SCI. MAR., 60 (Supl. 2): 209-218 SCIENTIA MARINA 1996

THE EUROPEAN ANCHOVY AND ITS ENVIRONMENT, *I. PALOMERA and P. RUBIÉS (eds.)*

Reproductive biology of anchovy (*Engraulis encrasicolus ponticus* Alexandrov 1927) in the Black Sea*

LEONID A. LISOVENKO[1] and DIMITRI P. ANDRIANOV[2]

[1] Russian Federal Institute of Fisheries and Oceanography (VNIRO), Moscow, Russia.
[2] P.P.Shirshov Institute of Oceanology, Moscow, Russia.

SUMMARY: Investigations on the reproductive biology of the anchovy conducted during the 1987-1992 period in the northwestern Black Sea, the main spawning area of this species in this sea, are summarized. The spawning takes place in summer in the warm upper layer, within a wide temperature range (16-28 °C). Reproduction occurs mostly in coastal waters, especially in estuarine areas with low salinity (7-18‰). The embryonic period lasts for about 24 hours (at 22.0-23.4 ° C) and the pelagic eggs are elliptical (long axis: 1.5-1.9 mm; short axis: 0.8-1.2 mm). By late summer, some of the young fish born at the very beginning of the spawning period may become mature at a body length of 55-65 mm and a weight of 1.2-2.4 g and take part in spawning. The spawning process is characterized by a clear daily rhythm: ripening and ovulation at about 9 p.m.; spawning from 9 p.m. to midnight; resting from midnight to 6 a.m.; forming of a new spawning batch from 6 a.m. to 9 p.m. Frequency of spawning depends on water temperature and varies during the spawning season, reaching its maximum -daily spawning- by the second half of June. On average, each female spawns more than 50 times a year. Individual batch fecundity depends on food availability, water temperature and body size. (Prepared by the Editors).

Key words: Anchovy, *Engraulis encrasicolus ponticus*, reproductive biology, Black Sea.

RESUMEN: BIOLOGÍA REPRODUCTIVA DE LA ANCHOA (*ENGRAULIS ENCRASICOLUS PONTICUS*, ALEXANDROV 1927) EN EL MAR NEGRO. – Se resumen las investigaciones sobre la biología reproductiva de la anchoa realizadas durante el período de 1987-1992 en el noroeste del mar Negro, el área principal de puesta de dicha especie en este mar. La puesta tiene lugar en verano, en las capas cálidas superficiales, dentro de un amplio margen de temperaturas (16-18 °C). La reproducción se efectúa principalmente en aguas costeras, especialmente en estuarios de salinidad reducida (7-18‰). El período embrionario dura unas 24 horas (a 22.0-23.4 °C) y los huevos pelágicos son elípticos (eje mayor: 1.5-1.9 mm; eje menor: 0.8-1.2 mm). A finales de verano, algunos de los individuos nacidos muy al principio del período de puesta pueden alcanzar la madurez a una talla de 55-65 mm y un peso de 1.2-2.4 g y tomar parte en la puesta. El proceso de freza se caracteriza por un claro ritmo diario: maduración y ovulación hacia las 21 horas; puesta de las 21 horas a medianoche; reposo de medianoche a las 6 horas; formación de una nueva puesta de las 6 horas a las 21 horas. La frecuencia de puesta depende de la temperatura del agua y varía a lo largo de la temporada de puesta, llegando al máximo -puesta diaria- en la segunda mitad de junio. Por término medio, cada hembra freza más de 50 veces al año. La fecundidad parcial individual depende de la disponibilidad de alimento, temperatura del agua y tamaño corporal. (Traducido por los Editores).

Palabras clave: Anchoa, *Engraulis encrasicolus ponticus*, biología reproductiva, mar Negro.

*Received June 10, 1995. Accepted April 10, 1996.

INTRODUCTION

Species of the genus *Engraulis* are typical representatives of pelagic fish communities in all oceans. Among other common ecological features they are characterized by a similar reproductive strategy to other pelagic fishes.

As a rule, all these are rather short cyclic fishes, batch spawners with protracted spawning seasons and high number of spawnings per year (Williams and Clarke, 1982; Hunter and Macewicz, 1985; Schaefer, 1987; Alheit, 1989). In *Engraulis*, including the Black Sea anchovy (*E. encrasicolus ponticus*), all above mentioned features are most pronounced (Hunter and Goldberg, 1980; Hunter and Leong, 1981; Alheit *et al.*, 1983; Tsuruta, 1987), effecting their predominance in pelagic fish communities.

The Black Sea anchovy has a reproductive strategy directed to increasing the quantity of eggs and larvae as an insurance of survival. In this sense, the Black Sea anchovy is a model subject. On the other hand, this anchovy is the most abundant pelagic fish of the Black Sea and the main object of fishing. So the knowledge of its reproductive peculiarities is necessary for directing a rational fishery.

The purposes of our research in reproductive biology of the Black Sea anchovy are to describe all qualitative and quantitative reproductive parameters: 1) Size and sex composition; 2) Size and age at maturity; 3) Period, duration and variability of spawning season; 4) Characteristics of oogenesis; 5) Type of spawning and number of spawning incidents; 6) Batch and individual annual fecundity; 7) Reproductive traits (expenses) of females; 8) Annual number of eggs spawned by population and annual energetic reproductive expenses of anchovy population. The final goal is to estimate the reproductive potential of the Black Sea anchovy and to determinate its position in the Black Sea ecosystem.

MATERIALS AND METHODS

Black Sea anchovy were collected on eight cruises of former USSR vessels during the 1987 to 1992 spawning seasons. The area sampled was the northwestern part of the Black Sea, from the shore of Crimea to the shore of Romania and Bulgaria (Fig. 1). This is the basic spawning area of anchovy in the Black Sea. To investigate diel rhythm of spawning, twelve stations during the cruises consisted of samples caught during 24-hour periods (Table 1). Each of the 12 stations usually included 8-10 samples collected by trawl at about 3-hour intervals in the same place (duration of trawling was 30 minutes; mouth of trawl width = 27 m and height = 7 m; trawl speed averaged 2.5 to 3 knots). The stations were taken in the places with the highest concentrations of spawning and feeding anchovy.

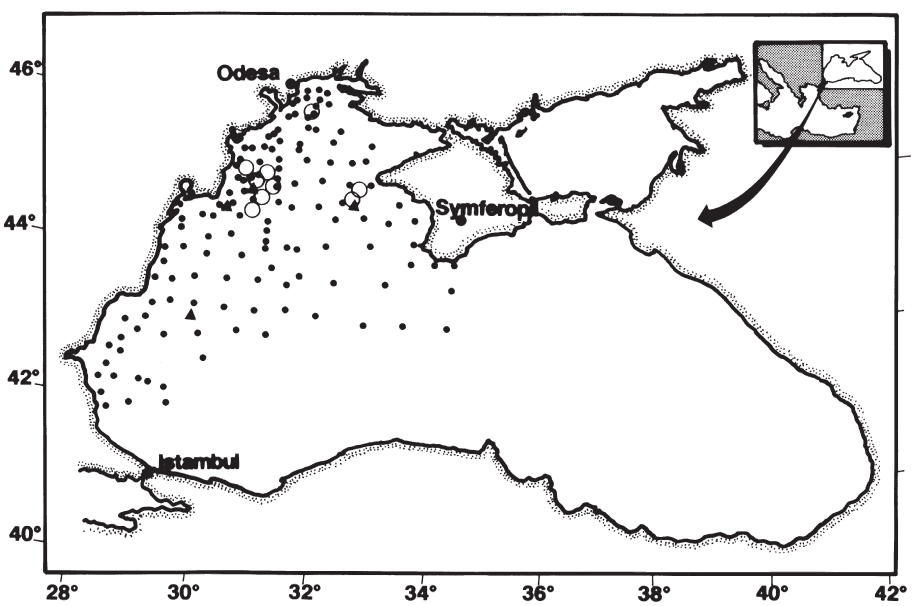

FIG. 1. – Map of standard trawl and ichthyoplankton surveys (dots) and location of trawl daily stations (circles), and anchovy young-of-the-year collection sites (triangles).

TABLE 1. – List of 24-h stations.

Station	Date	N trawls	N individuals	N ovaries analysed Oocyte size composition	Histology
1	23/24.06.1987	9	797	79	10
2	10/11.07.1987	9	544	0	0
3	25/26.05.1988	8	482	26	15
4	06/07.06.1988	8	422	100	50
5	24/25.07.1988	9	840	24	18
6	10/11.08.1988	10	856	44	15
7	20/21.06.1989	10	435	0	0
8	29/30.06.1989	6	187	0	0
9	06/07.07.1990	9	239	0	0
10	28/29.07.1990	8	317	0	0
11	02/03.08.1990	8	433	0	0
12	11/12.08.1990	10	390	0	0

One hundred anchovies were fixed with 10% formaldehyde from each catch. Anchovies were fixed immediately after taking the trawl on board. The following information was recorded: fork length, whole body weight, gutted fishes weight, sex, weight of ovaries or testes, and maturity stage was determined.

The stages of maturity were determined by the standard six-grade scale (Sakun and Butzkaya, 1968), modified for multiple spawning fishes (Oven, 1976).

The state of gonads was determined by the following: their size and colour; fullness of the blood vessels; size, colour and transparency of any oocytes; presence of a cavity in the gonads; and of blood in the cavity after spawning

GSI (gonadosomatic index) was calculated for males and females such that

$$GSI = \frac{\text{Gonad weight}}{\text{Gutted fish weight}} * 100$$

The process of oocyte growth and maturation was investigated using the "size composition" method and histological criteria. The size composition method consisted in examining size composition of oocytes in ovaries of fish at different stages of maturity. A small piece of ovarian tissue (weight from 10 to 40 mg) was sampled from the middle part of the right ovary in 10 females. All oocytes more than 150 mm in diameter were counted and measured.

Histotechnic was made by standard method (Roskin and Levinson, 1957). 8-10 mm slides were made and stained by the Hematoxylin-Eosin procedure. Oocytes were described within the limits of periods of protoplasmic growth, trophoplasmic growth and ripe.

Classification of oogenesis was based on the terminology of Götting (1961), Oven (1976) and Lisovenko (1985).

Growth rate in anchovy during the spawning seasons of these years was calculated by correlation-regression analysis of the actual size and weight data for females caught in the spawning grounds during the entire or most of the reproductive period.

Calculation of the difference between the average gonado-somatic index of the females caught immediately prior to the beginning of their laying of eggs (usually at 9 p.m.) and females taken upon the completion of their egg laying (usually at 3 a.m) was used as the principial method for assessing the amount of eggs laid by females and their dynamics throughout the spawning seasons. This indicator was chosen because of the following considerations:

(i) It had been found out earlier that the GSI, as an integrated indicator, virtually does not depend on the size of females, and in separate samples it correlates closely with the relative fecundity;

(ii) There is no need for special research because the GSI can easily be calculated using the data of the standard comprehensive biological analysis, and is sufficiently objective;

(iii) For an individual female it might be assumed that the difference between the weight of eggs before they are laid and after that corresponds to the amount of eggs laid, in other words to the batch fecundity of this female since the weight of ovary before the egg are laid includes the weight of hydratated eggs, diminishing by a portion relating to the weight of eggs laid after they are laid. Unfortu-

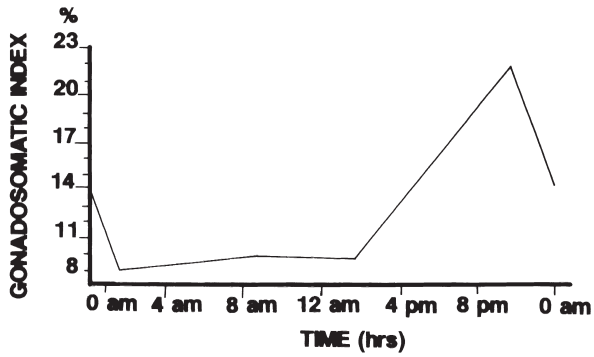

FIG. 2. – The diel dynamics of mean value of gonadosomatic indices of anchovy females (June 23-24, 1987).

nately, this characteristic cannot be calculated on the level of individual fish, and was calculated on the group level. Since daily stations were made at the same point, virtually on the same unit of concentration, and recognizing the simultaneouspattern of variations in GSI in all reproducing females, we assume that the average number of eggs laid can be assessed on the basis of comparison of the average GSI in pre- and post-spawning females.

In order to bring the relative batch fecundity in conformity with the difference between the average values of GSI before and after egg laying we used daily GSI dynamics data for the station made on June 23-24, 1987 (Fig. 2).

In this curve average GSI values for 3 p.m., 6 p.m., 9 p.m. are given only for the females at the IY-Y th stages of maturity which were to spawn next night. As is seen from the diagram the minimum average GSI value in fish at this station was recorded at 3 a.m, the maximum value at 9 p.m. (similar GSI dynamics were observed at all daily stations without exceptions). The difference between the maximum and minimum values (relative weight of eggs laid) was 14.8%.

The batch size and the relative fecundity (eggs per 1 g of gutted fish) in the maturing females caught at this daily station at 9 p.m. were calculated by the standard weight method. The average relative fecundity was 652.3 eggs/g. If we assume that this level corresponds to 14.8 percent or 0.148 g of the ovary weight per 1 g of gutted fish, one percent (0.01 part of the weight of gutted fish) would correspond to 44.1 eggs per 1 g of gutted fish. Based on those data it might be concluded that the weight of one egg would on the average make up 0.226 mg. This roughly corresponds to the actual weight of hydratated eggs from the ovaries of pre-spawning fish (9 p.m.). Those results were used for all daily stations in 1988 and 1990. In order to calculate the average relative fecundity of females at one or another daily station the average value of difference of GSI was invariably multiplied by 44.1 eggs.

RESULTS

The spawning season lasts from mid May, when water temperature is about 15-16 °C, to the middle or end of August when the temperature is about 25-26 °C. Anchovy spawns only in the upper warm layer (0-25 m), above the thermocline.

A number of results indicate that anchovy spawn simultaneously at night (9 p.m. to midnight). These include the diel dynamics of visible characteristics of gonads, gonosomatic index (GSI) of anchovy females (Figs. 2, 3), size composition of the oocytes in ovaries (Fig. 4), histological characteristics of ovary (Fig. 5) demonstrate that anchovy spawn

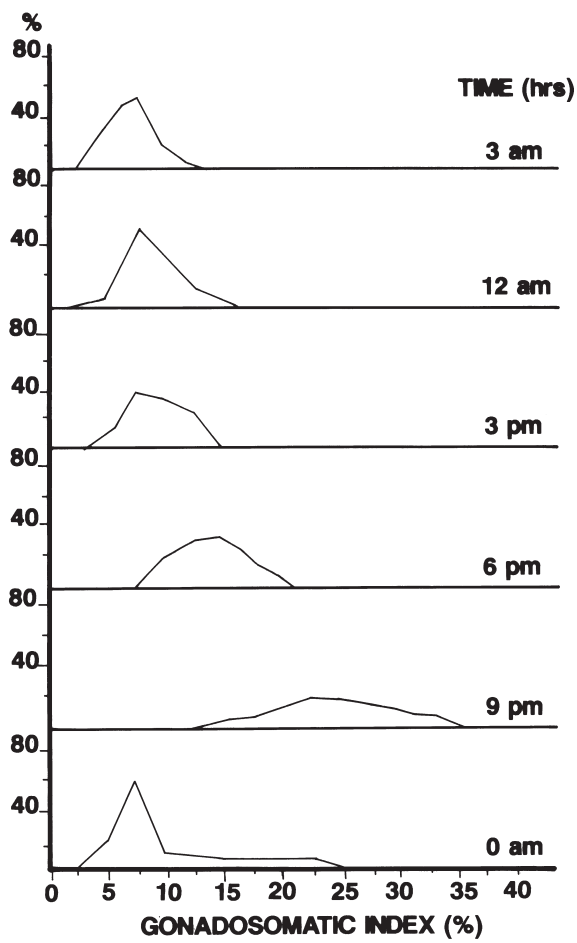

FIG. 3. – The diel dynamics of the frequency distribution of female gonadosomatic indices (June 23-24, 1987).

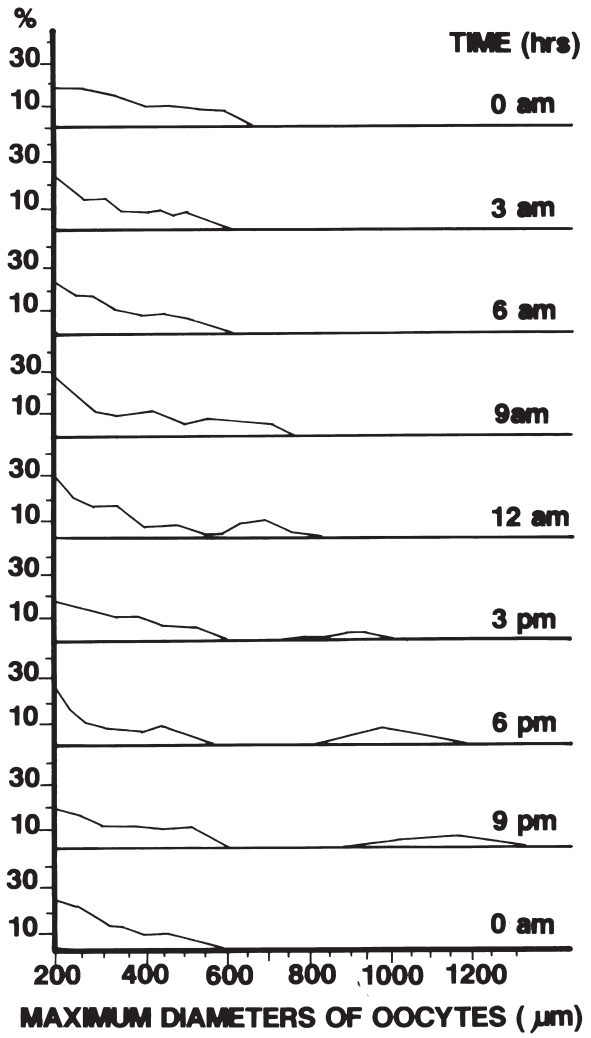

FIG. 4. – The diel dynamics of the frequency distribution of oocyte maximum diameter (mm) in anchovy ovaries (June 23-24, 1987).

simultaneously at night (9 p.m. to midnight). Accordingly, simultaneous changes are observed in ovaries of females of this species throughout the day related to preparation for the next spawning. The nucleus of the most mature oocytes are recorded to begin migration to the animal pole at about 9 a. m. At 10-11 a.m. hydration begins of the oocytes which will be laid on the coming night. At about 3 p.m. the formation of a batch of hydrated oocytes of the nearest spawning terminates. Hydratation and ovulation finish by 9 p.m.

The size and structure of postovulatory follicles demonstrate daily changes from midnight to 6 p.m. The morphology of postovulatory follicle at 6 and 9 p.m. is difficult to define because they often look like an "atretic body" and can be easily confused with follicular atresia.

It was concluded that it might be possible to estimate the relative number of the daily spawning females by using the histological criteria (the age of postovulatory follicles). A reliable assessment of the proportion of females spawning every day might be to estimate the relative number of females at the IY-Y stage of maturity (those with ovaries having hydrated eggs) between 3 p.m. and 9 p.m.

Estimates of the average relative quantity (relative weight) of the eggs laid by females can be made on the basis of the difference between the average gonadosomatic index (GSI) upon the completion of egg-laying (1-3 a.m.) and the average GSI just before the beginning of egg laying (8-9 p.m.).

Calculated by this method the relative quantity of eggs (percentage of the weight of gutted fish) and relative batch fecundity show considerable interannual differences (Fig. 6).

It was established that a small portion of Black Sea anchovies achieve sexual maturity and spawn in the first year of life, two to three months after hatching and at the end of the spawning season. Males of this species first achieve sexual maturity at lengths of 55 to 60 mm and weight of 1.2-1.5 g, and females at 60-65 mm and 2.1-2.4 g. Fish spawning for the first time measured 65-95 mm and weighed 2.1-4.2 g.

The percentage of fish completing maturation and ready for spawning is apparently less than 1 percent. In the size classes of young of the year over 80 mm, practically all males and females attain sexual maturity and begin to spawn. "Transitional" values of GSI between sexually immature and mature young of the year provisionally are thought to be 1.5%. The young of the year, like adults, are characterized by a pronounced daily rhythm of egg deposition, batched spawning, continuous oocyte development, and indeterminate fecundity.

The results of studying the dynamics of the weight of gutted female Black Sea anchovy in 1988 and 1990 (weight increment) are shown in Fig. 7. According to the results the weight of gutted female anchovy increased throughout the spawning season 1988 between May 28 and August 11 by on average 2.6 g (48.7%) (i.e. from 3.98 g to 5.92 g). The average weight of gutted female anchovy in 1990 during the period between June 30 and August 11, (40 days) changed from 6.41 g to 7.68 g (i.e. by 1.27 g, or by 19.7%). By way of extrapolation of these data to the beginning of the spawning season it was shown that in late May, 1990, the weight of gutted female anchovy was close to 5.3 g.

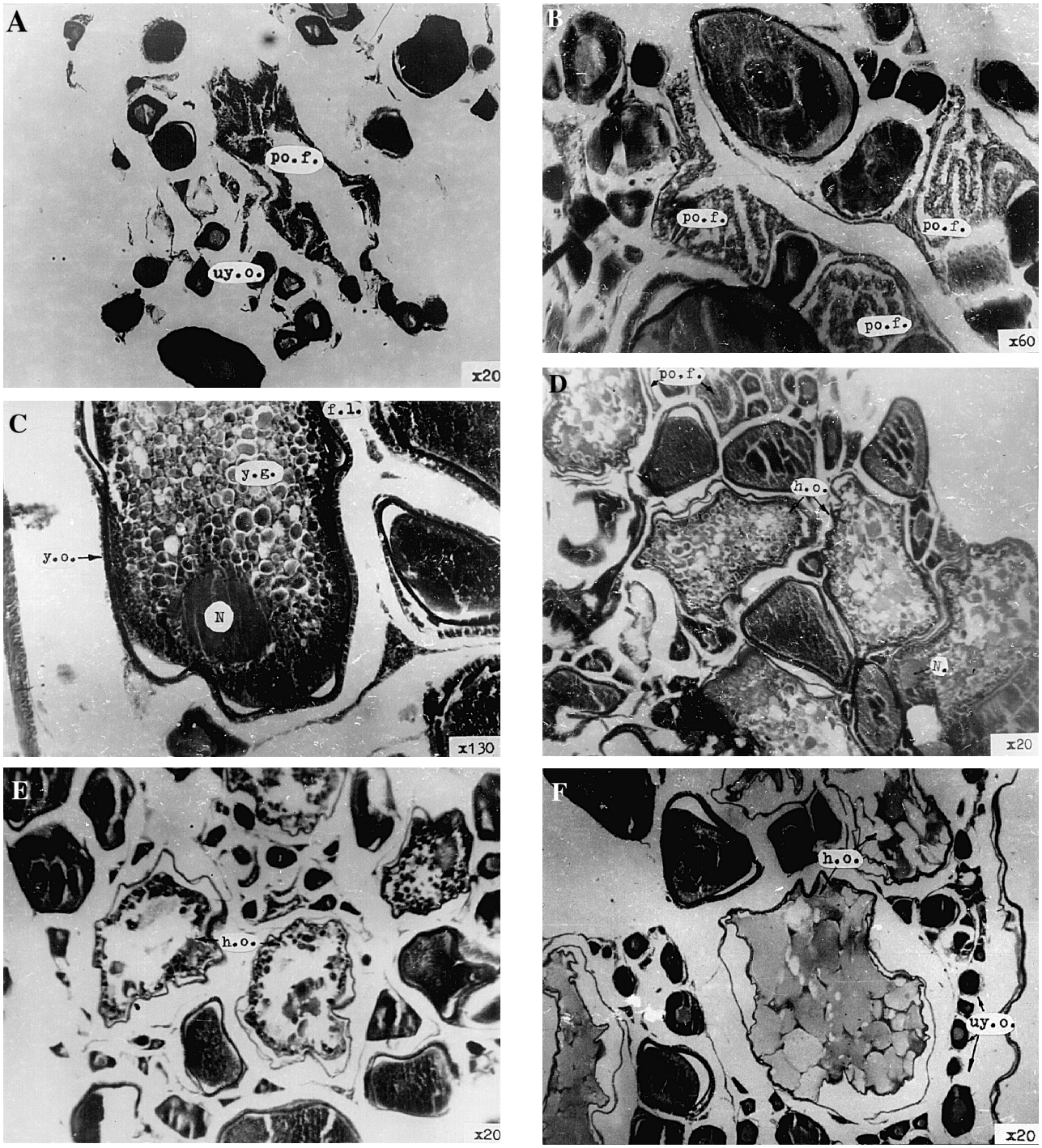

FIG. 5. – The diel dynamics of histological characteristics of anchovy ovaries. POF - postovulatory follicle; FL - follicle layer; UYO - unyolked oocytes; YO - yolked oocytes; YG - yolk globules; HO - hydrated oocytes; N - nucleus; FYP - forming yolk plates. Females caught: (a) 0-0.30 a.m. (VIn-IV stage of maturity); (b and c) 6-6.30 a.m. (IV stage); (d) 15-15.30 (IV stage); (e) 18-18.30 (IV-V stage); and (f) 21-21.30 (V stage).

Based on average relative fecundity estimates in the Black Sea anchovy and the average weight of gutted females obtained for each daily station in 1988 and 1990, the average absolute batch fecundity of spawned on the day of collection female anchovy and its dynamics during the spawning seasons of these years was calculated (Fig. 8). The average absolute batch fecundity during both spawning seasons passed through similar changes: gradual increase throughout the spawning season from the end of May till the end of July, and a rather sharp decline in early August. Given the common trend in

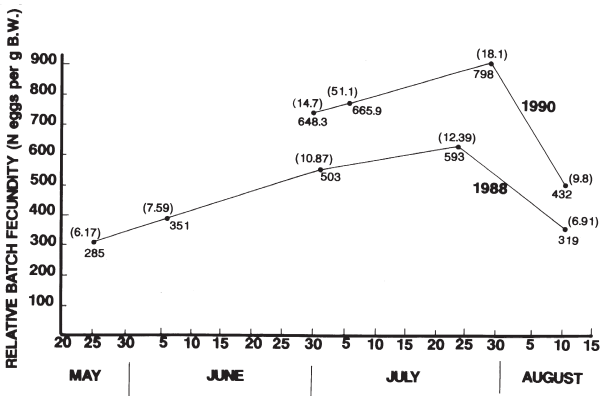

FIG. 6. – Seasonal dynamics and interannual differences of the relative quantity of eggs (percentage of the weight of gutted fish) and relative batch fecundity during spawning seasons 1988 and 1990.

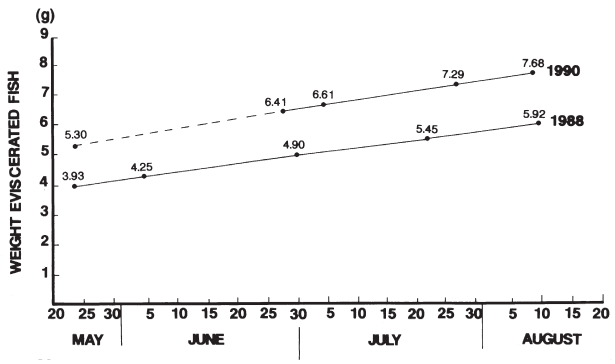

FIG. 7. The dynamics of the weight of gutted female Black Sea anchovy in 1988 and 1990 (weight increment).

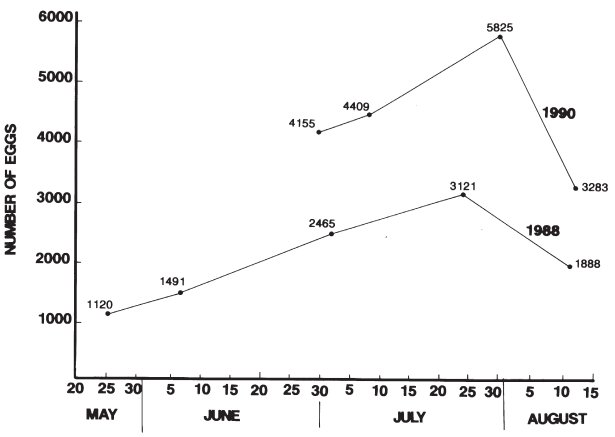

FIG. – 8. The seasonal dynamics of the calculated average absolute batch fecundity of eggs spawned on the day of collection of female anchovy (spawning seasons 1988 and 1990).

dynamics the average batch fecundity in 1990 was found to be nearly twice as great as in 1988.

Therefore, the assessment of the average number of eggs spawned on one day by all females, and of the total number of eggs spawned by one average female throughout the spawning season, required due consideration of the dynamics of the share of females spawning each day during these two seasons.

Despite some small interannual differences recorded in the dynamics of spawning females, we used the same spawning female share ratios as given in Fig. 9.

Based on the dynamics of the average absolute batch fecundity of spawning females (Fig. 8) and the dynamics of the share of spawning females (Fig. 9), dynamics of the average daily absolute batch fecundity was calculated with due regard to the nonspawning (missing the day) females for the two years (1988 and 1990) (Fig. 10).

The overall amount of eggs laid during the spawning season by one average female, as adjusted to the variations in the frequency of spawning (share of spawning females), was calculated on the respective scale as an area bounded by the curves obtained. The result was that the total number of eggs spawned by one average female during the spawning season was on average 138,203 in 1988, and 231,184 in 1990. Considering the average weight

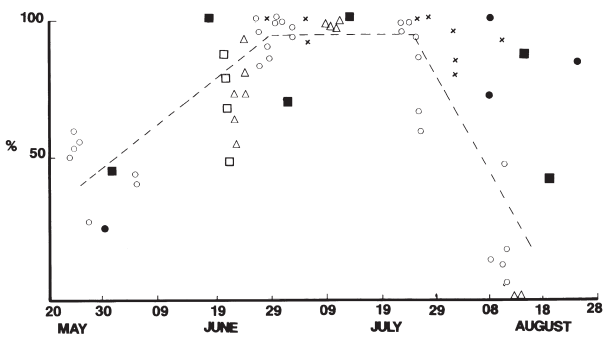

FIG. 9. Share of spawning females during spawning seasons (in % of fished females number). Δ - 1987; ● 1988; ○ - 1989; □ - 1990; × - 1991; ■ - 1992.

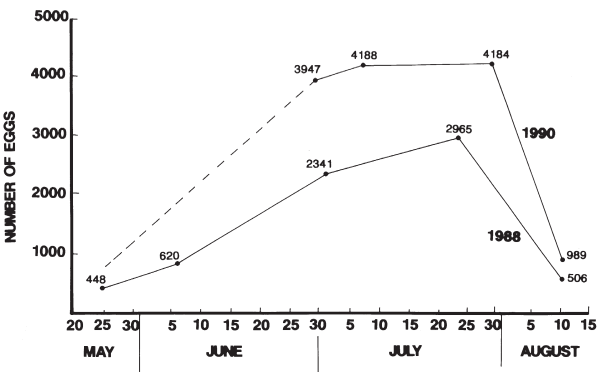

FIG. 10. – The seasonal dynamics of average absolute batch fecundity of average females (with due regard to the nonspawning females) during spawning seasons 1988 and 1990.

TABLE 2. – Quantitative reproductive parameters of the Black Sea anchovy population during 1988 and 1990.

Parameters	1988	1990
Total number of eggs spawned by one average female during the spawning season	138,203	231,184
Average weight of spawned eggs (g)	31.23	52.24
Energetic value of spawned eggs (cal)	24,876.54	41,613.12
Spawning stock biomass (t)	235,000	48,000
Number of producers	$42.7 \cdot 10^6$	$5.7 * 10^6$
Number of females	$21.36 \cdot 10^6$	$2.8 \cdot 10^6$
Number of eggs laid during the spawning season	$2.95 \cdot 10^{15}$	$0.663 \cdot 10^{15}$
Total weight (t)	667,200	149,700
Energetic value (cal)	$551 \cdot 10^{12}$	$197 \cdot 10^{12}$

and energetic value of one egg (0.226 mg, 0.18 cal.) this makes 31.23 g and 24,876.54 cal. in 1988, and 52.24 g and 41,613.12 cal. in 1990.

The results of egg number spawned by one average female during the spawning season and all anchovy stock's quantitative reproductive parameters calculations are shown in Table 2.

According to the spawning stock biomass estimates of the Black Sea anchovy obtained by YugNIRO there were 235,000 tons of parent stock of this species spawning in the entire water area of the Black Sea in 1988 whereas in 1990 the spawning stock biomass was only 48,000 tons.

This number can be used to calculate the total number of producers of this species. Given a sex ratio of 1:1, the average weight of one female in time of estimating 5.9 g, one male 5.1 g in 1988 (average weight of one fish 5.5 g), the value of 235,000 tons would correspond to 42.7 billion producers of which 21.4 billion are females. From this parent stock we estimated that 2.95 x 10^{15} eggs would be laid during the spawning season, their total weight being 667,200 tons and energetic value 551 x 10^{12} cal.

In 1990 the total weight of the spawning stock of 48,000 tons corresponds to 5.7 billion fish of which there were 2.9 billion females (mean weight of females 8.85 g and males 7.9 g; sex ratio 1:1). The absolute population fecundity of this stock (total number of eggs laid during the spawning season) was 0.663 x 10^{15} eggs, or 149,700 tons and energetic value 197.3 x 10^{12} cal.

DISCUSSION

We produced estimates of the main reproductive parameters of this species on the basis of a number of factors: the daily dynamics of spawning; the share of spawning fish; the amount of eggs spawned; spawning dynamics during two spawning seasons; and the estimated relative number of individual eggs corresponding to the relative weight of the eggs spawned (1%). The data obtained differ in principle from the previously made assumptions. It was detected that batch fecundity of anchovy does not remain constant during the spawning season. Instead, it goes up early during the spawning period, and declines again at its latter stage. This is related not only to the growth of fish during the spawning season, but also to the dynamics of the relative number of eggs spawned. A change in spawning frequency during the season was recorded for the first time by Hunter and Leong in Californian anchovy (Hunter and Leong, 1981), and was confirmed by our study. However, we found its occurrence to be much greater. While previous researchers believe that the anchovy spawn 3-4 batches of eggs (5,000-41,400 eggs) throughout the spawning season, or 9,000-10,000 eggs on average (Malyatsky, 1940; Smirnov, 1950; Chugunova and Petrova, 1954; Ambros, 1955, Tkacheva, 1955), our results indicate that the average number of eggs spawned by one female in various years was 138,000-231,000 . In other words, our view is that the actual number of eggs spawned by anchovy during a spawning season exceeds the previously suggested levels by at least one order of magnitude. This has to do with the newly obtained data on the frequency and multiplicity of spawning in this species based on the knowledge of the pattern of oogenesis previously obtained by Oven (1976), and examined in detail in our investigations.

Our results suggest an enormous reproductive potential of the Black Sea anchovy. Such high reproductive potential of the anchovy, in contrast to fishes of high latitudes, cannot be ensured by energetic resources accumulated in the female's body before spawning. Such egg production obviously is possible only if spawning stock are actively feeding during the entire spawning season. The results of research on the Black Sea anchovy feeding show that the energetic value of the food consumed by the anchovy is enough

for covering all the expenses of base metabolism, somatic growth and active reproduction.

In this connection the dynamics of batch fecundity and relative number of daily spawning females (spawning frequency) within the spawning season are becoming clear. Feeding activity, digestion rate and metabolism, of anchovy as well as other poikilotherms, are dependent on water temperature. Apparently, low spawning frequency and batch fecundity of Black Sea anchovy at the beginning of the spawning season can be accounted for by low water temperature.

The difference in the annual life history (cycle) of the Black Sea anchovy compared to the majority of fishes of high latitudes seems interesting. Although the anchovy has a pronounced hibernation period, in contrast to fishes of high latitudes, anchovy have not separated feeding and reproductive periods. Feeding and reproduction of anchovy take place simultaneously during the summer.

Such enormous reproductive potential of the anchovy, its short life cycle and rapid growth of yearlings result in wide, natural annual fluctuations of stock abundance and biomass. Abundance and biomass of anchovy are minimum in the spring, at the beginning of spawning. In summer and autumn abundance and biomass of anchovy increase several times due to the active reproduction and rapid growth, principally of young-of-the-year. The maxima are reached in November-December. In wintertime, as result of high natural mortality, the abundance and biomass of anchovy sharply reduce.

The Black Sea anchovy has extremely high reproductive potential and is characterized by high annual fluctuations in abundance and by the ability to rapidily restore biomass. Given these conditions, the danger of overfishing this species is decreasing. The anchovy is capable of restoring its abundance under fishery conditions of variable intensity. The most urgent measures for rational fishery include those directed at the preservation of the favorable reproductive conditions of this species (pollution control, river flow regulation, control of food competitors and consumers of eggs and young, making artificial upwellings and so on).

CONCLUSIONS

1. The spawning season of the Black Sea anchovy lasts from the middle of May to the second half of August. The peak of spawning is from the middle of June to the end of July.

2. Anchovy spawns only in the upper warm layer (0-25 m), above the termocline. During the spawning season the temperature varies from 16 °C (at the very begining of spawning) to 28 °C. It seems that the optimal temperature for anchovy spawning is 19-24 °C.

3. A small part of each new generation of anchovy reach sexual maturity and spawn two-three months after hatching, at the end of the spawning season. The next year, the new spawning generation is composed of mature individuals ready for spawning.

4. Black sea anchovy is a multiple spawning fish with a continuous type of oogenesis (terminology by Götting, 1961 and Oven, 1976). During the spawning season oocyte development is a continuous process involving all stages of oocytes. The fecundity of the Black Sea anchovy is clearly seasonally indeterminate (terminology by Hunter and Macewicz, 1985).

5. The Black Sea anchovy has a clear diel rhythm of spawning: riping and ovulation of egg from 9 p.m. to midnight; period of rest from midnight to 6 a.m.; forming the new spawning batch from 6 a.m.. to 9 p.m.

6. All reproductive parametres of Black Sea anchovy are very variable seasonally and annually. Within the spawning season one average female can produce about 50 batches of eggs. Total individual fecundity may achieve more than 200,000 eggs.

7. The extremely high reproductive potential of this species is based on a number of factors: early maturation, long period of spawning, multiplicity of spawning, high level of individual fecundity, high ability to restore reproduction.

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