SCI. MAR., 69 (2): 231-240 SCIENTIA MARINA 2005

Age and growth of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean*

ATHANASSIOS C. TSIKLIRAS[1,2], EMMANUIL T. KOUTRAKIS[2] and
KONSTANTINOS I. STERGIOU[1]

[1] Aristotle University of Thessaloniki, School of Biology, Department of Zoology, Laboratory of Ichthyology,
P.O. Box 134, 541 24, Thessaloniki, Greece. E-mail: atsik@bio.auth.gr
[2] Fisheries Research Institute, NAGREF, Nea Peramos, 640 07, Kavala, Greece.

SUMMARY: The round sardinella, *Sardinella aurita* Valenciennes, 1847, was sampled monthly from commercial purse-seine vessels in Kavala Gulf (northern Aegean Sea, Greece) for two complete year cycles (September 2000-August 2002). Its maximum total length and age were 248 mm and 5 years respectively. The length-weight relationship was $W=0.0062TL^{3.064}$ for males and $W=0.0059TL^{3.084}$ for females. The marginal increment analysis on scales (n=1352) confirmed annulus formation during February-March, which coincided with the lowest sea surface temperature prevailing in the study area. The marginal increment ratio for ages 1, 2 and 3 was positively correlated with sea surface temperature (all $r>0.4$, $P<0.05$). The parameters of the von Bertalanffy growth equation were: $L_\infty=248.678$ mm, $K=0.509$ yr^{-1} and $t_0=-0.881$ yr. The comparison of growth parameters for round sardinella, using the auximetric plot, from Mediterranean and northwest African waters indicated different growth patterns between the two areas.

Key words: age, growth, growth pattern, round sardinella, Aegean, Mediterranean.

RESUMEN: EDAD Y CRECIMIENTO DE LA ALACHA (*SARDINELLA AURITA*) EN EL MEDITERRÁNEO NORESTE. – La alacha, *Sardinella aurita* Valenciennes, 1847, se muestreó mensualmente durante dos ciclos anuales completos cycles (septiembre 2000-agosto 2002), a partir de barcas de cerco en el Golfo de Kavala (norte del mar Egeo, Grecia). La máxima longitud total y edad fue 248 mm y 5 años respectivamente. La relación talla edad fue $W=0.0062TL^{3.064}$ para machos y $W=0.0059TL^{3.084}$ para hembras. El análisis de incrementos marginales de las escamas (n=1352) confirmó la formación de anillos anuales durante febrero-marzo, lo que coincidió con las menores temperaturas superficiales del mar en el área de estudio. La relación de incrementos marginales para las edades 1, 2 y 3 estuvo positivamente correlacionada con la temperatura superficial del agua de mar ($r>0.4$, $P<0.05$). Los parámetros de la ecuación de crecimiento de von Bertalanffy fueron $L_\infty=248.678$ mm, $K=0.509$ años^{-1} y t_0 La comparación de parámetros de crecimiento de la alacha para el Mediterráneo y las aguas del noroeste de África indican diferentes patrones de crecimiento entre las dos áreas.

Palabras clave: edad, crecimiento, patrones de crecimiento, alacha, Egeo, Mediterráneo.

INTRODUCTION

The round sardinella, *Sardinella aurita* Valenciennes, 1847 (Pisces, Clupeidae) is a marine pelagic fish that is widely distributed throughout the tropical and subtropical seas of the world, including the entire Mediterranean and the Black Sea (Froese and Pauly, 2003). It is a key species inhabiting the ecosystem of the northwest African upwelling region (Bard and Koranteg, 1995).

It is commercially exploited in several southern Mediterranean countries (e.g. Egypt: Wassef *et al*., 1985; Libya: Pawson and Giama, 1985; Algeria: Bouaziz *et al*., 1998; Tunisia: Gaamour *et al*., 2001) and along the northwest African coast, where its population increase during the 1980s was known as

*Received May 14, 2004. Accepted September 29, 2004.

the ‘sardinella puzzle’ (Bard and Koranteg, 1995). The round sardinella is also of major commercial importance to the Greek purse-seine fishery, with 2215 metric tons landed in 2001, showing a 30-fold increase since 1990 (National Statistical Service of Hellas, 1990-2001). In Greece, it is used in the canning industry or as bait for other, highly profitable fisheries (e.g. bluefin tuna and swordfish). Prior to its recent establishment in the northern Aegean waters, as a result of hydrological changes (Bethoux and Gentili, 1999), its distribution was mainly confined to the southern Aegean (Ananiades, 1952).

The age and growth of round sardinella have been studied in the southern Mediterranean Sea (Navarro, 1932; Rossignol, 1955; Ben Tuvia, 1956; Pawson and Giama, 1985; Bouaziz *et al.*, 1998; Bouaziz *et al.*, 2001; Gaamour *et al.*, 2001) and northwest African waters (Pham-Thuoc and Szypula, 1973; Krzeptowski, 1981; Maxim and Maxim, 1987-88; Chesheva, 1998). In contrast, data on age and growth in the northern Mediterranean have only been provided for Greek waters (Ananiades, 1952).

In the present study, data on the age and growth of round sardinella in the northern Aegean Sea, the northern boundary of its Mediterranean distribution, are presented. These data are compared with those available from other areas of its distribution, using the auximetric plot (Cury and Pauly, 2000), in order to test whether the genetic differentiation of Mediterranean and Atlantic round sardinella stocks (Chikhi *et al.*, 1997) is also reflected in the growth performance of the species in these two large regions.

MATERIALS AND METHODS

Samples were collected onboard a commercial purse-seine boat fishing with artificial light at night. The boat was equipped with a purse-seine net (mesh size: 9 mm, bar length). Sampling was carried out on a monthly basis for two complete year cycles (September 2000 to August 2002) in the Kavala Gulf (northern Aegean Sea, Greece), at depths ranging between 31 and 65 m. Monthly sea surface temperature (°C) was recorded during sampling using a CTD probe (Ocean 301, Idronaut).

All samples were preserved in 8% formaldehyde buffered solution for two months. All fish were measured to the total (TL, mm), fork (FL, mm) and standard (SL, mm) lengths, the latter as defined by Holčik *et al.* (1989), weighed to the nearest 0.01 g (total weight, W), and sexed whenever possible. The relationships between different types of length were derived using linear regression. Consequently, the length-weight relationships ($W=aTL^b$) were determined for males, females and both sexes combined. The Fulton condition factor, $K_C=(W/TL^3)10^5$ (Le Cren, 1951), was calculated monthly and separately for the two sexes. Length-weight relationships were tested for differences between sexes using the analysis of t-test (Zar, 1999).

Scales from 1500 specimens were used for age estimation. Scales, which are of a cycloid ‘herring’ type (Chesheva, 1998), were extracted from the left flank, near the tip of the pectoral fin, washed and placed between slides. The scales (8-10 from each fish) were viewed using an image processing system consisting of a computer, a video camera fitted on an Olympus BH2 microscope, and the Optical Pattern Recognition System software package (Biosonics, 1986). Scales were read twice by the senior author at an interval of two months. They were read randomly to avoid bias in assigning ages. The scale radius was measured from the focus to the end of the scale on the left dorsal rim. Interpretation of annuli patterns was based on the criteria provided in Bagenal and Tesch (1978) and Chesheva (1998). Age classes were assigned based on the number of growth marks, the time of growth mark formation and the month the fish was collected. The date of birth for round sardinella was set at June, which approximately corresponded to the peak spawning period based on information on maturity stages, gonadosomatic index, and the presence of eggs and larvae in the study area (Tsikliras, 2004).

Validation of annual increment formation is a necessary prerequisite for ageing fish. Marginal increment analysis was used to validate the periodicity of growth increment formation (Beamish and McFarlane, 1983). The analysis was based on complete randomisation of samples, examination of two complete year cycles, and age specificity (Campana, 2001). The marginal increment ratio (MIR) for each specimen was estimated as follows:

$$MIR = \frac{S - r_n}{S} ,$$

where S is the scale radius and r_n is the radius of the most recent growth mark. Monthly mean marginal increments were calculated for each age with more than five specimens.

The relationship between total length and scale radius was examined using linear regression (TL= a+bS), from which back-calculated lengths at growth mark formation were estimated using the Fraser-Lee equation (Francis, 1990):

$$L_i = c + (TL - c)(\frac{S_i}{S}) \ ,$$

where L_i is the total length of the fish when growth mark i was formed, TL is the total length at time of capture, S_i is the distance from scale centre to growth mark i, S is scale radius and c is the intercept on length axis of the linear regression between total length and scale radius.

The growth curve was modelled using the von Bertalanffy growth equation (VBGE):

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

as well as its seasonalised counterpart (Pauly, 1998):

$$L_t = L_\infty(1 - e^{-K(t-t_0) - \frac{CK}{2\pi}\sin[2\pi(t-t_s)]}) \ ,$$

where L_t is the total length at age t, L_∞ is the asymptotic length, i.e. the mean length the fish in a population would reach if they were to grow indefinitely, K is a constant of dimension 1/t, expressing the rate at which L_∞ is approached, t_0 the theoretical age at which predicted mean length is zero, C expresses the amplitude of the seasonal growth oscillations, and t_s (summer point) expresses the phase of oscillations. The summer point equals t_w-0.5, where t_w (winter point) is that point at which minimum growth occurs (Pauly, 1998). If C=0, there is no seasonality in the growth and the equation reduces to the standard form of the von Bertalanffy function. For values of C close to 1, the amplitude of seasonality factor is maximal (Longhurst and Pauly, 1987). The mean observed lengths at age were used in order to assign equal weight to all observations. Growth parameters of both models were estimated iteratively using the Simplex minimisation algorithm of the STATISTICA statistical package (Statsoft, 1998). The measure of goodness of fit was the coefficient of determination.

The growth performance of a species can be captured by the growth index φ'=log$K$+2logL_∞ (Munro and Pauly, 1983), which can be used to compare growth rates between species and to evaluate growth performance potential under various environmental stresses (Pauly, 1994). The growth index is a species-specific constant related to the shape and the gill surface area of the species (Longhurst and Pauly, 1987).

Finally, the previously estimated growth parameters of different Mediterranean and northwest African round sardinella stocks (Table 1) were used to construct an auximetric double logarithmic plot of the parameter K against the corresponding estimate

TABLE 1. – Ageing methodology used (S: scales; LF: length frequency distribution; O: otoliths) and growth parameters (L_{max}: maximum reported total length; L_∞ asymptotic length; K: growth coefficient; t_0: age at zero length; t_{max}: maximum reported age; φ': growth index, as calculated in the present study from the growth parameters originally reported) for males (M) and/or females (F) of round sardinella of the Mediterranean Sea and northwest African coast.

Area	Method	Sex	L_{max}	L_∞	K	t_0	t_{max}	φ'	Reference
Mediterranean Sea									
Spain[1]	-	M, F	-	27.54	0.458	-0.382	4	2.541	Navarro, 1932
Greece[2]	S	M, F	27.00	32.57	0.288	-0.579	5	2.485	Ananiades, 1952
Israel	-	M, F	-	31.10	0.250	-1.800	5	2.383	Ben Tuvia, 1956
Algeria	LF	M	23.50	20.70	0.691	-0.194	5	2.471	Bouaziz *et al.*, 1998
Algeria	LF	F	25.50	24.24	0.540	-0.170	5	2.501	Bouaziz *et al.*, 1998
Algeria	LF	M, F	25.50	34.96	0.236	-0.707	4	2.460	Bouaziz *et al.*, 2001
Tunisia[3]	O	M	26.78	26.42	0.265	-1.920	7	2.314	Gaamour *et al.*, 2001
Tunisia[4]	O	F	27.35	29.73	0.239	-2.100	7	2.310	Gaamour *et al.*, 2001
Tunisia[5]	O	M, F	27.35	31.32	0.240	-2.580	7	2.268	Gaamour *et al.*, 2001
Northwest Africa									
Canary Islands[6]	-	M, F	-	34.61	0.306	-0.631	5	2.564	Navarro, 1932
Congo	-	M,F	-	31.00	0.693	-	5	2.823	Rossignol, 1955
Mauritania	S	M, F	41.00	40.70	0.326	-0.628	7	2.732	Pham-Thuoc and Szypula, 1973
Senegal[7]	S	M	38.12	40.69	0.274	-0.991	8	2.657	Krzeptowski, 1981
Senegal[8]	S	F	39.71	43.18	0.303	-0.955	8	2.751	Krzeptowski, 1981
Senegal[9]	S	M, F	39.71	42.12	0.283	-0.989	8	2.701	Krzeptowski, 1981
Senegal-Mauritania[10]	LF	M, F	44.47	45.22	0.364	-0.691	6	2.872	Maxim and Maxim, 1987-88
Mauritania[11]	S	M, F	39.10	41.63	0.261	-0.871	8	2.655	Chesheva, 1998

[1, 2, 6, 11] The von Bertalanffy growth equation was estimated from the mean lengths at age given by the authors,

[3, 4, 5, 10] Fork lengths converted to total lengths according to the equation given by the authors,

[7, 8, 9] Total lengths calculated according to the equation of Maxim and Maxim (1987-88) for the same area.

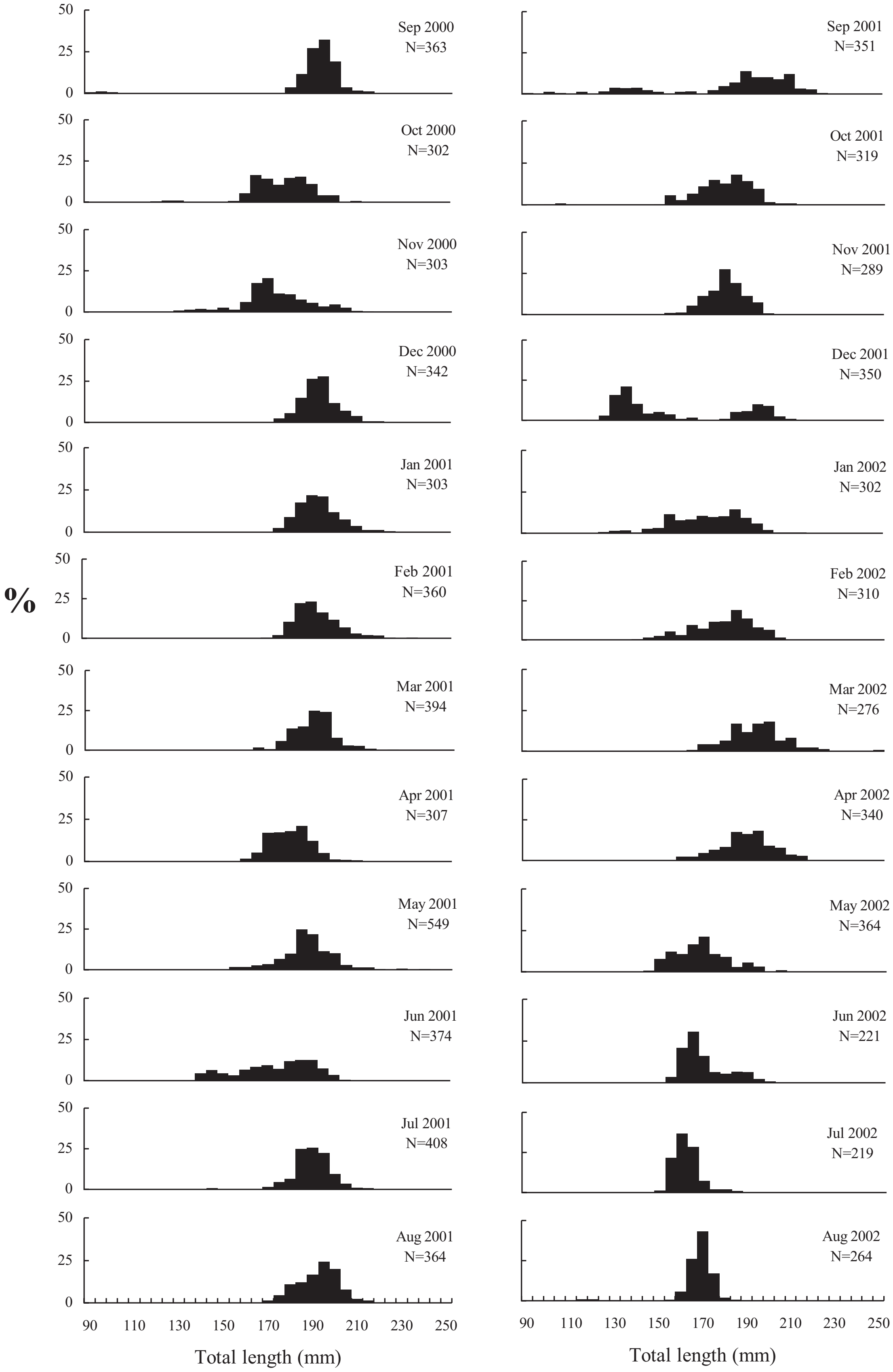

FIG. 1. – Monthly length frequency distribution of round sardinella, sexes combined, Aegean Sea (September 2000- August 2002).

of asymptotic length L_∞. Such a plot has been recently proposed for the comparison of within- and between-species growth performances (Cury and Pauly, 2000).

RESULTS

Overall, 8400 specimens were collected, 1500 of which were used for ageing and growth analysis. The length of round sardinella ranged between 84 and 248 mm TL (Fig. 1). The maximum size of females (102 to 248 mm TL) slightly exceeded that of males (97 to 243 mm TL), while the length of unsexed fish ranged from 84 to 105 mm TL. The three somatic lengths, i.e. total (TL), fork (FL) and standard (SL) length, were highly correlated to each other:

$FL= 1.468+0.879TL$ ($r^2=0.99$, $n=8400$, $P<0.01$),
$SL= -0.466+0.838TL$ ($r^2=0.99$, $n=8400$, $P<0.01$) and
$SL=-0.847+0.952FL$ ($r^2=0.99$, $n=8400$, $P<0.01$).

The length-weight relationship was $W=0.0062TL^{3.064}$ ($r^2=0.97$, $n=3274$, $S.E._b =0.009$) for males and $W=0.0059TL^{3.084}$ ($r^2=0.97$, $n=3434$, $S.E._b =0.008$) for females. The slope was significantly different between sexes (t-test: $t=8.621$, $P=0.006$), and significantly higher than the theoretical value of 3 for males (t-test, $t=6.572$, $P<0.001$) and females (t-test, $t=9.581$, $P<0.001$), indicating positive allometric growth for both sexes. The parameters a and b of the TL-W relationship exhibited monthly variations. The parameter a ranged between 0.00136 (females, April 2002) and 0.172 (males, September 2000), while b ranged between 1.963 (males, September 2000) and 3.586 (females, April 2002).

The Fulton condition factor varied between 0.66 (June 2001) and 0.81 (September 2000 and August 2001) for males (Fig. 2a) and between 0.68 (May 2001) and 0.82 (August 2002) for females (Fig. 2b). Despite its small amplitude, the condition factor exhibited a clear seasonal variability, with two maxima, one in early spring and one in late summer/autumn for both sexes, and one minimum, in late spring for females and in early summer for males. No relationship was found between condition factor and sea surface temperature (at $P<0.05$).

The mean monthly marginal increments of samples with one, two and three growth marks followed similar trends, with values declining precipitously in February and March (Fig. 3a). Growth mark formation occurred from January to March for ages 1 to 3 years, while sample size was inadequate for the monthly analyses of ages 4 and 5. The minimum marginal scale increments were recorded in March 2001 for the first study year and in February 2002 for the second one. The fact that during the course of a year, regardless of the number of growth marks present, the marginal increments underwent a pronounced decline only in late winter demonstrates that a single growth mark (=annulus) is formed in the scales of round sardinella each year. Annuli were not formed synchronously in all specimens, suggesting inter- and intra-age class variability in the timing of annulus formation. Mean monthly MIR for ages 1, 2 and 3 years were significantly ($r=0.46$, 0.45, 0.81 respectively, $P<0.05$ at all cases) positively correlated to SST (Fig. 3b).

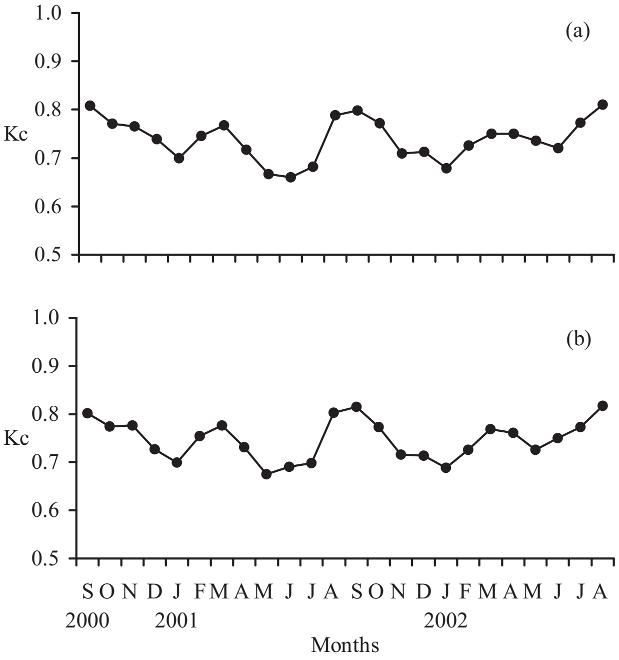

FIG. 2. – Monthly variation of Fulton condition factor (K_C) for male (a) and female (b) round sardinella, Aegean Sea (September 2000-August 2002).

The size of the fish from which scales were extracted ranged from 84 to 248 mm TL (Table 2). Out of the 1500 specimens used for age reading, 1352 were aged successfully (90.13%). The remaining ones were either damaged (6.46%) or inconclusive (3.41%). The scale nucleus is hardly distinguished, while growth marks are well defined but disappear from the rear (exposed) side of the scale. According to the annual growth marks present, the age of round sardinella in the northern Aegean Sea ranged from 0 to 5 years. One- and two-year-old fish were the dominant age classes in the catches,

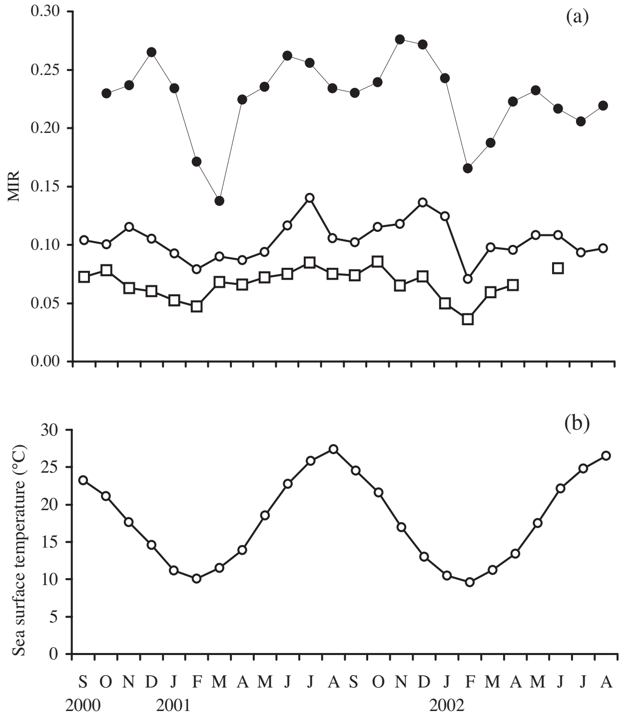

FIG . 3. – Monthly means of marginal increment ratio (MIR) for age I (solid circles), II (open circles) and III (open squares), for round sardinella (a), and sea surface temperature (°C) in the area (b) between September 2000 and August 2002.

accounting for 24.93 and 44.08% of the total aged individuals respectively (Table 2).

Scale radius was linearly correlated to fish length. The regressions of TL on S for males and females were:

$$\text{Males: } TL = 59.658+30.189S$$
$$(r^2=0.78, n=662, S.E._b=0.013, P<0.01),$$

$$\text{Females: } TL = 53.722+32.177S$$
$$(r^2=0.80, n=675, S.E._b=0.012, P<0.01).$$

TABLE 2. – The specimens of round sardinella used in growth analysis, Aegean Sea (2000-2002). Length: total length, TL, mm; N: number of specimens used for age reading; Aged: number of specimens successfully aged; I-V: number of annuli present on the scale.

Length	N	Aged	Annuli					
			0	I	II	III	IV	V
90	6	5	5					
100	7	5	5					
110	11	9	9					
120	23	19	19					
130	71	63	63					
140	65	51	51					
150	41	32	23	9				
160	67	52	1	51				
170	132	121		98	23			
180	172	153		96	57			
190	357	334		77	247	10		
200	316	297		6	227	64		
210	151	136			39	90	7	
220	64	54			3	36	15	
230	15	14				1	10	3
240	6	5						5
250	2	2						2
Total	1500	1352	176	337	596	201	32	10

The slopes (t-test, t=1.79, P=0.072) and the intercepts (t-test, t=0.062, P=0.95) did not differ significantly between sexes. Thus, the data were pooled for growth analysis and the combined slope was used for the back-calculation:

$$TL = 37.808+37.033S$$
$$(r^2=0.89, n=1352, S.E._b=0.009, P<0.01).$$

Mean back-calculated lengths at age indicated very rapid growth during the first year of life (59.83% annual growth increment), a decline in growth during the second year (16.27%) and rather constant growth during the third, the fourth and the fifth year (Table 3).

The VBGE parameters were (Table 4 and Fig. 4):

TABLE 3. – Mean back-calculated total lengths (in mm ± S.E.) at annulus formation, annual increment and % annual increment per age for round sardinella, Aegean Sea (2000-2002).

Annuli	Back-calculated lengths at annulus formation				
	I	II	III	IV	V
I	141.15±7.18				
II	134.94±7.91	173.28±3.63			
III	135.91±14.45	175.82±5.72	193.53±5.06		
IV	135.56±25.64	178.82±9.51	196.43±8.00	208.06±7.01	
V	137.48±67.97	179.24±26.74	202.52±15.68	218.15±14.07	228.88±22.09
Weighted mean	136.93	174.17	194.28	210.46	228.88
Annual increment	136.93	37.24	20.11	16.17	18.42
% Annual increment	59.83	16.27	8.79	7.07	8.05

TABLE 4. – Parameters estimates, standard errors (S.E.) and 95% confidence intervals for the standard and the seasonalised von Bertalanffy growth models for round sardinella, Aegean Sea (2000-2002).

Parameter	Estimate	S.E.	95% confidence intervals	
Standard growth model (r^2=0.99)				
L_∞ (mm)	248.678	3.592	241.494	255.862
K (yr^{-1})	0.509	0.057	0.395	0.623
t_0 (yr)	-0.881	0.127	-0.627	-1.135
Seasonalised growth model (r^2=0.99)				
L_∞ (mm)	249.948	4.496	240.956	258.940
K (yr^{-1})	0.494	0.043	0.408	0.580
t_0 (yr)	-0.856	0.081	-0.694	-1.018
C	0.400	0.153	0.094	0.706
t_w	0.815	0.119	0.577	1.053

$$L_t = 248.678(1 - e^{-0.509(t+0.881)})$$

$$L_t = 249.948(1 - e^{-0.494(t+0.856) - \frac{0.400 \times 0.494}{2\pi}\sin[2\pi(t-0.315)]}).$$

The predicted total lengths based on the VBGE were greater than the weighted back-calculated total lengths because annulus formation occurred in winter when the fish were on average about 5 months younger than the real age (Table 5). The round sardinella reached 61.6% of its L_∞ during the first year of life and 77.0% during its second year of life, values that closely agree with the corresponding back-calculated lengths. The computed values for C and t_w indicated that there is some degree of seasonality in growth, with the lowest growth occurring at about 8-9 months after the date of birth, that is, the growth rate is lower in February-March.

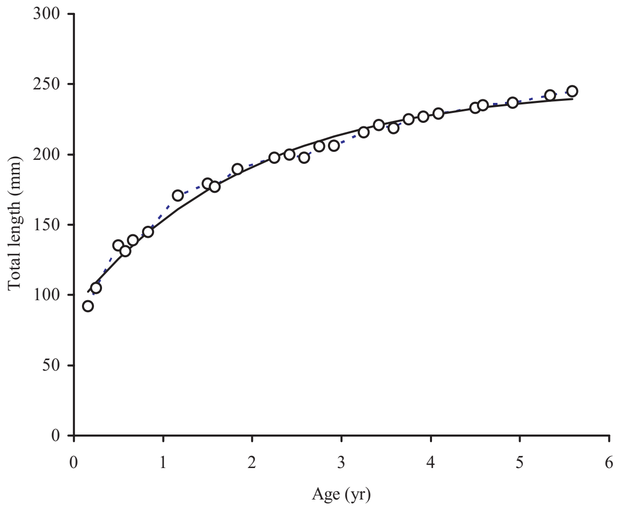

FIG. 4. – Standard (solid line) and seasonal (dashed line) von Bertalanffy growth curves fitted to monthly mean length-at-age data (open circles), for round sardinella in the Aegean Sea.

TABLE 5. – Back-calculated and predicted (standard and seasonalised von Bertalanffy growth models) total lengths (mm) at age (yr) for round sardinella, Aegean Sea (2000-2002).

Age	Back-calculated	von Bertalanffy	Seasonalised von Bertalanffy
1	136.93	153.17	116.51
2	174.17	191.24	168.55
3	194.28	214.12	200.30
4	210.46	227.87	219.67
5	228.88	236.14	231.48

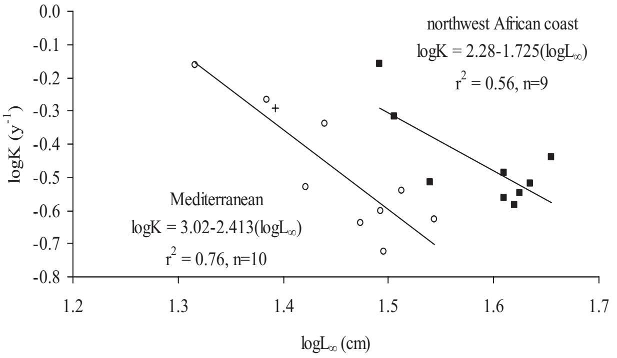

FIG. 5. – Auximetric plot for round sardinella for different areas of the Mediterranean (open circles), including the northern Aegean (cross), and the northwest African coast (solid boxes).

The ratio between maximum recorded length (L_{max}) and asymptotic length (L_∞) was 0.997. The φ′ value in the northern Aegean Sea was 2.491, similar to those estimated for the Aegean and other areas of the Mediterranean (Table 1). The mean growth index was significantly lower (t-test, t=7.57, P<0.001) for the Mediterranean stocks (φ′=2.423, S.E.=0.003) than for the northwest African coast ones (φ′=2.716, S.E.=0.003). The latter were characterised by higher lifespan, higher L_{max}, and for the same K, higher L_∞ than their Mediterranean counterparts (Table 1). This striking difference is nicely captured by the auximetric plot (Fig. 5). The log$K$-logL_∞ relationships were linear with negative slopes for both regions and differed significantly. The slope of the relationship, however, was not significantly (P>0.1) different from 0 when values from both regions were pooled together in the analysis.

DISCUSSION

Both male and female round sardinella exhibit positive allometric growth in the northern Aegean Sea, as has been previously reported for southern Mediterranean (Pawson and Giama, 1985; Bensahla Talet *et al.*, 1988; Gaamour *et al.*, 2001) and

Atlantic stocks (Fréon *et al.*, 1997), and in contrast to other Aegean areas (Petrakis and Stergiou, 1995; Moutopoulos and Stergiou, 2002; Koutrakis and Tsikliras, 2003). Such differences might be attributed to the fact that most of the above-mentioned studies did not include seasonal sampling, which is necessary because the condition of fish generally changes as a function of many factors (e.g. season, area, sex, maturity stage, feeding, sampling and preservation techniques; Le Cren, 1951). The condition factor increases in spring, when round sardinella start to feed upon the zooplankton organisms benefited from the high primary production (Tsikliras, 2004), and improve their condition for the forthcoming spawning. The robustness of the fish in late summer/autumn is attributed partly to the improvement of the condition after spawning and partly to the storage of energy for the winter.

In teleosts, the trends exhibited by the marginal increment analysis on scales or otoliths have frequently been used to validate the hypothesis that the growth zones on these structures are formed annually and can thus be used for ageing individual fish. The scales and the validating method of marginal increment analysis are particularly useful for short-lived species (Campana, 2001). The formation of annuli on scales has been attributed to various factors such as temperature, photoperiod and fish feeding (Bagenal, 1974). For the northern Aegean round sardinella, marginal increment analysis over two complete year cycles demonstrated the annual periodicity of growth increments on the scales, showing the potential use of scales for ageing purposes. Indeed, scales and marginal increment analysis have previously been used for round sardinella ageing in Mauritania (Chesheva, 1998). The coincidence of annulus formation of round sardinella with the lowest water temperatures, as is also indicated by the positive relationship between SST and MIR, might suggest that temperature is one of the most important factors in controlling the formation of growth marks in the study area. There is evidence that the formation of growth marks in scales and otoliths requires seasonal changes in water temperature of 4-5°C (Longhurst and Pauly, 1987). Indeed, the seasonal mean water column temperature difference in the study area was 6.5°C.

Clupeoids have a strong shoaling behaviour and tend to be relatively fast-growing and short-lived, rarely living beyond 5-10 years (Blaxter and Hunter, 1982). These characteristics were generally true of all Mediterranean and northwest African round sardinella stocks (Table 1). Round sardinella in the northern Aegean were characterised by a lower lifespan, lower $L_{\max}$ and L_∞, smaller length-at-ages than the northwest African stocks, and by lower $L_{\max}$ and L_∞ than most Mediterranean stocks. The natural population age structure of any species must have evolved (within the physiological capacity of each species) to optimise long-term persistence and maximise occupation of habitat in competition with other species (Longhurst, 1998). The observed longevity of round sardinella in the northern Aegean is similar to that previously reported for the Mediterranean Sea. The only exception is the Tunisian stock (lifespan: 7 yr; Gaamour *et al.*, 2001). Greater lifespan has only been reported for northwest African waters where round sardinella reach an age of 8 years.

In general, growth parameters of round sardinella in the northern Aegean agreed with those reported from previous studies in the Mediterranean (Table 1). The difference between back-calculated lengths-at-age and observed lengths-at-age is related to the formation of annuli 4-5 months before spawning, which in northern Aegean begins in June and lasts about two months (Tsikliras, 2004). The high overlap between successive age classes in terms of length for ages 2 to 4 years (Table 2) must be attributed to the ability of each individual to confront potential environmental stress as well as to the different growth opportunities for the fish born at the beginning and at the end of the spawning season. Not all populations are subjected to the same amount of stress and, in a Darwinian world, not even all individuals of a population react in a similar way to stresses such as starvation or unfavourable environment. High individual growth variability has also been reported by Pawson and Giama (1985) for round sardinella in Libyan waters, and did not allow the estimation of growth parameters. These authors attribute growth variability to different growth opportunities and the relatively extended spawning period.

The rapid early growth observed in the northern Aegean has also been previously reported for round sardinella on the northwest African coast (Boely, 1982), and also for a congeneric species, the oil sardine *S. longiceps*, on the southeast coast of India (Longhurst and Wooster, 1990). In contrast, Pawson (1990) reports that the smallest (110-124 mm TL) round sardinella caught in autumn were approximately 14 months of age. In the northern Aegean Sea, the growth of round sardinella juveniles is so rapid that they reach 130 mm at the age of 3-4 months (Fig. 4). Such differences in life history parameters among geographically closely related populations of round sardinella may be attributed to the phenotypic plasticity of the species and the ability to adapt and take advantage of environmental conditions (Cury and Fontana, 1988).

Life history theory predicts that there is a trade off between growth and reproduction in animals with indeterminate growth (Stearns, 1992), and especially in fish because female fecundity is a function of size (Wootton, 1998). The “reproductive drain hypothesis” suggests that adult fish grow less than juvenile fish because much of their energy is allocated to reproduction. In contrast, Pauly (1994) suggests that it may be the slowdown in growth that triggers reproduction. The rapid growth for round sardinella during the first year of life declined gradually in the subsequent years, probably because a certain amount of energy in excess of maintenance was allocated to reproductive needs. Round sardinella in the study area reached sexual maturity at the size of 155.0 and 168.33 mm (TL) for males and females respectively (Tsikliras, 2004), which correspond to an age of 1.03 years for males and 1.33 for females.

The L_{max} to L_∞ ratio is an important parameter in the context of life history theory (e.g. Longhurst and Pauly, 1987), as it shows the growth a fish achieves during its lifespan, expressed as a percentage of its potential growth (Beverton, 1963). The L_{max} to L_∞ ratio for a dataset of 74 Hellenic marine fish species ranged between 0.56 and 1.34, with a mean value of 0.90 (Stergiou, 2000). The computed value for round sardinella in the Aegean Sea, which falls within the reported range and very close to the mean value, suggests that round sardinella is able, within its maximum life span, to complete more than 99% of what would appear to be its potential growth range. Similar values have been reported before for several clupeid and engraulid species, including *Sardinella* spp. (Beverton, 1963).

Differences in growth patterns can be the result of differences in genetic structure and/or differences in temperature, density of food and diseases (Pauly, 1994; Wootton, 1998). The comparison of K and L_∞ of round sardinella from the Mediterranean Sea and the northwest African coast showed that the growth patterns between these two closely situated regions differed, with all the Mediterranean stocks forming one group. This agrees with the results of genetic studies on round sardinella based on mitochondrial DNA, which showed that there is no gene flow between Atlantic and Mediterranean stocks, and two genetically differentiated groups were identified (Chikhi *et al*., 1997). In addition, the food availability of the Mediterranean Sea is much lower and the prevailing temperatures much higher (Stergiou, 2000) when compared to the cold nutrient-rich waters in upwelling systems, such as the northwest African one (Mann and Lazier, 1996).

Despite the oligotrophic nature of the eastern Mediterranean, which has been characterised as a ‘marine desert’ (Azov, 1991), eutrophic areas do exist locally, especially along the northern Aegean coast because of the presence of the cold and nutrient rich Black Sea water and the freshwater discharge (Stergiou *et al*., 1997). Both factors favour fish growth and high biomasses, especially for pelagic fish such as round sardinella. Nevertheless, the L_{max} of round sardinella in the northern Aegean Sea is smaller than in the southern Mediterranean. Such a discrepancy might be due to the recent invasion and establishment of round sardinella in the northern Aegean Sea, the northern boundary of species’ distribution in the eastern Mediterranean. Additionally, the competition with other species for space and food may have not allowed for the immediate phenotypic adaptation of this characteristic to the species’ new environment.

ACKNOWLEDGEMENTS

The authors wish to thank two anonymous reviewers for their constructive comments.

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