7	24 \pm 4.8	29 February	21	28.0 \pm 12.0	48 \pm 8.5	23 March	

CD, mean collection date; L_T , total length; n, number of fish.

at age because the linear increasing tendency was not always consistent in each individual for the first 20 days studied.

TRADITIONAL APPROACH TO TEST THE BIGGER-IS-BETTER MECHANISM

The same data set used for AIM was used for the traditional approach. Differences in mean daily W_1 between the original population and the survivors were addressed using univariate repeat-measures ANOVA. The analysis was a mixed two-factor design, with cohort as an independent factor (*i.e.* between-subject factor, with cases arranged in rows) and W_1 or R_O at age as a repeated factor (*i.e.* within-subjects factor with numbers of repeated levels arranged in columns). All RM ANOVAs were achieved on balanced set of levels over age (*i.e.* truncated at 20th day to maximize the number of observations and repeat measures to compare with the survivors). As this species forms the first ring at the third day after hatching (Hayashi *et al.*, 1989), RM ANOVAs contained 18 levels over age. Because of the increasing trend in W_1 and R_O at age *post hoc* tests were not used; instead, linear trend analysis was used to evaluate if differences between the original population and the survivors were kept constant across age.

COVARIANCE MATRIX IN REPEAT-MEASURE ANALYSES

As R_O and W_1 are not independent across age the Huynh–Feldt's adjustment was used to decrease the d.f. when the F statistic was inflated by severe violation of the sphericity assumption (Crowder & Hand, 1990; Chambers & Miller, 1995). Multivariate repeat-measures ANOVA were also used to test for differences in R_O at age and W_1 at age in both the GLM and traditional approach. Models were fitted using SYSTAT (version 12, SYSTAT Software Inc., Richmond, CA, U.S.A.).

RESULTS

GENERAL LINEAR MODELS

The relationships L_T and age, R_O and age, and R_O and L_T were well described by linear regressions [Fig. 2 (a)–(c)]. Except for some values, which were far from the regression line, there was no apparent heterocedasticity in the residuals for the range of larvae collected [Fig. 2 (d)–(f)]. The residuals of L_T and age were highly correlated with residuals of R_O and age [$r = 0.82$; Fig. 3(a)]. Conversely, growth-rate effect (*i.e.* the relationship residuals of R_O and L_T and residuals of age and L_T) was markedly inferior [$r = 0.31$; Fig. 3(b)]. A strong correlation between residuals of L_T and age and R_O and age relationships means that individuals that were large for their age also had large otoliths for their age. A weak correlation between residuals of R_O and L_T and R_O and age means a weak tendency for fast-growing individuals to have small otoliths at a given L_T compared to slow-growing individuals. Thus, both the age effect (*i.e.* age-independent variability) and growth-rate effects on the otolith-size and fish-size relationship were not strong for *S. melanostictus*.

Hatch dates among age classes ranged from November to March, and distribution differed significantly among age classes (Table III). Hence, day of year was added to the GLMs as a numerical covariate. In a previous evaluation both interactions D_Y and age class and R_{STLOR} and age class were not

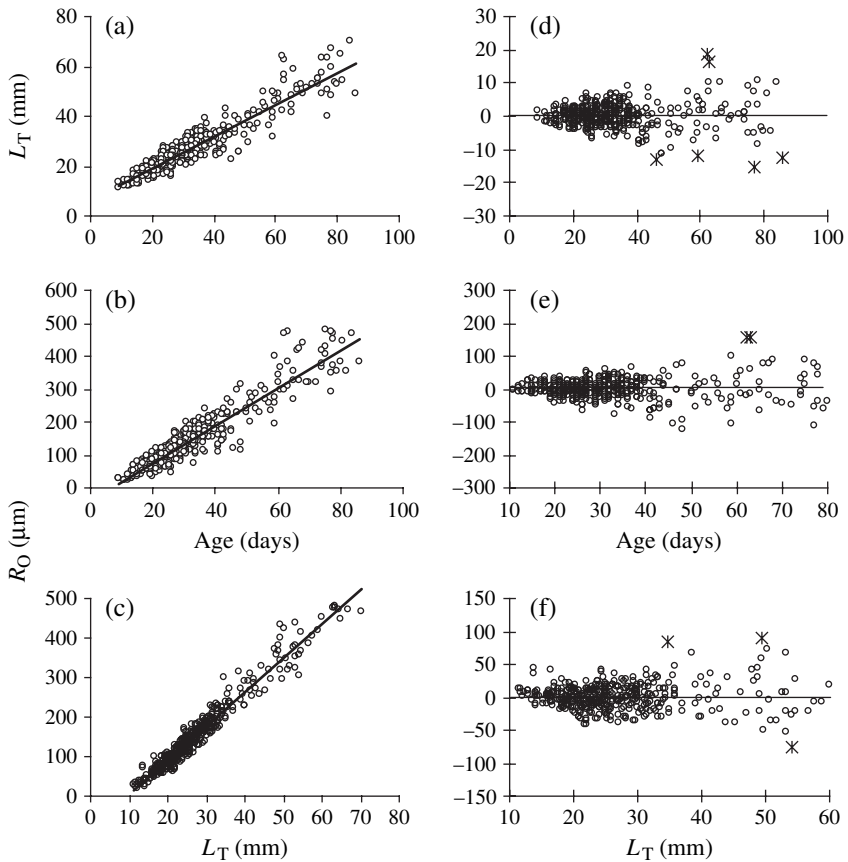


FIG. 2. Fitted models of (a) total length (L_T) and age ($y = 0.64x + 6.05$; $r^2 = 0.87$), (b) otolith radius (R_O) and age ($y = 5.71x - 37.33$; $r^2 = 0.90$) and (c) R_O and L_T ($y = 8.64x - 84.68$; $r^2 = 0.95$) relationships and (d), (e), (f) their respective residuals for *Sardinops melanostictus* larvae and early juveniles collected from October 2003 to March 2004 in Tosa Bay, southern Japan. *, data distant from the curve.

significant; hence, only the interaction between R_{SAOR} and age class was included in the models.

The statistical output for RM-GLMs can be separated in two parts: the first part encompassed the statistical significance to assess the overall effect of age class and other explanatory variables (see equation 1) in the model and the second part encompassed the statistical significance to assess the effect size of individual predictors. The second part included estimated coefficients, standardized coefficients, s.e., 95% CI and statistical probabilities for categorical and continuous predictors as well as for each repeated measurement. All these results were omitted for brevity.

The first part, summarized in Tables IV and V and Fig. 4, showed that both W_1 and R_O at age varied significantly among age classes (between-subject effect) on an overall context, but to see if such variations are significant for each repeat measure the least-square means (LSM) must be examined. LSMs (*i.e.*

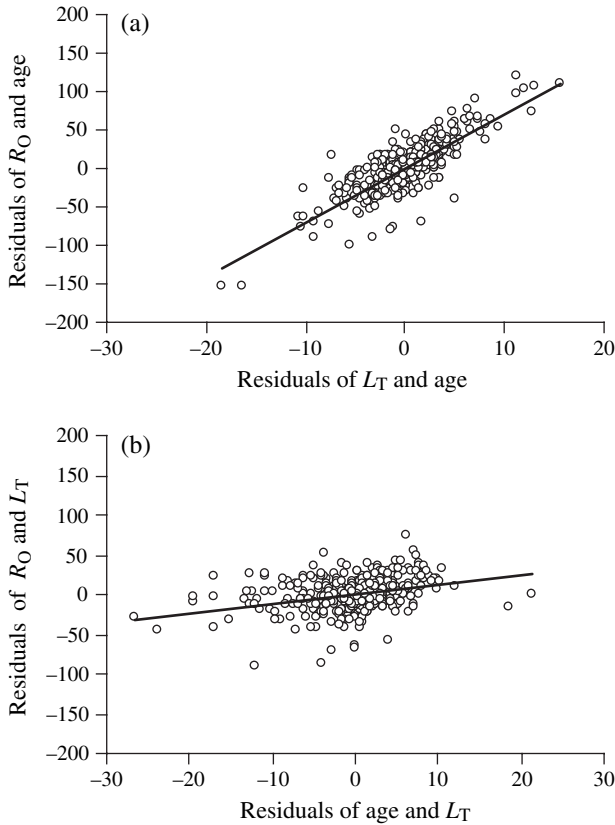


FIG. 3. (a) Age ($y = 7.05x - 0.005$; $r^2 = 0.66$, $P < 0.001$) and (b) growth-rate effects ($y = 1.16x - 0.002$; $r^2 = 0.1$, $P < 0.05$) on the fish-size and otolith-size relationship of larval *Sardinops melanostictus* for the 2003–2004 year class.

the predicted mean of W_I at age and R_O at age by the RM-GLMs) for each age class is a measure of growth averaged across all levels of the other factors involved. LSMs incorporate the influence of the following aspects: (1) some fish had either larger (*i.e.* positive residuals) or shorter (*i.e.* negative residuals) R_O

TABLE III. Two-side probabilities of two-sample Kolmogorov–Smirnov tests, for differences in hatch-date distributions between age classes of larval *Sardinops melanostictus* collected in Tosa Bay, southern Japan

Year class	Age class (day)	<i>n</i>	10–19	20–29	30–39	40–49	50–59
2003–2004	10–19	63					
	20–29	147	0.007				
	30–39	105	0.004	0.307			
	40–49	32	<0.001	0.020	0.001		
	50–59	18	0.042	0.133	0.172	0.004	
	>60	33	0.000	0.014	0.004	0.028	0.029

n, number of fish.

TABLE IV. Univariate repeat-measure GLMs for larval *Sardinops melanostictus* collected from October 2003 to March 2004 in Tosa Bay, describing the relationship between the increment width of sagittae as a dependent variable and day of year (D_Y), standardized residuals otolith radius (R_O) and relationship (R_{SORA}), standardized residuals of the R_O and total-length (L_T) relationship (R_{SORTL}), and 10 day interval age classes as independent variables

Source of variation	SS	d.f.	MS	F	W (d.f.)	P
Between-subject effects						
Age class	4.950	4	1.240	15.77		<0.001
D_Y	0.250	1	0.250	3.19		0.080
R_{STLOR}	0.330	1	0.330	4.23		0.040
R_{SOAR}	26.790	1	26.790	341.29		<0.001
Age class $\times R_{SAOR}$	14.550	4	3.640	46.32		<0.001
Error	24.180	323	0.080			
Within subject effects						
Time	5.220	3	1.740	24.89	0.836 (321)	<0.001
Time \times age class	1.310	12	0.110	1.57	0.947 (849)	0.157 (0.096)
Time $\times D_Y$	0.600	3	0.200	2.84	0.976 (321)	0.060 (0.037)
Time $\times R_{STLOR}$	0.370	3	0.120	1.78	0.982 (321)	0.140 (0.149)
Time $\times R_{SAOR}$	1.810	3	0.600	8.64	0.933 (321)	<0.001
Time $\times R_{SAOR} \times$ age class	1.788	12	0.149	1.95	0.948 (849)	0.026
Error	64.570	969	0.071			

P , probabilities between parenthesis correspond to Wilks' λ estimator; W , Wilks' λ for multivariate GLM of repeat measures over time. When no parenthesis is shown, $P < 0.001$ for univariate and multivariate GLMs.

for its age; (2) some fish had either larger (*i.e.* positive residuals) or shorter (*i.e.* negative residuals) R_O for its length; and (3) the day of the year when a given fish hatched as well as the potential interactions between them and over time, such as was shown by the high statistical significance for R_{SAOR} , lower but significant for R_{STLOR} , and statistically significant for day of year when repeated measurements were taken into account (Table IV). LSMs showed that older survivors grew faster and were larger at each level (*i.e.* at 5, 10, 15 and 20 days of their life) than the younger members collected, although the Tukey *pos hoc* test showed that differences were more marked for increment R_O at age. In addition, GLMs also showed that although W_I and R_O at age did not vary significantly among age classes when repeat measures were considered (time \times age class), the differences turned highly significant when the effect of R_{SAOR} was incorporated (time $\times R_{SAOR} \times$ age class).

AUTOREGRESSIVE-INDIVIDUAL METHOD (AIM)

In all R_O -at-age series for larvae and survivors of cohort A, the ACF showed a gradually decay with time [see Fig. 5(a) for a representative sample]. The PACF showed a significant high value at lag 1, which suggested that R_O at age were non-seasonal stationary series with 1 autoregressive parameter. ARIMA analysis confirmed that the R_O -at-age series were first order

TABLE V. Univariate repeat-measures GLMs for larval *Sardinops melanostictus* collected from October 2003 to March 2004 in Tosa Bay, describing the relationship between the otolith radii (R_O) at age of sagittae as dependent variable and day of year (D_Y), standardized residuals R_O and age relationship (R_{SOAR}), standardized residuals of the R_O and total length (L_T) relationship (R_{SORTL}) and 10 day interval age classes as independent variables

Source of variation	SS	d.f.	MS	F	W (d.f.)	P
Between-subject effects						
Age class	5.185	4	1.296	17.74		<0.001
D_Y	0.068	1	0.068	0.93		0.335
R_{STLOR}	0.643	1	0.643	8.80		0.003
R_{SOAR}	10.806	1	10.806	147.92		<0.001
Age class $\times R_{SAOR}$	6.147	4	1.537	21.04		<0.001
Error	23.596	323	0.073			
Within subject effects						
Time	60.884	3	20.295	2924.36	0.836 (306)	<0.001
Time \times age class	0.138	12	0.012	1.66	0.947 (849)	0.457 (0.07)
Time $\times D_Y$	0.157	3	0.052	7.54	0.976 (321)	0.006 (<0.001)
Time $\times R_{STLOR}$	0.022	3	0.007	1.07	0.982 (321)	0.308 (0.362)
Time $\times R_{SAOR}$	0.925	3	0.308	9.47	0.839 (321)	<0.001
Time $\times R_{SAOR} \times$ age class	0.819	12	0.868	9.86	0.835 (849)	<0.001
Error	6.725	969	0.007			

P , probabilities between parenthesis correspond to Wilks' λ estimator; W , Wilks' λ for multivariate GLM of repeated measures over time. When no parenthesis is shown, $P < 0.001$ for univariate and multivariate GLMs.

autoregressive models [*i.e.* ARIMA (1,0,0)]; hence, one autoregressive parameter was included in autoregression analysis. Results of individual fits are not shown (but see Table VI and Fig. 6 for a representative sample of autoregression and ordinary least-square regression). Slopes derived from autoregression showed that survivors grew faster than members from the original population (Fig. 7; ANOVA, $F_{1,257}$, $P < 0.001$). The interaction between cohort and population was not significantly different (ANOVA, $F_{3,257}$, $P > 0.05$).

TRADITIONAL APPROACH TO TEST THE BIGGER-IS-BETTER MECHANISM

For statistical comparison, the W_I series were truncated at the 21st day to maximize the number of observations and repeat measures to compare with the survivors. In general, two consistent patterns in daily W_I occurred: (1) an increase in W_I after first feeding through to the third week of larval life evidenced in members of the original population and survivors and (2) a progressive decrease in W_I throughout the second month evidenced in the survivors. In the four cohorts studied, however, univariate and multivariate repeat-measures ANOVA showed that the survivors had significantly wider W_I at age ($F_{1,257}$, $P < 0.001$; Wilks' $\lambda_{16,242}$, $P < 0.001$) and larger R_O at age ($F_{1,257}$, $P < 0.001$; Wilks' $\lambda_{17,241}$, $P < 0.001$) than the members of the original population

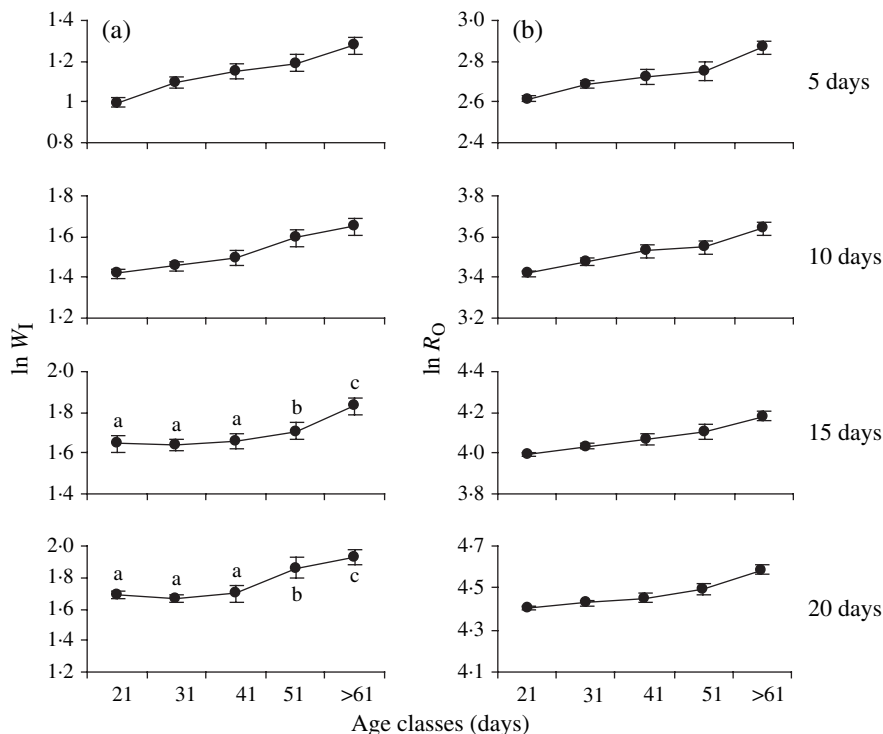


FIG. 4. Least-square mean \pm s.e. of \ln transformed (a) increment width (W_1) and (b) otolith radius (R_O) at 5, 10, 15 and 20 days after first feeding, classified by 10 day age classes of larval and juvenile *Sardinops melanostictus* for the 2003–2004 year class. Different lower-case letters denote significant differences (Tukey *post hoc* test, $P < 0.05$).

throughout the first 3 weeks of larval life in the four cohorts (Fig. 8). In both, I_W ($F_{1,257}$, $P < 0.001$) and R_O ($F_{1,257}$, $P < 0.001$), the linear trend accounted for a significant fraction of the variability over age.

DISCUSSION

GENERAL LINEAR MODELS

Former studies have demonstrated the utility of R_O at age to test growth–survival processes (Hovenkamp, 1992; Campana, 1996; Hare & Cowen, 1997; Cotano & Alvarez, 2003). These studies have assumed that larvae with a larger otolith also had a larger body size, and consequently comparison of average radius (as a proxy for growth) at a different point of the cohort history will standardize the confusing age and somatic-growth effects on otolith growth. In an alternative approach, both effects as well as the effect of hatch date in repeat-measures general linear models (RM-GLMs) were included to test for differences in both W_1 and R_O at age among age classes, and through this approach evidence was also found for the growth-rate and bigger-is-better mechanisms for this species. The statistical output from RM-GLMs is long

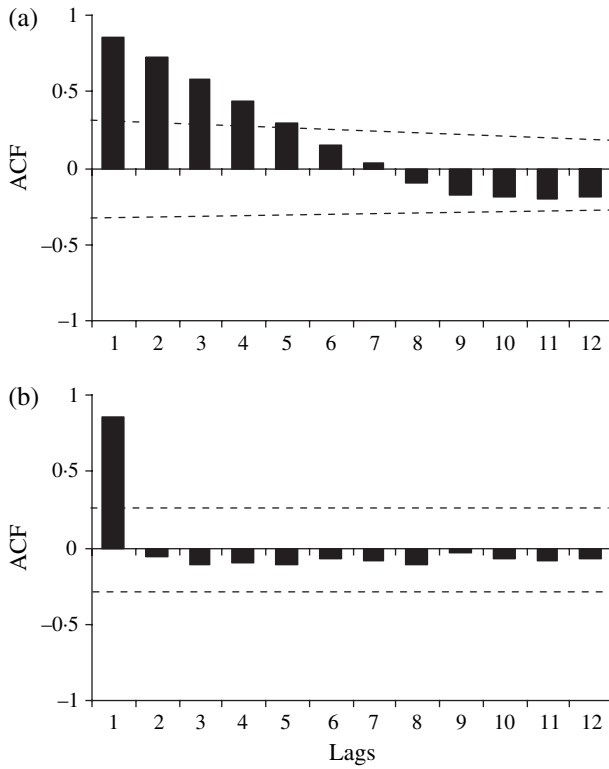


FIG. 5. Estimated (a) autocorrelation (ACF) and (b) partial autocorrelation (PACF) functions of otolith radii-at-age series for an individual from the original cohort A. ---, 2 s.e.

and complex and not easy to interpret from a biological point of view. When testing the differences in W_1 and R_O at age, however, the key aspect is the statistical inference derived from the ANOVA results as well as their effect size evaluated by the statistical significance of the estimated parameters.

TABLE VI. Illustrative example of the otolith radii-at-age relationships for individuals from the original and survivor populations of cohort A *Sardinops melanostictus*. Coefficients [intercept (a) and slope (b)] were estimated using maximum likelihood method in autoregression analysis

Population	Statistic	Coefficient	s.e.	T-ratio	P
Original	Φ_1	0.678	0.174	3.891	0.001
	a	-2.708	1.244	-2.182	0.043
	b	3.589	0.092	38.849	<0.001
	R_v	1.035			
Survivor	Φ_1	0.937	0.059	15.917	<0.001
	a	-9.521	0.293	-1.915	0.073
	b	6.521	0.293	22.245	<0.001
	R_v	2.668			

P, probability for regressive parameters; R_v , residual variance; Φ_1 , autoregressive parameters.

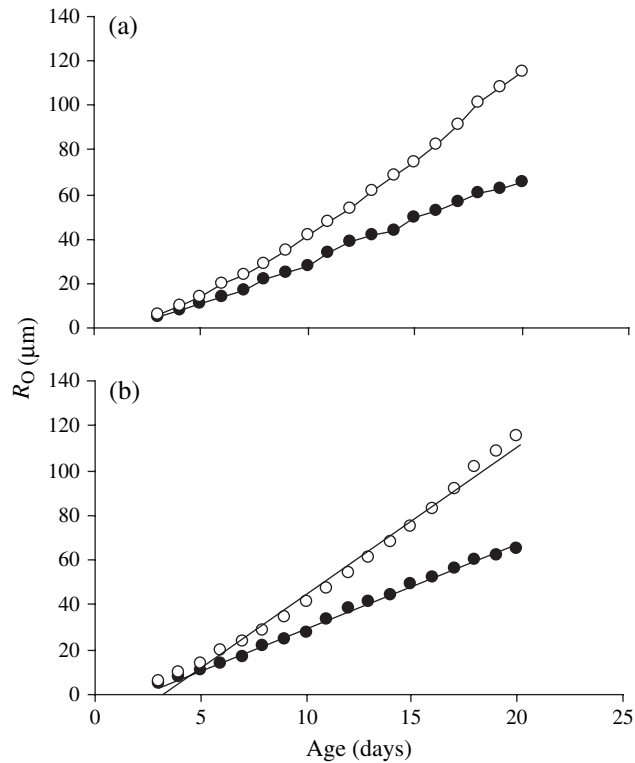


FIG. 6. (a) Autoregression fit for an individual from an original population (●) and a survivor (○) *Sardinops melanostictus*, as specified in Table VI. (b) Least-square regression is also given for the same individuals. The curves in (b) were fitted by: original $y = 6.72 (0.15)x - 15.42 (1.98)$ ($r^2 = 0.99$) and survivor $y = 3.65 (0.05)x - 3.4 (0.66)$ ($r^2 = 0.99$) (s.e. in parentheses).

In the present study, the standardized residuals of the age and R_O relationship, standardized residuals of the L_T and R_O relationship along with D_Y were used as covariates in GLMs, although strictly speaking a simpler GLM could also be applied with only age class and D_Y as explanatory variables, which also showed similar conclusions. Then, what is the difference between the simple RM-GLMs that only use age class as covariate and the extended GLMs with residual-based covariate? Residuals added as covariate reduce the variability when comparing least-square means of otolith size at age. For example, if no significant differences in W_1 at age as age-class increase were found in simple RM-GLMs, the conclusion would be that the growth-rate mechanism is not operating. A considerable amount of such variability, however, is associated with the growth rate and age effects, both of which can be approximated by the residual values. Consequently, the inclusion of residuals make comparison of otolith size at age among age classes more reliable, even when the age-growth effect and age effect on the otolith size and fish relationship are not severe as showed in the current study.

Unquestionably, the influence of residuals was higher in lower age classes than in older survivors because R_O at capture not only is closer to the last

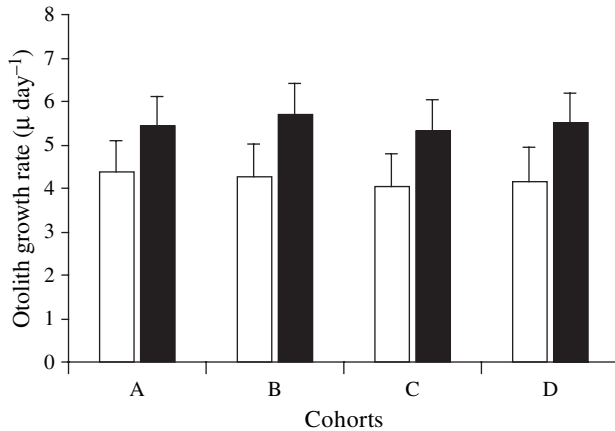


FIG. 7. Mean + s.e. otolith growth rates for the original population (□) and survivors (■) of *Sardinops melanostictus* estimated from individual-autoregressive fits of radii-at-age for cohorts A–D.

level of repeat measure used (*i.e.* at 20 days) but also because during the larval stage both age and growth-rate effects are expected to be more severe. Although in the current study, both the growth-rate effect and age effects on the R_O and L_T relationship were low, *i.e.* in most cases faster growing fish tended to have also larger otoliths at a given size than a slower growing fish [growth-rate effect; Fig. 3(b)], and in most cases an older fish also had a larger otolith [age effect; Fig. 3(a)], yet there was a 34% of variability accounted by the age-independent variability, which made the residuals of the R_O and age relationship highly significant between and within subject (*i.e.* over repeat measurements).

Results from least-square means from RM-GLMs showed that both W_1 and R_O at age significantly increased as age class increased showing that older fish (*i.e.* the survivors at a given age) always grew faster and were larger than the younger ones supporting the growth-rate and bigger-is-better mechanisms for this species. All this evidence suggests that the growth-rate and bigger-is-better mechanisms operated throughout the first 20 days of larval life, although the later mechanism appeared clearer in the current study presumably as a result of the major variability associated with growth rate *per se*. In addition, the intrinsically lower variability in W_1 and R_O at earlier stages than at older ones, a mechanism already documented in some clupeid larvae (Watanabe & Kuroki, 1997; Takasuka *et al.*, 2004a), would make easy to detect the growth-rate and bigger-is-better mechanisms at younger ages than at older ones.

AUTOREGRESSIVE-INDIVIDUAL METHOD

One of the difficulties in analysing otolith-based data is the autoregressive nature of the daily otolith increments (*i.e.* the error of the otolith growth rate at a given date may be influenced by the error of growth of previous days). Serial autocorrelation violates the assumption of serial independence required

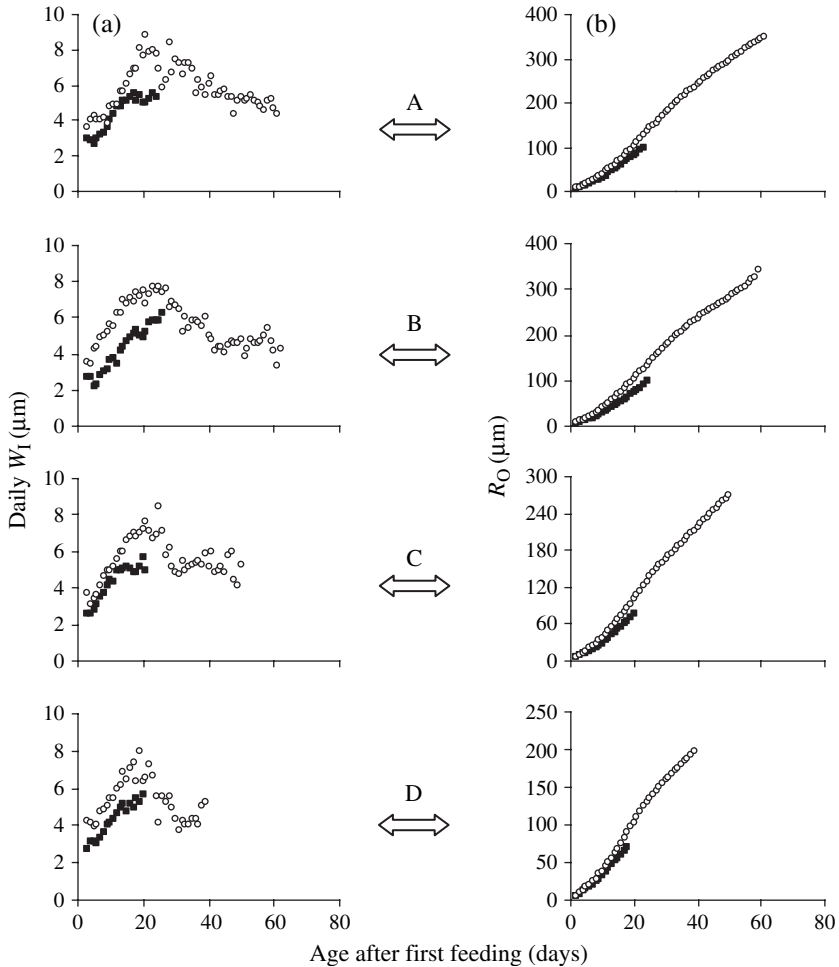


FIG. 8. Scatter plots illustrating mean (a) daily increment widths (W_1) and (b) radii (R_O) at age for individuals of the original population (■) and survivors (○) of *Sardinops melanostictus*, for the four hatched cohorts (A–D) specified in the Table II.

for most classical inference tests as well as making ordinary least-square estimates due to an inflated unjustified precision (Bence, 1995). To date, no study has analysed otolith-growth series of individual fishes to estimate the serial autocorrelation, although some studies have analysed time series of otolith-growth rate cross-matched to the calendar date (Gutierrez & Morales-Nin, 1986; Thorrold & Williams, 1989; Maillet & Checkley 1991; May & Jenkins, 1992; Ralston, 1995). Although the methodologies applied have differed between studies (cross-correlation analysis, transfer function models or regression models), the common outcome found has been the elevated serial autocorrelation of the daily otolith-growth series. The present study agrees in part with these findings, although both ARIMA and autoregressive regression showed that serial autocorrelation of R_O at age at the individual level was only

significant at lag 1, *i.e.* a given value of R_O at age was only significantly correlated with the previous value. When the serial autocorrelation was measured by AIM, further support for the growth–mortality hypothesis in this species was found. It could be argued that AIM deal with serial autocorrelation, although it could be more influenced by the age and growth-rate effects owing its individual-based nature. The AIM, however, can be useful when otolith and somatic growth are directly related, such as in the current study. Although the applicability of this method is computer intensive, the high performance of modern statistical software make this approach quite fast and reliable.

KEY ASSUMPTION

A key assumption in the current study common to the three methods used was that all individuals analysed originated from the same population. This assumption seems to be supported by the spawning biology and ecology of this species. Synchronizing with the reduction in population size, *S. melanostictus* has restricted its spawning area to costal areas in Tosa Bay in the Pacific side of the Shikoku Island (Kuroda, 1991; Kawasaki, 1993; Watanabe *et al.*, 1995). A fraction of spawned larvae in the coastal areas are transported northward to a high productive area (*i.e.* Kuroshio Extension) by the Kuroshio Current (Heath *et al.*, 1998). Hatched larvae may also be retained in Tosa Bay or transported offshore off the path of the Kuroshio by local wind-driven currents (Kishida *et al.*, 1994; Heath *et al.*, 1998; Watanabe & Nakamura, 1998). Larvae transported offshore across the Kuroshio experience high mortality and consequently they seem to be less important for recruitment (Nakata *et al.*, 1995; Zenitani *et al.*, 1996; Heath *et al.*, 1998). The importance to recruitment success of larvae retained in Tosa Bay is unknown. The fact that spawning occurs in this bay, however, suggest that there is an adaptive choice to maximize larval survival in coastal areas. In addition, at the currently low level of population size, the captured larvae are expected to have originated from the adult stock spawning in this bay. On the other hand, the three methods proposed depend upon the accuracy at which daily increment widths were measured. As daily increments are very distinctive in both the larval and juvenile stages for *S. melanostictus* (Hayashi *et al.*, 1989; Watanabe & Kuroki, 1997), however, it seems reasonable to infer a low influence of this factor in the conclusions derived from the present study.

GROWTH AND SURVIVAL

In the current study, the consistent results found among the three methods argues in favour that growth and mortality were directly related during the first three weeks of larval life of *S. melanostictus*, at least under the action of the two mechanisms tested (*i.e.* the bigger-is-better and growth-rate mechanisms). These results agree with previously published studies reporting that faster growing and larger fishes have enhanced advantages to deal with survivorship at a given moment in the sea. Conversely, the results contradict studies that have suggested that bigger is not always better based on the following evidence: (1) smaller sized fishes can gain advantage from a decreased rate of encounters

with predators (Taylor, 2003); (2) large body-size fishes have more melanophores, which can increase the probability that they will be detected by predators (Folkvord & Hunter, 1986; Fuiman, 1989); and (3) larger and fast-growing fishes can also have major swimming ability which can facilitate encounter rate with predators (Fuiman & Magurran, 1994; Cowan *et al.*, 1996; Paradis *et al.*, 1996). Furthermore, a recent study proposed the growth-selective hypothesis based on the growth-predation relationship for larval *E. japonicus* (Takasuka *et al.*, 2003). This hypothesis proposes that 'faster growing larvae will be less vulnerable to predation than slower growing conspecifics, even if they are the same size, at a given moment in the sea' (Takasuka *et al.*, 2003). More recently, Takasuka *et al.*, (2004a, b) did not find evidence for the bigger-is-better and stage-duration mechanisms for larval cohorts of this species in coastal waters. They found that growth rate of survivors were higher than for the original population, and they suggested that the differences in growth rate were mediated by predation. Conversely, in the current research on *S. melanostictus* growth-rate and bigger-is-better mechanisms seemed to be mutually dependent, operating synchronously during the larval stage of this clupeid. Further research focused to test the stage-duration and growth-predation hypotheses in *S. melanostictus* could provide a way to test to what extent the mechanisms associated to survival process fully differ between both clupeids.

The evidence either against or in favour of the bigger-is-better and growth-rate mechanisms support the view that growth is indeed affecting survival during the early life of fishes (either positive or negatively). What remains to be seen is to what extent the selective-mortality hypothesis is species specific, stage specific or mediated by the link between growth and predation such as suggested by Takasuka *et al.* (2003, 2004a, b) Unfortunately, most studies dealing with the growth and survival relationship published to date have been restricted to a single species and on small temporal and spatial scales (summarized in Table VII). Although comparisons can be spurious owing the differences in methodologies, the most common pattern seems to be a direct (*i.e.* positive) relationship between growth and survival for the larval stage. In addition, although perhaps simply coincidental these studies included young-of-the-year (YOY) fishes to reconstruct larval-growth patterns. Certainly, YOY fishes are the true survivors and if they were indeed faster growing and larger individual when they were larvae, their growth patterns should be stored in their otoliths. Consequently, it is reasonable to hypothesize that more reliable evidence could be found to test the growth and survival relationship when YOY fishes are included in the analyses.

The current paper gives further support for the framework of the growth-dependent mortality hypothesis documented for other marine fishes (Hovenkamp, 1992; Meekan & Fortier, 1996; Wright & Bailey, 1996; Van der Meeren, 2003; Nielsen & Munk, 2004) and provides two new approaches to take full advantage of statistical modules available in modern statistical software to analyse longitudinal data derived from otoliths. Certainly, reconstructions of past somatic-growth rates depend upon the degree of coupling between otolith and somatic-growth rate (Baumann *et al.*, 2005), and the published evidence to date suggests that decoupling occurs when growth controllers (*e.g.* temperature and

TABLE VII. Published studies in which otolith microstructure analysis was used to test the bigger-is-better (BIB), growth-rate (GR) and stage-duration (SD) mechanisms for tropical, subtropical and temperate fishes

Family	Species	Climate	BIB	GR	SD	Stage	Surv.	Meth.
Clupeidae	<i>Spratelloides gracilis</i> (1)	Tropical	+	+	ne	YOY	YOY	Tr
	<i>Engraulis japonicus</i> (2)	Temperate	-	-	-	Larvae	Larvae	Tr
	<i>Sardinops melanostictus</i> (3)	Subtropical	+	+	ne	Larvae	YOY	AC, Tr, AIM
	<i>Sardina pilchardus</i> (4)	Subtropical	+	+	ne	Larvae	YOY	AC
Gadidae	<i>Gadus morhua</i> (5)	Temperate	+	ne	ne	YOY	YOY	Other
	<i>Gadus morhua</i> (6)	Temperate	+	ne	ne	Larvae	Larvae	Other
	<i>Gadus morhua</i> (7)	Temperate	+	+	ne	Larvae	YOY	Tr
Labridae	<i>Symphodus roissali</i> (8)	Subtropical	+	ne	ne	Larvae	YOY	Tr
	<i>Symphodus ocellatus</i> (8)	Subtropical	+	ne	ne	Larvae	YOY	Tr
	<i>Thalassoma bifasciatum</i> (9)	Tropical	+	+	ne	Larvae	YOY	Tr
Osmeridae	<i>Halichoeres bivittatus</i> (9)	Tropical	+	+	ne	Larvae	YOY	Tr
	<i>Mallotus villosus</i> (10)	Polar	-	ne	ne	Larvae	Larvae	Other
Percidae	<i>Osmerus mordax</i> (11)	Temperate	+	+	ne	Larvae	YOY	Tr
	<i>Perca flavescens</i> (12)	Temperate	+	+	ne	YOY	YOY	Other
Pleuronectidae	<i>Pleuronectes platessa</i> (13)	Temperate	+	ne	ne	Larvae	Larvae	Other
	<i>Pomatomus saltatrix</i> (14)	Subtropical	+	ne	ne	Larvae	YOY	AC
Pomatomidae	<i>Oncorhynchus keta</i> (15)	Temperate	+	ne	ne	Larvae	YOY	Other
	<i>Oncorhynchus nerka</i> (16)	Temperate	+	ne	ne	Larvae	YOY	Other
	<i>Coregonus albus</i> (17)	Tropical	-	-	ne	Larvae	Larvae	Other
Coregonidae	<i>Coregonus lavaretus</i> (17)	Tropical	-	-	ne	Larvae	Larvae	Other

AC, collected individual were separated by age classes; AIM, autoregressive-individual method; Meth., methods; ne, not evaluated; Other, non-specified or cross-sectional length-on-age data; Stage, the developmental period at which the mechanisms were tested; Surv., survivors, the developmental stage from which growth patterns were re-constructed; Tr, traditional method. (1) Meekan *et al.*, 2006; (2) Takasuka *et al.*, 2004a; (3) Current study; (4) Alemany *et al.*, 2006; (5) Campana, 1996; (6) Meekan & Fortier, 1996; (7) Nielsen & Munk, 2004; (8) Raventós & Macpherson, 2005; (9) Searcy & Sponaugle, 2001; (10) Pepin *et al.*, 1992; (11) Sirois & Dodson, 2000; (12) Post & Prankevicius, 1987; (13) Hovenkamp, 1992; (14) Hare & Cowen, 1997; (15) Healey, 1982; (16) West & Larkin, 1987; (17) Urpanen *et al.*, 2005.

feeding) operates in extreme conditions (Mosegaard *et al.* 1988; Hare & Cowen, 1995; Baumann *et al.*, 2005). Then, if the growth-rate effect on the otolith size and fish size relationship is low, it would intrinsically imply that the environmental conditions associated to the growth controllers are relatively stable. As a corollary, the linear-growth pattern for the R_O and age, R_O and L_T and L_T and age relationships as well as the low growth-rate effect found in the current study seem to be proof that such conditions were operating for this species. Since otolith growth is a conservative process (Gutierrez & Morales-Nin, 1986; Secor & Dean, 1989) it is reasonable to expect less decoupling between otolith growth and somatic growth under optimal environmental conditions.

Evidence for the growth-rate and bigger-is-better mechanisms acquire special importance for *S. melanostictus* because cumulative mortality after the first-feeding stage has been suggested as the main factor determining the decline in population size in the last decade (Watanabe *et al.*, 1995). Indeed, if growth and mortality are related, drastic changes in the mechanisms affecting larval growth could trigger drastic changes in survival for this species. Unquestionably, many growth modifiers could be overlapping and hence be difficult to identify, but attention should be focused on the two main growth controllers (*i.e.* water temperature and food availability; Houde, 1997). In addition, the importance of growth for survival is also critical for *S. melanostictus* in coastal areas because highest growth rates have been documented for this species in nearshore nursery grounds (Watanabe & Kuroki, 1997). If the growth-rate and bigger-is-better mechanisms are operating on a species that tends to maximize spawning in coastal areas, then nearshore areas could always contain potential survivors, which would be vulnerable to the Shiraso fishery.

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