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EFFECTS OF ENVIRONMENTAL CHANGES ON EARLY STAGES AND REPRODUCTION OF ANCHOVY (*ENGRAULIS ENCRASICOLUS* L.) IN THE ADRIATIC SEA

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ABSTRACT

Anchovy spawns in the Adriatic from (March) April to October (November). Egg production and the quantity of yolk-sac larvae follow the changes of primary production and zooplankton quantity during the spawning season, with the phase lag of about two months. Investigations of long-term fluctuations of egg production, quantity of larvae and postlarvae showed that increase of egg production was followed by increase of the quantity of postlarvae but also with the increase of their instantaneous mortality rates. These fluctuations were positively correlated with the fluctuations in temperature, salinity, primary production and zooplankton quantity, with the phase lag of one year. Since 1978 these "regular" fluctuations have been disturbed. The anchovy biomass decreased, while the temperature, salinity, contents of nutrients and primary production have been continuously increasing in the entire Adriatic. It seems that these changes were the consequence of a low frequency period of climatic change, probably amplified by the antropogenic eutrophication.

Key words: Anchovy, early-life history stages, environmental changes, reproduction, Adriatic Sea

INTRODUCTION

Early stages of the anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), have been studied in the Adriatic for more than 100 years. Graeffe (1888) was the first who reported its eggs in the plankton of Northern Adriatic during the summer months. This report was published in the same year when the anchovy eggs were described for the first time by Raffaele (1888). Later on, numerous scientists studied various aspects of the early life stages of Adriatic anchovy up to nowadays. The number of studies related to the ecology of planktonic stages and to the adult anchovy is considerably higher than those related to other fishes. Therefore it follows that anchovy is the most intensively studied fish species in the Adriatic.

The attention paid to the studies of both early stages and adult anchovy is, to a large extent, the consequence of the anchovy's abundance in the catch of pelagic fish in the Adriatic. For example, during the period from 1962 to 1973 the catch of the anchovy made 47% of the mean annual catch of pelagic fish. However, since 1978 the decrease of anchovy biomass was observed. This caused decrease of the catch, and in the period from 1977 to 1989 anchovy catch was only 28.7% of the total pelagic fish catch in the Adriatic.

The aim of this paper is to review basic information about the early life stages of the Adriatic anchovy, and to provide an explanation of the causes of the recent biomass decrease of this fish.

ELEMENTARY DATA

A) Spawning season

Numerous authors (Steuer, 1910; Stiasny, 1910; Vatova, 1928; Gamulin, 1940, 1964; Varangolo, 1964a, b, 1965; Vučetić, 1957, 1964, 1975; Zavodnik, 1967, 1970; Štirn, 1969; Merker & Vujošević, 1972; Regner, 1972, 1979, 1985; Picinetti *et al.*, 1979, 1980; Regner *et al.*, 1985) found anchovy eggs in plankton during the April-October period, and sometimes also in March and November. It seems that the increased sea temperatures in January and February affect earlier occurrence of the anchovy eggs (Regner, 1972). The earliest record was of

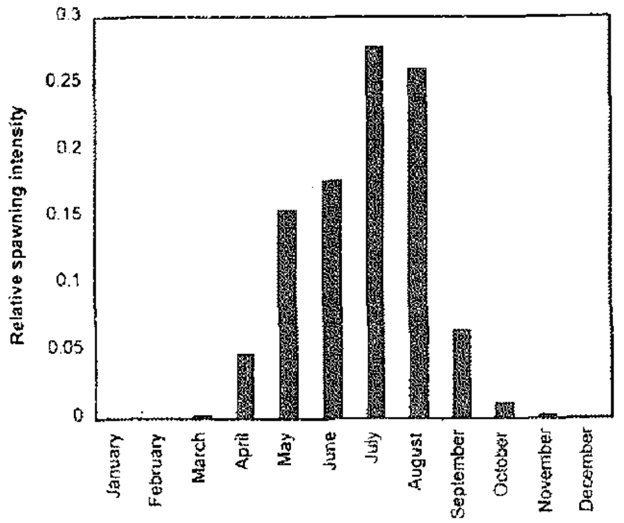


Fig. 1: Long-term means of relative spawning intensity of the Adriatic anchovy.
Sl. 1: Povprečne vrednosti relativne intenzivnosti drstenja jadranskega inčuna v daljšem časovnem obdobju.

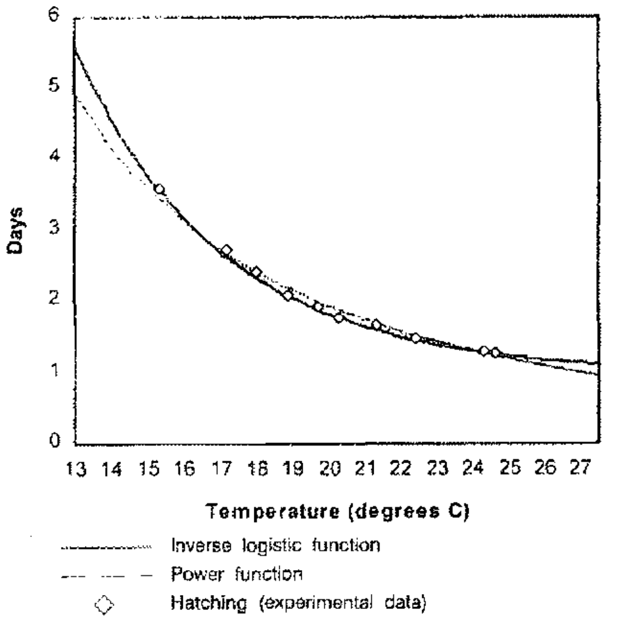


Fig. 2: Temperature-dependent development of anchovy eggs fitted with inverse logistic (---) and power (- -) functions.
Sl. 2: Temperaturna odvisnost razvoja inčunovih iker (inverzna in potenčna odvisnost).

a single egg found in the Gulf of Venice at the end of February 1967 (Zavodnik, 1970).

Maximum of eggs in plankton may appear, depending on characteristics of the spawning seasons and spawning areas, at any time during the period between May and September. Very often, curves of the spawning intensity are polymodal. Generally, maximum egg production occurs in open waters earlier than in coastal ones.

Long-term means, calculated from the data of different authors, show that about 85% of the anchovy eggs in the Adriatic are produced in the May-August period. The production of eggs is highest in July (Fig. 1).

The relationship with the temperature and salinity during the spawning season was studied by Vučetić (1957), Varangolo (1965), Štirn (1969), Zavodnik (1970), Merker & Vujošević (1972), Regner (1972, 1979, 1985). The results obtained show that anchovy spawns within temperature ranges of 11.6-27.5°C in the Northern Adriatic, and 13.12-27.32°C in the Central and Southern Adriatic, with the maximal egg production at temperatures between 17°C and 22°C. In the Northern Adriatic anchovy spawns within 9.1 and 38.5 ppt salinity ranges, and within 33.8 and 39.6 ppt in the Central and Southern Adriatic. Maximal egg production may occur at any of the aforementioned salinities (Regner, 1979, 1985).

Positive correlation was found between the quantity of anchovy eggs and the number of phytoplankton cells, as well as with the zooplankton dry weight (Vučetić, 1975). Analysis of long-term data (1962-1976 period) showed that production of anchovy eggs and the quantity of larvae followed primary production and the zooplankton spring peaks with the phase lag of about two months (Regner, 1979, 1985). This phase lag may be related to the intensive feeding of adult anchovy in the pre-spawning period. Such a correlation was not found for the quantity of postlarvae (stages after the yolk-sac resorption). It was assumed that their survival was connected to the quantity of microzooplankton which was found to be their main food in the Central Adriatic (Regner, 1971).

The catch of juveniles was analyzed in the Gulf of Manfredonia (Rizzoli, 1983). The largest quantities were observed in December, and again in April and May. So far there are no studies on the ecology of juveniles in the wider areas of Adriatic, except in the area of Novigradsko more (Sinovčić, 1992).

B) Daily period of spawning

Anchovy spawns in the Central Adriatic in the evening, between 7 and 9 p.m. (Vučetić, 1957). According to Varangolo (1964a) maximum spawning in the Northern Adriatic takes place between 6 and 8 p.m.

C) Temperature-specific development times of eggs and larvae, growth of larvae and postlarvae

During the 1976 and 1977 spawning seasons, anchovy eggs, larvae, and postlarvae were reared under experimental conditions in order to estimate their temperature-developmental time relationship, and growth rates of larvae and postlarvae as influenced by temperature (Regner, 1979, 1985). The relationship between egg development and temperature was fitted with four different functions. The power function:

$D = 1788.4199 \times T^{-2.290236}$ (1),

where *D* is the developmental time in days, and *T* is the temperature in °C, was used for all estimates of anchovy developmental times. The best fit was obtained with inverse logistic function with the parameters:

$D = 1 / 1.012896 \times [1 + e^{4.914322 - (0.257451 \times T)}]$ (2),

(Regner, 1979, 1985), and therefore this function was used for all the estimates of developmental times of anchovy eggs since 1979. This function gives better estimates particularly at lower temperatures (Fig. 2).

For the estimates of instantaneous mortality rates of eggs, residence times and the mean ages of particular developmental stage have to be known. Thus, to obtain residence times and mean ages of stages (stages were described by Regner, 1979, 1985) the value of D obtained from equations (1) or (2) has to be corrected with the following factors:

Stage	Residence time correction	Mean time correction
I+II	0.1630	0.0815
III	0.0795	0.2028
IV	0.1506	0.3178
V	0.0837	0.4350
VI	0.1925	0.5731
VII	0.1173	0.7280
VIII	0.1046	0.8389
IX	0.0628	0.9226
X	0.0460	0.9770

Value of D has to be divided with the residence time correction factor, while for the estimate of the mean age it has to be multiplied with the correction for the mean time.

For the egg mortality estimates during biomass assessments the smaller number of stages has been used:

Stage	Residence time correction	Mean time correction
A (I-IV)	0.395	0.198
B (V-VII)	0.393	0.592
C (VIII-IX)	0.165	0.871
D (X)	0.046	0.977

Developmental time for larvae from hatching to yolk-sac resorption was fitted with the power function, the parameters of which were:

$D = 270065.2744 \times T^{-3.8079}$ (3),

where *D* is time in days, and *T* is temperature.

Larval growth up to the yolk-sac resorption was approximated with Farris (1960) and von Bertalanffy (1938) functions, while the growth of postlarvae was approximated with exponential functions (Regner, 1979, 1985). In 1980, data obtained on larval and postlarval growth were fitted again with Gompertz function, which gave better fit then previously used equations. The form of the Gompertz function used for the estimates of growth was:

$l_t = a \times e^{-be^{-ct}}$ (4),

where l_t is length of larva in the time *t*, *a* is the asymptote, while *b* and *c* are constants.

As far as larvae were concerned, the constants (*b, c*) of equation (4) were found to be temperature dependent. This relationship can be expressed as:

$a = 0.20466 + 0.369659 \times T - 0.00893519 \times T^2$
$b = 0.335907 + 0.001603 \times T$
$c = 7.87357 - 0.841969 \times T + 0.028809 \times T^2$,

where *T* is temperature in °C.

For the postlarvae, only the data obtained for the mean temperature of 21.30°C were consistent enough to be fitted with Gompertz function (Regner, 1980). The parameters of the Gompertz function obtained for the growth at this temperature level were:

$l_t = 27 \times e^{-2.532e^{-0.086t}}$ (5).

Growth of postlarvae was also estimated from the daily growth increments of the otoliths of the postlarvae collected during the cruises along the Eastern Adriatic coast in August 1989 (Regner & Dulčić, 1990) and July/August 1990 (Dulčić & Kraljević, 1996). The parameters of the Gompertz functions were:

Parameters	a	b	c
Regner & Dulčić (1990)	27.315	2.0517	0.0892
Dulčić & Kraljević (1996)	29.664	3.0311	0.1211

It is interesting that the parametes of the Gompertz functions obtained either from the measured lengths of postlarvae reared in experimental conditions, or from the counting otolith daily increments of postlarvae caught from the plankton after the twelve years, do not differ very much (Regner & Dulčić, 1990).

The age of anchovy larvae and postlarvae was estimated for the following standard length groups:

Larvae (SL, mm)
I - 2.38
II - 2.39 - 3.03
III - 3.04 - 3.68
Postlarvae (SL, mm)
I - 3.99
II - 4.00 - 5.99
III - 6.00 - 7.99
IV - 8.00 - 9.99
V - 10.00 - 11.99
VI - 12.00 - 13.99
VII - 14.00 -15.99

VIII - 16.00 - 17.99
IX - 18.00 - 19.99
X - 20.00 - 21.99

Residence time of length group can be estimated with the equation:

$$\Delta t = -1/c \ln [(1/b \ln a/l_{t(i+1)}) - \ln (1/b \ln a/l_{ti})] \quad (6),$$

where Δt is the residence time, while l_{ti} and $l_{t(i+1)}$ are initial and final lengths of each length group, while *a*, *b*, and *c* are the parameters of the equation (4). For the estimate of mortality rates the number of larvae and postlarvae from each length group have to be divided with the residence time.

The mean age from hatching of n-th length group can be estimated with the equation:

$$t_n = \sum_{i=1}^{n-1} \Delta t_i + \Delta t_n/2 \quad (7),$$

where Δt_i are residence times of length groups, obtained from equation (6).

D) Length-weight relationship of anchovy larvae and postlarvae

The relationship between standard lengths and dry weights was studied on the artificially reared larvae and postlarvae (Regner, 1983). It was found that larvae showed initial increase of the W/L ratio, which decreased later during yolk-sac resorption. Length-weight relationship in postlarvae was approximated with the power function, the exponent of which was 3.32, indicating positive alometric relationship.

E) Feeding of postlarvae

The feeding of postlarvae of the size from 3.0 to 8.0 mm standard lengths was investigated during the 1968 and 1969 spawning seasons in the Central Adriatic (Regner, 1971). It was found that the food consisted mostly of copepod eggs, nauplii and copepodites. The mean percent of postlarvae with the food in the digestive tract was, depending on size, between 10 and 43%.

F) Horizontal and vertical distribution

Horizontal distribution of anchovy eggs during the spawning season in the Adriatic was studied by numerous authors either in local areas (Gamulin, 1940; Varangolo, 1965; Štirn, 1969; Vučetić, 1971; Regner, 1972; 1979, 1985; Casavola *et al.*, 1987) or on larger scale in the Northern, Central and Southern Adriatic (Steuer, 1913; Piccinetti *et al.*, 1979, 1980; Gamulin & Hure, 1983; Regner *et al.*, 1985).

According to the aforementioned authors, anchovy spawns in the Adriatic above the depths of about 200 m, which corresponds with the Adriatic shelf. Thus, its eggs

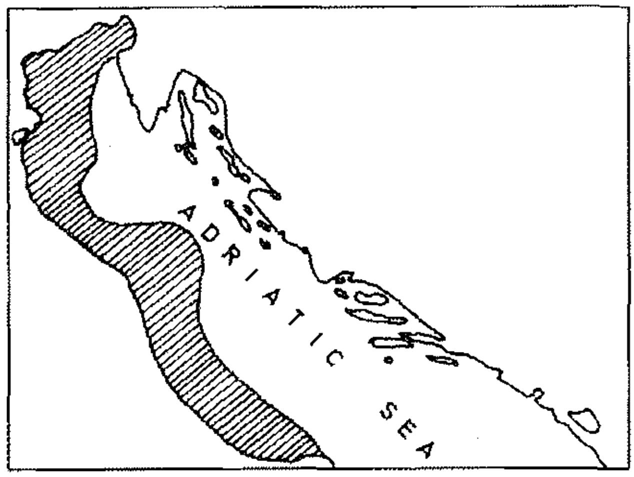


Fig. 3: The main spawning area (shaded) of the Adriatic anchovy.
Sl. 3: Glavno (osenčeno) drstišče jadranskega inčuna.

can not be found only in the areas deeper than 200 m - above the Jabuka pit in the Central Adriatic and above the Southern Adriatic pit.

Analysis of the long-term data shows that the main spawning area of the anchovy can be relatively clearly distinguished in the Adriatic (Regner *et al.*, 1985). In this area the probability that the mean daily egg production during the period of the maximum spawning intensity will be more than 100 eggs m^{-2} day^{-1} is higher than 90%. The area covers the shallow Northern Adriatic (with the exception of the zone along the western coast of the Istrian peninsula which is under the influence of relatively oligotrophic waters of the incoming Adriatic geostrophic current), and the zone along the western coast, to the Gargano peninsula (Fig. 3). Sometimes high production of anchovy eggs can be found around Palagruža island. In fact, this area is under the influence of the outflows of Italian rivers, especially of the river Po. In other areas, along the eastern Adriatic coast and in the channels between the islands along the eastern coast, as well as along the western coast from the Gargano peninsula to the Otranto straight, the intensity of spawning is substantially lower than in the main spawning area.

The anchovy egg and larvae surveys which covered almost the entire area of the Adriatic shelf were relatively numerous. For example, 11 cruises have been performed in the Northern, Central and a part of Southern Adriatic during the 1976-1990 period only for anchovy biomass estimates. However, most of the surveys have been carried out only once or twice during the spawning season. Therefore, little is known about the shifting of spawning centers during the spawning season, if the Adriatic is considered as a whole. The knowledge of transport and survival of larval stages is even more scarce. Only one analysis of the mortality rates of anchovy larvae and postlarvae in the entire area of the

Northern and Central, and a part of Southern Adriatic was carried out on the material collected in July 1978 (Piccinetti *et al.*, 1982).

The surveys throughout the spawning season were relatively scarce. They have been performed over relatively limited areas, mainly in the shallow Northern Adriatic. According to these surveys, centres of spawning within this part of the main anchovy spawning area move during the spawning season either in cyclonic (Vučetić, 1964; Varangolo, 1965) or in anticyclonic direction (Štirn, 1969).

These displacements are presumably affected by the specific water circulation in the Northern Adriatic. The circulation of surface waters in the Adriatic is basically cyclonic, with the northwest incoming flow along the eastern coast and southwest outgoing flow along the western coast (Zore, 1956). Owing to the bottom topography, this current forms four relatively permanent gyres with the northwesternmost one in the Northern Adriatic. The horizontal density gradients, combined with coastal river runoff of fresh water are capable of driving cyclonic circulation in the Northern Adriatic, which during the summer may be modified by two separate circulation cells (Malanotte-Rizzoli & Bergamasco, 1983). The wind stress (NE direction) may accelerate cyclonic circulation. On the contrary, if the wind direction is SE it can generate anticyclonic circulation along the west coast of the Northern Adriatic (Betello & Bergamasco, 1991; Rajar & Četina, 1991). This explains the differences in the direction of the moving of anchovy spawning centres found by different authors. Besides, the influence of these gyres on the rates of the mixing of oligotrophic waters of incoming geostrophic current and eutrophic waters of the river Po outflow is very important, because the rates of both horizontal and vertical mixing regulate the intensity of primary and secondary production. Together with the direction of currents is, no doubt, essential for the intensity of the spawning of anchovy in this area, as well as for the more or less successful survival of its planktonic stages. So far there were no detailed studies on the influence of the Northern Adriatic circulation on the transport and survival of anchovy larval stages. This should be one of the main tasks in the future investigations.

Along the Eastern Adriatic coast, where the anchovy spawning is not so intensive, some other geophysical factors may be of some importance for the reproduction of this fish. During the last two cruises, performed in July 1989 and August 1990 for the anchovy biomass assessment along the Eastern Adriatic coast, the distribution of daily egg production was compared with the vertical distribution of isotherms along the transects. This comparison showed that the egg production was most intensive in the areas of upwelling (Regner, *pers. comm.)*

Obvious influnce of the atmosphere - sea interaction on the distribution of anchovy spawning centre points out that both short and long-term climatic changes may be the principal factors that regulate reproduction of the Adriatic anchovy.

Vertical distribution of the anchovy planktonic stages was also studied in the Adriatic. Varangolo (1965) found maximal density of anchovy eggs 1 m below the surface, while Ghirardelli (1967) and Specchi (1968) reported maximum egg concentration in 7-27 cm layer. After Regner (1972), eggs were most abundant in the upper 10 m, while larvae and postlarvae were found in maximal densities in 10-20 m layer. The larger quantities of larvae and postlarvae found near the surface during the night indicated their diurnal vertical migrations.

G) Long-term fluctuations

Long-term fluctuations of the anchovy early stages were studied only in the eastern part of the Central Adriatic (Vučetić, 1971; Regner, 1974; Regner, 1979, 1985).

Considerably large fluctuations of total annual number of anchovy eggs through the period between 1959 and 1969 were accounted for the changes of amount of advection of the eastern Mediterranean water into the Adriatic (Vučetić, 1971). Later it was found that the fluctuations of the annual quantity of the anchovy eggs coincided with the fluctuations of primary production (Regner, 1974).

The more detailed studies on the relationships between annual means of egg production, number of postlarvae and their mean mortality rates with the annual means of abiotic and biotic factors (temperature, salinity, primary production and quantity of zooplankton) were carried out for the period of fifteen years (1962-1976) (Regner, 1979, 1985). It was found that the fluctuations of egg and postlarvae quantities were positively correlated with the fluctuations of temperature, salinity, primary production, with the phase lag of about 1 year. Mean instantaneous mortality rates of postlarvae were negatively correlated with the aforementioned factors. Thus, it may be supposed that survival of the postlarvae is more successful in the years of higher organic production, probably due to the decreased intraspecific competition. Spectral analysis of all long-term data showed periodicity of 2-3, 5-7, and 9-11 years. Since the similar periods were found out in annual variations of air pressure in Trieste and Venice (Polli, 1955), as well as in fluctuations of sardine catch (Regner & Gačić, 1974), it is possible that the reproduction of anchovy, regarding the long-term periods, is controlled by climatic changes, which affect the dynamics of the water masses and fluctuations of organic production in the Adriatic. The mechanism of this control seems to act through the changes of atmosphere - sea interactions. These changes depend on changes of air pressure gradients over the Mediterranean and on intensity of penetration of polar air towards the Mediterranean, *i.e.* on dis-

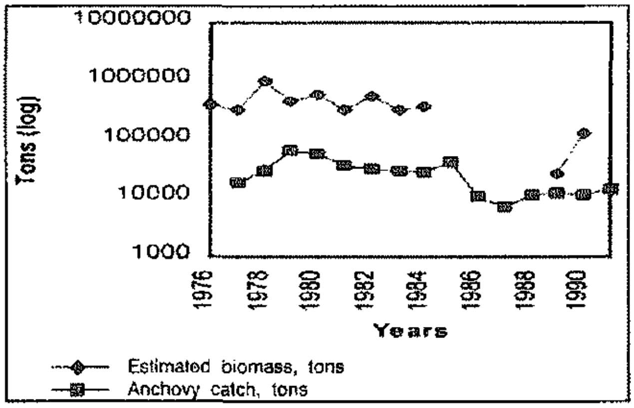


Fig. 4: Relationship between the estimated biomass and the catch during the period of decrease of the anchovy population in the Adriatic.
Sl. 4: Razmerje med ocenjeno biomaso in ulovom v obdobju upadanja inčunove populacije v Jadranskem morju.

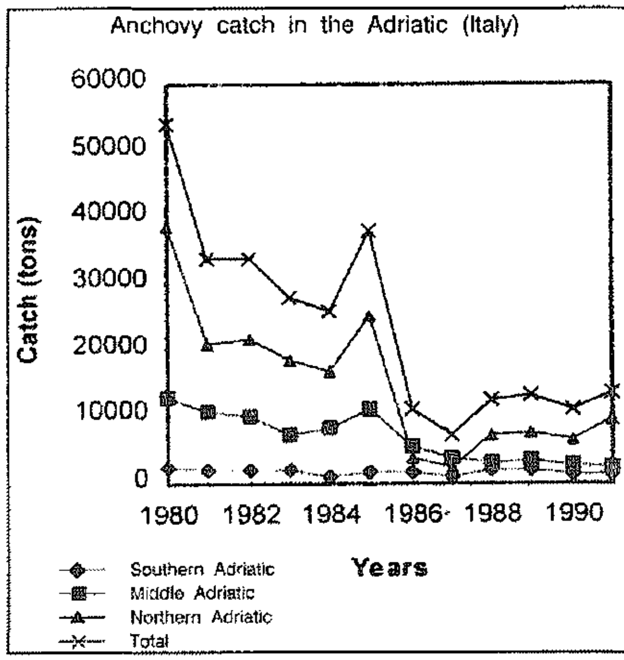


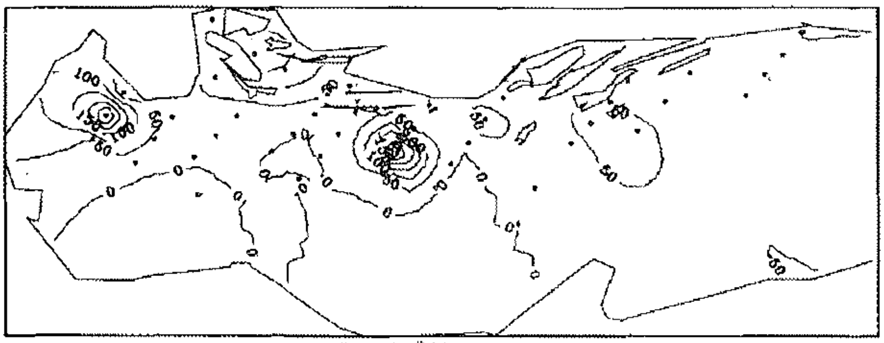
Fig. 5: Data on Italian catch in the Northern, Central, and Southern Adriatic during the period of anchovy population decrease.
Sl. 5: Podatki o italijanskem ulovu inčunov v severnem, srednjem in južnem Jadranu v obdobju upadanja inčunove populacije.

placements of large baric centres such as Icelandic cyclone and Syberian anticyclone (Zore-Armanda, 1969). Fluctuations of these climatic factors affect the intensity of penetration of the water masses of the Eastern Mediterranean intermediary layer (Buljan, 1963), which carry relatively large quantities of nutrients. They also intensify general water circulation, as well as the rates of mixing of water masses in the Adriatic (Zore-Armanda, 1991). In the years of intensified advections of the eastern Mediterranean waters, the primary and secondary productions increase (Pucher-Petković & Zore-Armanda, 1973). These changes of production may be assumed as the main factor which regulates the reproduction of anchovy in the Adriatic.

Further investigations have shown that after 1978 these "regular" fluctuations were disturbed. Long-term estimates of the anchovy biomass in the Adriatic, with both egg production (Regner *et al.*, 1985; Dulčić, 1993) and acoustic methods (Azzali *et al.*, 1990), showed a continuous decrease since 1978. Stock has almost collapsed during the years 1986-1987, and began to recover in the years 1989-1990 (Fig. 4). The catch of the anchovy in the Adriatic, which was 62,492 tons in 1979, fell down to only 7,055 tons in 1987.

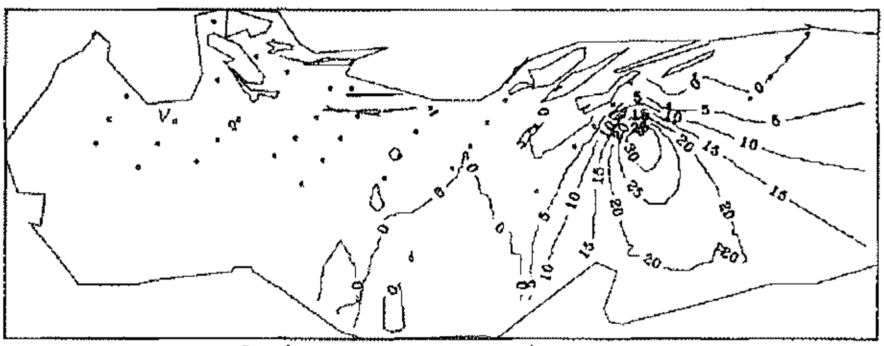
Since the biomass assessments by both methods applied showed that the anchovy stock was not overfished, some other explanations had to be found for this decrease.

From the mid-seventies onwards some changes, which may be the cause of the anchovy stock decrease, took place in the Adriatic. The constant increase of sea surface temperatures and salinity was observed, together with the decrease of sea water transparency and oxygen saturation in bottom layers (Zore-Armanda *et al.*, 1987; Zore-Armanda, 1991). These changes were followed by the increase of primary production (Pucher-Petković *et al.*, 1987), indicating that the Adriatic ecosystem went through a relatively long period of eutrophication. Just during this period some unusual changes in the distribution of some species took place in the Adriatic. For example, the large masses of gilt sardine *(Sardinella aurita)*, which was always present but not abundant in the Souhern Adriatic, spread since 1975 over the entire Adriatic, and in 1979 reached even the Gulf of Trieste (Gamulin, 1975; Kačić, 1975; Regner, 1977). The fish retreated to the Southern Adriatic in the second half of the eighties. As this fish spawns during the summer months, it can be a competitor to the anchovy postlarvae. A similar phenomenon happened with the population of jellyfish *Pelagia noctiluca* which exploded and covered large parts of the Adriatic during the period from 1977 to 1985 (Vučetić, 1982, 1985). This jellyfish is known as a predator of fish eggs and larvae. Since its quantities were the most numerous during the spawning season of anchovy, it may be assumed that this phenomenon also negatively influenced the recruitment of anchovy population. However, the anchovy stock decrease, although evident, was not so great during the period of the massive occurrence of *Pelagia noctiluca* (Vučetić & Alegria-Hernandez, 1987). On the contrary, the sharp decrease of the anchovy stock began just in 1985 (Figs. 4 and 5).

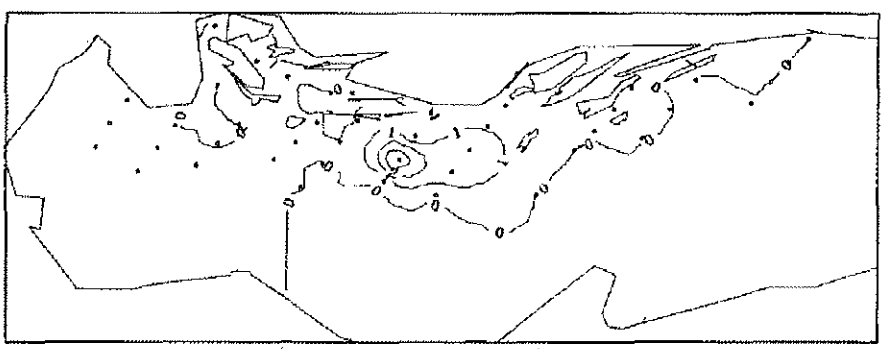


Eggs/m²/day, 1989

Larvae, mean age 2.9 days, 1989



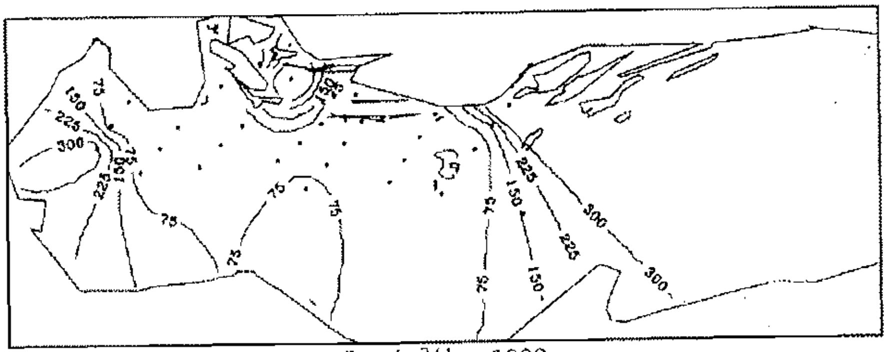
Postlarvae, mean age 7.8 days, 1989



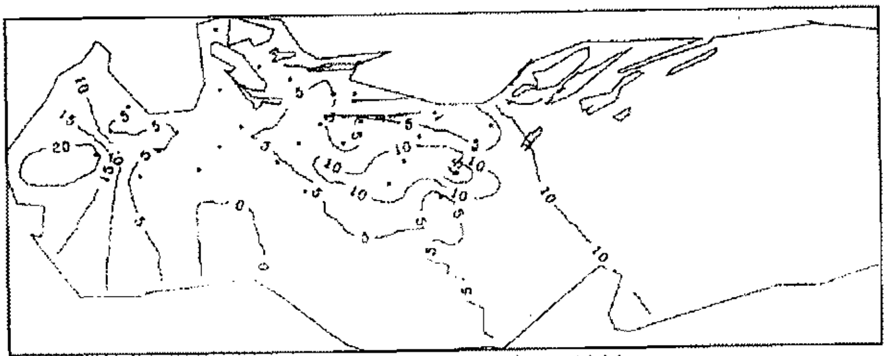
Postlarvae, mean age 12.3 days, 1989

Fig. 6: Horizontal distribution of anchovy eggs, larvae, and postlarvae (N/m²/day) along the Eastern Adriatic coast in August, 1989.

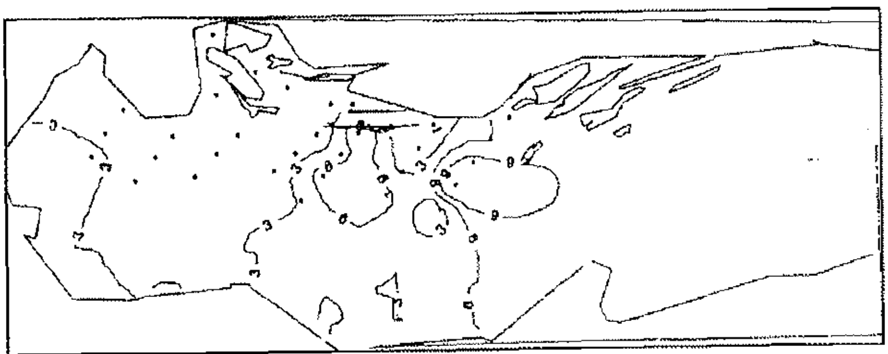
Sl. 6: Horizontalna razširjenost inčunovih iker, ličink in preobraženih ličink (N/m²/dan) vzdolž vzhodnojadranske obale v avgustu 1989.



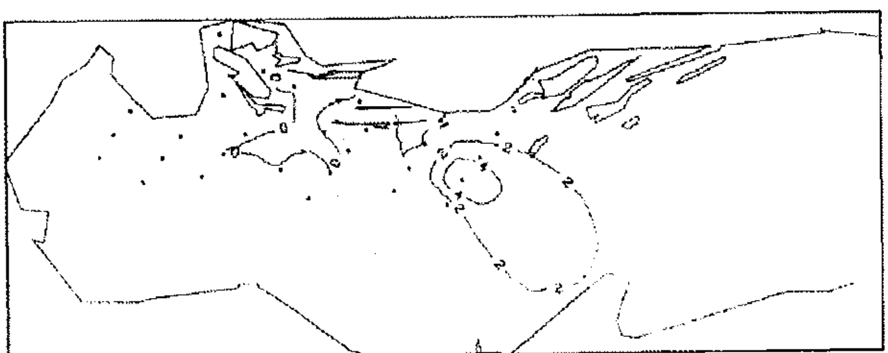
Eggs/m2/day, 1990



Larvae, mean age 2.9 days, 1990



Larvae, mean age 7.9 days, 1990



Larvae, mean age 12.4 days, 1990

Fig. 7: Horizontal distribution of anchovy eggs, larvae, and postlarvae (N/m²/day) along the Eastern Adriatic coast in July, 1990.
Sl. 7: Horizontalna razširjenost inčunovih iker, ličink in preobraženih ličink (N/m²/dan) vzdolž vzhodnojadranske obale v juliju 1990.

At the same time, from the beginning of the eighties, the summer blooms of phytoplankton and benthic diatoms started to spread in the Adriatic Sea. Initially they were limited to smaller enclosed or semienclosed polluted areas, and they lasted for a relatively short time. The surface affected by the blooms increased from year to year, especially in the shallow Northern Adriatic, and along the western Adriatic coast, to the Gargano peninsula (Marasović & Pucher-Petković, 1987; Marchetti *et al.*, 1988; Todini & Bizzari, 1988; Marasović *et al.*, 1994). The period of blooms prolonged to the entire warmer season, coinciding with the spawning period of anchovy. Finally, during the period between 1986 and 1989, the blooming of plankton and benthic diatoms covered almost all the shallow parts of the Adriatic, particularly central and western parts of the Northern Adriatic, just the main spawning area of anchovy. In all the areas affected by the blooms, mucous matter released by diatoms was dispersed in dense patches, from the bottom to the surface. These blooms began to decrease in 1990. Time series of Italian catch of the anchovy (Fig. 5) show the sharpest decrease of the catch in the Northern Adriatic just in these years. This indicates that the anchovy was seriously affected by the blooms.

The spawning of the anchovy during the 1989 spawning season in the Northern Adriatic showed the lowest egg production in June, July and August, ever recorded in this area. Only one centre of more intensive spawning was detected in August in the area 10-20 miles off the western Istrian coast, in the zone of relatively oligotrophic waters of the incoming geostrophic current. The mortality rates of larvae were unusually high, while older postlarvae were not found in plankton (Dulčić, 1995). Moreover, during the anchovy egg surveys along the eastern Adriatic coast in 1989, it was found that anchovy postlarvae from the age classes of ~ 8 and 12 days were completely absent not only in the Northern Adriatic but also in the northern parts of the Central Adriatic (Fig. 6). The situation in 1990, when blooms began to decrease, was slightly different. Postlarvae from 8 days age class were found in large parts of the Northern Adriatic, but those 12 days old were still absent (Fig. 7).

This would mean that during the relatively long period of changes which caused eutrophication in the Adriatic, conditions for the reproduction of anchovy gradually deteriorated, using the permanent decrease of the population. Finally, during the 1986-1989 period of massive blooms, the population almost collapsed. Intensive blooms in the main spawning area of the Adriatic anchovy changed chemical properties of the water (Legović & Justić, 1994), qualitative and quantitative composition of phyto- (Marasović & Pucher-Petković, 1985; Fanuko, 1989) and zooplankton (Regner, 1987), which affected negatively both adult fish and larval stages. Besides all possible direct or indirect effects, it can be supposed that the patches of the mucous matter may irritate adult fish even physically, and act as a traps for larvae and postlarvae (Dulčić, 1995). Therefore, it seems that especially during the mentioned periods of massive blooms fish was forced to reproduce in relatively "clean" oligotrophic waters of the Central and Southern Adriatic,-instead in its main spawning areas. It seems that during this period anchovy population recruited mostly from the waters of the eastern coast of Central and Southern Adriatic, and probably from waters of the western coast of the Southern Adriatic (in the area between the Gargano peninsula and Otranto). The conditions for the reproduction are not so favourable in these areas as they are in the traditional spawning area where the effects of eutrophication have been most pronounced. Since the temperature and salinity increased during this period, it seems that this eutrophication was the consequence of the period of low frequency climatic change, the effects of which could be intensified by the anthropogenic eutrophication. After all, it is known that this kind of phytoplankton blooms occurred from time to time in this area. These blooms were recorded, for example, in 1890-1891, 1903, 1905, 1921, 1927, 1931 (Fonda-Umani *et al.*, 1989; Regner, 1991), when anthropogenic influence was not so obviously intensive as it is nowadays. However, it seems that the reproductive potential of anchovy is considerably high, because stock began to increase immediately after decrease of the blooms intensity (Fig. 4).

CONCLUSIONS

It is evident from this review that numerous investigators studied various aspects of the early life history stages of the Adriatic anchovy. Together, their results give relatively comprehensive picture of the embryonic development and growth, seasonal and daily intensity of spawning, horizontal and vertical distribution and long-term fluctuations of anchovy planktonic stages in the Adriatic.

It is also evident that the results obtained were dispersed within the long period of time, and that the intensity of investigations, as well as the number of investigated parameters, varied from one area to another. Thus, the data obtained are not consistent enough, and it is not easy to compare them. On the other hand, some factors essential for the better understanding of reproduction and recruitment of this important species for the Adriatic fisheries have been studied only occasionally and in very restricted areas. Besides, very little is known about juvenile anchovy. The simultaneous targeted studies of both adult fish and early life stages were never performed in the Adriatic. The same situation is with the comparative studies of the influence of dynamics of water masses, as well of production, quantity and distribution of microzooplankton on the transport and survival of anchovy postlarvae. Those were, among the others, the main reasons that it was not possible to forecast the collapse of the anchovy population in the 1986-1989 period, although the decrease in the anchovy population has been observed on time.

Therefore, for the future projects some systematic multidisciplinary investigations have to be planned. Investigations have to be designed in a way which will enable a better understanding of the processes essential for the success of survival of the anchovy postlarvae and juveniles, *i.e.* for the success of recruitment. They should encompass physical oceanography, phyto- and zooplankton production with the emphasis on the studies of microzooplankton, together with studies of transport, condition and survival of postlarvae and juveniles, and the state of the adult part of population. They have to be performed throughout the year, and most intensively in the main spawning area. Since the basic period of fluctuation of anchovy population in Adriatic must be covered, they should last three years at least.

POSLEDICA SPREMEMB V MORSKEM OKOLJU NA ZAČETNE RAZVOJNE STOPNJE IN RAZMNOŽEVANJE INČUNA *ENGRAULIS ENCRASICOLUS* L. V JADRANSKEM MORJU

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POVZETEK

Začetni razvojni stadiji inčuna Engraulis encrasicolus *v Jadranskem morju so bile prvič preučevani že pred dobrim stoletjem. Graeffe (1888) je bil prvi, ki je poročal o ikrah, odkritih v poletnih mesecih v planktonu severnojadranskega morja. To poročilo je bilo objavljeno prav tistega leta, ko je inčunove ikre opisal Raffaele (1888). Pozneje so se raziskavam o začetnih razvojnih stadijih jadranskega inčuna posvetili še mnogi drugi znanstveniki, in treba je reči, da je število raziskav, povezanih z ekologijo planktonskih stadijev in z odraslimi inčuni, precej večje, kot jih je bilo opravljenih za druge vrste rib. Tako seveda lahko trdimo, da je inčun najintenzivneje preučevana riba v Jadranu.*

Avtor je v pričujočem članku želel napraviti pregled znanja o planktonskih stadijih inčuna v Jadranu. Razmnoževalno območje te vrste v Jadranu je zelo široko, saj se inčun drsti v globinah do 200 m, vendar je njegovo glavno drstišče v evtrofiziranih vodah zahodnega dela plitkega severnega Jadrana in ob italijanskem obrežju vse do Garganskega polotoka. Inčun se v Jadranu drsti od (marca) aprila do oktobra (novembra), in sicer v vodah s temperaturo med 11,6 in 27,6 °C in slanostjo med 9,1 in 39,6 ppt. Produkcija in število ličink z rumenjakovo vrečko sledita spremembam v primarni produkciji in biomasi zooplanktona med drstenjem, s približno dvomesečnim odmikom v razvojni stopnji.

Čas razvoja iker in ličink jadranskega inčuna kot tudi krivulje rasti ličink in preobraženih ličink je avtor izračunal v eksperimentalnih razmerah. Krivulje rasti preobraženih ličink so bile začrtane tudi na osnovi otolitnih določevanj starosti. Nadrobne raziskave o dolgoročnih nihanjih v produkciji inčunovih iker, številu ličink in preobraženih ličink kot tudi o stopnji takojšnje umrljivosti preobraženih ličink so bile opravljene v srednjem Jadranu med letoma 1962 in 1976. Pokazale so, da je povečani produkciji iker sledila povečana abundanca preobraženih ličink in hkrati povečana stopnja njihove takojšnje umrljivosti. Ugotovljeno je bilo, da so ta nihanja neposredno povezana z nihanji v temperaturi, slanosti, primarni produkciji in količini zooplanktona, z enoletnim odmikom v razvojni stopnji.

Že od leta 1978 so ta "redna" nihanja povsem porušena. Zmanjšala se je biomasa inčunov, medtem ko se temperatura, slanost, vsebnost nutrientov in primarna produkcija nenehno povečujejo v celotnem Jadranu. Videti je, da so bile te spremembe posledica nizkofrekvenčne periode podnebnih sprememb, na kar je bržkone vplivala tudi antropogena evtrofikacija. Ker je evtrofikacija prizadela predvsem plitki severni Jadran in pas ob italijanskem obrežju do Garganskega polotoka, se zdi, da je ta pojav negativno vplival na razmnoževanje inčuna v njegovih glavnih drstiščih.

Ključne besede: inčun, zgodnji razvojni stadiji, spremembe v morskem okolju, razmnoževanje, Jadransko morje

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