Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea*

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SUMMARY: This paper is a review of the knowledge on the anchovy planktonic stages in Adriatic sea. The area of reproduction of this species is very wide in the Adriatic since the anchovy will spawn anywhere down to the depth of 200 m. However the main spawning area is in the eutrophic waters of the western part of the shallow northern Adriatic and along the Italian coast to the peninsula of Gargano. Anchovy spawn in the Adriatic generally from April to October, in the temperature and salinity ranges of 11.6 - 27.6°C and 9.1 - 39.6 ppt, respectively. Developmental times of Adriatic anchovy eggs and larvae, as well as the growth curves of larvae and postlarvae, were estimated under experimental conditions. The growth curves of postlarvae were also estimated from otolith readings. Biomass assessments of Adriatic anchovy by means of egg production method was made possible by the known temperature-development relationships, as well as the knowledge of the residence times of particular developmental stages. Spawning biomass was estimated in the northern and middle Adriatic during the period from 1976 to 1990. Detailed investigations of long-term fluctuations of anchovy egg production, quantity of larvae and postlarvae, as well as of instantaneous mortality rates of postlarvae, were performed in the middle Adriatic for the period from 1962 to 1976. Fluctuations of egg production and larval abundance were found positively correlated with fluctuations of temperature, salinity, primary production and zooplankton quantity, with a lag of one year. As eutrophication particularly affected the shallow northern Adriatic and the zone along the Italian coast as far as the peninsula of Gargano, it seems that this phenomenon negatively affected the reproduction of the anchovy in its main spawning areas.

Key words: Anchovy, Engraulis encrasicolus, eggs and larvae, reproduction, Adriatic.

RESUMEN: EFECTO DE LOS CAMBIOS AMBIENTALES EN LOS PRIMEROS ESTADIOS Y EN LA REPRODUCCIÓN DE LA ANCHOA EN EL ADRIÁTICO. – Este trabajo es una revisión de los conocimientos sobre los estados planctónicos de la anchoa en el Adriático. El área de reproducción de esta especie en el Adriático es muy amplia, abarcando todas las zonas de profundidad inferior a 200 m. Sin embargo, el área principal se encuentra en las aguas eutróficas y poco profundas de la zona nor occidental y a lo largo de las costas italianas, hasta la península de Gargano. En general, la puesta se produce de abril a octubre, en un rango de temperaturas de 11.6 - 27.6°C y de salinidades de 9.1 - 39.6 ppt. Se estimaron la duración del desarrollo de huevos y larvas y las curvas de crecimiento de larvas y postlarvas bajo condiciones experimentales. También se estimaron las curvas de crecimiento de las postlarvas a partir de lectura de otolitos. La evaluación de la biomasa de anchoa mediante el método de producción de huevos fue posible conociendo las relaciones entre desarrollo y la temperatura, así como los tiempos de residencia de estadios de desarrollo concretos. Se estimó la biomasa en puesta en el Adriático norte y medio, duran- te el período 1976-1990. En el Adriático mediu se realizaron investigaciones detalladas sobre fluctuaciones a largo plazo de la producción de huevos, abundancia de larvas y postlarvas y tasas de mortalidad de postlarvas, para el período 1962-1976. Se encontró una correlación positiva entre la producción de huevos y la abundancia de larvas con las fluctuaciones de temperatura, salinidad, producción primaria y abundancia de zooplancton, con un retraso de un año. Parece que la eutroficación que afecta las aguas someras del Adriático norte y la zona de la costa Italiana afecta negativamente a la reproducción de la anchoa en sus principales áreas de puesta (Traducido por los editores).

Palabras clave: Anchoa, Engraulis encrasicolus, huevos y larvas, reproducción, Adriático.

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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 that eggs of this fish were found in the plankton of the northern Adriatic during the summer months. In the same year Raffaele (1888) first described anchovy eggs. Later on, numerous scientists studied various aspects of the early life stages of Adriatic anchovy. The number of studies related to the ecology of the planktonic stages and to the adult anchovy is considerably higher than those related to other fishes. Therefore it follows that the anchovy is the most intensively studied fish species in the Adriatic.

The attention paid to both early life 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 was 47% of the mean annual catch of pelagic fish. However, since 1978 a decrease of anchovy biomass has been observed. This caused a decrease in the catch, and in the period from 1977 to 1989, anchovy was only 28.7% of the total pelagic fish catch of the Adriatic.

The aim of this paper is to give basic information about early life stages of the Adriatic anchovy, and to try to explain the causes of the recent decrease of the biomass of this fish.

ELEMENTARY DATA

**Spawning season**

Anchovy eggs are found in plankton during the period April–October, and sometimes from March to November (Steuer, 1910; Stiasny, 1910; Vatova, 1928; Gamulin, 1940, 1964; Varagnolo, 1964a, 1965; Vucetic, 1957, 1964, 1975; Zavodnik, 1970; Stirn, 1969; Merker and Vujosevic, 1972; Regner, 1967, 1970, 1972, 1979/85; Piccinetti et al., 1979; Piccinetti et al., 1980; Regner et al., 1985; Regner and Dulcic, 1994). The production of eggs is the highest in July (Fig. 1).

A positive correlation was found between the quantity of anchovy eggs and the number of phytoplankton cells, as well as with zooplankton dry weight (Vucetic, 1975). Analysis of long term data (1962-1976) showed that (i) production of anchovy eggs and the quantity of larvae followed primary production and (ii) the zooplankton peaks with the 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 water.

About 85% of anchovy eggs in the Adriatic are produced in May-August (Gamulin, 1940, 1964; Varagnolo, 1964a; Merker and Vujosevic 1972; Regner, 1972, 1979/85; Piccinetti et al., 1979; Piccinetti et al., 1980; Regner et al., 1985; Regner and Dulcic, 1994). The production of eggs is the highest in July (Fig. 1).

The relationship with temperature and salinity during the spawning season has been well studied (Vucetic, 1957; Varagnolo, 1965; Stirn, 1969; Zavodnik, 1970; Merker and Vujosevic, 1972; Regner, 1972, 1979/85). Results show that anchovy spawns within temperature ranges of 11.60-27.50°C in the Northern Adriatic, and 13.12-27.32°C in the Middle and Southern Adriatic, with the maximal egg production between 17-22°C. In the Northern Adriatic anchovy spawn in 9.10-38.50 ppt salinity ranges, and in 33.80-39.60 ppt in the Middle and Southern Adriatic. Maximal egg production may occur at any of the aforementioned salinities (Regner, 1979/85).

A positive correlation was found between the quantity of anchovy eggs and the number of phytoplankton cells, as well as with zooplankton dry weight (Vucetic, 1975). Analysis of long term data (1962-1976) showed that (i) production of anchovy eggs and the quantity of larvae followed primary production and (ii) the zooplankton peaks with the
phase lag of about two months (Regner, 1979/85). 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 linked to the quantity of microzooplankton which was found to be their main food in the Middle Adriatic (Regner, 1971).

The catch of juvenile anchovy was analyzed in the Gulf of Manfredonia (Rizzoli, 1983). The largest quantities were observed in December, and again in April and May. To date there are no studies on the ecology of juveniles in the wider areas of Adriatic.

Daily period of spawning

In the Middle Adriatic anchovy spawns in the evening, between 19:00 and 21:00 hours (Vucetic, 1957). According to Varagnolo (1964b) maximum spawning in the Northern Adriatic takes place between 18:00 and 20:00 hours.

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 in experimental conditions in order to estimate the relationship between temperature and developmental time, and between temperature and growth rates of larvae and postlarvae (Regner, 1979/85). Four different functions were fitted to represent the relationship between egg development and temperature. The following power function was used for estimates of anchovy egg developmental times in the paper by Regner (1979/85).

\[ D = 1788.4199 \times T^{2.290236} \]  

(1)

where \( D \) is the developmental time in days, and \( T \) is the temperature in °C. However the best fit was obtained with the inverse logistic function with the parameters:

\[ D = \frac{1}{1.012896 \left[ 1 + e^{4.914322 - (0.257451 \times T)} \right]} \]  

(2)

(Regner, 1979/85). Therefore this function was used for all estimates of developmental times of anchovy eggs since 1979. This function gives better estimates particularly in lower temperatures (Fig. 2).

To determine instantaneous mortality rates of eggs information is required on residence times and the mean ages of particular developmental stage. Thus, to obtain residence times and the mean ages of stages (see Regner, 1975/85) the value of \( D \) obtained from equations (1) and (2) has to be corrected with the factors presented at Table 1.

The value of \( D \) has to be divided with the residence time correction factor. The estimate of the mean age has to be multiplied with the correction for the mean time.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Residence time correction</th>
<th>Mean time correction</th>
</tr>
</thead>
<tbody>
<tr>
<td>I + II</td>
<td>0.1630</td>
<td>0.0815</td>
</tr>
<tr>
<td>III</td>
<td>0.0795</td>
<td>0.2028</td>
</tr>
<tr>
<td>IV</td>
<td>0.1506</td>
<td>0.3178</td>
</tr>
<tr>
<td>V</td>
<td>0.0837</td>
<td>0.4350</td>
</tr>
<tr>
<td>VI</td>
<td>0.1925</td>
<td>0.5731</td>
</tr>
<tr>
<td>VII</td>
<td>0.1173</td>
<td>0.7280</td>
</tr>
<tr>
<td>VIII</td>
<td>0.1046</td>
<td>0.8389</td>
</tr>
<tr>
<td>IX</td>
<td>0.0628</td>
<td>0.9226</td>
</tr>
<tr>
<td>X</td>
<td>0.0460</td>
<td>0.9770</td>
</tr>
</tbody>
</table>

TABLE 1. – Residence time and mean age correction factors by egg stage needed to determine instantaneous mortality rates of anchovy eggs.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Residence time correction</th>
<th>Mean time correction</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (I - IV)</td>
<td>0.395</td>
<td>0.198</td>
</tr>
<tr>
<td>B (V - VII)</td>
<td>0.393</td>
<td>0.592</td>
</tr>
<tr>
<td>C (VIII - IX)</td>
<td>0.165</td>
<td>0.871</td>
</tr>
<tr>
<td>D (X)</td>
<td>0.046</td>
<td>0.977</td>
</tr>
</tbody>
</table>

TABLE 2. – Correction factors by group of egg stages used to determine anchovy egg mortality.
Table 2 shows correction factors for the groups of stages used to determine egg mortality for biomass assessments.

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

\[ D = 270065.2744^T^{3.8079} \] (3),

where \( D \) is time in days, and \( T \) is the 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, 1979/85). In 1980, data obtained on larval and postlarval growth were fitted again with Gompertz functions, which gave better fit than previously used equations. The form of the Gompertz function used for the estimates of growth was:

\[ l_t = ae^{-be^{-ct}} \] (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 of equation (4) were found to be temperature dependent. This relationship can be expressed as:

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

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 a Gompertz function (Regner, 1980). The parameters of the Gompertz function obtained for the growth at this temperature level were:

\[ l_t = 27.315^e^{-2.0517e^{-0.0802t}} \] (5).

Growth of postlarvae was also estimated from the daily growth increments of the otoliths of the postlarvae collected during the cruise along the Eastern Adriatic coast performed in August 1989 (Regner and Dulcic, 1990). The parameters of Gompertz function were:

\[ l_t = 27.315^e^{-2.0517e^{-0.0802t}} \] (6).

It is interesting to observe that the parameters of the Gompertz functions obtained either from the measured lengths of postlarvae reared in experimental conditions, or from counting otolith daily increments of planktonic postlarvae after twelve years, do not differ too much.

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

\[ \Delta t = -\frac{1}{c} \ln \left( \frac{1}{b l_{i+1}} \right) - \ln \left( \frac{1}{b l_i} \right) \] (7),

where \( \Delta t \) is the residence time, while \( l_i \) and \( l_{i+1} \) are initial and final lengths of each length group defined (Table 3), while \( a \), \( b \) and \( c \) are the parameters of equation (4). To estimate mortality rates, the number of larvae or postlarvae from each length group (Table 3) have to be divided with the residence time.

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

\[ \bar{i}_n = \sum_{i=1}^{n-1} \Delta t_i + \frac{\Delta t_n}{2} \] (8),

where \( \Delta t_n \) are residence times of length groups, obtained from equation (7).

### Length-weight relationship of anchovy larvae and postlarvae

The relationship between standard length and dry weight was studied on artificially reared larvae and postlarvae (Regner, 1983). It was found that larvae showed an initial increase of the W/L ratio, which decreased after the anchovy reached the stage of

<table>
<thead>
<tr>
<th>Length Group</th>
<th>Standard Length Range</th>
</tr>
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<tbody>
<tr>
<td>Larvae (SL, mm)</td>
<td>2.38 - 3.03</td>
</tr>
<tr>
<td>II</td>
<td>2.39 - 3.03</td>
</tr>
<tr>
<td>III</td>
<td>3.04 - 3.68</td>
</tr>
<tr>
<td>IV</td>
<td>3.69 - 4.33</td>
</tr>
<tr>
<td>V</td>
<td>4.34 - 5.00</td>
</tr>
<tr>
<td>VI</td>
<td>5.01 - 6.00</td>
</tr>
<tr>
<td>VII</td>
<td>6.01 - 7.00</td>
</tr>
<tr>
<td>VIII</td>
<td>7.01 - 8.00</td>
</tr>
<tr>
<td>IX</td>
<td>8.01 - 9.00</td>
</tr>
<tr>
<td>X</td>
<td>9.01 - 10.00</td>
</tr>
</tbody>
</table>

| Postlarvae (SL, mm) | 3.99 - 4.99 |
| II | 4.00 - 5.99 |
| III | 5.00 - 6.00 |
| IV | 6.00 - 7.00 |
| V | 7.00 - 8.00 |
| VI | 8.00 - 9.00 |
| VII | 9.00 - 10.00 |
| VIII | 10.00 - 11.99 |
| IX | 11.00 - 12.99 |
| X | 12.00 - 13.99 |
| XI | 13.00 - 14.99 |
| XII | 14.00 - 15.99 |
| XIII | 15.00 - 16.99 |
| XIV | 16.00 - 17.99 |
| XV | 17.00 - 18.99 |
| XVI | 18.00 - 19.99 |
| XVII | 19.00 - 20.99 |
| XVIII | 20.00 - 21.99 |

Table 3. Length groups defined to estimate age of anchovy larvae and postlarvae.
yolk-sac resorption. Length-weight relationship in postlarvae was approximated with a power function, the exponent of which was 3.32, indicating a positive allometric relationship.

Feeding of postlarvae

The feeding of postlarvae from 3 to 8 mm standard length was investigated during the 1968 and 1969 spawning seasons in the Middle Adriatic (Regner, 1971). It was found that 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%.

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; Varagnolo, 1965; Stirn, 1969; Vucetic, 1971; Regner, 1972, 1979/85; Casavola et al., 1987) or over all the northern, middle and southern Adriatic (Steuer, 1913; Piccinetti et al., 1979, 1980; Gamulin and Hure, 1983; Regner et al., 1985).

According to the aforementioned authors, anchovy spawns in all parts of the Adriatic where depths do not exceed 200 m, i.e., in the area of Adriatic shelf. Thus, its eggs cannot be found in the areas deeper than 200 m (above Jabuka pit in the middle Adriatic and above 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/m²/day is higher than 90%. The area covers shallow northern Adriatic waters (with the exception of the zone along the western coast of the Istrian peninsula which is under the influence of the 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 Palagruza island. In fact, this area is under the influence of the outflows of Italian rivers, especially of the river Po. In the 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 larva surveys which covered almost the entire area of the Adriatic shelf were relatively numerous. For example, for anchovy biomass estimates alone 11 cruises have been performed over the northern, middle and part of the southern Adriatic during 1976-1990 (Regner, 1990). However, most of the surveys have been performed 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. 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 middle, and part of the southern Adriatic, was done on the material collected in July 1978 (Piccinetti et al., 1982).

Surveys throughout the spawning season were relatively scarce. They were performed over relatively limited areas, mainly in the shallow northern Adriatic. According to these surveys, centers of spawning within this part of the main anchovy spawning area move during the spawning season either in cyclonic (Vucetic, 1964; Varagnolo, 1965) or in anticyclonic directions (Stirn, 1969).

These displacements are obviously 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, the most northwesterly one
being 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 and 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 and Bergamasco, 1991; Rajar and Cetina, 1991). This explains differences in the movement of anchovy spawning centers found by different authors. Besides, the influence of these gyres on the rates of mixing of oligotrophic waters of incoming geostrophic current on the one hand and eutrophic waters of river Po outflow on the other hand is very important. The rates of both horizontal and vertical mixing regulate the intensity of primary and secondary production in this most productive area of the Adriatic sea. Intensity of production, together with the direction of currents is, with no doubt, essential for the intensity of anchovy spawning in this area, as well as for the more or less successful survival of its planktonic stages. There is a lack of detailed studies on the influence of northern Adriatic circulation on the transport and survival of anchovy larval stages. This should be one of the main tasks of future investigations.

In the other areas, such as along the eastern Adriatic coast, where anchovy spawning is not so intensive, some other geophysical factors may be of importance for the reproduction. During the last two cruises, performed in July 1989 and August 1990 to assess anchovy biomass 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 upwelling areas (Regner, unpublished data).

Obvious influence of the atmosphere-sea interaction on the distribution of anchovy spawning centers 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. Varagnolo (1965) found maximum densities of anchovy eggs 1 m below the surface, while according to Ghirardelli (1967) and Specchi (1968) maximum egg concentration was in the 7-27 cm layer. According to 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.

LONG-TERM FLUCTUATIONS

Long-term fluctuations of anchovy early life stages were studied only in the eastern part of middle Adriatic (Vucetic, 1971; Regner, 1974; Regner, 1979/85).

Considerably large fluctuations in the total annual number of anchovy eggs through the period between 1959 and 1969 were accounted for by changes in the amount of advection of the eastern Mediterranean water into the Adriatic (Vucetic, 1971). Later it was found that fluctuations of the annual quantity of anchovy eggs coincided with fluctuations of primary production (Regner, 1974). More detailed studies on the relationships between annual mean egg production, number of postlarvae and their mean mortality rates with the annual mean values of abiotic and biotic factors (temperature, salinity, primary production and quantity of zooplankton) were carried out for a period of fifteen years (1962-1976) (Regner, 1979/85). It was found that fluctuations of egg and postlarvae quantities were positively correlated with the fluctuations of temperature, salinity, primary production, with a 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 postlarvae is more successful in years of higher organic production, probably due to decreased intraspecific competition. Spectral analysis of all long-term data showed periodicity of 2-3, 5-7 and 9-11 years. Since similar periods were found in annual variations of air pressure in Trieste and Venice (Polli, 1955), as well as in fluctuations of sardine catches (Regner and Gacic, 1974), it is obvious that the reproduction of anchovy, over the long-term period, is controlled by climatic changes which affect the dynamics of the water masses and organic production in the Adriatic. The mechanism of this control seems to act through 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 displacements.
of large baric centers such as Icelandic cyclone and Siberian 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 eastern Mediterranean waters, the primary and secondary production increase (Pucher-Petkovic and Zore-Armanda, 1973). These changes of production may be assumed as the main factor which regulate 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 were performed by egg production (Regner et al., 1985; Regner, 1990) and acoustic methods (Azzali et al., 1990). Long-term stock assessment using the annual egg production method overestimated anchovy biomass, due to the underestimated batch fecundity and spawning frequency. (Regner, 1990). However, although estimates obtained by acoustic and egg production methods were significantly different, fluctuations of biomass derived from both methods showed very good mutual correlation, and both time series were strongly correlated with the statistical data on the anchovy catch in the Adriatic. They also showed a continuous biomass decrease since 1978. Stock 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 to only 7,055 tons in 1987 (GFCM statistical bulletin no. 7, 1989; Annuario Statistico della Zootecnia, Pesca e Caccia, Rome, years 1980-1992; Statisticki bilten SFRJ, Belgrade, years 1976-1991).

Since biomass assessments by both methods (the acoustic method may be considered more reliable) showed that the anchovy stock was not overfished, some other explanations had to be found for this decrease.

From the mid seventies, a number of change took place in the Adriatic. A constant increase of sea surface temperatures and salinity was observed, together with a decrease of sea water transparency and oxygen saturation in bottom layers (Zore-Armanda et al., 1987; Zore-Armanda, 1991). These changes were followed by an increase of primary production (Pucher-Petkovic et al., 1987), indicating that the Adriatic ecosystem was passing through a relatively long period of eutrophication. Just during this period some unusual changes in the distribution of certain species took place. For example, large masses of gilt sardine (Sardinella aurita, Vallenciennes), which was always present but not abundant in the southern Adriatic, spread since 1975 over all the Adriatic, and in 1979 reached the Gulf of Trieste (Gamulin, 1975; Kacic, 1975; Regner, 1977). The fish retreated to the southern Adriatic in the second half of eighties. As this fish spawns during the summer months, it can be a competitor to the anchovy postlarvae.

A similar phenomenon happened with the jellyfish Pelagia noctiluca which exploded and covered large parts of the Adriatic during the period from 1977 to 1985 (Vucetic, 1982, 1985). This jellyfish is known as a predator of fish eggs and larvae. Since its quantities were most numerous during the spawning seasons of anchovy, it may be assumed that this phenomenon also negatively influenced recruitment of anchovy population. However, the anchovy stock decrease, although evident, was not still too steep during the period of the massive occurrence of Pelagia noctiluca (Vucetic and Alegria-Hernández, 1987). On the contrary, the sharp decrease of the anchovy stock began in 1986 (Figs. 4 and 5).

At the same time, from the beginning of eighties, the summer blooms of phytoplankton and benthic diatoms started to spread in the Adriatic sea. Initially they were limited to smaller enclosed or semi-

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**Fig. 4.** – Relationship between estimated biomass and catch during the period of the decrease of the anchovy population in the Adriatic.
enclosed polluted areas, and lasted for a relatively short time. The surface affected by the blooms was increased from year to year, especially in the shallow northern Adriatic, and along the western Adriatic coast to the peninsula of Gargano (Marasovic and Pucher-Petkovic, 1987; Marchetti et al., 1988; Todini and Bizzari, 1988; Marasovic et al., 1994). The period of blooms prolonged 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 shallow parts of the Adriatic, particularly central and western parts of the northern Adriatic, 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 catches of the anchovy (Fig. 5) show the sharpest decrease of the catch in the northern Adriatic in these years. This indicates that 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 center of more intensive spawning was detected in August 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 the plankton (Regner, 1994). Moreover, during the anchovy egg surveys along the eastern Adriatic coast in 1989, anchovy postlarvae from age classes of ~ 8- and 12-days were completely absent from the northern Adriatic and the northern parts of the middle Adriatic (Fig. 6). The situation in 1990,
when blooms began to decrease, was slightly different. Postlarvae from the 8-days age class were found in large parts of the northern Adriatic, but those of 12-days old were still absent (Fig. 7).

During the relatively long period of changes which caused eutrophication in the Adriatic, conditions for reproduction of anchovy have gradually deteriorated, causing the permanent decrease of the population. Finally, during the 1986-1989 period of massive blooms, the population has almost collapsed. Intensive blooms in the main spawning area of the Adriatic anchovy changed the chemical properties of the water (Legovic and Justic, 1994), and both the qualitative and quantitative composition of phytoplankton (Marasovic and Pucher-Petkovic, 1987; Fanuko, 1989) as well as zooplankton (Regner, 1987), which affected both adult fish and larval stages negatively. Additional to any possible direct or indirect effects, mucous matter associated with these blooms likely irritate adult fish and act as a traps for larvae and postlarvae (Regner, 1994). Therefore, it seems that during periods of massive blooms fish were forced to reproduce in relatively “clean” oligotrophic waters of the middle and southern Adriatic instead of in its main spawning areas. It seems that during this period, anchovy population was recruited mostly from the waters of the eastern coast of middle and south Adriatic, and probably from the 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 temperature and salinity were increasing 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 anthropogenic eutrophication. After all, it is known that phytoplankton blooms of this kind occur 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 the anthropogenic influence was not so intensive as it is nowadays. However, it seems that the reproductive potential of anchovy is considerably higher because stock began to increase immediately after the blooms intensity decreased (Fig. 4).

**CONCLUSIONS**

It is evident from this review that numerous investigators have studied various aspects of the early life history stages of the Adriatic anchovy. Together, their results give a 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 results obtained varied with time, and that the intensity of investigations, as well as the number of investigated parameters changed 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. Furthermore, very little is known about juvenile anchovy. Simultaneous studies of both adult fish and early life stages have never been performed in the Adriatic. Similarly, comparative studies on the influence of the dynamics of water masses, production, quantity and distribution of microzooplankton on the transport and survival of anchovy postlarvae have never been carried out. Those were, among others, the main reasons why it was not possible to forecast the collapse of the anchovy population in 1986-1989 period, although the decrease of anchovy population was observed at the time.

Future research must be systematic and multidisciplinary. Investigations have to be designed in a way which will enable a better understanding of the processes essential for the success of survival of anchovy postlarvae and juveniles, i.e. for the success of recruitment. They should encompass a number of areas: physical oceanography; phyto and zoo-plankton production including microzooplankton; transport, condition and survival of postlarvae and juveniles; and the state of the adult population. Studies should be performed throughout the year, and most intensively in the main spawning area. Since the basic period of fluctuation of anchovy population in the Adriatic must be covered, they should last three years at least.

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