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Trends in various biological parameters of the European sardine, *Sardina pilchardus* (Walbaum, 1792), in the Eastern Mediterranean Sea*

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SUMMARY: In this study we present the longest time series available concerning various biological parameters of sardine in Greek waters. Biweekly samples were collected within a single day in clusters from random collections of the total landed catch derived from different vessels operating in the Northwest Aegean Sea, between July 1996 and June 2000. Total length (TL) was measured for 51.246 individuals. In addition, for a sub-sample of 50 individuals per sampling period, gross body weight and gonad weight were also measured to the nearest 0.1 and 0.01 g respectively. The analysis of the biweekly length-frequencies showed that the dominant length classes ranged between 130 and 160 mm TL. The mean biweekly TL decreased significantly ($r=-0.525$, $P<0.05$) with time during the study period. The same was also true for the maximum TL ($r=-0.46$, $n=77$, $P<0.001$). In contrast, the exponent b of the length-weight relationship increased significantly ($r=0.358$, $P<0.05$) with time. No relationship was found between the gonadosomatic index and b ($r=-0.13$, $P>0.05$). The parameters of the seasonalized von Bertalanffy growth equation and mortality and exploitation rates, based on monthly length-frequencies, were also estimated. The decline in the mean TL and the increase in the slope b of the length-weight relationship are discussed in relation to the recent increase in the effort expended on sardine populations and within the framework of density-dependent effects on growth.

Key words: long-term changes, growth, length-weight relationship, *Sardina pilchardus*, Eastern Mediterranean, Aegean Sea.

INTRODUCTION

The European sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) are the two most important small-sized pelagic species in Greek waters. A study on genetic distances, based on electrophoresis, and of morphometric and meristic characters using multivariate analysis does not indicate separate stocks of sardine in the Aegean Sea (Spanakis *et al*., 1989). Sardine comprises about 12% of the mean total reported landings (Stergiou *et al.*, 1997a) and 23% of the North Aegean ones (Stergiou and Pollard, 1995). It is mainly caught using purse seiners at depths less than 60 m, making up about 20% of the total purse seine catch, as well as using beach seiners, small netters and, to a lesser extent, trawlers (Stergiou *et al*., 1997a). Sardine landings exhibit a clear seasonal cycle, with catches being much higher during the October-May period, when sardine schools migrate to the coasts for spawning (Stergiou *et al*., 1997a; Stergiou and Lascaratos, 1997; Giannoulaki *et al*., 2001). During 1964-1990, the total sardine landings fluctuated around 10,000-12,000 t and sharply increased to 20,000 t in 1992, following the decline of the anchovy landings from 25,000 t in

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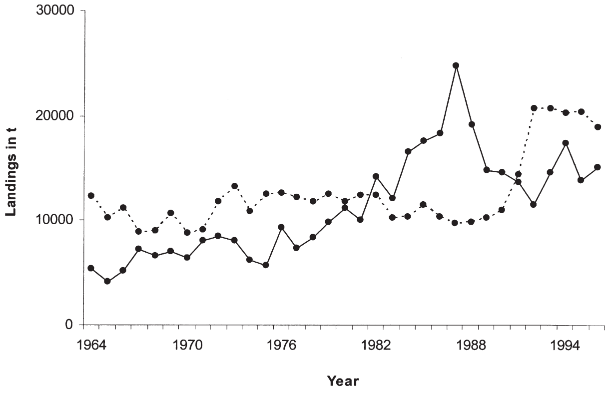

FIG. 1. – Annual catches of anchovy (continuous line) and sardine (dotted line) in Greek waters, 1964-1997.

1987 to about 10,000 t in 1992 (Fig. 1). The analysis of sardine landings using a variety of statistical tools (Stergiou, 1989, 1990, 1991, 1992; Stergiou and Christou, 1996; Stergiou *et al.*, 1997b; Stergiou and Lascaratos, 1997) indicate: (a) persistence of landings; (b) landing periodicity of 2-3 and 4-5 years; (c) that climate might affect long-term trends and short-term variation in the landings; and (d) variability and replacement of anchovy by sardine landings are not due to chance, and that wind activity over the North Aegean Sea might act as a forcing function.

There are many published studies concerning various aspects of sardine biology, ecology and fisheries in Greek Seas (physiology: Machias and Tsimenides, 1995, 1996; age, growth and reproduction: Laskaridis, 1948; Tserpes and Tsimenides, 1991; Machias *et al.*, 2001; Koutrakis *et al.*, 2001; Ganias *et al.*, 2000, 2001b; migration: Giannoulaki *et al.*, 1999; eggs and larvae: Yannopoulos *et al.*, 1973; Daoulas and Economou, 1986; Machias *et al.*, 2001; Ganias *et al.*, 2001a; genetics: Spanakis *et al.*, 1989; Machias *et al.*, 2001; daily egg production: Somarakis *et al.*, 2001; echo-abundance and distribution: Machias *et al.*, 1996, 2001; Maravelias *et al.*, 1997; Giannoulaki *et al.*, 2001; fisheries: for a review see Stergiou *et al.*, 1997a). Nevertheless, there is an absence of regular, long time series of data on growth, maturity, biomass and recruitment of sardine, and other pelagic species, throughout the Greek Seas. This is because experimental sampling and surveys are generally highly discontinuous at both temporal and spatial scales, a fact representing an impediment to the study of the effects of environmental variability on small pelagic species. Within this context, an effort was made in 1996 for the establishment of a long time series, the longest one for the Eastern Mediterranean Sea, of various biological parameters of sardine based on biweekly samples collected from the commercial landings of the purse-seine fleet in the Northwest Aegean Sea.

Fishing has important effects on the demographic structure of the exploited stocks (e.g. Jennings *et al.*, 2001; Stergiou, 2002). The increased fishing effort expended on sardine stocks since the early 1990s (Fig. 1) occurred with a 34% decrease in the North Aegean sardine biomass in 1996 when compared to that of 1995 (Machias, unpubl. data). In this study we tested whether such an increase in the effort expended on sardine populations is reflected in the trends in the biweekly length-frequencies, the mean total length, the exponent b of the length-weight relationship and the gonadosomatic index of sardine during July 1996-June 2000. In addition, growth and mortality rates were also estimated.

MATERIAL AND METHODS

Biweekly random samples were collected from the commercial landings of the purse-seine fleet at the fishing port of Nea Michaniona (northern rim of the Thermaikos Gulf) from July 1996 to June 2000. Samples were taken within a single day in two or three clusters from random collections of the total landed catch derived from different vessels operating in the Northwest Aegean Sea. No data were collected for the period between 15th December and 1rst March of each year, because purse-seine fishing in the Greek Seas is banned during that period. The sampling frequency ranged from 7 to 17 days, with a mean sampling frequency of 15.14 days (± SE=0.44).

Total length (TL) was measured to the nearest mm for 51.246 individuals. In addition, for a subsample of 50 individuals per sampling period, gross body weight (W) and gonad weight (W_g) were also measured to the nearest 0.1 and 0.01 g, respectively. Sex was macroscopically identified.

The above mentioned data were consequently used for the estimation of the following biological parameters: (a) biweekly length-frequencies; (b) arithmetic mean TL per sampling period; (c) TL-W relationship, $W=a(TL)^b$; (d) gonadosomatic index (GSI; Nikolsky, 1963): $GSI=100(W_g/W)$; and (e) growth parameters, K, L_∞, C and WP, of the seasonalized von Bertalanffy (1938) growth equation (Pauly, 1998). The latter were estimated from the monthly length-frequencies using various routines of FiSAT (ELEFAN I: "Scan K-values", "response surface" and "automatic search" routines: Gayanilo *et al.*, 1994; Gayanilo and Pauly, 1997). The seasonalized growth equation is (Pauly, 1998):

$$L_t = L_\infty[1-e^{(-K(t-to)-(CK/2\pi)\sin(2\pi(t-ts)))}],$$

where K is the curvature parameter, L_∞ is the asymptotic length, C is the amplitude of growth oscillation and WP is the winter point related with the summer point t_s ($WP = t_s+0.5$) indicating the time of the year when growth is slowest. For the computation of the von Bertalanffy parameters, we used as an initial range of L_∞ the following values: (a) the 95% confidence interval, CI, of the maximum length L_{max}' estimates; and (b) the estimate of L_∞ derived from the Powell-Wetherall method (Powell, 1979; Wetherall, 1996; Pauly, 1986), applied to all samples pooled together. Both methods are implemented in FiSAT (Gayanilo *et al.*, 1994; Gayanilo and Pauly, 1997) and briefly presented below. L_{max}' is estimated from the set of n extreme values of the largest specimen in each sample (L*) using the regression:

$$L^* = a + 1/a\ (P),$$

where P is the probability associated with the occurrence of an extreme value, 1/a is a measure of dispersion, and L_{max}' is the intercept of the regression line with the probability associated with the nth observation. P is computed for any extreme value from $P = m/(n+1)$ where m is the position of the value, ranked in ascending order and n is the number of L* values (Gayanilo *et al.*, 1994; Gayanilo and Pauly, 1997). According to the Powell-Wetherall method, the smallest length fully recruited to the gear (L') and the mean length of a fish with length larger than L' (L_{mean}) are related as follows:

$$(L_{mean}-L') = a+b\ (L'),$$

where:

$$L_{mean}= [(L_\infty+L')/(1+(Z/K)],$$

from which:

$$L_\infty = -a/b$$

and

$$Z/K = -(1+b)/b.$$

Finally, total mortality (Z) estimates were derived from the length-converted catch curve (Pauly, 1984):

$$\ln(N_i/\ \Delta t_i) = a + b(t_i),$$

where N_i is the number of fish in length class i, Δt_i is the time needed for the fish to grow through length class i, t_i is the age (or the relative age, computed with $t_0 = 0$) corresponding to the mid-length of class i, and the arithmetic value of the slope b is an estimate of Z. Consequently, natural mortality (M) was estimated from the growth parameters and the mean annual water temperature in the study area (i.e. 15°C) using Pauly's (1980) empirical equation, fishing mortality (F) from the relationship F = Z-M and the exploitation ratio (E) from the relationship E = F/Z (Pauly, 1983; Pauly and Morgan, 1987).

RESULTS

In total, the TL of sardine ranged between 8 and 21 cm (mean length = 14.48 cm ± SE = 0.64). The

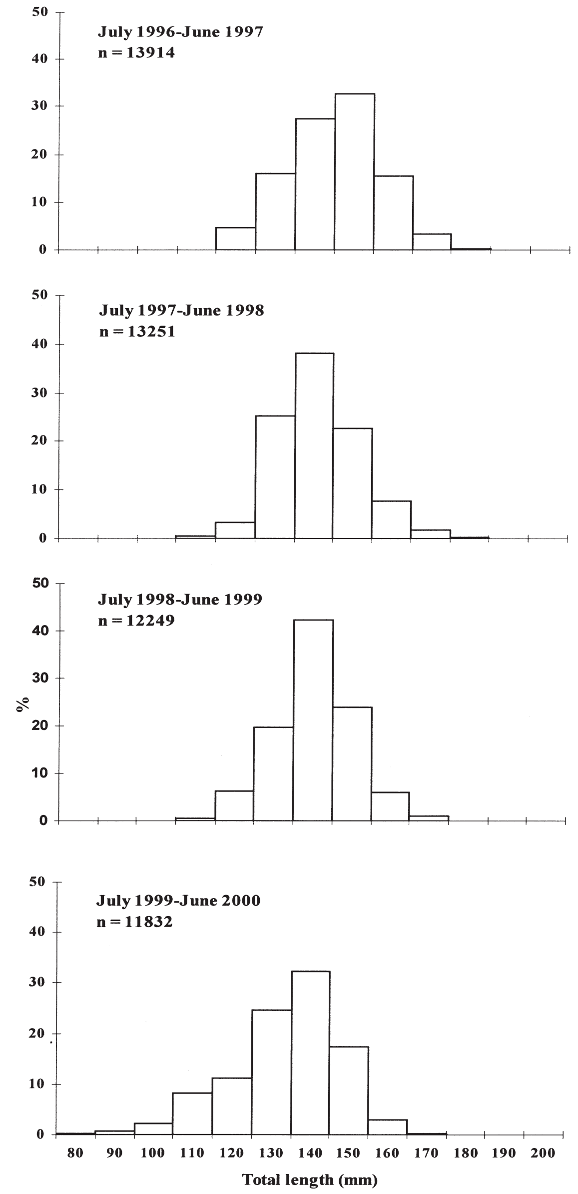

FIG. 2. – Annual length-frequency distribution of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

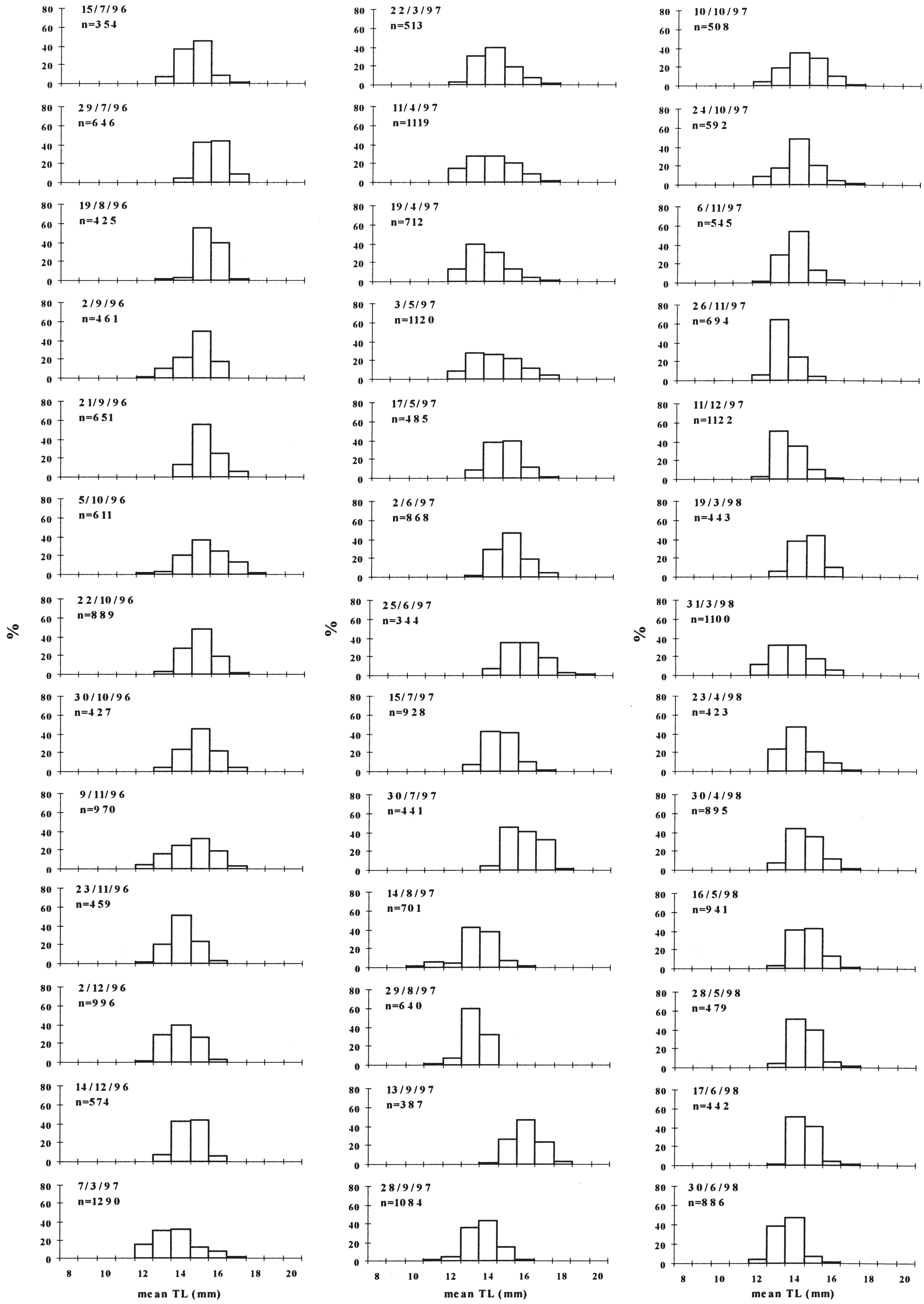

FIG. 3. – Biweekly length-frequency distribution of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

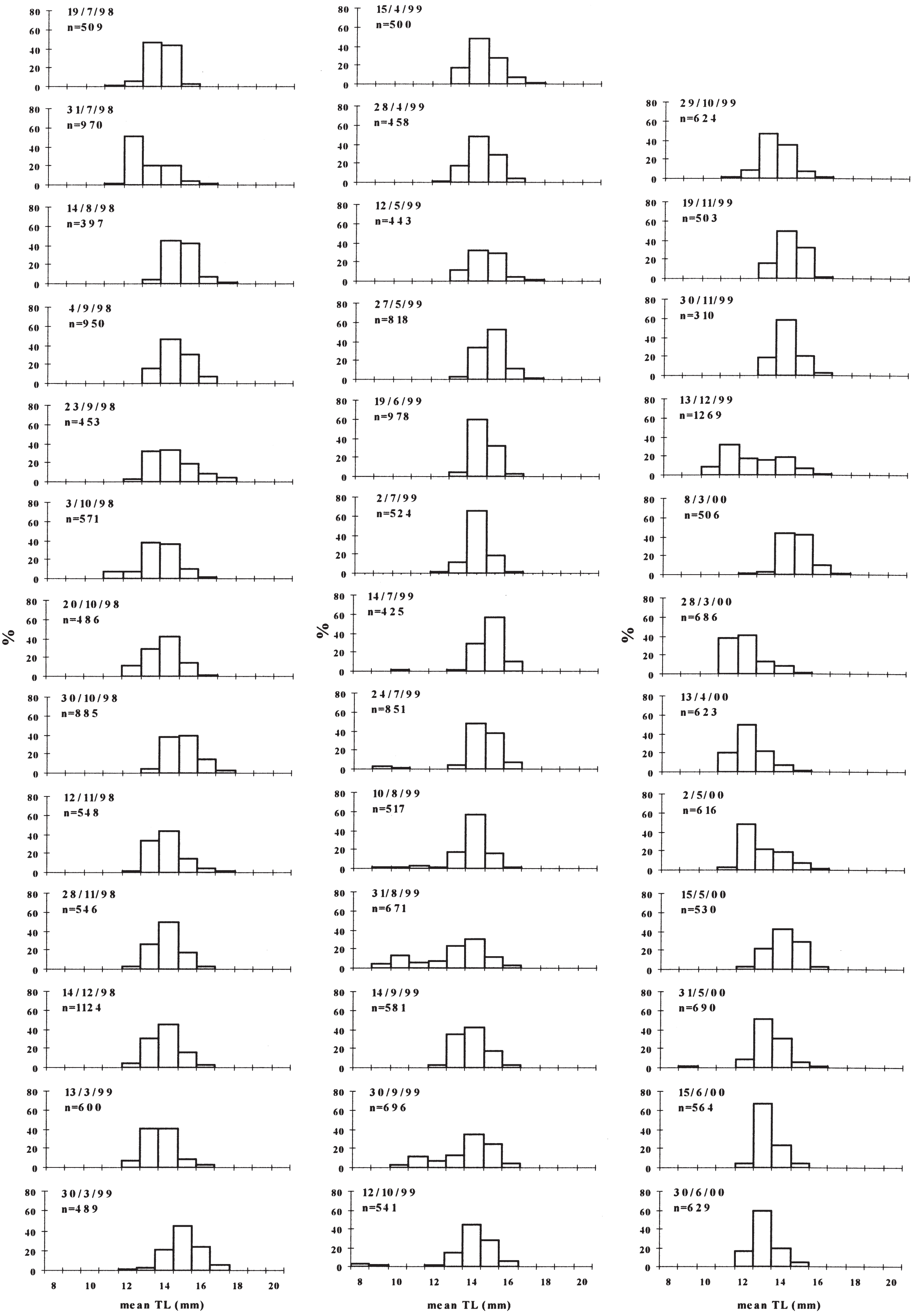

FIG. 3 (Cont.). – Biweekly length-frequency distribution of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

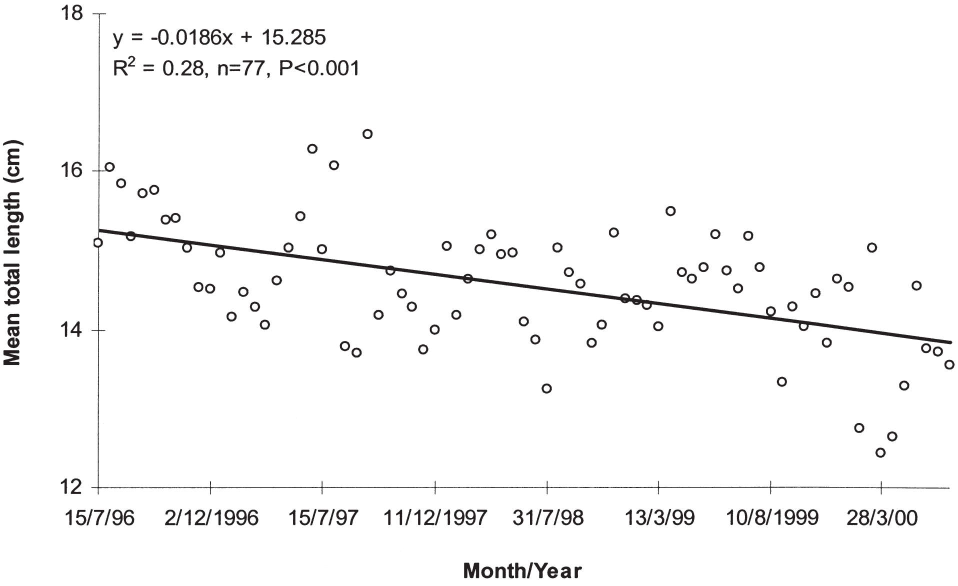

FIG. 4. – Biweekly mean total length (in cm) of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

annual length-frequency distribution exhibited a mode at 15 cm in 1996-1997 and at 14 cm in 1997-2000 (Fig. 2). During July 1999-June 2000, the percentage of the smallest individuals (TL<13 cm) was higher whereas that of the larger ones lower than those in the previous years (Fig. 2). The biweekly length-frequency distributions (Fig. 3) displayed modes at 15-16 cm for the first year, at 14-15 cm for the second and third year and at 13-14 cm for the last study year during May to September. The smallest individuals (12-14 TL cm for 1996-1999 and 11-13 cm TL for 1999-2000) were recorded during October-April whereas during the last study year very small individuals (TL<11 cm) were also recorded during July-October.

The mean biweekly TL declined significantly (r=-0.525, n=77, P<0.001) with time (Fig. 4). Because the smallest individuals were recorded in October-April, the relationship between mean TL and time was also analyzed for May-September and October-April separately. In both cases, the mean biweekly TL declined significantly with time (May-September: r = -0.471, n=39, P<0.005; October-April: r = -0.624, n=38, P<0.001). The maximum TL also declined with time (figure not shown; r=-0.46, n=77, P<0.001).

The exponent b of the length-weight relationship was 3.041 for females, 3.116 for males and 3.153 for sexes combined (Fig. 5). The exponent b for sexes combined exhibited a seasonal cycle, with the highest values generally occurring, with few exceptions, from March to September-October, and also

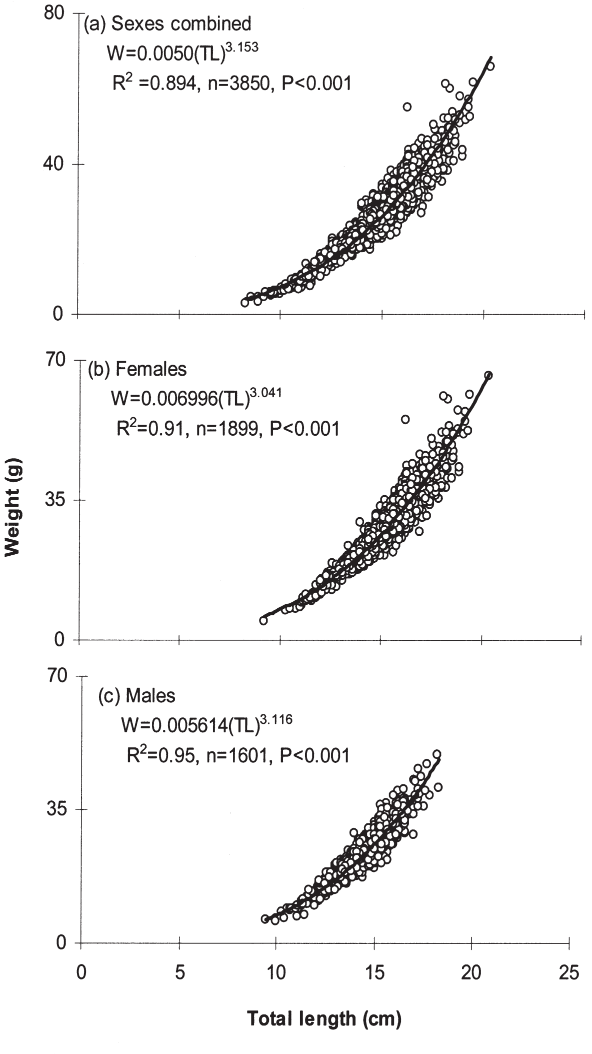

FIG. 5. – Length-weight relationships of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

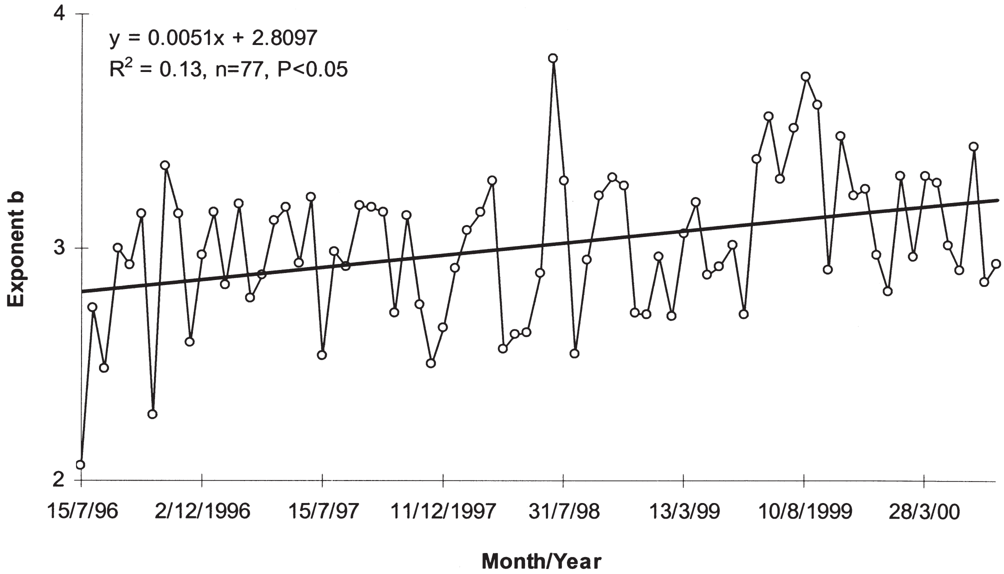

FIG. 6. – Temporal variation in the exponent b of the length-weight relationship of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

increased significantly ($r=0.358$, $n=77$, $P<0.002$) with time (Fig. 6). It was also negatively correlated with the mean TL over the study period ($r=-0.29$, $n=77$, $P<0.05$).

The GSI (Fig. 7) also exhibited a clear bimodal seasonal cycle, with peaks during November-April and lowest values during May-September, with the importance of the secondary peak increasing with time. No relationship was found between GSI and the exponent b of the length-weight relationship ($r = -0.13$, $n=77$, $P>0.05$).

The estimated L'_{max} was 20.27 cm (95% CI: 19.63-20.90 cm) (Fig. 8a) whereas the Powell-Wetherall method provided the following estimates: $(L_{mean}-L')=2.81-0.131(L')$ ($r=-0.98$, $P<0.001$), from which $L_\infty=21.45$ cm and $Z/K=6.64$ (Fig. 8b). For the estimation of the growth parameters, the initial range of L_∞ values used in the different ELEFAN routines was from 19.63 to 21.45 cm TL. The following combination of growth parameters was finally selected ($R_n=0.83$; with R_n being an index of goodness of fit):

$$L_t = 20.8[1-e^{(-0.86(t-to)-(0.86*0.6/2\pi)\sin(2\pi(0.1)))}].$$

The parameters of the length-converted catch curve were $\ln(N_i/ \Delta t_i) = 19.88 -5.65(t_i)$ ($r^2=0.997$)

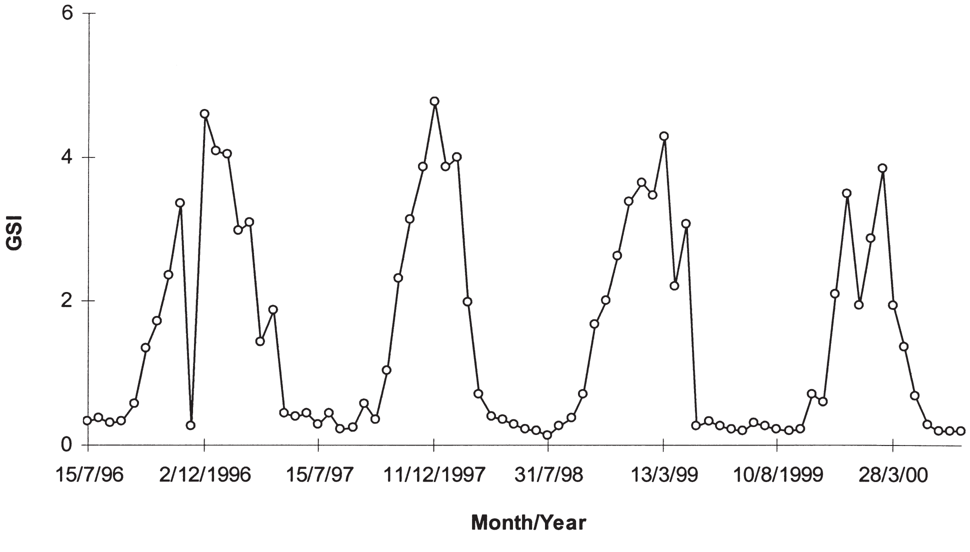

FIG. 7. – Temporal variation of the gonadosomatic index (GSI) of sardine, *Sardina pilchardus*, in the Northwest Aegean Sea, 7/1996-6/2000.

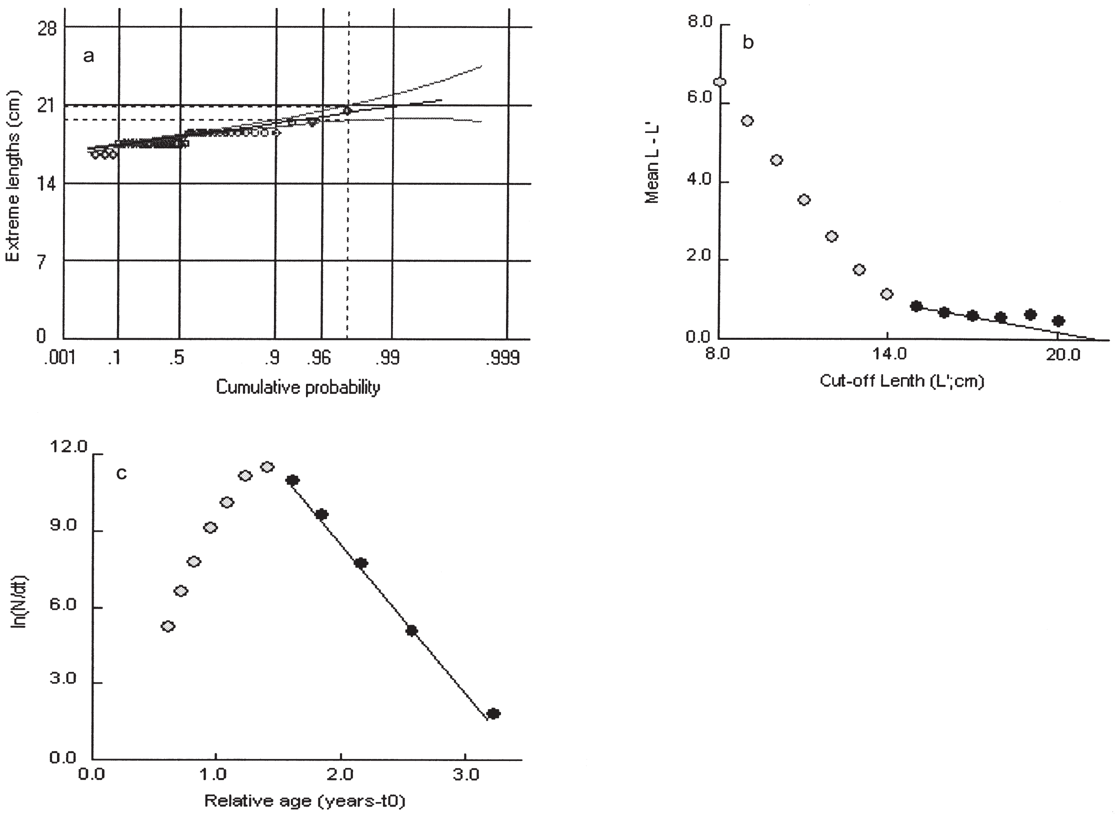

FIG. 8. – (a) Estimation of maximum length (L_{max}'), (b) the Powell-Wetherall plot for estimating L_∞ and Z/K, and (c) length-converted catch curve for sardine in the Northwest Aegean Sea, 7/1996-6/2000 (see text for details).

and the mortality estimates were Z=5.65 yr^{-1} (95% CI: 5.05-6.25 yr^{-1}) (Fig. 8c), M=1.34 yr^{-1} and F=4.31 yr^{-1} whereas E=0.76.

DISCUSSION

The annual length-frequencies of sardine were unimodal (Fig. 2), a fact clearly indicating that landings are based exclusively on one year-class, as is also the case in the NE Aegean (i.e., Thracian Sea: Koutrakis *et al.*, 2001; Kallianiotis *et al.*, 2001), the Central Aegean Sea (Ganias *et al.*, 2001a) and the northwestern Mediterranean (Pertierra and Perrotta, 1993). The maximum recorded TL for the last study year was 18.9 cm (Fig. 2), which was larger than that recorded in the Thracian Sea during October 2000-July 2001 (TL=17.3; Koutrakis *et al.*, 2001), a fact indicating that a further decline in TL may have taken place in 2001. The maximum recorded TL in the study area was also larger than that reported from the Ionian and Central Aegean Sea during 1999-2001 (18 and 18.4 cm, respectively: Machias *et al.*, 2001).

The exponent b of the length-weight relationship for sexes combined was similar to that estimated for sardine in the Ionian and Central Aegean Seas during 2000-2001 (b=3.15; Machias *et al.*, 2001) and slightly smaller than that estimated for October 2000-July 2001 in the Thracian Sea (b=3.29; Koutrakis *et al.*, 2001).

In the study area, sardine was characterized by high K and L_∞ values, when compared to estimates from other areas, being comparable to those estimated from otoliths' readings in the Western Mediterranean (Table 1). The North Aegean Sea, including the Thermaikos Gulf, is generally considered as a relatively eutrophic area, being characterized by higher plant pigment concentrations, influenced by nutrient input from the Black Sea, freshwater runoff and anthropogenic eutrophication, than those prevailing in the remaining parts of the Greek Seas (Stergiou and Georgopoulos, 1993; Stergiou *et al.*, 1997a). Accordingly, the relative abundance and density of small pelagic fishes, as indicated by echo surveys, are higher in the North Aegean Sea than in the remaining parts of the Greek Seas (Stergiou *et al.*, 1993; Machias *et al.*, 1996; Machias *et al.*, 2001).

TABLE 1. – Growth parameters of sardine, *Sardina pilchardus*, within its distributional area.

Geographic area	L_∞ (cm)	K (yr^{-1})	Method	Reference
Central-east Atlantic	24.6	0.37	Otoliths	Krzeptowski (1983)
W. Mediterranean	20.08	0.234	Otoliths	Pertierra and Morales-Nin (1989)
W. Mediterranean	21.21	0.18	Length-frequency	Pertierra and Morales-Nin (1989)
W. Mediterranean	21.2	0.31	Length-frequency	Pertierra and Morales-Nin (1989)
W. Mediterranean (Alboran)	20.69	0.69	Otoliths	Alemany and Alvarez (1993)
W. Mediterranean (Gulf of Vera)	19.9	0.93	Otoliths	Alemany and Alvarez (1993)
W. Mediterranean (Alacant)	17.41	0.84	Otoliths	Alemany and Alvarez (1993)
W. Mediterranean (Valencia)	18.02	0.65	Otoliths	Alemany and Alvarez (1993)
W. Mediterranean (Gulf of Lions)	18.18	0.7	Otoliths	Alemany and Alvarez (1993)
E. Adriatic (Croacia)	20.5	0.46	Scales	Sinovcic (1984)
N. Aegean and Ionian (Greece)	18.12	0.3	Scales	Tserpes and Tsimenides (1991)
NW Aegean (Greece)	20.80	0.86	Length-frequency	Present study

Sardine, like other temperate clupeids, is a multiple spawner producing several discrete batches of oocytes within the reproductive period (Ganias *et al*., 2001a; Somarakis *et al*., 2001), relying on energy stored as fat rather than liver glycogen for reproduction, with individuals not spawning at periods of high food abundance, but storing energy as fat for later reproductive activity (Somarakis *et al*., 2000). The analysis of the sardine GSI in the study area (Fig. 7) indicated that spawning takes place during the colder part of the year, in November-April. This is also true of the Central Aegean and Ionian Seas (Machias *et al*., 2001), the Thracian Sea (Koutrakis *et al*., 2001) as well as in other areas of the Mediterranean Sea and off the Moroccan and Spanish coasts of the Atlantic Ocean (e.g. Delgado and Fernandez, 1985; Alvarez and Alemany, 1996; Quintanilla and Perez, 2000; Froese and Pauly, 2000; FishBase online: www.fishbase.org). In contrast, spawning in the North Sea and Black Sea takes place in the summer (June to August: FishBase online). It must be noted that based on the biweekly GSI, the reproductive period of sardine in the North Aegean extends over 4-6 months (Fig. 7) as is also the case for the Thracian Sea (Koutrakis *et al*., 2001) and the Central Aegean Sea (Machias *et al*., 2001). In contrast, in the Ionian Sea the reproductive activity of sardine extends over about 2-4 months which are shifted towards spring (Machias *et al*., 2001; Somarakis *et al*., 2001). Finally, it is noteworthy that the increase in the importance of the secondary GSI peak with time (Fig. 7) must be related to the decrease in the mean TL with time (Fig. 4), given that smaller sardines generally spawn later than larger ones (Machias *et al*., 2001). It must be pointed out that although GSI describes the reproductive condition of sardine before and after the peak of reproduction it does not adequately describe the reproductive condition within the reproductive period (Ganias *et al*., 2001a).

In general, growth is affected by a variety of factors, such as food quantity and quality, temperature and environmental heterogeneity, and growth itself affects maturation (Wootton, 1990). The marked decline in the mean sardine TL during 1996-2000 (Fig. 3) followed: (a) the sharp increase in the sardine landings during 1992-1997 with a concurrent decline in anchovy landings (Fig. 1) (see also Koutrakis *et al*., 2001; Kallianiotis *et al*., 2001); and (b) the 34% decrease in the North Aegean sardine biomass in 1996 when compared to 1995 (A. Machias, unpubl. data). In addition, sardine discarding has been greatly reduced in recent years, with the length structure of discarded specimens being similar to that of the retained ones (Kallianiotis *et al*., 2001). The above-mentioned facts together with the high exploitation rate estimated for the study period (E=0.76) indicate that intense fishing, by removing the largest individuals, may be implicated in such a decline in the maximum and mean TL of sardine during 1996-2000. Fishing generally affects the age and length structure of fisheries stocks (e.g. Jennings *et al*., 2001; Stergiou, 2002) and fishing-induced declines in the length structure have also been observed for other sardine species of the world (e.g. Japanese sardine: Kawasaki, 1992; Hiyama *et al*., 1995). Yet, the effect of other factors, such as for instance adverse environmental conditions and low food density (e.g. for North Aegean Sea: Somarakis *et al*., 1997, 2000; Stergiou and Lascaratos, 1997; Japanese sardine: Wada and Kashiwai, 1991; Hiyama *et al*., 1995), acting in a synergetic or not fashion with fishing, cannot be ruled out. In any case, given that the reproductive traits (i.e., fecundity, spawning frequency, egg size) of sardine are length-depended (Ganias *et al*., 2001b; Somarakis *et al*., 2001), a decrease in the mean TL of sardine may lead to a decline in the total population reproductive output and offspring survival (Trippel *et al*., 1997). This, coupled with climate-induced changes in the biological production of the North Aegean Sea (e.g. Stergiou *et al*., 1997a) may lead to long term fluctuations in sardine abundance. These issues require further studies.

The decline in the mean TL (Fig. 3) went along with an increase in the exponent b of the length-weight relationship (Fig. 5), which may indicate a density-dependent effect. In general, density-dependent effects on growth are commonly reported for fish populations (e.g. sardine: Wada and Kashiwai, 1991; Hiyama *et al*., 1995; herring: Heath *et al*., 1997; silver hake: Ross and Almeida, 1986; eel: De Leo and Gatto, 1996). The underlying mechanism involves relaxation of competition for available food resources at low population densities (e.g. Jennings *et al*., 2001). Thus, a decrease in the abundance of large sardines in the North Aegean could result in more quantity of food being available for small sardines and/or small individuals gain faster weight in the absence of intra-specific competition. Yet, density-dependence is not always easy to prove (Jennings *et al*., 2001) and in fact other mechanisms for density-dependent growth may also be implicated (e.g. the relationship between school size and population density and its effect on growth: Bakun, 1989; Bakun and Cury, 1999; amplified size-dependent predation during population declines: Bakun, 1989). This clearly indicates the need for an "integrated ecosystem view of marine resource population dynamics" (Bakun, 1989), such as the paradigmatic approach undertaken for the Peruvian anchovy (Pauly and Tsukayama, 1987; Pauly *et al*., 1989), which will account for spatial and temporal variability in a variety of both biological and environmental parameters.

The trends in the biological characteristics of sardine reported here must be taken into account when designing management plans, and their incorporation into various assessment models may considerably reduce uncertainty in estimations and increase predictability. The fact that there were only four years of data does not allow us to statistically address many of the issues discussed above. However, monitoring of the biological parameters of sardine in the study area is ongoing, and an effort will be made to relate such changes with environmental ones.

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REFERENCES

Alemany, F. and F. Alvarez. – 1993. Growth differences among sardine (*Sardina pilchardus* Walb.) in Western Mediterranean. *Sci. Mar*., 57(2-3): 1993.

Alvarez, F. and F. Alemany. – 1996. Birthday analysis and its application to the study of recruitment of the Atlanto-Iberian sardine *Sardina pilchardus*. *Fish. Bull*. (U.S.), 95: 187-194.

Bakun, A. – 1989. Mechanisms for density dependent growth in Peruvian anchoveta: Alternatives to impact on the regional scale food supply. In: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. *ICLARM Conference Proceedings*, 18: 235-243.

Bakun, A. and P. Cury. – 1999. The "shool trap": a mechanism promoting large-amplitude out-of-phase population oscillations of small pelagic fish species. *Ecol. Let*., 2: 349-351.

Bertalanffy, L. Von. – 1938. A quantitative theory of organic growth (Inquiries on growth laws II). *Hum. Biol*., 10(2): 181-213.

Daoulas, Ch. and A. N. Economou. – 1986. Seasonal variation of egg size in the sardine, *Sardina pilchardus* Walb., of the Saronikos Gulf: causes and a probable explanation. *J. Fish Biol*., 28: 449-457.

De Leo, G.A. and M. Gatto. – 1996. Trends in vital rates of the European eel: Evidence for density-dependence? *Ecol. Appl*., 6: 1281-1294.

Delgado, A. and M.A.R. Fernandez. – 1985. Datos sobre la biología de la sardina (*Sardina pilchardus* Walb., 1972) capturado por los cerqueros españoles en Africa Occidental de 1976 a 1982. *Simp. Int. Afl. Afr., Inst. Inv. Pesq. (Barcelona)*, Vol. II: 935-955.

Froese, R. and Pauly, D. (eds.) – 2000. *FishBase 2000: Concepts, design and data sources*. ICLARM, Manila.

Ganias K., S. Somarakis, E. Caragitsou, C. Koutsikopoulos, A. Machias and A. Theodorou. – 2001a. Differential egg production of sardine off the central Hellenic coasts in December 1999. *Proc. 36th CIESM Congr.*, 36: 268.

Ganias K., S. Somarakis, C. Koutsikopoulos, E. Caragitsou, A. Machias, N. Tsimenides and A. Theodorou. – 2000. Oceanographic, planktonic and biological study of the sardine reproduction in the coastal areas of central Greece. *Hellenic Fish. News*, 233: 41-48 (in Greek).

Ganias K., S. Somarakis, A. Machias, C. Koutsikopoulos, P. Christopoulos, N. Tsimenides and A. Theodorou. – 2001b. Can simple gonadal indices be used to describe the reproductive condition of multiple spawners like sardine? *Proc. 10th Greek Symp. Ichthyol.*, 10: 97-100.

Gayanilo, F.C.Jr. and D. Pauly. – 1997. The FAO-ICLARM Stock Assessment Tools (FiSAT) Reference Manual. *FAO Computerized Information Series (Fisheries)*, 8: 262 pp.

Gayanilo, F.-C. Jr., P. Sparre and D. Pauly. – 1994. The FAO-ICLARM stock assessment tools (FiSAT) user's guide. FAO, Rome 1994.

Giannoulaki M., A. Machias and N. Tsimenides. – 1999. Ambient luminance and vertical migration of sardine (*Sardina pilchardus*). *Mar. Ecol. Progr. Ser*., 173: 275-288.

Giannoulaki M., A. Machias, C. Coutsikopoulos, S. Somarakis, L. Manousakis and N. Tsimenides. – 2001. The distribution of sardine (*Sardina pilchardus*) in Central Aegean and Ionian Sea. *Proc. 10th Greek Symp. Ichthyol.*, 10: 61-64.

Heath, M., B. Scott and A.D. Bryant. – 1997. Modelling the growth of herring from four different stocks in the North Sea. *J. Sea Res.*, 38: 413-436.

Hiyama, Y., H. Nishida and T. Goto. – 1995. Interannual fluctuations in recruitment and growth of the sardine, *Sardinops melanostictus*, in the Sea of Japan and adjacent waters. *Res. Popul. Ecol.*, 37: 177-183.

Jennings, S., Kaiser, M.J., Reynolds, J.D., 2001. Marine fisheries ecology. Blackwell Science, London, UK.

Kallianiotis, A., P. Vidoris, A. Argyrokastritis, V. Kosmidis, K. Euthimiadis and A. Argyri. – 2001. Landings and catch per unit effort of the purse seine fishery of the fleet of Kavala. *Proc. 10th Greek Symp. Ichthyol.*, 10: 73-76.

Kawasaki, T. – 1992. Mechanisms governing fluctuations in pelagic fish populations. *S. Afr. J. Mar. Sci.*, 12: 873-879.

Koutrakis, M., A. Tsikliras and N. Kamidis. – 2001. On the biology of sardine Sardina pilchardus (Walbaum, 1792) in the Gulf of Kavala. *Proc. 10th Greek Symp. Ichthyo.*, 10: 69-72.

Krzeptowski, M. – 1983. Biological characteristics of the sardine (*Sardina pilchardus* Walb.) off west Sahara. *Acta Ichthyol. Piscatoria*, 13(1): 13-36.

Laskaridis, K. – 1948. Study of the biology of the sardine (*Clupea pilchardus* Walb.) in Greek waters. *Proc. Hellenic Hydrobiol. Fish. Bull.,* 85: 561-568.

Machias, A., S. Somarakis, M. Giannoulaki, K. Ganias, E. Maraveya, L. Manousakis, N. Tsimenides, A. Magoulas, E. Caragitsou, A. Siapatis, K. Anastasopoulou, C. Koutsikopoulos, N. Fragopoulou, E. Tzanatos, M. Isari, P. Christopoulos, M. Georgiadis, A. Ramfos and D. Vavoulis. – 2001. Evaluation of the southern Greek sardine stocks. Institute of Marine Biology of Crete (IMBC), Final Report (Contract No 98/039).

Machias, A., S. Somarakis and N. Tsimenides. – 1996. Comparative distribution of anchovy and sardine in the North Aegean basin: June 1995. *Proc. 17th Scient. Symp. Greek Soc. Biol. Sci.*, 17: 135-137.

Machias, A. and N. Tsimenides. – 1995. Biological factors affecting the swimbladder volume of sardine (*Sardina pilchardus*). *Mar. Biol.*, 123: 859-867.

Machias, A. and N. Tsimenides. – 1996. Anatomical and physiological factors affecting the swim-bladder cross-section of the sardine *Sardina pilchardus*. *Can. J. Fish. Aquat. Sci.*, 53: 280-287.

Maravelias, C.D., A. Machias, S. Somarakis and N. Tsimenides. – 1997. Spatial distribution of pelagic species in the northern Aegean Sea: use of geostatistics and environmental variables. *Proc. 5th Hellenic Symp. Oceanogr. Fish.,* 5(2): 119-122.

Nikolsky, G. V. – 1963. *The ecology of fishes*. Academic Press. 352 pp.

Pauly, D. – 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cons*., 39(3): 175-192.

Pauly, D. – 1983. Some simple methods for the assessment of tropical fish stocks. *FAO Fish. Techn. Pap*., 234: 52 pp.

Pauly, D. – 1984. Length-converted catch curves: a powerful tool for fisheries research in the tropics (Part II). *Fishbyte (ICLARM)*, 2(1): 17-19.

Pauly, D. – 1986. On improving operation and use of the ELEFAN programs. Part II. Improving the estimation of L_. *Fishbyte (ICLARM)*, 4(1):18-20.

Pauly, D. – 1998. Tropical fishes: patterns and propensities. *J. Fish Biol.*, 53 (Suppl.): 1-17.

Pauly, D. and G.R. Morgan. – 1987. Length-based methods in fisheries research. *ICLARM Conf. Proc*., 13: 468 pp.

Pauly, D., P. Muck, J. Mendo and I. Tsukayama (eds.). – 1989. The Peruvian Upwelling Ecosystem: Dynamics and Interactions. *ICLARM Conf. Proc*., 18: 438 pp.

Pauly, D. and I. Tsukayama. (eds.). – 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of changes. *ICLARM Stud. Rev*., 15: 351 pp.

Pertierra, J.-P. and B. Morales-Nin. – 1989. Sardine growth in the Catalan Sea (NW Mediterranean) determined by means of otolith interpretation and length-frequency data. *Sci. Mar.*, 57(2-3): 821-826.

Pertierra, J. P. and R. G. Perrota. -1993. On the popoulation dynamics of sardine, *Sardina pilchardus* Walbaum, 1792, from the Catalan sea (northwestern Mediterranean). *Sci. Mar.*, 57(2-3): 235-241.

Powell, D.G. – 1979. Estimation of mortality and growth parameters from the length-frequency in the catch. *Rap. P.-V. Réun. ICES*, 175: 167-169.

Quintanilla, L. and N. Perez. – 2000. Spawning frequency of sardine *Sardina pilchardus* (Walb.) off the Spanish North Atlantic coast in 1997. *Fish. Res.*, 45: 73-79.

Ross, M. and F.P. Almeida. – 1986. Density-dependent growth of silver hakes. *Trans. Am. Fish. Soc*., 115: 548-554.

Sinovcic, G. – 1984. Summary of biological parameters of sardine (*Sardina pilchardus* Walb.) from the central Adriatic. *FAO Fish. Rep*., 290: 147-148.

Somarakis, S., K. Ganias, C. Koutsikopoulos, A. Machias and C. Papaconstantinou. – 2001. Applying the daily egg production method (DEPM) to small sardine stocks in the Eastern Mediterranean (Central Greece). Working Doc., ICES Study Group on the Estimation of spawning biomass for sardine and anchovy (SGSBSA), Lisbon, 22-25/10/2001, 21 pp.

Somarakis, S., I. Kostikas, N. Peristeraki and N. Tsimenides. – 1997. Fluctuating asymmetry in the otoliths of larval anchovy *Engraulis encrasicolus* and the use of developmental instability as an indicator of condition in larval fish. *Mar. Ecol. Progr. Ser.,* 151: 191-203.

Somarakis, S., E. Maraveya and N. Tsimenides. – 2000. Multispecies ichthyoplankton associations in epipelagic species: Is there any intrinsic adaptive function? *Belgian J. Zool.*, 130 (suppl. 1): 125-129.

Spanakis, E., N. Tsimenides and E. Zouros. – 1989. Genetic differences between populations of sardine, *Sardina pilchardus*, and anchovy, *Engraulis encrasicolus*, in the Aegean and Ionian seas. *J. Fish Biol.*, 35: 417-437.

Stergiou, K.I. – 1989. Modeling and forecasting the fishery of pilchard, *Sardina pilchardus* in Greek waters using ARIMA time series models. *J. Cons.*, 46: 16-23.

Stergiou, K.I. – 1990. An autoregressive model of the anchovy *Engraulis encrasicolus* fishery in the eastern Mediterranean. *Fish. Bull. (U.S.)*, 88: 411-414.

Stergiou, K.I. 1991. Describing and forecasting the sardine-anchovy complex in the eastern Mediterranean using vector autoregressions (VAR). *Fish. Res.*, 11: 127-141.

Stergiou, K.I. – 1992. Variability of monthly catches of anchovy *Engraulis encrasicolus* in the Aegean Sea. *Fish. Bull. US*, 90: 211-215.

Stergiou, K.I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. *Fish. Res*., 55(1-3): 1-9.

Stergiou, K.I. and E.D. Christou. – 1996. Modeling and forecasting annual fisheries catches: comparison of regression, univariate and multivariate time series methods. *Fish. Res.*, 25: 103-138.

Stergiou, K.I., E.D. Christou, D. Georgopoulos, A. Zenetos and C. Souvermezoglou. – 1997a. The Hellenic seas: Physics, Chemistry, Biology and Fisheries. *Oceanogr. Mar. Biol. Ann. Rev.*, 35: 415-540.

Stergiou K.I., E.D. Christou and G. Petrakis. – 1997b. Modeling and forecasting monthly fisheries catches: comparison of regression, univariate and multivariate time series methods. *Fish. Res.*, 29: 55-95.

Stergiou, K.I. and D. Georgopoulos. – 1993. The distribution of phytoplankton pigments and the fishery of anchovy (*Engraulis encrasicolus*) in the Hellenic Seas. *Naga (the ICLARM Quartely)*, 16(2): 34-37.

Stergiou, K.I. and A. Lascaratos. – 1997. Climatic variability and the anchovy/sardine ratio in Hellenic waters. *Geojournal*, 41(3): 245-254.

Stergiou, K. I., C. Papaconstantinou, M. Kleanthous and A. Fortouni. – 1993. The relative abundance and distribution of small pelagic fishes in the Aegean Sea. *Fresenious Environ. Bull.,* 2: 357-362.

Stergiou, K.I. and D.A. Pollard. – 1995. A spatial analysis of the commercial fisheries catches from the Greek Aegean Sea. *Fish. Res.,* 20: 109-135.

Trippel, E.A., O.S., Kjesbu and P. Solendal. – 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: R.C. Chambers and E.A. Trippel (eds.), *Early life history and recruitment in fish populations*. pp. 31-62. Chapman and Hall, New York.

Tserpes, G. and N. Tsimenides. – 1991. Evaluation of growth rate differences in populations of *Sardina pilchardus* (Walbaum, 1792) (Clupeidae) from the Aegean and Ionian Seas. *Cybium*, 15(1): 15-22.

Wada, T. and M. Kashiwai. – 1991. Feeding ground selection of

Japanese sardine with stock fluctuation. *Bull. Hokkaido Natl. Fish. Res. Inst.*, 55: 197-204.

Wetherall, J.A. – 1986. A new method for estimating growth and mortality parameters from length-frequency data. *Fishbyte (ICLARM)*, 4(1): 12-14.

Wootton, R.J. – 1990. *Ecology of teleost fishes.* Chapman and Hall, New York.

Yannopoulos, A., S. Yannopoulos and C. Sotiriades-Vlahos. – 1973. On the occurrence of ichthyoplankton in the Saronikos Gulf, Aegean Sea. Anchovy and sardine in 1969-70-71. *Rev. Trav. Instit. Peche Maurit. Nautes*, 37(2): 177-181.