

Reproductive biology of round sardinella (*Sardinella aurita*) in the north-eastern Mediterranean

ATHANASSIOS C. TSIKLIRAS and EFTHIMIA ANTONOPOULOU

Aristotle University of Thessaloniki, School of Biology, Department of Zoology, Laboratory of Animal Physiology, UPB 134, 541 24, Thessaloniki, Greece. E-mail: atsik@bio.auth.gr

SUMMARY: The reproductive biology of round sardinella, *Sardinella aurita* Valenciennes, 1847, was studied for the first time in the north-eastern Mediterranean Sea. Round sardinella has gained much attention lately because of its biomass increase, which might be the result of climatic changes occurring across the Mediterranean Sea. Monthly samples were collected on board commercial purse-seiners for two complete year cycles (September 2000 to August 2002). Round sardinella is a gonochoristic fish. The overall female to male ratio was not statistically different ($P=0.34$) from unity, although it varied monthly and with the length of the fish. The seasonal changes in the gonadosomatic index and the macroscopic characteristics of gonads showed that round sardinella in the northern Aegean spawns between May and July. Male round sardinella reach first sexual maturity at a smaller total length than females (155.0 and 168.3 mm respectively). Mean absolute fecundity (F_A) increased exponentially with body length ($F_A=0.0949 \times L^{4.22}$) and weight ($F_A=511.19 \times W^{1.02}$), with an average of ~21,000 oocytes produced per spawning female. Relative fecundity (F_R) ranged between 242 and 681 oocytes/g of body weight (average: 445 oocytes/g). The frequency distribution of oocytes showed that round sardinella produces a single batch of oocytes. In general, the reproductive characteristics of round sardinella in the north-eastern Mediterranean Sea differed when compared to stocks from other areas of its distribution.

Keywords: sex-ratio, maturity, fecundity, spawning, round sardinella, Aegean, Mediterranean.

RESUMEN: BIOLOGÍA REPRODUCTIVA DE LA ALACHA (*SARDINELLA AURITA*) EN EL MEDITERRÁNEO NE. – La biología reproductiva de la alacha, *Sardinella aurita* Valenciennes, 1847 fue estudiada por primera vez en el Mediterráneo NE. Esta especie ha sido recientemente motivo de atención debido a su incremento de biomasa, que podría ser debido a cambios climáticos en el Mediterráneo. Se obtuvieron muestras mensuales a bordo de barcos de pesca con artes de cerco durante dos ciclos anuales completos (Septiembre de 2000-Agosto de 2002). La alacha es una especie gonocorista. Globalmente, la proporción de sexos no fue estadísticamente ($P=0.34$) diferente de la unidad. Los cambios estacionales en el índice gonadosomático y en las características macroscópicas de las gónadas mostraron que la época de puesta de la alacha en el norte del mar Egeo tiene lugar entre Mayo y Julio. Los machos de la alacha alcanzaron la madurez sexual a una talla total inferior a la de las hembras (155.0 y 168.3 mm, respectivamente). La fecundidad media absoluta (F_A) se incrementó exponencialmente con la talla ($F_A=0.0949 \times L^{4.22}$) y peso ($F_A=511.19 \times W^{1.02}$), con una media de ~21,000 oocitos producidos por hembra madura. La fecundidad relativa (F_R) osciló entre 242 y 681 oocitos/g de peso corporal (promedio: 445 oocitos/g). La distribución de frecuencias de los oocitos mostró que la alacha produce una única cohorte de oocitos. En general, las características reproductivas de la alacha del Mediterráneo NE son distintas de las observadas en poblaciones de otras áreas de su distribución.

Palabras clave: proporción de sexos, maduración sexual, fecundidad, puesta, alacha, Mar Egeo, Mediterráneo.

INTRODUCTION

Fish have developed reproductive strategies and traits that ensure the survival of the species under variable and often unfavourable conditions (Potts

and Wootton, 1984). The reproductive strategy of each species is expressed by certain characteristics such as age and size fecundity, time duration and frequency of spawning, size at first maturity and reproductive behaviour (Potts and Wootton, 1984;

Wootton, 1998). All these characteristics are useful for managing fisheries (Jennings *et al.*, 2001), particularly for single species pelagic fisheries.

Round sardinella, *Sardinella aurita* Valenciennes, 1847 (Pisces, Clupeidae), is a widely distributed, middle-sized pelagic fish. The distribution of the species is tropical and subtropical often associated with major upwelling systems (Durand *et al.*, 1998; Froese and Pauly, 2003, www.fishbase.org). Its range extends to the western and eastern Atlantic Ocean, the Pacific Ocean, the entire Mediterranean Sea and occasionally the Black Sea (Bauchot, 1987). Round sardinella is a stenothermic and stenohaline species (Binet, 1982; Longhurst and Pauly, 1987; Fréon and Misund, 1999). Until about twenty years ago, it was only sporadically found in the northern Aegean Sea and its distribution was confined to the warmer and more saline southern Aegean waters (Ananiades, 1952). As a typical opportunistic species (Cury and Fontana, 1988), it has invaded the northern Aegean Sea waters over the last twenty years mainly due to climatic changes (Bethoux and Gentili, 1999). This is also the case in the Adriatic Sea (Kačić, 1984). However, an adaptation of the species to the local environmental conditions should not be excluded (Cury and Fontana, 1988).

The commercial exploitation of round sardinella in the Greek seas has steadily increased since the early 1990s (National Statistical Service of Hellas, 1990-2002) because it is in high demand by the canning industry and as bait for the profitable tuna and swordfish fisheries. Total landings increased from 69 t in 1990 to 2733 t in 2002. The main part of the landings is caught by the purse-seiners using light attraction (60-80%), while the remaining part is caught by small scale fisheries (i.e. netters, beach seiners and small 'sardine-nets') and bottom trawlers (Tsikliras, 2004a). Using pelagic trawls is prohibited in Greek waters.

The reproductive biology of round sardinella has been thoroughly studied in the western (Bakun and Parrish, 1990; Fréon *et al.*, 1997) and eastern Atlantic (Fontana, 1969; Pham-Thuoc and Szypula, 1973; Cury and Fontana, 1988; Roy *et al.*, 1989; Quatey and Maravelias, 1999). In contrast, information is limited for the Mediterranean stocks and focused on the southern part of the sea. Size and age at maturity have been studied in Algerian (Bouaziz *et al.*, 2001) and Tunisian waters (Gaamour *et al.*, 2001); time and duration of spawning in Egyptian (Wassef *et al.*, 1985), Algerian (Bensahla Talet *et al.*, 1988) and Tunisian waters (Gaamour *et al.*, 2001); and fecundity in Algerian (Bensahla Talet *et al.*, 1988) and Tunisian waters (Gaamour *et al.*, 2001). Data on its reproductive biology in Greek waters is very scarce (time and duration of spawning: Ananiades, 1952), which is the case for many eastern Mediterranean stocks (Stergiou *et al.*, 1997).

The aim of the present study is to investigate the following aspects of the reproductive biology of round sardinella in the northern Aegean Sea: (a) the time and duration of the spawning season; (b) the annual reproductive cycle, in terms of seasonal changes in the gonadosomatic index and maturity stages; (c) the sex-ratio; (d) the size at first sexual maturity; and (e) the fecundity.

The aim of the present study is to investigate the following aspects of the reproductive biology of round sardinella in the northern Aegean Sea: (a) the time and duration of the spawning season; (b) the annual reproductive cycle, in terms of seasonal changes in the gonadosomatic index and maturity stages; (c) the sex-ratio; (d) the size at first sexual maturity; and (e) the fecundity.

MATERIAL AND METHODS

Monthly samples were collected from Kavala Gulf (40°52'N, 24°25'E, northern Aegean, Greece) on board a professional boat using a commercial purse seine net (length: 800 m, height: 90 m and mesh size: 9 mm bar length) between September 2000 and August 2002 (Fig. 1). Each monthly sample consisted on average of 331 individuals (ranging between 212 and 549). Additional samples (906 individuals) were collected just prior to the spawning period of the species using an unselective gear (beach seine with

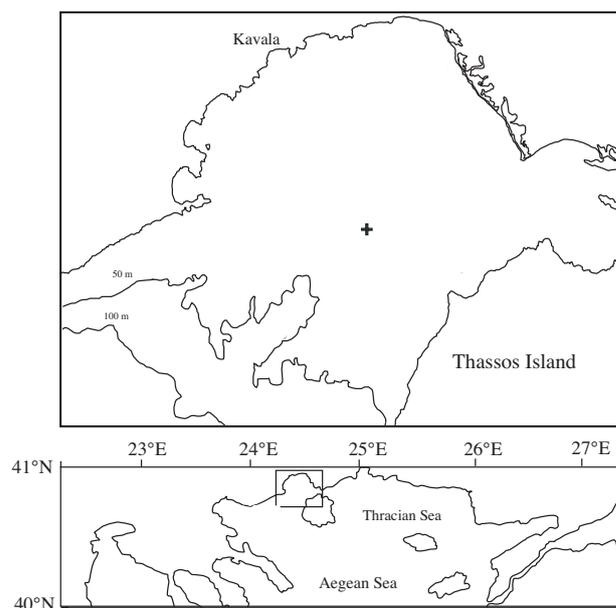


FIG. 1. – Map of the study area (Kavala Gulf, northern Aegean Sea, Greece) showing the station at which temperature data was recorded (+). The depth contours of 50 and 100 m are also indicated.

cod-end mesh size of 8 mm, bar length), to avoid biased results taken with selective gear, which could give an inaccurate estimation of size at maturity (Jennings *et al.*, 2001). The beach seine samples were only used for estimating size at maturity. Furthermore, sea surface temperature (SST, °C) was recorded monthly, using a CTD probe (Fig. 1).

Fish samples were immediately fixed on board in formaldehyde solution (8%, buffered) and were measured (total length, L, mm) and weighted (total weight, W, g) in the laboratory. Total length ranged between 97 and 243 mm for the males and between 102 and 248 mm for the females (monthly length frequency distribution is given by Tsikliras *et al.*, 2005b). Gonad weight (GW) was recorded to the nearest 0.01 g. In overall, 7942 individuals were sexed and the maturity stages were determined using the six stage key of Nikolskii (1963). A χ^2 goodness-of-fit test (Zar, 1999) was undertaken to compare the female:male (F:M) ratios (per month and within the size groups), with a hypothesized sex-ratio of 1:1. Sex and maturity stages were determined macroscopically.

The gonadosomatic index [$GSI=(GW/W)\times 100$] describes the relative size of gonads and is used as an index of reproductive activity (Wootton, 1998). Absolute fecundity (F_A) was determined in a sample of 105 gonads collected prior to spawning (stage V, Nikolskii, 1963) and preserved in Gilson's fluid (Bagenal and Braum, 1978). Oocytes were counted volumetrically (Bagenal and Braum, 1978) and oocyte diameter was measured under a microscope. The relationship between F_A and length or weight was described using the exponential equation: $F_A=ax^b$, which after a logarithmic transformation takes the form $\log F_A=\log a+b(\log x)$, where x is either length or weight and a , b are the regression constants. To assign equal weight to all size classes, mean F_A per length class was used (Živkov and Petrova, 1993). Relative fecundity (F_R) was considered as the number of eggs per unit of body weight (Nikolskii, 1963).

The logistic model is commonly used as a mathematical description of the relation between body size and sexual maturity (e.g. Echeverria, 1987). The length at which 50% of the individuals attained sexual maturity (L_{50}) was estimated by fitting a logistic curve to the relationship between the percentage of mature fish (P) and length class (L):

$$P = e^{(v_1+v_2L)} / (1 + e^{(v_1+v_2L)}),$$

and

$$L_{50} = -v_1/v_2.$$

The proportion of mature fish for each 5 mm length class was estimated by sex and v_1 , v_2 were calculated using the method described by Petrakis and Stergiou (1997), as adopted for maturity studies (Stergiou, 1999). For the estimation of L_{50} , mature individuals were considered those that were classified at stages IV to VI, while those classified at stages I to III were considered immature. A test for over-dispersion was performed by comparing the deviance statistic Δ to the χ^2 distribution on $N-2$ degrees of freedom (Petrakis and Stergiou, 1997). The data are over-dispersed if $\Delta > \chi^2$. Finally, the age at 50% maturity and the dimensionless ratio L_{50}/L_∞ (where L_∞ is the asymptotic value of L), which expresses the proportion of the potential growth span of the species covered before maturation (Beverton, 1992), were calculated using the growth parameters previously estimated by Tsikliras *et al.* (2005b).

RESULTS

Sex-ratio

Round sardinella is a gonochoristic fish. External morphological and colour differentiation is not observed at any stage of its life cycle (monomorphism). In overall, 4014 (50.54%) out of the 7942 individuals sexed were females, and 3928 (49.46%) were males. The F:M ratio was 1.02:1 and did not differ significantly ($\chi^2=0.91$, $P=0.34$) from unity. Yet, the F:M ratio exhibited a monthly variation from 0.13 in June 2002 to 1.67 in December 2001. The size-specific sex-ratio showed that the number of males and females was equal for lengths lower than 160 mm, whereas the number of males was higher for length classes of 160 (F:M=0.43, $\chi^2=73.79$, $P<0.001$) and 170 mm (F:M=0.71, $\chi^2=27.39$, $P<0.001$). The sex-ratio did not differ statistically from unity for length classes of 180 (F:M=0.92, $\chi^2=1.85$, $P=0.179$) and 190 mm (F:M=0.96, $\chi^2=0.72$, $P=0.402$). Females generally dominated at lengths greater than 200 mm (Fig. 2).

Gonad weight

The weight of the testes ranged between 0.59 and 9.91 g (average 1.55 g, S.D.=0.81) for males with

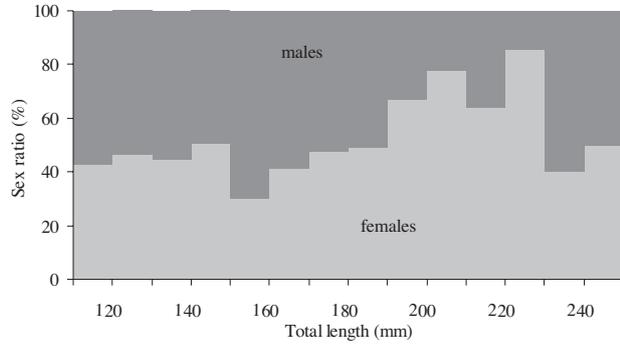


FIG. 2. – Sex-ratio (%) as a function of total length (L, mm) for round sardinella, Aegean Sea.

length ranging between 159 and 243 mm. Similarly, the ovary weight ranged between 0.33 and 5.52 g

(average 1.54, S.D.=0.88) for females with length ranging between 160 and 230 mm. Testes and ovaries accounted for 4.84% and 4.41% of the total weight respectively. An analysis of variance revealed the statistical difference in the average proportion of sexual organs to the fish body weight ($F=5.32$, $P=0.021$).

Time of spawning and maturity stages

The analysis of GSI indicated that the gonads of both sexes started to develop around April and matured fully a month later (Fig. 3a and b). Mean monthly SST (Fig. 3c) was 0.5 to 1°C higher during the first study year (mean: 18.15, range: 10.07-

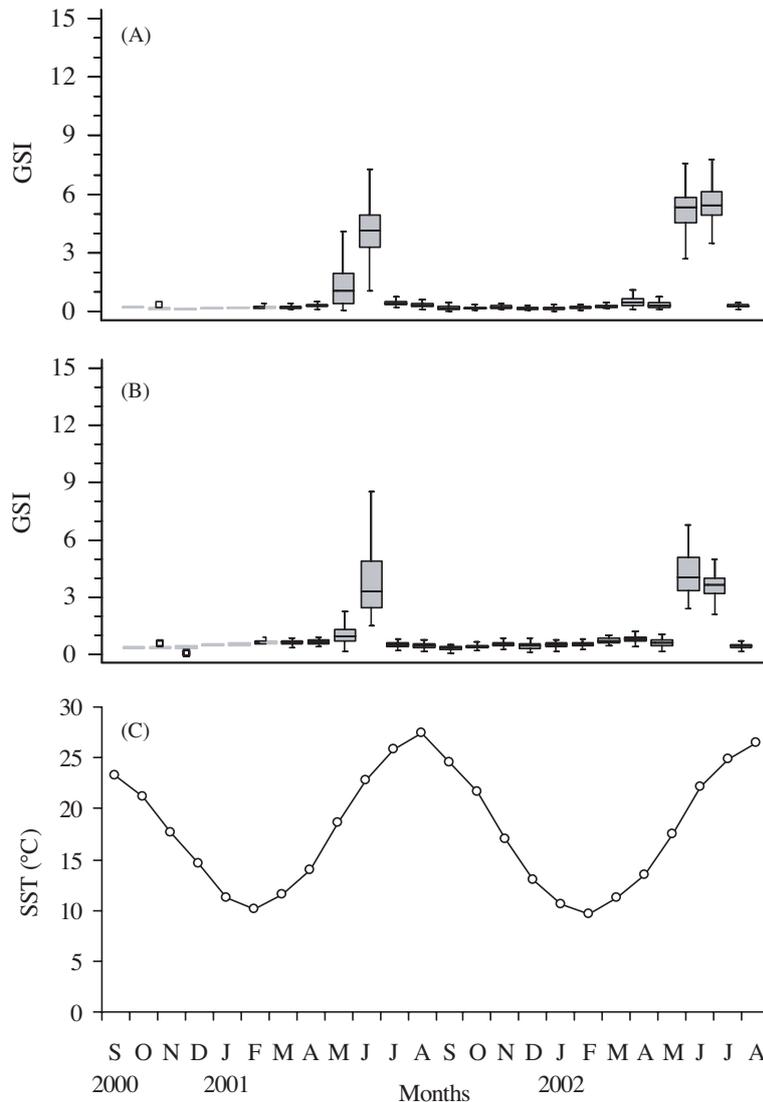


FIG. 3. – Monthly variation of (A) male and (B) female round sardinella gonadosomatic index (GSI) between September 2000 and August 2002. The rectangular part of the plot extends from the lower to the upper quartile; the centre lines within each box show the location of the sample medians; the squares indicate outliers. (C) Monthly variation of mean sea surface temperature (SST, °C) in the northern Aegean Sea (September 2000-August 2002).

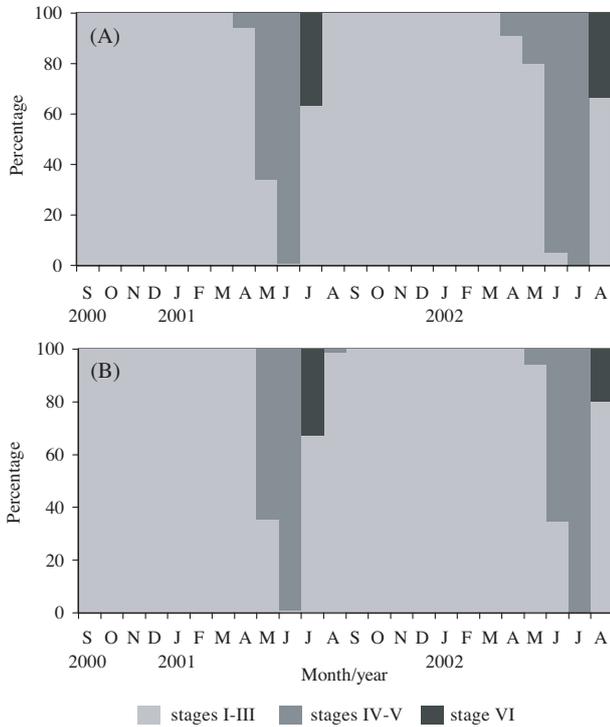


FIG. 4. – Monthly percentage of maturity stages of (A) male and (B) female round sardinella, Aegean Sea.

27.41) compared to the second one (mean: 17.67, range: 9.62-26.51).

The spawning season of the species is confined to a specific period of the year and begins in May or June. Sexually mature individuals were only caught during May, June and July (Fig. 4). The first mature males and females (stages IV and V) appeared in April and May respectively. In June, almost all specimens of both sexes were mature and in July, 36.7% of males and 24.5% of females were spent (stage VI), while the rest were at stage II (Fig. 4). All individuals of both sexes were resting (stage II) between September and March with the exception of some immature (stage I) specimens caught in September and October 2001.

Size at maturity

The L_{50} was 155.0 mm for males and 168.3 for females (Fig. 5). The smallest mature male and female were 135 and 136 mm, respectively. All females with a length greater than 215 mm and all males with a length greater than 205 mm were mature. The parameters of the equations describing the relationship between the proportion of mature fish and length class are shown in Table 1. The L_{50}/L_{∞} was 0.62 for males and 0.67 for females.

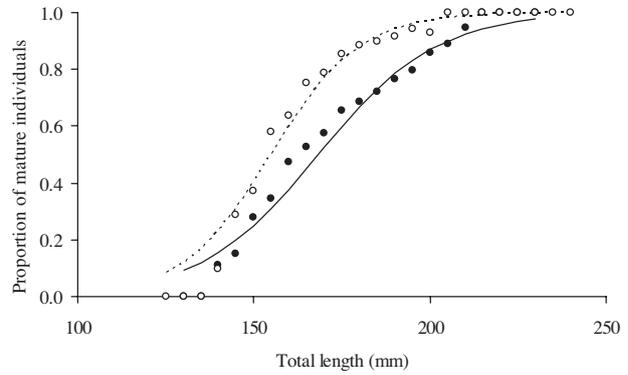


FIG. 5. – Estimated (line) and observed (dots) proportion of mature at length (L, mm) round sardinella, Aegean Sea (females: solid circles, males: open circles).

Based on the growth parameters of the species (Tsikliras *et al.*, 2005b), the age at 50% maturity for males and females was 1.03 and 1.33 years respectively.

Fecundity and oocyte diameter

Absolute fecundity (F_A) exhibited high variability among females and ranged between 9,700 (S.D. of 4 subsamples=632) and 72,700 (S.D. of 4 subsamples=9,449) oocytes, corresponding to females with $L=164$ mm and $L=228$ mm respectively (mean=20,976, S.D.=7,741, $n=105$). Relative fecundity (F_R) ranged between 242 and 681 oocytes/g. An average of 445 (S.D.=98) oocytes/g was produced. Mean F_A increased exponentially with length and weight:

$$F_A = 0.0949 \times L^{4.22}, r^2 = 0.91, P < 0.01, n = 8 \text{ (Fig. 6a)}$$

TABLE 1. – Estimated mean length (L_{50} , mm) and age (t_{50} , yr) at which 50% of the fish are sexually mature and the parameters of the equations describing the logistic relationship between the proportion of mature fish (P) and body length (L) for male and female round sardinella, Aegean Sea.

Parameter estimates	Females	Males
Length range (mm)	129-230	125-243
v_1	- 10.10	-12.40
v_2	0.060	0.080
SE v_1	0.851	1.024
SE v_2	0.005	0.006
L_{50} (mm)	168.33	155.00
t_{50} (yr)	1.33	1.03
Lower 95 % CL L_{50}	165.30	151.89
Upper 95 % CL L_{50}	171.01	157.60
L_{25} (mm)	150.02	141.27
L_{75} (mm)	186.64	168.73
Deviance statistic (Δ)	22.655	35.237
Degrees of freedom	19	23
χ^2	30.143	35.175
r^2	91.06	90.09

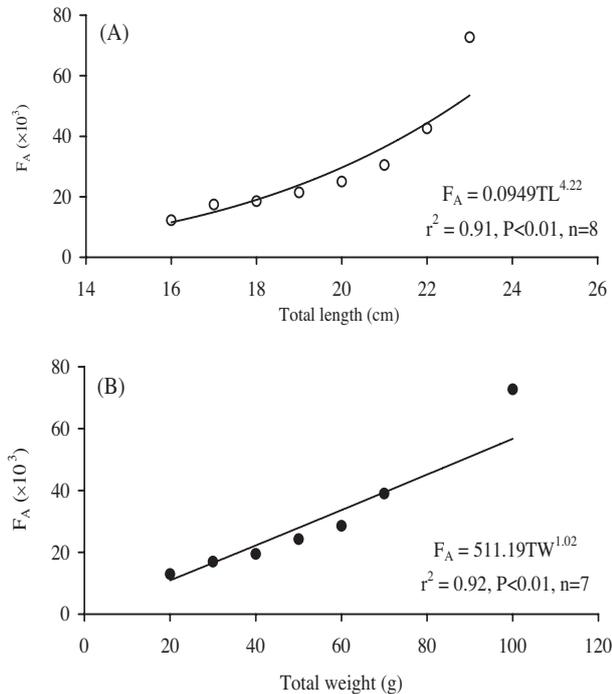


FIG. 6. – Mean absolute fecundity (F_A) of round sardinella as a function of (A) total length (L , cm) and (B) body weight (W , g).

$$F_A = 511.19 \times W^{1.02}, r^2 = 0.92, P < 0.01, n = 7 \text{ (Fig. 6b).}$$

In all stages of ovarian development, a permanent stock of oocytes smaller than 0.20 mm was observed. The average oocyte diameter just before spawning (oocytes >0.20 mm, stage V) was 0.44 (range: 0.20–0.76 mm, S.D.=0.05). There was no correlation between oocyte diameter and length ($r=0.056$, $P=0.55$). The unimodal frequency distribution of oocyte diameter showed that round sardinella is a determinate spawner producing a single batch of oocytes (Fig. 7).

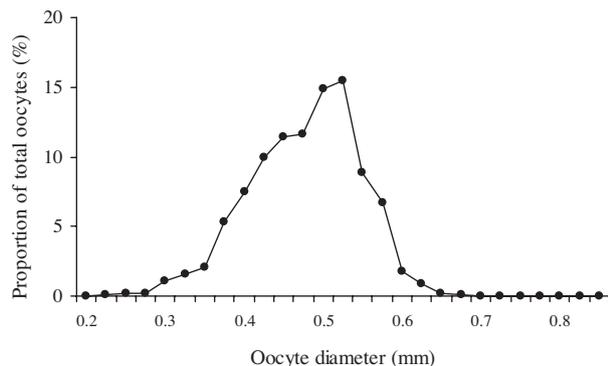


FIG. 7. – Size distribution of oocytes in the ovary of round sardinella just prior to spawning (early June 2001), Aegean Sea. A total of 105 females were used, the total length of which ranged between 156 and 228 cm.

DISCUSSION

Sex ratio

An overall balanced sex-ratio was found in the present study, which is in agreement with the results previously reported for round sardinella in Venezuelan waters (Fréon *et al.*, 1997). In contrast, Boely and Champagnat (1970), and Gaamour *et al.* (2001) noted a female dominated population in Senegalese and Tunisian waters respectively. The differences in the size-specific sex-ratio were also reported for Libyan waters (Pawson and Giama, 1985) and were related to sexual differences in growth, mortality or energetic cost of reproduction. Females generally dominated the higher length classes in the northern Aegean, Algerian (Bensahla Talet *et al.*, 1988) and Tunisian waters (Gaamour *et al.*, 2001), while differences in the size-specific sex-ratios have been reported for other Mediterranean marine fishes (e.g. Stergiou *et al.*, 1996).

Gonad weight

The testes frequently represent a much lower proportion of the total fish weight than the ovaries (Wootton, 1998). This sexual dimorphism, however, was not observed in round sardinella from the northern Aegean Sea. Moreover, the size of testes may relate to the mode of fertilization and the distance between the two sexes during spawning because external fertilization in the open sea requires greater amounts of sperm, and hence large testes, to ensure a higher rate of fertilization of the dispersed oocytes (Wootton, 1998). Additionally, the prespawning strategic behaviour of female round sardinella (Ben Yami, 1976) and other clupeoids (Blaxter and Hunter, 1982) may result in the dissemination of the two sexes and thus the need for larger sperm quantities than in other species. Male and female round sardinella in the northern Aegean Sea exhibited similar growth (and hence mortality) rates (Tsikliras *et al.*, 2005b), indicating that the same pattern persists for their entire lifespan.

Time of spawning and maturity stages

The spawning of round sardinella in the northern Aegean occurs in one episode every year in early summer (May to July), according to the monthly variation of the GSI and the maturation stages of the fish.

As in most marine fishes, the time of spawning of round sardinella has evolved as a mechanism to ensure the synchronization of larvae appearance and the peak of primary production (i.e. the favourable conditions for offspring survival; Cushing, 1975; Blaxter and Hunter, 1982). However, the onset of the spawning season of round sardinella varied between the two study years probably owing to temperature differences, with GSI being positively correlated with temperature (Tsikliras, 2004b). The existence of a positive relationship between GSI and temperature does not necessarily imply a direct effect of temperature or an effect of temperature alone on the onset of spawning. Population-related changes and other factors such as food availability (e.g. Roy *et al.*, 1989) may also play a role. In the northwest Mediterranean, inter-annual differences in the duration and onset of reproduction of round sardinella were related to temperature differences (Palomera and Sabatés, 1990). Moreover, Ben Tuvia (1960) noted that the gonad maturation of round sardinella begins at sea temperatures greater than 20 °C and Ettahiri *et al.* (2003) also related the spawning of round sardinella with high water temperatures. The process of gonad maturation and spawning in round sardinella may, however, be delayed due to unfavourable feeding or environmental conditions (Quatey and Maravelias, 1999). Due to the flexible strategy that results from its demographic plasticity (Cury and Fontana, 1988) and its wide geographical range, round sardinella might be a model species for understanding climate change-mediated effects on fish populations.

The reproductive period of round sardinella in the present study was short and lasted two months. Indeed, the breeding season of fishes inhabiting environments with pronounced seasonal climatic variations is almost invariably confined to a brief and specific period of the year (Bye, 1984). The duration of spawning of round sardinella might be short due to the presence of the sympatric clupeoids, the European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758) and European sardine, *Sardina pilchardus* (Walbaum, 1792) in the northern Aegean Sea. Increased antagonism occurs among clupeoid fishes at certain stages of their life cycles (Palomera and Sabatés, 1990), which has caused the evolution of different reproductive strategies to avoid antagonism in early and more vulnerable life stages (Wang and Tzeng, 1997). The temporal succession (Caragitsou *et al.*, 1997, Wang and Tzeng, 1997) and spatial segregation (Palomera and Sabatés, 1990) of sympatric clupeoid larvae reduces competition for habitat and maximizes resource utilization (Wang and Tzeng, 1997).

The duration of round sardinella's spawning is more extensive in the southern Mediterranean Sea (Tunisia, Egypt, Algeria, Libya: Table 2) and is probably attributed to the warmer climate compared to that of the northern Aegean. In other areas of its distribution (Table 2), the reproduction of round sardinella is highly variable regarding the time and duration of spawning. Consequently, its reproduction lasts throughout the year off the north-west African coast (Fontana, 1969), exhibiting intra-annual varia-

TABLE 2. – Spawning period and other reproductive parameters (L_{50} : size at maturity, mm; F_A : absolute fecundity; F_R : relative fecundity; F:M: female to male ratio) of round sardinella in several areas of its distribution.

Area	Months												L_{50} (mm)	F_A ($\times 10^3$)	F_R	F:M	Reference		
	J	F	M	A	M	J	J	A	S	O	N	D							
<i>Mediterranean</i>																			
Aegean 2001			•	•											155.0 (M), 168.3 (F)	9.7-72.7	242-681	1.02	Present study
Aegean 2002					•	•									140 (M), 150 (F)	–	–	–	Present study
Aegean					•	•	•								–	–	–	–	Ananiades, 1952
Egypt					•	•	•	•							–	–	–	–	Wassef <i>et al.</i> , 1985
Libya					•	•	•	•							–	–	–	–	Pawson and Giama, 1985
Algeria						•	•	•	•						–	–	–	–	Bensahla Talet <i>et al.</i> , 1988
Tunisia						•	•	•							141 (M), 152 (F)	8.3-43.2	240-480	1.20	Gaamour <i>et al.</i> , 2001
Algeria															141 (F)	–	–	0.99	Bouaziz <i>et al.</i> , 2001
<i>Atlantic</i>																			
Canary Islands	•	•	•												–	–	–	–	Navarro, 1932
NW Africa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	–	–	–	–	Fontana, 1969
NW Africa	•														–	29-303	–	–	Pham-Thuoc and Szypula, 1973
Senegal			•	•	•	•	•								–	–	–	–	Cury and Fontana, 1988
Ghana			•	•				•	•	•					–	–	–	–	Cury and Fontana, 1988
Ghana					•			•	•	•	•				167 (M), 171 (F)	–	–	–	Quatey and Maravelias, 1999
Brazil															–	–	–	–	Matsuura, 1996
Venezouela	•	•													197	–	–	0.99	Fréon <i>et al.</i> , 1997

tions with one (Fontana, 1969), two (Cury and Fontana, 1988), or even three (Quaatey and Maravelias, 1999) peaks of reproductive activity.

Size at maturity

Round sardinella males in the northern Aegean Sea were smaller and younger at maturity than females. Indeed, in short-lived species, maturation usually occurs at the end of the first year of life (Beverton, 1963). Bimaturism, which is common in species with promiscuous mating, external fertilization and indeterminate growth (Stearns, 1992), is also observed in other round sardinella populations (Quaatey and Maravelias, 1999; Gaamour *et al.*, 2001). In general, higher L_{50} values have been reported for Atlantic stocks of round sardinella (Venezuelan waters, Ghana waters: Table 2). In the Mediterranean, however, round sardinella reaches sexual maturity at a smaller size (Table 2). Age and size at maturity vary among closely related species, among populations within species and among individuals within populations, suggesting that they can respond rapidly to natural selection (Stearns, 1992). Size and age at first maturity depend on environmental and genetic factors (Wootton, 1998; Sampson and Al-Jufaily, 1999), but can be influenced by other factors such as long-term fishing pressure (Jennings *et al.*, 2001). The latter may pose a severe impact on size at maturity forcing the population to mature at a smaller size in order to ensure the survival of the species (Olsen *et al.*, 2004).

The L_{50}/L_{∞} ratio is generally smaller for large-sized species and larger for small-sized ones (e.g. Beverton, 1963; Longhurst and Pauly, 1987), which is also true for the Mediterranean fishes (Tsikliras *et al.*, 2005a). The L_{50}/L_{∞} ratio for a dataset of 24 Hellenic marine fish species ranged between 0.33 and 0.74 with a mean value of 0.48 (Stergiou, 2000). The computed value for round sardinella ranks the species within the reported range and close to the maximum value. Beverton (1963) reported a range of ratios between 0.62 and 0.80 for clupeids, and a value of 0.65 for *Sardinella* spp., which agrees closely with the value calculated in the present study.

Fecundity and oocyte diameter

The absolute fecundity (F_A) of round sardinella in the northern Aegean Sea exhibited high variability

among individuals of the same size. This can be the result of either genetic differences among the females, or environmental conditions or a combination of both (Stearns, 1992; Wootton, 1998). The fecundity of round sardinella in the northern Aegean is close to the lower limit of the range reported so far for the species in both the Mediterranean and Atlantic Seas (Table 2). An important parameter accounting for these differences is the maximum recorded length in these areas, which is lower in the northern Aegean (max $L=248$ mm) when compared to the northwest African coast (max $L=410$ mm; Pham-Thuoc and Szypula, 1973) and southern Mediterranean (max $L=292$ mm; Bensahla Talet *et al.*, 1988), the reason being that F_A is a function of length (e.g. Wootton, 1998). However, on a unit body mass basis, the above differences were balanced. Thus, in Algerian waters relative fecundity (F_R) ranged between 246 and 933 oocytes/g, which is very close to that of the northern Aegean (Table 2).

The mean F_A in the present study was strongly correlated with length and weight. The positive correlation of F_A with length has been reported for round sardinella populations in the Mediterranean (Bensahla Talet *et al.*, 1988; Gaamour *et al.*, 2001) and the eastern Atlantic (Pham-Thuoc and Szypula, 1973). The parameter b of the relationship between F_A and length is higher than those reported for round sardinella in Tunisian waters (Gaaamour *et al.*, 2001) and lies close to the upper limit of the previously reported values for other fishes (Wootton, 1998). The reproductive potential, as reflected in the increase in F_A with length, indicates that round sardinella allocates more energy to reproduction as it grows. This is supported by the asymptotic decline of round sardinella's growth with age (Tsikliras *et al.*, 2005b). Such trade offs are common in fish, with the trade off between growth and present reproduction being potentially significant because female fecundity is a function of body size (Wootton, 1998). Besides body length and weight, which largely determine the fecundity of fish (see also Trippel and Neil, 2004; Tsikliras *et al.*, 2005a), the physiological condition of maternal stock, expressed as total lipid energy, is also very important in estimating the number of eggs produced and predicting the subsequent recruitment (Marshall *et al.*, 1999).

The frequency distribution of oocyte diameter indicated that, besides the permanent stock of primary oocytes, the oocytes of round sardinella in the northern Aegean Sea developed synchronously,

which is also the case for round sardinella in Libyan waters (Pawson and Giama, 1985). Although the frequency distribution of oocyte diameter is an indicator of the nature of spawning in fishes and the presence of more than one group of yolked eggs is an accepted criterion that more than a single spawning takes place (Blaxter and Hunter, 1982), further histological examination of the gonads and hormonal profile studies are required to ensure the single batch spawning of the species.

ACKNOWLEDGEMENTS

The authors would like to thank Mrs V. Papantoniou for her help in the laboratory, Drs K.I. Stergiou and E.T. Koutrakis and two anonymous reviewers for their helpful suggestions and criticisms.

REFERENCES

- Ananiades, C.I. – 1952. Quelques considérations biométriques sur l'allache (*Sardinella aurita* C. V.) des eaux grecques. *Prak. Hell. Hydrobiol. Inst.*, 5: 5-45.
- Bagenal, T.B. and E. Braum. – 1978. Eggs and early life history. In: T.B. Bagenal (ed.), *Methods for Assessment of Fish Production in Freshwaters*, pp. 165-201. Blackwell Scientific Publications, Oxford.
- Bakun, A. and R.H. Parrish. – 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). *J. Cons.*, 46: 269-283.
- Bauchot, M.L. – 1987. Poissons osseux. In: W. Fischer, Schneider, M. and M.-L. Bauchot (eds.), *Fishes FAO d'identification des espèces pour les besoins de la pêche: Méditerranée et mer Noire. Zone de pêche 37. Volume II. Vertèbres.*, pp. 861-1422. Food and Agricultural Organisation of the United Nations, Rome.
- Ben Tuvia, A. – 1960. Fluctuations in the stock of *Sardinella aurita* and its dependence on temperature and rain. *FAO Fish Biol. Synop.*, 14: 287-312.
- Ben-Yami, M. – 1976. *Fishing with light*. FAO Fishing News Books, England.
- Bensahla-Talet, A., Y. Mortet and J.A. Tomasini. – 1988. Relations masse-longueur, sex-ratio et reproduction (saison de ponte, fécondités) de *Sardinella aurita* (Val. 1847) des cotes Oranaises (Algerie). *Rapp. Comm. int. Mer Médit.*, 31 V-II: 14.
- Bethoux, J.P. and B. Gentili. – 1999. Functioning of the Mediterranean Sea: past and present changes related to freshwater input and climate changes. *J. Mar. Syst.*, 20: 33-47.
- Beverton, R.J.H. – 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, 154: 44-67.
- Beverton, R.J.H. – 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.*, 41 (Suppl. B): 137-160.
- Binet, D. – 1982. Influence des variations climatiques sur la pêcherie des *Sardinella aurita* ivoiro-ghanéennes: relation sécheresse-surpêche. *Oceanol. Acta*, 5: 443-452.
- Blaxter, J.H.S. and J.R. Hunter. – 1982. The biology of the clupeoid fishes. *Adv. Mar. Biol.*, 20: 1-223.
- Boely, T. and C. Champagnat. – 1970. Observations préliminaires sur *Sardinella aurita* (C. et V.) des cotes sénégalaises. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, 159: 176-181.
- Bouaziz, A., A. Bennoui, B. Brahmi and R. Semroud. – 2001. Sur l'estimation de l'état d'exploitation de la sardinelle (*Sardinella aurita* Valenciennes, 1847) de la région centre de la cote algérienne. *Rapp. Comm. int. mer Médit.*, 36: 244.
- Bye, V.J. – 1984. The role of environmental factors in the timing of reproductive cycles. In: G.W. Potts and R.J. Wootton (eds.), *Fish Reproduction: Strategies and Tactics*, pp. 187-205. Academic Press, London.
- Caragitsou A., K. Siapatis, K. Anastassopoulou, C. Papaconstantinou. – 1997. Seasonal distribution of ichthyoplankton in Aegean Sea. In: *Proc. Fifth Hell. Symp. Oceanogr. Fisher.*, vol. II, pp. 143-145, 13-17 April, Kavala, Greece.
- Cury, P. and A. Fontana. – 1988. Compétition et stratégies démographiques comparées de deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) des cotes ouest-africaines. *Aquat. Living Resour.*, 1: 165-180.
- Cushing, D.H. – 1975. *Marine Ecology and Fisheries*. Cambridge University Press, London.
- Durand, M.-H., P. Cury, R. Mendelssohn, C. Roy, A. Bakun and D. Pauly. – 1998. *Global versus Local Changes in Upwelling Systems*. ORSTOM, Paris.
- Echeverria, T.W. – 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fish. Bull.*, 85: 229-250.
- Ettahiri, O., A. Berraho, G. Vidy, M. Ramdani and T. Do Chi. – 2003. Observation on the spawning of *Sardina* and *Sardinella* off the south Moroccan Atlantic coast (21-26° N). *Fish. Res.*, 60: 207-222.
- Fontana, A. – 1969. Etude de la maturité sexuelle des sardinelles *Sardinella eba* (Val.) et *Sardinella aurita* (C et V) de la région de Pointe-Noire. *Cah. ORSTOM, Sér. Océanogr.*, 7: 101-114.
- Fréon, P. and O.A. Misund. – 1999. *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment*. Blackwell Fishing News Books, London.
- Fréon, P., M. El Khattabi, J. Mendoza and R. Guzman. – 1997. Unexpected reproductive strategy of *Sardinella aurita* off the coast of Venezuela. *Mar. Biol.*, 128: 363-372.
- Froese, R. and D. Pauly. (eds.). – 2003. FishBase, World Wide Web electronic publication. <www.fishbase.org>, 10 September, 2003.
- Gaamour, A., H. Missaoui, L. Ben-Abdallah and A. El Ahmed. – 2001. Paramètres biologiques de la sardinelle ronde (*Sardinella aurita* Valenciennes, 1847) dans la région du Cap Bon (canal siculo-tunisien). GFCM, 26-30 March 2001, Kavala, Greece. (www.faocopemed.org/en/sac/docs.htm)
- Jennings, S., M.J. Kaiser and J.D. Reynolds. – 2001. *Marine Fisheries Ecology*. Blackwell Science, London.
- Kaćić, I. – 1984. Gilt sardine (*Sardinella aurita* Val.) in Adriatic Sea. *Nova Thalass.*, 6: 371-373.
- Longhurst, A.R. and D. Pauly. – 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego.
- Marshall, C.T., N.A. Yaragina, Y. Lambert and O.S. Kjesbu. – 1999. Total lipid energy as a proxy for total egg production by fish stocks. *Nature*, 402: 288-290.
- Matsuura, Y. – 1996. A probable cause of recruitment failure of the Brazilian Sardine *Sardinella aurita* population during the 1974-75 spawning season. *S. Afr. J. Mar. Sci.*, 17: 29-35.
- National Statistical Service of Hellas. – 1990-2002. *Statistical Yearbooks*. NSSH, Athens.
- Navarro, F. – 1932. Nuevos estudios sobre la alacha (*Sardinella aurita* C.V.) de Baleares y de Canarias. *Notas Resum. Inst. Esp. Oceanogr.*, 60: 1-35.
- Nikolskii, G.V. – 1963. *The ecology of fishes*. Academic Press, London and New York.
- Olsen, E.M., M. Heino, G.R. Lilly, M.J. Morgan, J. Bratney, B. Ernande and U. Dieckmann. – 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932-935.
- Palomera, I. and A. Sabatés. – 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the north-western Mediterranean. *Sci. Mar.*, 54: 61-67.
- Pawson, M.G. and M.S. Giama. – 1985. A biological sampling problem illustrated by the population structure and growth patterns of *Sardinella aurita* at Tripoli, Libya. *Environ. Biol. Fish.*, 12: 143-154.
- Petrakis, G. and K.I. Stergiou. – 1997. Size selectivity of diamond and square mesh codends for four commercial Mediterranean fish species. *ICES J. Mar. Sci.*, 54: 13-23.

- Pham-Thuoc and J. Szygula. – 1973. Biological characteristic of gilt sardine *Sardinella aurita* Cuv. et Val. 1847 from northwest African Coast. *Acta Ichthyol. Piscat.*, 3: 19-37.
- Potts, G.W. and R.J. Wootton. – 1984. *Fish Reproduction: Strategies and Tactics*. Academic Press, London.
- Quaatay, S.N.K. and C.D. Maravelias. – 1999. Maturity and spawning pattern of *Sardinella aurita* in relation to water temperature and zooplankton abundance off Ghana, West Africa. *J. Appl. Ichthyol.*, 15: 63-69.
- Roy, C., P. Cury, A. Fontana and H. Belvèse. – 1989. Spatio-temporal reproductive strategies of the clupeoids in West African upwelling area. *Aquat. Living Resour.*, 2: 21-29.
- Sampson, D.B. and S.M. Al-Jufaily. – 1999. Geographic variation in the maturity and growth schedules of English sole along the U.S. west coast. *J. Fish Biol.*, 54: 1-17.
- Stearns, S.C. – 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- Stergiou, K.I. – 1999. Intraspecific variations in size- and age-at-maturity for red bandfish, *Cepola macrophthalma*. *Environ. Biol. Fish.*, 54: 151-160.
- Stergiou, K.I. – 2000. Life-history patterns of fishes in the Hellenic Seas. *Web Ecol.*, 1: 1-10.
- Stergiou, K.I., P. Economidis and A. Sinis. – 1996. Sex ratio, spawning season and size at maturity of red bandfish in the western Aegean Sea. *J. Fish Biol.*, 49: 561-572.
- Stergiou, K.I., E.D. Christou, D. Georgopoulos, A. Zenetos and C. Souvermezoglou. – 1997. The Hellenic seas: physics, chemistry, biology and fisheries. *Oceanogr. Mar. Biol. Ann. Rev.*, 35: 415-538.
- Trippel, E.A. and S.R.E. Neil. – 2004. Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (*Melanogrammus aeglefinus*) in relation to body size and condition. *Can. J. Fish. Aquat. Sci.*, 61: 2097-2110.
- Tsikliras, A.C. – 2004a. *Biology and population dynamics of round sardinella (Sardinella aurita Valenciennes, 1847) in Kavala Gulf (Northern Aegean Sea, Greece)*. Ph. D. thesis, Aristotle University of Thessaloniki, Greece.
- Tsikliras, A.C. – 2004b. Spawning pattern of round sardinella, *Sardinella aurita* Valenciennes, 1847, in relation to sea surface temperature (northern Aegean Sea, Greece). *Rapp. Comm. int. Mer Médit.*, 37: 449.
- Tsikliras, A.C., E. Antonopoulou and K.I. Stergiou. – 2005a. Reproduction of Mediterranean fishes. In: K.I. Stergiou and D.C. Bobori (eds), *Fish and more, Proc. 3rd FishBase Mini Symp.*, pp. 37-40. University Studio Press, Thessaloniki, Greece.
- Tsikliras, A.C., E.T. Koutrakis and K.I. Stergiou. – 2005b. Age and growth of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean. *Sci. Mar.*, 69: 231-240.
- Wang, Y.T. and W.N. Tzeng. – 1997. Temporal succession and spatial segregation of clupeoid larvae in the coastal waters off the Tanshui River Estuary, northern Taiwan. *Mar. Biol.*, 129: 23-32.
- Wassef, E., A. Ezzat, T. Hashem and S. Faltas. – 1985. Sardine fishery by purse-seine on the Egyptian Mediterranean coast. *Mar. Ecol. Progr. Ser.*, 26: 11-18.
- Wootton, R.J. – 1998. *Ecology of Teleost Fishes*. Kluwer Academic Publishers [Fish and Fisheries Series, no. 24], Dordrecht, The Netherlands.
- Zar, J.H. – 1999. *Biostatistical Analysis*. Prentice-Hall, New Jersey.
- Živkov, M. and G. Petrova. – 1993. On the pattern of correlation between fecundity, length, weight and age of pikeperch *Stizostedion lucioperca*. *J. Fish Biol.*, 43: 173-182.

Scient. ed.: F. Piferrer

Received October 13, 2004. Accepted September 26, 2005.