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ECOLOGY OF PLANKTONIC STAGES OF THE ANCHOVY, *ENGRAULIS ENCRASICOLUS* (Linnaeus, 1758), IN THE CENTRAL ADRIATIC

EKOLOGIJA PLANKTONSKIH STADIJA BRGLJUNA, *ENGRAULIS ENCRASICOLUS* (Linnaeus, 1758), U SREDNJEM JADRANU

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The results of analyses of spatial-temporal distribution and survival of anchovy planktonic stages collected from the open sea and channel area for fifteen years and from the coastal area for nine years are presented. This study was undertaken to contribute to the knowledge of their ecology as well as of the fluctuations in their numbers to show what caused them in the first place.

Temperature effects on egg developmental time and the rate and properties of growth of anchovy larvae and postlarvae under experimental conditions were examined for the purpose of these analyses. Mathematical approximations of these relationships were also made. They provided the basis for the calculations of the age of anchovy developmental stages in the plankton. Global, monthly and annual mean mortality coefficients of anchovy eggs and larval stages were calculated from the known age from which the periods of specific mortality were also established.

Egg production and the numbers of anchovy larvae and postlarvae per unit time and area were calculated for each individual sample from known egg developmental time as affected by temperature and from mortality coefficients. Thus the data on plankton catches were made intercomparable irrespective of the time and place they were realized at.

The analysis of long-term monthly means showed that spatial-temporal distribution of anchovy planktonic stages during spawning season was affected more by the dynamics of biotic environmental factors (primary production and zooplankton quantity) than by that of the abiotic ones (temperature, salinity).

The study of the relationship between anchovy planktonic stages and adult anchovy catches from the study area showed that during intensive reproduction anchovy were far less accesible.

Long-term egg production fluctuations, the numbers and survival of anchovy postlarvae were observed in relation to the above mentioned abiotic and biotic environmental fac-

tors and anchovy catch fluctuations applying the spectral analysis method.

The similarity between oscillation periods of all analysed parameters led to the conclusion that the entire anchovy population responded to environmental changes with a phase lag of about a year. It seems to be largerly affected by the trophic basis changes.

Calculated basic oscillation period provide a good basis for eventual long-term forecast of anchovy population fluctuations in the Adriatic.

1. INTRODUCTION

Anchovy, *Engraulis encrasicolus* (Linnaeus, 1758) are the only representatives of *Engraulidae* family in the Mediteranean and therefore in the Adriatic, as well. They count among the pelagic species of small size thus that in the Adriatic they reach not more than 205 mm in length (Mužinić, 1972). They are distributed in the Atlantic, from the western coasts of Africa up to Bergen, as well as in the North Sea, Baltic, Mediterranean and Black Sea. They are widely distributed in the Adriatic inhabiting all its parts down to 210 m depth (Mužinić, 1973).

Anchovy are significant in the Yugoslav pelagic fish catch. In the 1961—1974 period the average Yugoslav anchovy catch was 3490.9 tons (Stočarstvo i ribarstvo, 1962—1975) after the average sardine (*Sardina pilchardus* Walb.) catch of 11632.7 tons and the average sprat (*Sprattus sprattus* L.) catch of 3596.3 tons. Anchovy make 16.7% of the total Yugoslav pelagic fish catch which was 20949.2 tons in the 1961—1974 period.

On the other hand, with the average catch of 23734.8 tons anchovy made up even 63.4% of the Italian average pelagic fish catch in the Adriatic which was 27428.34 tons in the same period (Annuario statistico della pesca e della caccia, 1962—1973; GFCM STATISTICAL Bull., 1, 1976).

Making up 46.64%, anchovy quantities of 27225.7 tons were the highest in the total average Yugoslav and Italian pelagic fish catch of 58377.54 tons in the same period.

Up to now, a large number of authors have studied both the adult anchovy and their planktonic stages owing to their high proportions in the catch as well as to their relatively high commercial importance. However, since a number of questions concerning this fish species have remained unanswered their ecology should further be given great attention. Therefore the researches the results of which are published in this paper were carried out in order to contribute to the better knowledge of ecology of their planktonic stages in the Adriatic.

1.1. A REVIEW OF THE STUDIES OF ANCONOVY PLANKTONIC STAGES CARRIED OUT UP TO NOW

Anchovy eggs were for the first time described by Raffaele (1888) on the basis of the plankton material collected from the Gulf of Naples. After him an anchovy egg is of elypsoid shape and its longer diameter is

1.15 — 1.25 mm. Capsule structure is smooth with no pores and/or grooves. Large vesicles cover most of the yolk which has no oil globules. The first description of anchovy larvae was given by Wenckebach after Ehrenbaum (1905—1909). According to Ehrenbaum's (1905—1909) data from the North Sea the larva is 4 mm long. Fage (1920) made the detailed description of anchovy postlarvae of 4—50 mm in lenght. D'Ancona (1931) described in detail anchovy larvae and postlarvae from the Gulf of Naples. Yolk sac of the larva is elongated backward. Chorda is relatively thick with two rows of cells. The intestine is thin, stright and ends at the ventral end of the primordial fin. Larva has neither mouth opening nor pharynx. It's eyes are unpigmented. On its ventral side there is a lot of pigment cells along the intestine. After D'Ancona larva transforms in postlarva at 4—5 mm length. In postlarva the yolk sac is resorbed, eyes are pigmented and silver, otocysts are very big. Mouth opening is formed already at the end of larval stage before the yolk sac complete resorption. Primordial fin is diminished and rays occur in dorsal, anal and caudal fins. Dorsal fin is formed at the level of anal opening. Pigment cells extend along the intestine, at the end of tail fin and on the lower body side from the anal opening to the tail. Point shaped melanophore is formed above the anal opening. The longest postlarva described by D'Ancona was 33 mm in length.

The first data on anchovy eggs in the Adriatic plankton were given by Graeffe (1888) who reported anchovy to spawn in the northern Adriatic in summer months. After the results of the previous investigations (Steuer, 1910; Stiasny, 1910; Vatova, 1928; Gamulin, 1964; Varagnolo, 1964; Vučetić, 1964; Varagnolo, 1965; Zavodnik, 1967; Štirn, 1969; Zavodnik, 1970 for the northern Adriatic; Gamulin, 1940; Vučetić, 1971; Regner, 1972; Vučetić, 1975 for the central Adriatic; Vučetić, 1957; Merker and Vujošević, 1972 for the southern Adriatic and Piccinetti *et al.*, 1979 for a part of the southern Adriatic, as well as for the central and northern Adriatic) anchovy eggs are ordinarily taken from plankton in April—October. Zavodnik (1970) reported a record of one anchovy egg in the Gulf of Venice at the end of February 1967, which is the earliest reported record of anchovy eggs in plankton. Results of the central Adriatic investigations (Vučetić, 1971; Regner 1972) show that the season of anchovy egg occurrence in plankton may sometimes extend from March to November. The increased sea temperature in January and February seems to affect the earlier occurrence of eggs in the area (Regner, 1972).

After the records of the afore-mentioned authors, anchovy egg maximum numbers occur in May—June and August—September respectively. Maximum numbers occur in the open central Adriatic earlier than in the coastal neritic waters (Vučetić, 1971; Regner, 1972; Piccinetti *et al.*, 1979).

Studies of the seasonal aspect of anchovy egg occurrences in the Adriatic included also the collection of data on water temperature, salinity and density ranges within which these occurrences tako place. Anchovy eggs were recorded from the northern Adriatic at temperature ranging from 11.6 to 27.5°C (Štirn, 1969; Zavodnik, 1970) with maximum numbers at temperature of about 22°C, and 9.1 — 38.5‰ salinity (Varagnolo, 1965; Štirn, 1969; Zavodnik, 1970). After these authors, anchovy eggs are more numerous in the northern Adriatic at lower salinity values. In the central and southern Adriatic anchovy eggs were found at 13.17—27°C temperature range (Vuče-

tić, 1957; Merker and Vujošević, 1972; Regner, 1972) with maximum numbers at 18—20°C (Regner, 1972) and at 33.86—38.69‰ salinity range (Merker and Vujošević, 1972; Regner, 1972) with maximum number at 34—38‰ salinity (Regner, 1972). Anchovy egg maxima were found to occur within a considerably narrow water density range, 26.6—27.4 σt in the open central Adriatic and 24.13—24.81 σt in its coastal part (Regner, 1972).

Effects of some of the biotic factors on the seasonal anchovy egg distribution was studied in addition to the water temperature, salinity and density effects. Comparing the eleven-year mean anchovy egg quantities during the spawning season with the long-term dry weight means and number of individual zooplankton groups, Vučetić, (1975) finds that the variations in anchovy egg quantities during the spawning season coincide with the variations in zooplankton dry weight and phytoplankton quantity in the coastal area and the zooplankton dry weight maxima in the open sea. After this author the adaptation of adult fish to certain feeding conditions before and during the spawning season accounts for this phenomenon.

Taking together the results of the investigations of all the foregoing authors the conclusion arrived at is that during the spawning season anchovy eggs are present all over the Adriatic at depths not exceeding 150—200 m. Anchovy eggs are either not found at all or rarely found in small numbers in the areas of greater depths such as the South Adriatic Pit and Jabuka Pit. The investigations carried out up to now does not provide the basis for an authoritative picture of the anchovy eggs quantitative relations between different Adriatic areas since different authors collected material with different gear and differently expressed quantities (per plankton net haul, per unit volume, per square metre).

The investigations in the central Adriatic showed that anchovy eggs were more numerous in the coastal and open sea than in the channel area (Gamulin, 1940; Vučetić, 1971; Regner, 1972). The investigations of anchovy spawning in the northern Adriatic, from the outer side of island Dugi otok to the coasts of Istra, Vučetić (1964) showed that during the spawning season the areas of anchovy spawning were displaced from the open sea towards the coasts of Istra. Varagnolo (1965) found for the Gulf of Venice that spawning centres were also shifting towards the coast as well as along the coast in a counterclockwise direction. The findings of both of those authors show that spawning centres in the northern Adriatic are in fact shifting in the direction of the prevailing Adriatic surface current. On the contrary, Štirn (1969) established quite the opposite direction of spawning centres shifting. And finally, the only investigations so far which collected material from a relatively large number of stations covering a large part of the Adriatic in a relatively short time (Piccinetti *et al.*, 1979) showed that in 1976 anchovy eggs occurred in the largest number in the Gulf of Trieste, close to the river Po delta and in the open Adriatic from the level of the Susak Island to the northern margin of the Jabuka Pit as well as round the Palagruža Island.

Further on, vertical anchovy egg distribution was also studied in the Adriatic. Vučetić (1957) and Gamulin (1964) concluded that anchovy eggs were distributed in the surface layers. On the basis of egg quantities in the catches from different depth layers by vertical hauls of plankton net

fitted closing facility (Regner, 1972) it was found that eggs were mainly distributed in the upper ten metres. By a series of plankton net horizontal hauls at different depths Varagnolo (1965) and Čmovž (1973) took the largest number of eggs at 1 m depth below the surface. Studying the zooplankton microdistribution Ghirardelli (1967) and Specchi (1968) found the greatest concentrations of anchovy eggs in the 7—27 cm depth layer. After these records it may be concluded that the anchovy eggs are floating immediately beneath the surface.

Vučetić (1957) and Varagnolo (1964a) observing the occurrence of individual embryonic egg stages in plankton by a series of successive catches realized at shorter time intervals over few days determined approximately the period of the day in which anchovy are spawning, as well as an approximate duration of their embryonic development. Vučetić reported that anchovy spawned in the Mljet Island Lakes between 7 and 9 o'clock p.m. and that their embryonic development took up to 40 hours at 20—21°C temperature and about 24 hours at 27°C. After Varagnolo, who studied the area of Chioggia, anchovy spawn between 6 and 8 o'clock p.m. and embryonic development requires 4 days at 16.5°C to 1 day at 27—28°C.

Studying the shape and size of anchovy eggs from different Mediterranean and Black Sea areas, Lugovaja (1963) found the eggs from the central Adriatic to be larger and more elongated (means of both diameters were 1.36 × 0.63 mm) and those from the northern Adriatic smaller and more oval (means of both diameters 1.20 × 0.50 mm). This author accounted it for by a salinity decrease going northwardly from the central Adriatic. Anchovy egg size was found to vary from 1.2 — 1.84 × 0.48 — 0.67 mm in the central Adriatic. It was recorded that the eggs were smaller at the end of spawning period than at its beginning (Regner, 1972). This is held to be due to the later sexual maturation of smaller and younger fish, which as a rule, have smaller eggs. It was, as well, found that anchovy eggs were larger in the open part of the central Adriatic than in the coastal part nevertheless the salinity was lower in the coastal area (Regner, 1973). This could be the result of the spawning of smaller and younger fish in the coastal area.

Egg mortality and survival in the Adriatic are very little known. Comparing the quantities of alive eggs with those of dead eggs in individual stages Regner (1972) found the greatest mortality at first development stages. Calculating egg mortality by the same method Picinetti *et al.*, (1979) give an average mortality of the Adriatic anchovy of about 98% taking from the beginning to the end of embryonic development. Mortality causes and the intensity of effects of eventual predators are, for the time being, almost completely unknown.

Long-term fluctuations of anchovy egg numbers were also studied in the central Adriatic. Considerable increases in the total number of eggs were recorded from the coastal and channel area in the 1959—1969 period. These increased quantities were recorded in the open sea in 1961, 1968 and 1969. This increase in the number of eggs was accounted for by the periodical more intensive ingressions of the eastern Mediterranean water into the Adriatic (Vučetić, 1971). Carrying larger quantities of nutrients (Buljan, 1953) this water causes an increase of the Adriatic organic production. It was noted for the same area that the variations in total anchovy egg numbers in

plankton coincided with the variations in the mean annual primary production values (Regner, 1974). The effect of primary production is indirect realized probably through the increased production of zooplankton on which the adult anchovy feed.

And finally, three attempts have been made up to now to assess the quantites of sexually mature anchovy in the Adriatic on the basis of egg quantities in plankton. Namely, if the egg quantities in plankton, spawning season duration and magnitude of fish spawning area are known on the one side and weight and fecundity of females and the number of batches in one season as well as the quantitative relations between sexually mature females and males on the other, the biomass of sexually mature part of the population may be calculated. First attempt was made by Štirn (1969) who calculated that anchovy biomass was 250 000 tons in the northern Adriatic in 1965. Vučetić (Karlovac *et al.*, 1974) assessed anchovy biomass to reach 190 000 tons in the whole Adriatic. In 1976 Piccinetti *et al.*, (1979) found that the biomass of this was approximately 927 000 tons in a part of the southern Adriatic and in the central and northern Adriatic.

Apart from eggs, the problems of the Adriatic anchovy larvae and postlarvae have been much less studied.

Data on anchovy larvae and postlarvae were for the first time given by Karlovac (1963) on the basis of the material collected during the HVAR Expedition cruises covering the whole open Adriatic in 1948—1949. After this autor anchovy larvae and postlarvae occur in plankton from May to November with maximum numbers in July—September. Larger concentrations of larval stages were recorded between the Premuda Island and the northern margin of the Jabuka Pit as well as round the Palagruža Island. Further, Karlovac (1967) found that the density of the central Adriatic larvae and postlarvae in the open waters and channels exceeded that in the closed bays and that the time of their occurrence in plankton is opposite to the time of sardine larval stages occurrence. In the central Adriatic anchovy larvae and postlarvae were taken from plankton from April to November with maxima in June and August. It was found that they occurred within approximately the temperature, salinity and density ranges of egg occurrence (Regner, 1972). The larvae and postlarvae reach maximum numbers within 17.8—21.7°C temperature range, 35.00 — 38.58‰ salinity range and 24.5 — 27.0 σt density range (Karlovac, 1963; Regner, 1972).

Vertical distribution of anchovy larvae and postlarvae was also studied in the Adriatic. Larvae and postlarvae were found to be most numerous in the 10—20 m depth layer in the central Adriatic, while in the surface layer (0—10 m) they may be found only by night what indicates the nyctohemeral migrations (Regner, 1972). Studying the vertical distribution in the Mediterranean and Adriatic Čmovž (1973) recorded the highest concentrations of anchovy larval stages at 25—50 m.

It was found that in the Adriatic anchovy the change of larva in postlarva, i. e. the change from passive to active feeding took place at lengths of 3.1 — 3.5 mm (Duka, 1963) and/or of 2.8 — 3.9 mm (Regner, 1972).

Adriatic anchovy postlarval feeding has been studied on two occassions. Duka (1963) found that anchovy fed mainly on copepod developing stages. After this author index of gut fullness ranges from 68.28 in younger postlarvae

(3.6 — 6.0 mm in length) to 39.05 in older postlarvae (6.1 — 12.0 mm in length) and these postlarvae feed during the light period of the day with a brake at noon hours. Regner (1971) found similar food composition in anchovy from the central Adriatic. After this author the percentage of postlarvae which reach the food is higher in the coastal and channel areas than in the open sea.

The only data sources on larval and postlarval anchovy survival are those from the central Adriatic. It was observed that the number of postlarvae immediately upon the yolk sac resorption was considerably reduced if compared with that of larvae. On this basis it was concluded (Regner, 1972) that in this stage anchovy were in the »critical« period which, after Hjort (1914), occurs in many fish species at the transition from passive to active feeding owing to the lack of adequate food. The percentages of total quantity of older anchovy postlarvae (of 8.00—9.99 mm in legth) in relation to total egg quantity found during individual spawning seasons were, further, calculated for the same area in 1968—1971. These calculations, used as a rough indicator of survival, showed that survival ranged between 0.5 and 1.0%. The comparison of the percentage of survived postlarvae and the total annual number of postlarvae with the annual primary production means showed their positive correlation which indicated that the better availability of food was the basis for the better survival of anchovy postlarvae (Regner, 1974).

The already given account of the researches so far of the anchovy planktonic stages in the Adriatic shows that a relatively large number of authors have studied their ecology in detail. Comparing the results of these investigations with everything known of the other Adriatic planktonic fish stages, it may be concluded that in this respect anchovy are besides sardine, the best studied Adriatic fish species.

All the earlier data referring the anchovy eggs, irrespective whether including their seasonal distribution or long-term fluctuations have been based upon the comparison of egg quantities expressed per net haul, per cubic metre or under a square metre. Since, however, the time of embryonic development is proportional to the environmental temperature, eggs accumulated in plankton are, dependently on temperature, spawned during different number of days. This shows that the intercomparison of egg quantities cannot give a proper image of spawning intensity. To make the data intercomparable, the number of eggs recorded from a sample should, after Tanaka (1973), be divided by the number of days necessary for the complete embryonic development at the water temperature at time of sampling. Further, to give an approximately real insight into the spawning intensity expressed as a quantity of eggs spawned per unit time and area, the correction for eggs mortality should be made. Only thus elaborated samples are intercomparable irrespective of the time and place of sampling. Since no more precise data on egg development speed in relation to temperature have been available, neither mortality nor spawned egg quantities could be calculated. At the same time there are no data on larval and postlarval growth rates in relation to temperature, except those of Kornilova (1955) for 22—24°C temperature. Therefore mortality, i. e. survival could not be calculated either.

2. STUDY AREA

The studies were carried out at a transversal profile which goes almost straight south from Split. It includes the station *Kaštela Bay* (43°41'N 16°22'E), *Pelegrin* (43°12'N 16°19'E) and *Stončica* (43°00'N 16°20'E). These stations are distributed thus that they cover a relatively closed coastal area, the channel area and an area affected by the open sea. The Institute of Oceanography and Fisheries in Split has a long-term series of data on physical and chemical parameters as well as on the primary and secondary organic production collected from these stations (Fig. 1).

The depth of the *Kaštela Bay* Station is 42 m. The bay in which this station is located is characterized by the large variations of oceanological factors due to the land closeness, bay's shallowness and freshwater inflows. The bay is relatively closed, surrounded by the Kozjak Mountain, northern coast of the Čiovo Island and Marjan Peninsula. On the one side it is connected with the adjacent sea through a narrow and shallow strait near Trogir and

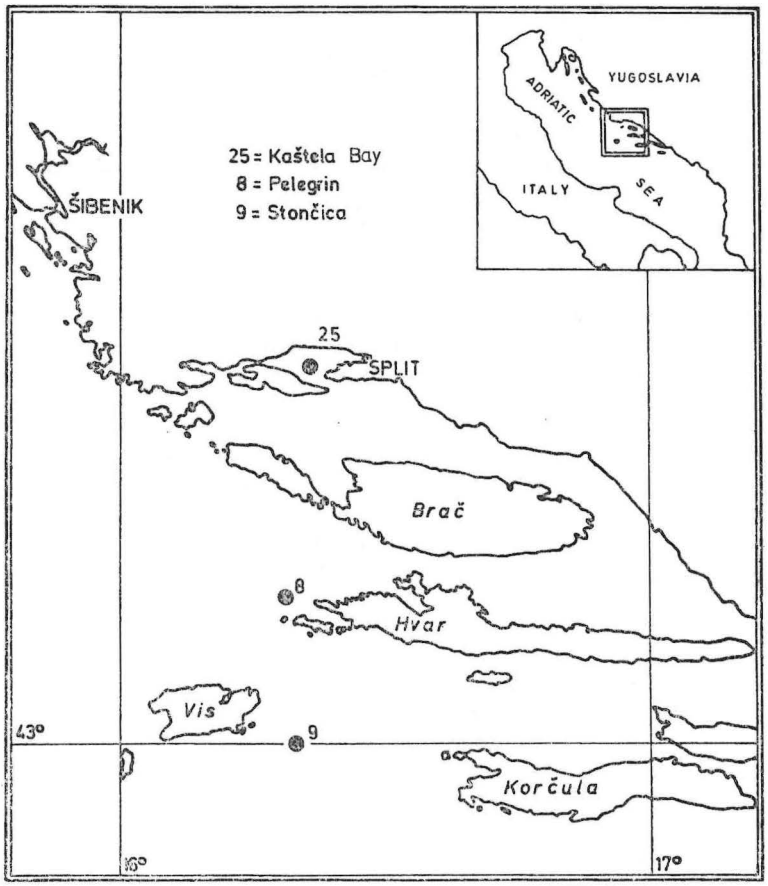

Fig. 1. The area of investigations

on the other through a strait between the Čiovo Island and Marjan Peninsula of 0.9 miles in width and 51 m greatest depth. The area of the Bay is 61 square kilometers with the mean depth of 23 m (Zore-Armanda, 1955). The greatest recorded depth is 45 m.

The fresh water inflows originate in the Jadro River drainages and submarine springs (Alfirević, 1966).

Its bottom is mainly muddy, only somewhere rocky.

After Buljan and Zore-Armanda (1971) annual surface temperature variations range between 7—8°C and 25°C, and in some places the temperature even reaches 28.05°C. According to the long-term observations by the same authors mean temperature of 0—30 m depth water column vary from 12.02°C to 22.19°C. Minimum sea temperatures of the Kaštela Bay occur in February and maximum in August (surface) and October (bottom layers). Salinity variations are also considerable ranging from 28.17—38.19‰ on the surface and/or from 34.58—38.04‰ in the 0—30 m water column. Minimum salinity values are recorded in December and January and maximum in August.

Sea currents of the Kaštela Bay are variant due to the small depth, strong local wind forcings and poor tidal currents. After Zore-Armanda (1975) mean resultant current speed is 6 cm/sec on the surface, 4 cm/sec in the intermediate layer and 3 cm/sec in the bottom layer. The greatest current speeds occur in the autumn and winter months. Resultant current directions are W, NW in spring and early summer, E in summer, particularly in the surface layer, and S in winter (Zore-Armanda, 1974). It was also calculated that the exchange of the entire bay's water mass with the Brač channel took place twice in a month's period and that the inflow somewhat exceeded the outflow (Zore-Armanda, 1975).

The primary production measurements by Steeman-Nielsen method by means of radioactive carbon (C^{14}) showed that, dependently on the year, it varied in the Kaštela Bay within the 103.2—177.4 g C/m^2 range per year with maxima in winter and spring periods (Pucher-Petković, 1970). This area seems to begin to show the signs of eutrophication due to the organic pollution originating from the town of Split effluents. The evidences of eutrophication were found in increased cell number and summer phytoplankton maximum (Pucher-Petković, 1975).

Mean zooplankton biomass value (dry weight) obtained from the long-term means is 7.7 mg/^{3}. Maxima occur in this area in the warmer part of the year in the months of March, May and August (Vučetić, 1971a).

Pelegrin Station is close to the Cape Pelegrin of the Hvar Island. Its depth reaches 78 m. This station is affected both by the land and by the open sea, thus the hydrographic properties vary less here than in the Kaštela Bay and more than in the open sea. Bottom is of sandy-detritic structure (Gamulin-Brida *et al.*, 1971).

Temperature ranges from 12.07° to 24.°C and salinity from 36.89 to 38.71‰ (Buljan and Zore-Armanda, 1966).

Current of W direction is prevalent in spring, and of NE direction in autumn. Current speeds vary from 13—23 cm/sec (Zore-Armanda, 1975).

There is no available data on primary production at this station, since primary production was not studied here by the radioactive carbon method.

However, the long-term observations of phytoplankton quantity expressed as a number of cells per litre of sea water show that phytoplankton quantities are considerably smaller here than in the Kaštela Bay and still higher than at Stončica Station (Pucher-Petković in Karlovac *et al.*, 1974).

Mean zooplankton biomass value is 4.8 mg/m^3 with maxima in March and May (Vučetić, 1971a).

Stončica Station is 4 nautical miles south from the Cape Stončica of the Vis Island, with depth of 107 m. Bottom structure is the same as that at Pelegrin Station.

This station is affected by the open sea thus that the temperature and salinity variations are lesser than at the preceding stations.

Annual surface temperature value varies from 13.52 to 23.88°C and salinity from 37.39 to 38.55‰ (Buljan and Zore-Armanda, 1966).

Resultant surface current directions at Stončica Station are NW in winter, N in spring, SE in summer and SW in autumn. E direction prevails in the intermediate layer nevertheless the W and NW direction speeds are highest. In the colder part of the year S direction is prevalent in the bottom layer what is probably in connexion with the outflow of the cooled coastal water which flows out towards the open sea close to the bottom. In the warmer part of the year the alternative occurrences of W and SE directions are recorded. Current speeds vary from 1—14 cm/sec on the surface, 5—13 cm/sec in the intermediate layer and from 3—16 cm/sec in the bottom layer (Zore-Armanda, 1968).

Primary production of organic matter varies at this station dependently on the year, from 44.4 to 92.2 g C/m^2 per year (Pucher-Petković et Zore-Armanda, 1973). As it may be seen the primary organic production is considerably less here than in the Kaštela Bay. This is probably due to that the nutrient concentrations are lower here than in the costal area (Buljan *et al.*, 1975). Maximum organic matter production occures at this station in winter (December-January) and spring (May-June).

Zooplankton biomass is, on an average, 3.8 mg of dry matter per cubic metre. Higher dry weight values occur from March to May with the marked maximum in April (Vučetić, 1971a).

The long-term observations of all the stations of the study area show that salinity and nutrient quantities are periodically increased what after Pucher-Petković and Zore-Armanda (1973) produces favourable effects for the primary and secondary organic production, both in this area and in the whole Adriatic. These salinity and production relation changes are, after Buljan (1953), due to periodical intensified ingressions of the more saline eastern Mediterranean water into the Adriatic.

3. MATERIAL AND METHODS

Stations Stončica and Pelegrin were sampled from January 1962 to December 1976, and the Kaštela Bay Station from February 1968 to December 1976. All samplings were made on monthly basis by m/v BIOS and m/v PREDVODNIK. A total of 176 2—4 day cruises were realized.

At all stations the zooplankton samples were obtained by double vertical hauls with a plankton net of »Helgoland« type (K ü n n e, 1933). Net's mouth aperture diameter is 143 cm with 1.6 m^2 area. Net of silk No. O with 0.516 mm mesh size was towed at a speed of 0.5 m/sec, viz. at about 1 knot. Material collected by both hauls was kept in the same jar and fixed in 2% neutralised formol solution in the sea water.

Net was towed from bottom to surface, at Stončica and Pelegrin from 75 m and in the Kaštela Bay from 30 m depth.

Data on the sea temperature and salinity were collected simultaneously with zooplankton samplings at each of the stations. These data were taken from standard oceanographic levels, i. e. from 0, 10, 20 and 35 m at the Kaštela Bay Station, from 0, 10, 20, 30, 50 and 75 m at Pelegrin and from 0, 10, 20 30, 50, 75 and 100 m at Stončica.

Collected zooplankton material was further worked out in the laboratory. Prior to sorting, zooplankton samples were sedimented for 24 hours in 1 l beaker in order to obtain the data on the overall plankton volume. Volume was expressed in cubic centimeters. Material was then examined under binocular microscope at 10 times enlargement and the complete ichthyoplankton separated. From the rest, the anchovy planktonic stages were extracted and counted. Anchovy planktonic stages were determined after D' A n c o n a (1931).

Planktonic stages were classified according to the following scale:

1. Egg stage, from fertilization to hatching.
2. Larval stage, from hatching to the complete yolk sac resorption. As a rule, only pectoral fins are differentiated in this stage. Mouth opening has not yet developed, eyes are not pigmented. At termination of this stage mouth is opened and eye pigmentation begins.
3. Postlarval stage initiates with the complete yolk sac resorption. Mouth is well formed, eyes pigmented and the differentiation of dorsal, ventral, and caudal fins begins. Body loses its transparency and pigmentation is increased.

The classification given for sardine in the GFCM Studies and Reviews, No. 1 (1957) was used to classify anchovy eggs with respect to the embryonic development. This classification was adapted to anchovy thus that eleven stages (I—XI) were modified to ten (I—X).

I stage includes non-fertilised and fertilised eggs in which cleavage has not yet started. It ends with the cleavage beginning.

II stage starts with the occurrence of two blastomeres and extends to the beginning of gastrulation.

III stage begins with the occurrence of gastrulation cavity. At the end of this stage the blastodisc covers about one-third of the yolk.

IV stage begins with the embryo distinction along the median line, head formed on the embryo is clearly distinctive since it is wider that other embryo's parts. At the end three-thirds of the yolk are covered by blastodisc.

V stage begins with the three-thrids of the yolk been enclosed by blastodisc and lasts till the blastopore is closed. The folds of dorsal fin are visible on embryo. Eye bubbles become discernable at the end of this stage.

VI stage begins from the closing of blastopore and appearance of eye bubbles and lasts till the beginning of tail separation from the yolk sac. Eyes extend almost to the half head. Somites formation begins. Embryo thickens all its length long and pupils become distinct.

VII stage begins with the separation of tail from the yolk sac and ends when tail is one-third as long as the body. Tail top is rounded and is still in the same plane with the body. Fin folds are clearly visible around the tail part.

VIII stage begins with tail flexing laterally. Ventral fold of primordial fin is as wide as the embryo's body. At the end of this stage tail top is pointed and the tail is bent at and angle of 90 degrees with respect to the its position at the end of seventh stage.

IX stage begins when the tail is back in the plane of the embryo's body, which is turned up at an angle of 90 degrees with rescept to the one at the end of stage VIII. It ends when the free body part is half as long as the body.

X stage begins when tail exceeds one half the body length and ends with the larva hatching from egg.

Thus classified eggs were counted and the number of dead eggs in the sample was separately recorded. The eggs with opaque yolk with destroyed vesicles, partly or fully split in the perivitelline space were taken as dead eggs. If these eggs reached the stage in which the embryo was developed it was frequently destroyed or in an unnatural position.

The alive and dead anchovy eggs and undamaged larvae and postlarvae were measured under a binocular microscope at a 10×4 enlargement by means of an ocular-micrometer with 0.0375 mm precision. Longer and shorter diameters were taken in eggs. Standard length (LS) from the top of snout to tail fin base was measured in larvae and postlarvae, since their tails were frequently damaged. Measured larvae and postlarvae were thereafter sorted into length groups on the basis of the data on growth experimentally obtained.

Quantity of anchovy eggs, larvae and postlarvae was expressed as a number of individuals below a square metre of the sea surface. The following equation given by Tanaka (1973) was used for this calculation:

$$Y = \frac{X}{A \cdot \frac{D}{d} F} \qquad (3.1)$$

where Y is the number of specimens under a square metre, X the number of specimens in the plankton sample, A area of net aperture, D length of a path or water column over which the net was towed, d maximum reached depth and F filtration efficiency.

As already mentioned the area of aperture of »Helgoland« plankton net is 1.6 m^2. Since there were always performed two hauls the net aperture should be multiplied by 2 to obtain the A value. Accordingly A is 3.2 here. Since plankton catches were always realized by vertical hauls the D/d ratio is ~ 1 and therefore negligible. Filtration efficiency (F) was not separately calculated for »Helgoland« net type. Since the aim of this study was to obtain the intercomparable data on the quantity of anchovy planktonc stages in the study area and not the absolute data, the F values was taken to be approximately 1. Accordingly, the number of specimens under a square metre was calculated thus that:

$$Y = \frac{X}{3.2} \qquad (3.2)$$

As it has already been mentioned in the chapter 1.1, results expressed in this way, particularly those concerning anchovy eggs, are not intercomparable. Namely, egg quantity in the plankton is, to a large extent, dependent on the presence of a larger or smaller number of embryonic stages, which, further, depends on the embryonic developmental time, i. e. on the temperature of the environment. To make the data on catches realized at different temperatures intercomparable a further correction should be made by means of the equation which after Tanaka (1973) is as follows:

$$Y' = \frac{X}{D \cdot K} \qquad (3.3)$$

where Y' is the number of eggs spawned below a square metre per day, Y number of eggs below a square metre from the equation (3.2), D time of embryonic development at defined temperature expressed in days and K mortality correction. Thus calculated Y' value gives the spawning intensity, i.e. the number of planktonic eggs »produced« by females per unit area per day. Therefore, hereinafter this value will be called egg production.

In order to obtain the necessary data for the correction of anchovy egg quantity with respect to sea temperature and mortality, as well as for the calculation of larval and postlarval mortality several experiments were run in 1976 and 1977.

Time of egg development as influenced by temperature was studied on three occasions, on 6 September 1976 at mean temperatures of 15.38 and 20.04°C, on 29 June 1977 at temperature of 17.90, 19.50, 21.00 and 24.10°C, and on 23 July 1977 at temperature of 17.14, 18.73, 22.05 and 23.88°C. The experiments could not be run at more than four temperatures at a time and we were forced to carry them out in a succession. Larval and postlarval growth was studied during these experiments whenever the quantity permitted. For this purpose three separate experiments were carried out, started on 24 August, 8 September and 16 September 1977. Thus the larval growth was studied at ten mean temperatures of 16.7, 17.77, 18.7, 19.02, 19.6, 21.1, 21.3, 21.88, 21.98 and 24.05°C and postlarval growth at three temperatures of 19.02, 21.3 and 24.05°C.

Material for the studies of anchovy egg development speed was obtained by artificial fertilization of mature eggs. To obtain mature individuals for

artificial fertilization adult anchovy were caught by pelagic trawl in the Kaštela Bay and Šolta Channel in the close vicinity of the Institute of the Oceanography and Fisheries. Thus the fertilised eggs could be placed in the incubation facility soon after fertilization. Pelagic trawl was towed by motor vessel BIOS for 40—50 minutes at a speed of 3.7 knots at depth between 20 and 40 m. Fishing was always carried out during evening hours since it was known that anchovy spawn at this period of the day (V u č e t i ć, 1957; V a r a g n o l o, 1964a). Alive and undamaged anchovy individuals were put in a container with the sea water and the males and females with the gonads in the VI maturity stage separated (S i n o v č i ć, 1978), that is immediately prior to spawning. The method of »dry fertilization« was applied. Eggs with sperm were left for 10—15 minutes out of water and thereupon the previously filtered sea water with streptomycin sulphate in 30 mg/l concentration was gradually added. The time at which the water was added was taken to be the time of fertilization. Thus the fertilization was carried out at 22.35^h on 6 September 1976, at 21.20^h on 29 June 1977 and at 22.45^h on 23 July 1977. Since the fertilization was carried out on board it was not possible to maintain the constant water temperature. It was recorded that at the time of fertilization temperatures were 20.5°C, 24.00°C and 24.50°C. Not later than 30—40 minutes after fertilization eggs were brought into the laboratory. A part of the material was placed in the thermostatic chamber (constant temperature laboratory room) and a part was kept at the temperature of the laboratory to study the fertilization efficiency.

Eggs for the experiments initiated on 24 August, 8 September and 16 September 1977 which were intended exclusively for the study of the characteristics of larval and postlarval growth, were collected from the Kaštela Bay plankton by a cylindric-conic, silk Nr. 3, 0.333 mm mesh size plankton net of 196 cm length and 57 cm aperture diameter. Net was hauled twice for 10—15 minutes at a speed of 1 knot. Undamaged eggs of most frequently the IV embryonic development stage were extracted and incubated at 21—22°C temperature. A number of eggs were placed in the thermostatic chamber immediately before hatching.

Eggs, larvae and postlarvae were kept in the thermostatic chamber of $4 \times 3 \times 2.2$ m dimensions fitted a facility for maintenance of constant air temperature of the 0—25°C range with the $\pm$ 1°C precision. Parax bottles of 1.5 l capacity were used as incubation jars in the experiments started on 6 September 1976 and 29 June 1977, and rectangular glass tanks of $27 \times 19 \times 9$ cm dimensions for the rest of the experiments. Bottles were filled to 1.5 l with filtered sea water and tanks to 5 l. The water was added a 30 mg/l streptomycin sulphate concentration to prevent bacterial reproduction. Both the bottles and tanks were immersed in 22.5 l plastic black tanks with the fresh water. The temperature of each time on of these incubators was always kept at a constant temperature of the thermostatic chamber while other incubators were heated by a 1000 W heater connected through a contact thermometers immersed in the fresh water. This allowed the rearing tank to be maintained at the temperature higher than that of the thermostatic chamber. During the experiments thermometers for temperature control were continuously immersed in the sea water. The sea water was continuously aerated by means of an air pipe vith about 1 m^3/min flow.

Each thermostatic facility was illuminated with two 100 W bulbs. All the bulbs were connected through an authomatic switch which maintained a 15 h light- 11 h dark regime.

The sea water level in the vessels was noted and distilled water was added every 24 hours to prevent the salinity increase due to evaporation. During egg incubation water was not replaced. However, during larval and postlarval incubation it was replaced every 3—4 days. Due to the small quantity of water, observations of salinity were made only occasionally. It was established that salinity varied within relatively narrow limits (36.75 — 38.78‰).

Temperature was measured to the nearest 0.1°C every 2—7 hours in egg experiments, every 10—12 hours in larval experiments and once a day in postlarvae ones. The highest temperature deviations from mean values varied from —1.18 to +1.32°C in the experiment of 23 July 1977 at mean temperature of 23.88°C, and the lowest ones of —0.2 to +0.1°C in the experiment of 29 June 1977 at mean temperature of 24.1°C.

During experiments 10 to 15 eggs were taken every 2—7 hours and observed by binocular microscope at 4 × 10 enlargement for embryonic stage control and thereupon the eggs were placed back into the incubator. Larvae and younger postlarvae were measured every 10—12 hours and older postlarvae every other day. Like in the material collected from the plankton, their standard lenght (LS) was taken under 4 × 10 enlargement with the precision of 0.0375 mm. Both larvae and postlarvae were measured alive in the small quantity of water and upon measurement they were preserved in 2% neutralised formol diluted in the sea water. Two months later they were remeasured to establish to what extent had the preserved specimens shrank. Dependently on the available quantity the measured samples contained from 1—16 specimens. An approximate time of occurrence of morphological changes such as the mouth opening, eye pigmentation and yolk sac resorption was also observed in larvae.

In some of the experiments initiated on 23 July, 24 August and 16 September 1977, dead eggs, larvae and postlarvae were collected and counted to make an approximate estimation of mortality during experiments.

Postlarvae were fed with »wild plankton« which mainly contained nauplii and copepodites. In the experiment of 23 July 1977 plankton was supplied by a pump with the flow rate of 20 l/min. The sea water pumped passed through a plankton silk sieves of 0.516, 0.333, 0.250, 0.060 and 0.010 mm diameter. Plankton which did not passed through a 0.010 mm sieve was given as a food to postlarvae. Since this way of providing food proved to take too much time and did not give sufficient food quantity, for the 24 August and 16 September 1977 experiments food was collected by plankton nets of 34 cm mouth aperture and 104 cm total length. Food for younger postlarvae was caught by a net of nylon material with 0.037 mm mesh size and for older postlarvae with 0.060 mm mesh size net. Nets were hauled in the surface layer two times for 20 minutes. The caught plankton was filtered the same manner as in the case with the pump. 1 ml of sea water was taken from the filtered material and microscoped. Nauplii and copepodites were counted to establish the plankton concentration which should be aded to the containers to keep the food concentration constant. Food was supplied once a day and the nauplii concentration was taken as a measur of food quantity. In 23 July and 24 August 1977 experi-

ments the nauplii concentration was maintained at 5 individuals per ml of water in the tanks and in 8 September and 16 September 1977 experiments at 10 individuals per ml of water.

Results obtained by working out both the *in situ* collected material as well as that of the experiments, were further analysed by mathematical and statistical methods.

4. RESULTS AND DISCUSSIONS

4.1. TIME OF EGG DEVELOPMENT, RATES AND CHARACTERISTICS OF ANCHOVY LARVAL AND POSTLARVAL GROWTH AS INFLUENCED BY TEMPERATURE

Results

The principal goal of the experiments with eggs, larvae and postlarvae of anchovy was to obtain the data on the time of their development and growth rates as affected by temperature. However, some other data were also obtained during these experiments such as those on the survival of eggs, larvae and postlarvae.

Data on anchovy egg mortality were obtained only from the experiments carried out at 17.14 and 24.10°C temperatures in which at the beginning the number of eggs was 865 and 606 respectively. At 17.14°C temperature 171 larvae were hatched, i.e. 19.8% eggs survived. Since the experiment at 24.10°C temperature was continued even after hatching, it was not possible to establish an accurate number of hatched larvae. After an estimation on the basis of counted dead eggs in the final developmental stage and the first dead larvae upon hatching, about 67% eggs survived.

The highest egg mortality was found to occur up to the IV—V stages, while it was particularly low in the later stages (Fig. 2).

Data on larval and postlarval mortality were obtained during the experiments at 19.02, 21.30, 21.88 and 24.05° temperatures. Counting of dead individuals included not only the larvae and postlarvae found on the bottom of the basin but also those which were caught for length measurements.

Counting of dead individuals showed that the mortality rate in larvae was almost constant up to the yolk sac resorption (Fig. 3). The highest mortality up to the yolk sac resorption was recorded at lowest temperature (47% survived) and the lowest mortality at highest temperature when 80% of larvae survived.

Further, as shown by Fig. 3, a sudden increase in mortality occurred not later than 1.2 days upon the yolk sac resorption at all the temperatures except at the 24.05°C one. It may be assumed that they starved to death after the transition to exclusively active feeding. As soon as larvae attained the length of about 3.8 mm, mortality became negligibly low and was due only to the fact that some of them were used for length measurements. The lowest percentage of survived postlarvae before they attained the above mentioned length was recorded at 21.30°C (about 6%) and the highest at 21.88°C (about 14%). This relatively small difference in survival percentage shows that the postlarvae were exposed to almost the same mortality causes in all the experi-

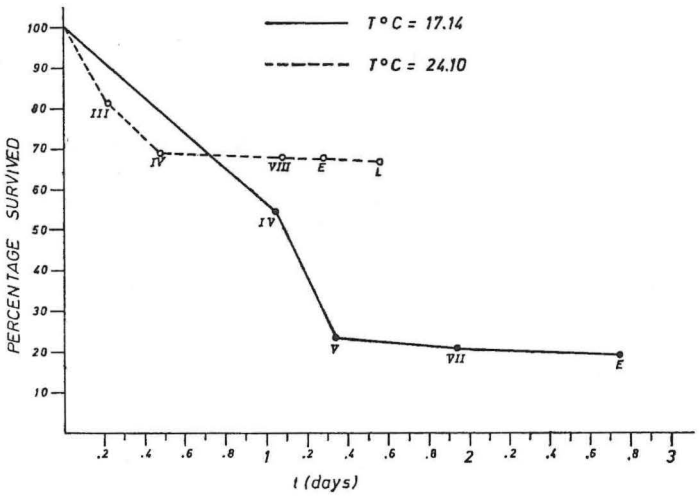

Fig. 2. Survival of anchovy eggs under experimental conditions. Stages are given by Roman numerals
E = time of hatching
L = larval stage

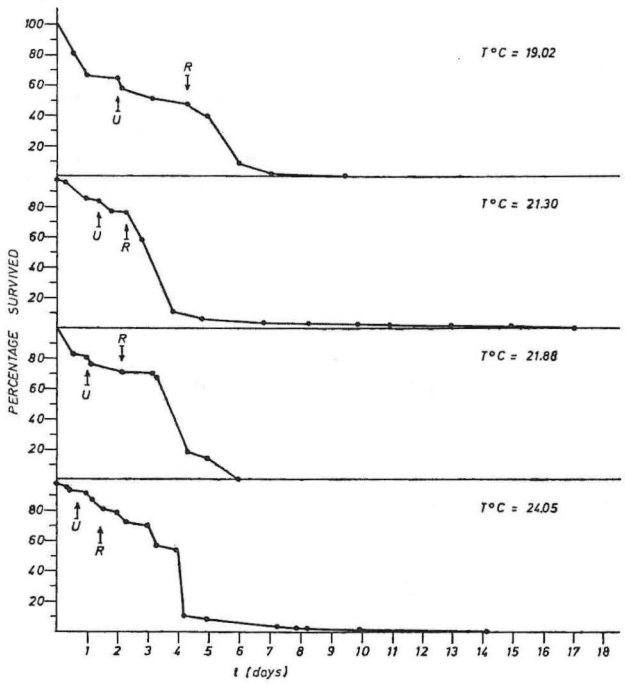

Fig. 3. Survival of anchovy larvae and postlarvae under experimental conditions
U = mouth opening
R = yolk sac resorption

ments. Any time before anchovy eggs were placed in the incubation vessels they were observed under a binocular microscope. Those observations, carried out 30—40 minutes after fertilization, showed that cleavage had already begun in almost all the eggs and that either the first two or four blastomeres had been formed. This means that eggs were at the beginning of the II stage of embryonic development. Nevertheless the sea water temperature at fertilization was high (20.5, 24.00 and 24.50°C), this is indicative of the fact that the first embryonic stage, from spawning and fertilization to the occurrence of the first two blastomeres takes very little of the time needed for an overall embryonic development.

Results of the examination of anchovy eggs left at ambiental temperature for 2 hours after the fertilization are given in Table 4.1.1.

Table 4.1.1. Percentage of fertilized anchovy eggs by artificial »dry« method

Date	Anchovy eggs			
	Total	II stage (fertilized)	I stage (unfertilized)	% Fertilized
06. 09. 1976.	163	142	21	87.12
29. 06. 1977.	104	96	8	92.31
23. 07. 1977.	148	126	22	85.14

On the basis of the data from Table 4.1.1. mean percentage of fertilized eggs was calculated to be 87.71%.

Results obtained on the basis of the experiments with anchovy eggs incubated at different temperatures showed that higher the environmental temperature the development of this fish, as well as that of other poikilotherms, was faster. Egg development at the lowest temperature of 15.38°C took 86.10 hours (3.59 days) and at the highest temperature of 24.10°C only 30.63 hours (1.28 days). Mean time between hatching of first and last larva was taken as the total developmental time. Developmental time as well as the time of beginning of each of the embryonic stages at all ten temperatures is given in Table 4.1.2. It was established that the relation of developmental time to temperature was not linear.

Four equations were used for the interpretation of anchovy egg developmental time curve as related to temperature, to study which one gives the best mathematical approximation.

— modified thermal sum equation used first by Reibisch (1902) and given after Alderdice and Velsen (1978) for the study of fish egg development in relation to temperature:

$$D = \frac{C}{T - a} \qquad (4.1.1),$$

then:

$$D = 10^{a} \cdot 10^{-bT} \text{ (Ahlstrom, 1943)} \qquad (4.1.2),$$

further the «inversely logistic equation« (Davidson, 1944)

Table 4.1.2. Developmental time of eggs as affected by temperature (parts of the hour are given by decimals; E. p. — the beginning of hatching; E. k. — the end of hatching; D — total developmental time).

Temperature									
15.38		17.14		17.90		18.73		19.50	
Hours	Stage	Hours	Stage	Hours	Stage	Hours	Stage	Hours	Stage
0	I	0	I	0	I	0	I	0	I
9.10	II	1.23	II	2.45	II	1.23	II	2.47	II
13.60	II	11.03	II/III	4.70	II	10.82	II	4.62	II
18.10	III	13.70	III	8.70	II	13.52	IV	8.77	III
45.08	V	15.65	III	12.04	III	15.55	IV	11.92	IV
61.20	VI/VII	22.03	IV	14.25	III	22.00	V	14.17	IV
69.80	VIII	24.33	IV	22.15	IV	24.28	V/VI	21.71	V
80.03	X	26.20	IV/V	25.29	V	26.17	VI	25.34	VI
83.83	E. p.	30.47	V	28.39	V	30.43	VI	28.32	VI
88.92	E. k.	33.32	V	31.20	VI	33.28	VI	31.24	VII
		34.78	VI	33.40	VI	**34.75**	VII	33.35	VII
86.10	$\bar{D}$	36.28	VI	36.87	VI	36.25	VII	36.84	VII/VIII
		37.95	VI	39.24	VI/VII	37.92	VII	39.20	VIII
		39.58	VI	41.34	VII	39.57	VII/VIII	41.17	IX
		45.33	VII	43.42	VII	45.28	VIII/IX	45.17	X E. p.
		45.62	VII	45.42	VII	47.65	IX/X	46.74	E. k.
		49.87	VII/VIII	47.82	VII	48.42	X E. p.		
		55.33	VIII	49.00	VII	51.58	E. k.	45.95	$\bar{D}$
		58.63	VIII/IX	51.37	VIII				
		61.57	IX	55.00	X	50.00	$\bar{D}$		
		64.25	X E. p.	57.00	X E. p.				
		67.25	E. k.	59.34	E. k.				
		65.75	$\bar{D}$	58.17	$\bar{D}$				

Table 4.1.2. — continued

Temperature									
20.04		21.00		22.05		23.88		24.10	
Hours	Stage	Hours	Stage	Hours	Stage	Hours	Stage	Hours	Stage
0	I	0	I	0	I	0	I	0	I
9.01	III	2.62	II	1.23	II	1.23	II	2.65	II
13.40	IV	4.50	II	10.70	IV	10.47	IV	4.39	III
41.75	E. p.	8.85	III	13.40	IV/V	13.22	V	8.99	IV/V
43.43	E. k.	11.87	IV	15.42	V	15.25	V/VI	11.65	V
		14.07	IV	21.98	VI	21.90	VII	13.84	V/VI
42.59	$\bar{D}$	21.97	VI	26.10	VII	24.08	VII	21.74	VII
		25.32	VI	30.42	VII/VIII	26.03	VIII	25.09	VIII/IX
		28.24	VII	33.17	VIII/IX	30.25	X E. p.	28.09	IX
		31.09	VII	34.42	X E. p.	32.25	E. k.	29.17	X E. p.
		33.27	VIII	36.25	E. k.			32.09	E. k.
		36.74	VIII/IX			31.25	$\bar{D}$		
		38.67	X E. p.	35.34	$\bar{D}$			30.63	$\bar{D}$
		40.80	E. k.						
		39.73	$\bar{D}$						

$$D = \frac{1}{C}(1 + e^{a+bT}) \qquad (4.1.3),$$

and

$$D = C\,T^{-b} \text{ (Lasker, 1964)} \qquad (4.1.4).$$

In all the equations D is developmental time in hours, T temperature in °C. In equation (4.1.4) C is the constant, whereas a is theoretical temperature of development threshold. Values a, b and c in the equations (4.1.2) and (4.1.4) are constants. In the equation (4.1.3) C is the asymptote whereas a and b are constants.

In all the equations mean constant values were calculated by the linear regression method. Further, correlation coefficients as well as their significance levels were calculated in all the equations comparing the following values:

$$r\left(T_i; \frac{1}{D_i}\right) \qquad (4.1.1),$$

$$r\,(T_i;\ \log D_i) \qquad (4.1.2),$$

$$r\,(e^{bT_i};\ D_i) \qquad 4.1.3),$$

$$r\,(\log T_i;\ \log D_i) \qquad (4.1.4),$$

where i is every i^{th} datum.

Calculated correlation coefficients showed high statistical significance in all used equations (Table 4.1.3). However, as it may be seen from the correlation coefficient values, the (4.1.3) equation gave best approximation, (4.1.4) coming next.

Table 4.1.3. Calculated means of constants, correlation coefficients and their significance levels. Egg developmental time calculated by each separate equation for the temperatures of 15.38, 20.04 and 24.10°C. Egg developmental time is expressed in hours. * — Developmental time in the experiment at defined temperature

Equation	$\bar{C}$	$\bar{a}$	$\bar{b}$	r	p	D 15.38	D 20.04	D 24.10
1. $D = \frac{C}{T - a}$	460.7	9.495	—	0.976	0.001	78.28	43.69	31.54
2. $D = 10^{a} \cdot 10^{-bT}$	—	2.651439	—0.049463	—0.975	0.001	77.75	45.73	28.80
3. $D = \frac{1}{C}(1 + e^{a+bT})$	0.042204	4.914322	—0.257451	0.999	0.001	85.25	42.24	30.22
4. $D = C\,T^{-b}$	42922.0767	—	—2.290236	—0.993	0.001	82.09 86.10*	44.77 42.59*	29.35 30.63*

Even though the best approximation of the anchovy egg developmental time was obtained by the application of the »inversely logistic« equation (4.1.3), the equation (4.1.4) for the calculation of the developmental time of anchovy eggs in the plankton was used owing to its simplicity.

Therefore all further calculations were carried out by the equation:

$$D = 1788.4199 \cdot T^{-2.290236} \qquad (4.1.5)$$

in which the time of development was expressed in days since C value was divided by 24.

The time needed to reach the end of each of the embryonic stages was as well calculated by the application of equation (4.1.4). It could not, however, be calculated for the first stage, since, as it has been already mentioned, it took very short time. The *b* values were found to vary between —2.23942 to —2.421353 with the mean value of —2.33222. This shows that, taking into account an eventual error in determination of the time of the end of one stage and the beginning of the next one at different temperatures and errors in mathematical calculations, the curve slopes were the same for all stages and they may be given for each of the stages by the *b* value from equation (4.1.5). Further, *C* constant values calculated for each individual stage were divided by the value of the constant for the total developmental time.

$$K_i = \frac{C_i}{C_{uk}}; \; i = II—X \qquad (4.1.6),$$

and thus *K* koefficients of the relation between the time of reaching the end of any of the embryonic developmental stages (i) and the time needed for the complete development (C_{uk}) were obtained. In this way the age of any temperature may be calculated by multiplying the *C* values from equation (4.1.5) with *K* coefficient from Table 4.1.4.

Table 4.1.4. C constant correction coefficients for individual development stages

Stage	II	III	IV	V	VI	VII	VIII	IX	X
K_i	0.162	0.245	0.395	0.476	0.669	0.778	0.890	0.053	1

Percentages of the time of each individual stage, except the first one, were also calculated in relation to the total developmental time by means of the following expression:

$$P = \frac{Dst_i - Dst_{i-1}}{Duk} \cdot 100,$$

where *P* is the time of each individual stage in percentages, Dst_i the end of each individual stage, Dst_{i-1} the end of the preceding stage and *Duk* total developmental time. The results obtained are given in Table 4.1.5.

Table 4.1.5. The time taken by each individual stage expressed as the percentage of the time needed for total development

Stage	II	III	IV	V	VI	VII	VIII	IX	X
P	16.30	7.95	15.06	8.37	19.25	11.73	10.46	6.28	4.60

After the results obtained, the II, IV and VI stages took most of the time while the X stage takes the least.

Fig. 4 gives the total time of egg development at studied temperatures and mathematically calculated curves for both the total development and that of the each individual stage.

Together with the measurements of larval and postlarval lengths, the data on an approximate time of occurrence of morphological changes in larvae, such as the beginning of mouth opening formation and eye pigmentation were also obtained during experiments as well as an approximate time of the complete yolk sac resorption, i.e. of the transformation to postlarvae (Table 4.1.6). Mouth opening formation and eye pigmentation were found to occur simultaneously.

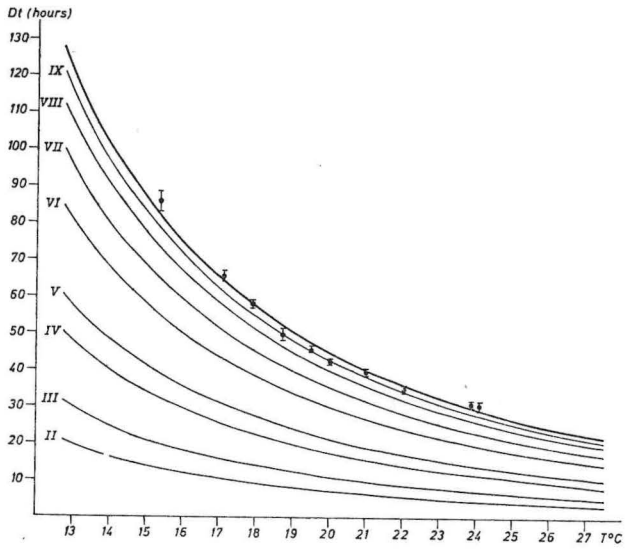

Fig. 4. Developmental time of anchovy eggs as influenced by temperature
Roman numerals mark the end of each individual stage

Results of length measurements showed that the length increment in larvae, from hatching to transformation to postlarvae averaged 1.08 mm (Table 4.1.7).

Table 4.1.6. Results of length (LS) measurements of anchovy larvae and postlarvae studying their growth at different temperatures (t = time in days, parts of the day expressed in decimals; N = number of measured individuals; l = mean length; O = mouth opening and eye pigmentation; R = yolk sac resorption)

Temperature							
16.70				16.77			
t	N	Range	$\bar{l}$	t	N	Range	$\bar{l}$
0	6	2.36—2.70	2.51	0	5	2.36—2.55	2.44
1.10	3	3.11—3.49	3.28	0.52	5	2.89—3.23	3.10
2.30	3	3.19—3.73	3.51	2.00	3	3.26—3.71	3.43
3.10	3	3.41—3.45	3.45^{o}	3.16	3	3.38—3.49	3.46^{o}
4.10	3	3.45—3.64	3.51	4.29	3	3.34—3.53	3.43
				4.96	3	3.53—3.75	3.61^{r}
				7.00	3	3.53—3.75	3.66
		18.70				19.02	
0	11	2.18—2.43	2.35	0	5	2.36—2.55	2.44
0.45	13	3.00—3.45	3.18	0.05	5	3.15—3.34	3.23
1.40	12	3.38—3.93	3.58	0.99	3	3.21—3.28	3.33
2.48	9	3.38—3.68	3.51^{o}	1.96	3	3.41—3.56	3.50^{o}
3.45	10	3.38—3.75	3.50	3.13	3	3.34—3.53	3.47
				4.30	3	3.45—3.60	3.55^{r}
				4.96	3	3.26—3.79	3.54
				7.00	3	3.71—3.90	3.80
				9.42	2	4.76—5.55	5.16
		19.60				21.10	
0	3	2.47—2.63	2.54	0	2	2.51—2.55	2.53
0.57	1	—	3.23	0.82	1	—	3.30
0.77	2	3.23—3.56	3.40	1.50	1	—	3.60^{o}
1.70	1	—	3.53^{o}	2.00	1	—	3.64
3.60	1	—	3.60^{r}				
2.50	1	—	3.60				
		21.30				21.88	
0	7	2.39—2.68	2.52	0	5	2.36—2.55	2.44
0.29	3	3.08—3.15	3.10	0.51	4	3.19—3.34	3.25
0.94	3	3.30—3.56	3.47	0.99	4	3.38—3.56	3.46^{o}
1.38	4	3.41—3.60	3.56^{o}	1.97	3	3.38—3.56	3.46
1.79	3	3.23—3.41	3.29	2.13	3	3.41—3.53	3.46^{r}
2.29	3	3.38—3.41	3.40^{r}	3.29	3	3.19—3.49	3.34
4.79	3	3.45—3.64	3.55	5.96	4	3.46—4.31	3.82
6.79	1	—	4.61				
8.96	2	6.19—6.98	6.59				
10.89	1	—	7.80				
12.95	1	—	7.80				
12.95	1	—	10.31				
14.92	1	—	11.33				
17.01	2	10.91—15.11	13.01				

Table 4.1.6. — continued

Temperature							
21.98				24.05			
t	N	Range	$\bar{l}$	t	N	Range	$\bar{l}$
0	16	2.25—2.59	2.45	0	10	2.32—2.56	2.47
0.48	12	3.03—3.49	3.27	0.28	10	3.09—3.35	3.16
0.95	1	—	3.60	0.67	7	3.32—3.56	3.45^{o}
1.07	9	3.23—3.90	3.58^{o}	1.23	7	3.15—3.55	3.49
2.04	9	3.34—3.86	3.65^{r}	1.42	9	3.34—3.64	3.47^{r}
				2.22	9	3.38—3.60	3.51
				3.27	10	3.38—3.83	3.62
				4.21	10	3.19—3.45	3.35
				5.23	9	3.01—3.56	3.28
				8.10	5	3.98—5.10	4.63
				10.17	3	4.90—6.75	5.95
				14.10	4	8.70—12.45	9.96

Table 4.1.7. Length of anchovy larvae (in mm) at hatching, mouth opening and eye pigmentation and transformation to postlarvae (complete yolk sac resorption)

	N	Range	$\bar{X}$	S. D.
Hatched larvae	60	2.18—2.70	2.46	$\pm$ 0.110
Mouth opening, eye pigmentation	45	3.23—3.90	3.50	$\pm$ 0.143
Yolk sac resorption	30	3.34—3.86	3.54	$\pm$ 0.139

The experiments also showed that mouth formation and yolk sac resorption occur earlier at higher temperatures than at the lower ones (Table 4.1.6). Mathematical analysis of the relation between the time between hatching and the beginning of these changes and temperature showed that it, as well as in eggs, may be given by the equation (4.1.4). It was found that the time of mouth opening and eye pigmentation may be calculated by the equation

$$D = 412428.585 \cdot T^{-4.1562} \qquad (4.1.7),$$

and the time of the complete yolk sac resorption by the equation

$$D = 270065.2774 \cdot T^{-3.8079} \qquad (4.1.8),$$

where D is time expressed in days and T temperature in °C.

Calculated curves are given in Fig. 5.

Coefficients of correlation between the time and temperature were calculated, like for eggs. They were found to be —0.979 and —0.977 respectively and after t-test, significant for the high significance level of $P < 0.001$.

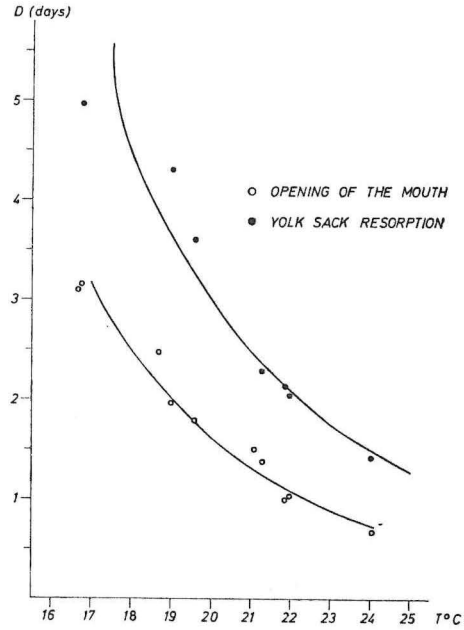

Fig. 5. Developmental time of anchovy larvae as influenced by temperature

Results of larval length measurements showed their very fast growth at the beginning, which slowed down considerably after mouth opening formation and eye pigmentation. Thereafter by the end of the yolk sac resorption larval growth was very slow. Even a decrease in larval mean length was recorded in this phase (Fig. 6).

To describe anchovy larval growth up to the yolk sac resorption the following equations were used:

$$l_t = K \log t \quad \text{(Farris, 1960)} \qquad (4.1.9),$$

and

$$l_t = A - Be^{-ct} \quad \text{(von Bertalanffy, 1938)} \qquad (4.1.10),$$

where l_t from equations (4.1.9) and (4.1.10) are larval lengths in time t, and t is time in days. The A value in equation (4.1.10) is asymptote, while K (4.1.9), B and c (4.1.10) are constants.

Values K, A, B and c were separately calculated for each individual temperature. To compare the statistical significance of these two equations, the correlation coefficients were calculated for the pairs:

$$r(\log t_i;\ l_{t_i}) \qquad \text{in the equation} \qquad (4.1.9) \text{ and}$$

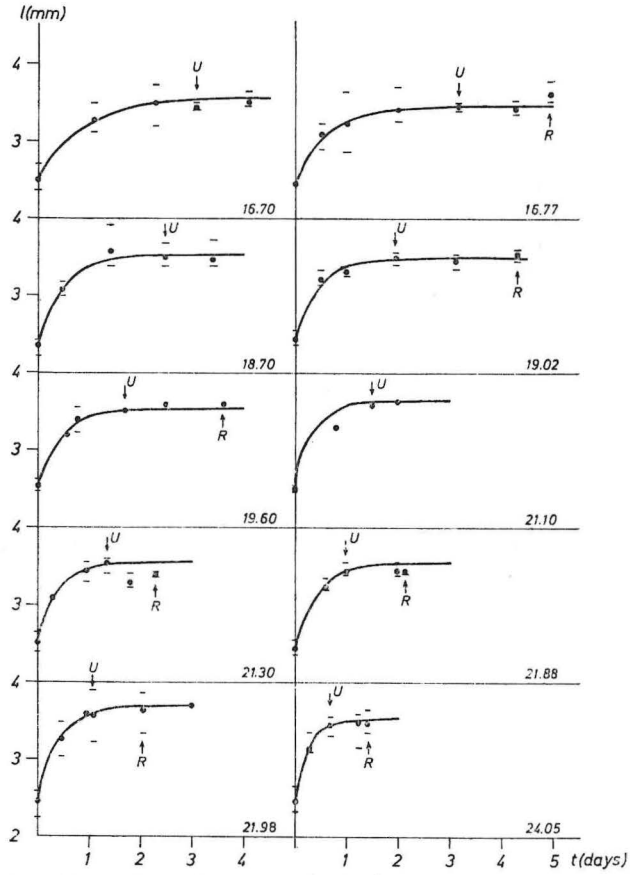

Fig. 6. Anchovy larvae growth curves
U = Mouth openning
R = Yolk sac resorption

$$r\,(t_i;\ \ln A - l_{t_i}) \qquad \text{in the equation} \qquad (4.1.10)$$

The results obtained for each individual temperature at which the experiments were carried out are given in Table 4.1.8.

Mean correlation coefficient value was found to be $r = 0.883$ for the equation (4.1.9) and $r = -0.900$ for the equation (4.1.10). However, the equation (4.1.10) was statistically significant at a considerably higher number of temperatures (Table 4.1.8). Accordingly, the intercomparison of the equations (4.1.9) and (4.1.10) showed the latter to be better for the description of the growth of larvae. Therefore, the equation (4.1.10) was used for further calculations.

Table 4.1.8. shows that the mean value $A = 3.56$ and $B = 1.09$.

Table 4.1.8. Values of constants, correlation coefficients and significance levels of the equations (4.1.9.) and 4.1.10.). * statistically insignificant

T°C	$l_t = K \log t$ (Farris, 1960)			$l_t = A - Be^{-ct}$ (von Bertalanffy, 1938)				
	K	r	P	A	B	c	r	P
16.70	0.3878	0.786	*	3.58	1.07	—1.1264	—0.893	0.05
16.77	0.4475	0.944	0.02	3.45	1.01	—1.6778	—0.798	*
18.70	0.3776	0.817	*	3.53	1.18	—2.1103	—0.941	0.1
19.02	0.3347	0.957	0.02	3.48	1.04	—2.3289	—0.967	0.05
19.60	0.4443	0.948	0.02	3.54	1.00	—2.2723	—0.998	0.05
21.00	0.9123	0.980	*	3.66	1.13	—2.8954	—0.999	0.02
21.30	0.3238	0.643	*	3.56	1.04	—2.6964	—0.683	*
21.88	0.3113	0.856	*	3.56	1.12	—2.2537	—0.861	0.1
21.98	0.5878	0.879	*	3.71	1.26	—2.4063	—0.931	0.05
24.05	0.4549	0.930	0.1	3.52	1.05	—4.1572	—0.926	0.05
r		0.883					—0.900	

Calculated mean value of asymptote A is very close to the mean length of larvae at the complete yolk sac resorption (Table 4.1.7). As seen in Fig. 6 larval growth curves calculated by the equation (4.1.10) showed very good agreement with the experimentaly obtained data on the growth of larvae.

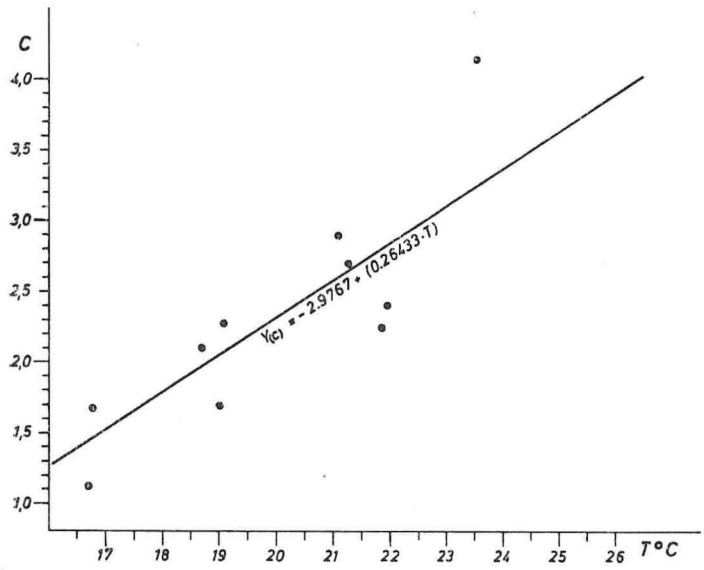

Fig. 7. Relation between the anchovy larvae growth rate coefficient (c) as influenced by temperature

It was further observed that the growth of larvae was faster at higher temperature i.e. that slope coefficients (c) of the growth curve increased with temperature (Fig. 7). By linear regression the relation between the c coefficient and temperature may be calculated by the equation:

$$c = -2.9767 + 0.26433\,T \qquad (4.1.11),$$

where T is temperature in °C. Correlation coefficient of c value and temperature was calculated to be r = 0.768 and, after t-test, it is significant for the significance level $P < 0.01$ what is indicative of the good statistical correlation of these two parameters. This renders possible the calculation of larval growth rate at any temperature by the following equation:

$$l_t = 3.56 - 1.09\,e^{-ct} \qquad (4.1.12),$$

where exponent c may be calculated for given temperature from the equation (4.1.11).

An approximate age of larvae may also be calculated by the following equation, particularly of those up to the mouth formation and eye pigmentation, if their length and the temperature of the environment are known,

$$t = \frac{1}{c} \ln \frac{1.09}{3.56 - l_t} \qquad (4.1.13),$$

where time is expressed in days.

The aim of the experiments with postlarvae was to rear them until they attain about 10 mm in length, since it was the greatest length of postlarvae caught by plankton net during field investigations. However, this was achieved only in the experiments carried out at temperatures of 21.30 and 24.05°C. In addition to these temperatures the data on the growth of postlarvae could also be obtained at temperature of 19.02°C (Table 4.1.6).

After the results obtained (Table 4.1.6), at the beginning the postlarvae grew slowly and later faster and faster. The best growth was observed at 21.30°C temperature. This may be accounted for by the fact that in this experiment the concentration of plankters was kept at 10 individuals per mililitre of water while in the other experiments this concentration was 5 ind/mil.

It was found that the growth of postlarvae may be given by the equation:

$$l_t = ae^{ct} \text{ (Ahlstrom, 1954)} \qquad (4.1.14),$$

where l_t is length in time t, and a and c are the constants. Constants for this equation were, like for the other ones, calculated by the linear regression from its linearized form. Correlation coefficients for the pairs r (t_i; ln l_{ti}) were calculated for each individual temperature. Since this growth equation is applicable to the growth of postlarvae beyond the yolk sac resorption (Fig. 8) the value t_0 may be calculated from the equation (4.1.8). On the basis of the equations (4.1.14) and (4.1.8), the following characteristics of the growth of postlarvae were obtained:

$$l_t(19.02) = 3.39\ e^{0.073021\,t} \quad (r = 0.941;\ P < 0.05)$$
$$l_t(21.30) = 3.13\ e^{0.101963\,t} \quad (r = 0.978;\ P < 0.001)$$
$$l_t(24.05) = 3.20\ e^{0.07931\,t} \quad (r = 0.967;\ P < 0.01)$$

Values of correlation coefficients and t-test show that the equation applied is, for all three temperatures, significant for the high significance levels.

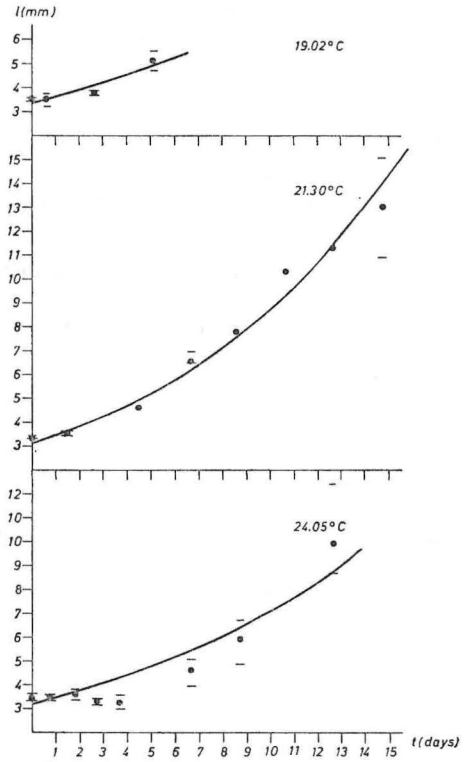

Fig. 8. Anchovy postlarvae growth curves

Distribution of exponent c values shows the growth of postlarvae to be slowest at the lowest temperature, and slightly faster at 24.05°C temperature. Faster growth at 21.30°C than at 24.05°C may be, as already mentioned, accounted for by the higher food concentration in the former experiment. Nevertheless, distribution of c values indicates that at the same food concentrations postlarvae grew somewhat faster if a temperature was higher. Therefore, the relation of coefficient c to temperature was calculated. It was obtained that:

$$c = -0.018522 + 0.004813 \cdot T \qquad (4.1.15),$$

but that the relation obtained is not statistically significant.

It was calculated that the mean value of the constant $\bar{a} = 3.24$. It should, in fact, represent the mean length of postlarvae at which they assume the growth characteristics which may be approximated by the equation (4.1.14).

Since this growth type is shown by postlarvae of 3.54 mm mean length (Table 4.1.7) beyond the yolk sac resorption, the calculated a value is considerably lower than the actual one. This is probably due to the decrease in the mean length of postlarvae upon the transition to active feeding (Table 4.1.6) since the data on all the length measurements were used in the calculation of the constants of equation (1. 1.14). Therefore the growth of postlarvae may be given by the equation.

$$l_t = 3.54\, e^{ct} \qquad (4.1.16),$$

where 3.54 is the mean length of larvae at the time of transition to postlarvae, whereas coefficient c may be calculated for the any temperature from equation (4.1.15). An approximate age of a postlarva may be calculated on the basis of this equation if its length and environmental temperature are known:

$$t = \frac{1}{c} \ln \frac{l_t}{3.54} \qquad (4.1.17),$$

where, to obtain the age of postlarva from hatching, the time between hatching and complete yolk sac resorption calculated from the equation (4.1.8) should be added to the required time.

The age of living larvae and postlarvae may be calculated by the equations (4.1.13) and (4.1.17). To calculate an approximate age of larvae and postlarvae caught from the plankton and preserved in 2% formol solution, the shrinkage of preserved larvae and postlarvae had to be examined. This was done thus that all the larvae and postlarvae reared experimentally were remeasured two months upon being preserved in formol. It was found that the mean length of alive specimens was 4.10 mm and that of the preserved ones 3.65 mm. Accordingly, an average shrinkage of 10.9% took place in formol.

It was calculated by the linear regression that the relation between the length of alive specimens and that of the preserved ones may be given by the equation:

$$l_k = -0.10842 + 0.9743 \cdot l_z \qquad (4.1.18),$$

where l_k is the length of preserved larvae or postlarvae and l_z the length of alive larvae or postlarvae in milimeters. Correlation coefficent was calculated to be 0.993 and $P < 0.001$. On the basis of this equation, the mean length of the preserved newly hatched larvae would be 2.29 mm and mean length of larvae in which the mouth formation and eye pigmentation have begun would be 3.30 mm. Mean length of larvae with the completely resorbed yolk sac would be 3.34 mm.

On the basis of these data an approximate age of preserved larvae may be calculated by the equation:

$$t = \frac{1}{c} \ln \frac{1.09}{3.36 - l_t} \qquad (4.1.19),$$

and that of postlarvae

$$t = \frac{1}{c} \ln \frac{l_t}{3.34} \qquad (4.1.20),$$

where A value from the equation (4.1.13) and a value from the equation (4.1.17) were recalculated for the preserved individuals on the basis of the equation (4.1.18).

DISCUSSION

Two periods of increased mortality were observed in the course of experiments, in eggs in the period from hatching to the end of the fifth stage of embryonic development, and in postlarvae upon the yolk sac resorption and transition to exclusively active feeding.

Since the predators are excluded under experimental conditions, the effects of pathogenic microorganisms and damages due to the hitting of eggs against jar's walls while they are carried by water current caused by air supply, are the most probable causes of egg mortality. The effects of microorganisms seem likely to be excluded since the antibiotic applied proved very successful. Namely, the microbiological water control carried out on two occasions did not show any bacterial presence (Krstulović, personal communication). In addition, even the concentrations of streptomycin sulphate lower than our proved very efficent (Shelbourne, 1963; Forrester and Alderdice, 1973). Therefore, it may be concluded that mechanical shocks were probably the main cause of egg mortality. According to the obtained results it appears that anchovy eggs are not equally susceptible to mechanical shocks throughout their development. Namely, the end of the period of increased mortality (Fig 3) coincides with the end of the fifth embryonic stage, when the yolk is completely overgrown by blastodisc i. e. when blastopore is closed. Similar was recorded for pacific halibut *Hipoglosus stenolepis* (Forester and Alderdice, 1973). These authors found that eggs were particularly susceptible to mechanical damages in the early stage of blastoderm cap and immediately prior to the closing of blastopore. After their findings, eggs with narrow perivitelline space were particularly susceptible to mechanical shocks. Anchovy eggs count among these egg types.

Since all the egg incsbation jars were of the same shape and capacity and aerated by the pumps of came capacity, which caused approximately the same water turbulence, it may be assumed that eggs incubated at temperatures of 17.14°C and 24.10°C were exposed to the shocks of approximately the same intensity. Therefore, the difference in percentage of survival (19.8% and 67% survived eggs respectively) may be accounted for by the longer exposure of eggs during more sensitive stages at lower temperatures at which the development lasts longer.

It should be mentioned that an increased number of dead anchovy eggs in early stages was observed in their natural environment, as well (Pavlovskaya, 1955; Dehnik, 1963; Regner, 1972). Nevertheless the expe-

rimental conditions cannot be compared with those in nature, it seems that mechanical shocks play a certain role in nature, as well. Namely, Pavlovskaya (1955) found an increased percentage of dead eggs of anchovy in the Black Sea when waves exceeded 3 degrees of Beaufort scale.

Mortality rate of larvae was rather stable (Fig. 3) in all the experiments in which the mortality was observed. Mortality increased suddenly after the yolk sac resorption. While the mortality of larvae, like that of eggs, may in the first place, be explained in terms of mechanical shocks the increased mortality of postlarvae immediately upon the yolk sac resorption is due to their starvation after transition to active feeding. It seems that the plankton net of 0.037 mm mesh size could not provide sufficient food quantity for younger postlarvae, and therefore the net which more dense silk should be used for further experiments. Pump collecting of food seems to have proved more suitable, since it was observed that at 24.05°C temperature experiment in which this method was applied the mortality increase occurred two days and a half after the yolk sac resorption, i. e. it somewhat »lagged« (Fig. 3). On the other hand it seems that the rest of postlarvae had sufficient food caught with the 0.060 mm mesh size net. Namely, as shown by the experiments, when postlarvae exceeded a length of about 3.8 mm, there was practically no dying at all. Otherwise, the occurrence of high mortality upon the transformation of larvae to postlarvae was recorded in a rather large number of larval fishes artificially reared such as northern anchovy (Lasker *et al.*, 1970; O'Connel and Raymond, 1970), mullet (Kuo and Shehadeh, 1972) plaice (Spectorova *et al.*, 1974), sea bass and sea bream (Barnabe, 1976; Villani, 1976). This mortality is most frequently attributed to the insufficient quantity of food.

The analysis of the obtained curve of anchovy egg development time as influenced by temperature showed that it could be well approximated by the equations (4.1.3) and (4.1.4). However, it should be pointed out that different authors successfully approximated the egg development by different equations. Thus for example, Blaxter (1956) and Ryland *et al.*, (1975) gave the herring (*Clupea harengus* L.) and plaice (*Pleuronectes platessa* L.) egg development by the thermal sums equations (4.1.1). Alderdice and Velsen (1978) approximated the development of salmon (*Oncorhynchus tshavitscha*) eggs by the Belehradek's modifictaion of thermal sun equation. The equation (4.1.4) was succesfully applied by Lasker (1964) to show the egg development and the time upon which the mouth opening and eye pigmentation took place in pacific sardine (*Sardinops caerulea*). This may, at first sight, lead us to conclude that the shapes of curves of egg developmental time as influenced by temperature vary from one species to another. It seems, however, that a part of the curve which lies within the wider limits of optimum temperature valence for any of the fish species may be rather well approximated by any of the equations used for this purpose. Rather considerable deviations in the application of different equations occur, after Alderdice and Velsen (1978) only in the part of curves which lies close to pessimum.

The comparison of our results with the earlier results of the studies of anchovy egg developmental time in relation to temperature shows that developmental time from our experiments agrees mainly with the records of

Kornilova (1955), Nikolskii (1957) and (Vučetić) (1957), particularly if the temperatures that Nikolskii and Kornilova reported are used as lower temperature limits (Table 4.1.9).

Table 4.1.9. The developmental times of anchovy eggs as affected by temperature, after different authors

	Regner			Kornilova	Nikolskii	Vučetić	Varagnolo
T°C	Experiment	Equation (4.1.3)	(4.1.4)	(1955) (exp. data)	(1957) (in situ)	(1957) (in situ)	(1964) (in situ)
15.00		91.58	86.93		65		
15.38	86.10						
16.00		76.17	74.98				
17.00		64.26	65.26				85
17.14	65.75						
17.90	58.17						
18.00		55.05	57.25				
18.73	50.00						
19.00		47.93	50.59				68
20.00		42.43	44.98				
20.04	42.59						
21.00	39.73	38.20	40.22				53
22.00		34.90	36.16	38—39			
22.05	35.34						
23.00		32.35	32.66				
23.38	31.25						42
24.00		30.39	29.63	38—39		40	
24.10	30.63						
25.00		28.87	26.98		29		32
26.00		27.69	24.66				
27.00		26.79	22.62		29	24	28

This agreement shows that the results obtained may be applied for the calculation of anchovy egg development time all over the area of their distribution, and even for their subspecies in the Black Sea. On the other hand, the results of Varagnolo (1964a) show broad disagreement with ours particularly at lower temperatures, where differences reach even 20 hours. The data of Nikolskii show also disagreement with ours for lower temperatures. This difference may be easily understood since longer the development its duration is more difficult to be established from the material collected *in situ*.

The process of mouth opening and eye pigmentation was found to initiate when anchovy larvae attain a mean length of 3.500 mm and the transformation of larvae to postlarvae, that is the complete yolk sac resorption at a mean length of 3.54 mm (Table 4.1.7). These length agree with the mean length of 3.10 mm and 3.14 mm respectively of the individuals preserved in 2% formol. Obtained data show broad agreement with the experimental

data of Kornilova (1955) after which the eye pigmentation in the Black Sea anchovy starts at lengths of 3.0—3.4 mm, whereas the yolk is resorbed at 3.6—4.0 in length.

After the results obtained temperature considerably affects the time between hatching and mouth opening and eye pigmentation as well as the time between hatching and transformation of larvae to postlarvae. This dependence on temperature was already recorded by Lasker (1964) in the pacific sardine larvae. This author approximated this dependence by the equation (4.1.4) which proved suitable for anchovy as well. The results agree well with the only earlier reports on the time between hatching and mouth opening and that between hatching and transformation to postlarvae, given by Kornilova (1955) for the Black Sea anchovy within the 22—24°C interval on temperature. This shows that the coefficients of the equations (4.1.7) and (4.1.8) may be used for the calculation of mouth opening and transformation to postlarvae for the whole area of anchovy distritbution.

Measurements of anchovy larval length from hatching to the transformation to postlarvae showed their fast growth up to approximately mouth opening and sudden growth decceleration thereupon.

Graphical representations of the growth of different fishes such as pacific sardine, *Sardinops caerulea* (Lasker, 1964), herring, *Clupea harengus,* (Blaxter and Hempel, 1963), sardine, *Sardina pilchardus,* (Blaxter, 1969), nothern anchovy *Engraulis mordax* (Kramer and Zweifel, 1970), mullet, *Mugil cephalus* (Kuo and Shehadeh, 1972) and plaice, *Pleuronectes platessa,* (Ryland, *et. al.,* 1975), show that the curves are very similar to the curves we obtained for anchovy in the present study (Fig. 6).

After Blaxter (1969), Farris (1959) distinguishes three stages of larval length growth: an early stage of fast growth, stage of slow growth before the complete yolk sac resorption and thereupon the stage of negative growth if there is no sufficient food available. If we exclude the third stage, which, as will be shown, is a pathological phenomenon, the first two stages given by Farris correspond to the curve of anchovy larvae described by the equation (4.1.10). It seems, therefore, that the growth of larvae of different fish species may be described by this equation.

This type of anchovy larval growth, and, as it seems according to the above mentioned authors, of that of other fish larvae, may perhaps of explained in terms of »re-orientation« in the utilization of the yolk sac reserves. Namely, after the records of Blaxter and Hempel (1966), larvae, utilize the yolk for two fundamental purposes, partly for tissue forming and partly as a source of energy for total metabolism. Three components of metabolism may be distinguished, growth metabolism, metabolism for the maintenance of vital functions, and metabolic processes which release the energy for movement. The interrelations of these three components change in the course of the growth of larvae. After Blaxter and Hempel the efficiency of yolk utilization for the purpose of growth decreases with the growth increment, whereas, on the other hand, after Ryland *et al.,* (1975) the yolk sac resorption rate remains constant throughout the period of the growth of larvae. This may be indicative of the fact that in the later period of their life larvae utilize the yolk more for other processes than for the growth. The utilization of the yolk is likely »oriented« to anatomic-morphological changes such as the opening of mouth and intestine, eye pigmentation

and similar as well as to the higher motility of larvae which search for prey upon the mouth opening. This »orientation« of the yolk utilization may result in the decrease of growth.

Another possible explanation of this type of growth of anchovy larvae is that by the increase in the larval weight metabolic requirements are so increased that the efficiency of the yolk utilization for the purpose of growth decreases and the growth deccelerates (Blaxter and Hempel, 1966). This assumption is more probable since it is in agreement with the statement of Von Bertalanffy (1938) that catabolism begins to increase in relation to anabolism with the increase of volume in relation to the surface, which occurs in animals during growth. This finally leads to a stagnation if catabolism and anabolism get equal.

The linear correlation between the growth speed of anchovy larvae and temperature (Fig. 7; equation 4.1.11) shows that temperature affects growth what apparently is the result of the acceleration of all the processes in an organism at higher temperatures. Ryland *et al.*, (1975) found that the rate of the yolk sac utilization by plaice (*Pleuronectes platessa*) larvae showed linear increase with temperature increase. However, studying the relation between the growth rate coefficient of plaice larvae and temperature these authors did not find linear correlation since after an increase of growth rate with temperature it suddenly decreased at temperatures higher than 8°C. This, however, may be due to the fact that temperatures higher than 8°C belong to the area of the upper pesimum of temperature valence of plaice. This is supported by the records of Johansen and Krogh (1914) who, after Ryland *et al.* (1975) found that plaice larvae growth was considerably delayed at 12°C. This may be indicative of the fact that linear correlation of larval growth and temperature may be expected withing the rather wide optimum limits, and that, going towards the upper or lower pessimum, considerable deviations, that is growth decceleration, may be expected.

Length decrease, recorded in our experiments at yolk sac resorption and in the youngest postlarvae (Table 4.1.6 and Figs. 6 and 8) is, for sure, the result of starvation during transition to active feeding. Namely, Love (1962) finds that due to starvation, larvae begin to consume their own tissues, what results in degradation of colagene filaments, muscles growing feeble, increase in body water content and loss in length. These larvae have already reached the state called »the point without return« after Blaxter and Hempel (1963). This means that they would die even if the sufficient food were provided, since they have got to weak to take food. Even though the larvae are still alive, this state means their ecological death. Since these larvae swim much slower than those which reached sufficient food, their proportionally high presence in samples we used for measurements may be accounted for by the fact that it was much easier to catch them by pipette than the well fed larvae. Anyway, it seems that these individuals should not be taken into account in calculations of growth rate.

Studies of the growth of postlarvae showed that their growth was somewhat faster at higher temperatures (equation 4.1.15). However, growth of postlarvae was faster at 21.30°C temperature than at 24.05°C. This may be accounted for by the fact that food concentration was maintained at approximately 10 nauplii/ml in 21.30°C experiment and at only about 5 nauplii/ml in 24.05°C experiment. This means that postlarvae which had more available

food grew faster irrespective of the lower temperature. Considerable influence of food on the growth of postlarvae was shown by O'Connel and Raymond (1970) for postlarvae of northern anchovy (*Engraulis mordax* Girard) and Wyatt (1972) for the plaice (*Pleuronectes platessa* L.) postlarvae. They studied postlarval growth at the same temperatures and different food concentrations and found that they grew faster if the concentration of food was higher. Concentration of food however, seems to affect the growth of postlarvae to a limited extent. This was found by O'Connel and Raymond who showed that growth of postlarvae was faster up to the concentration of 8 nauplii/ml. However, no differences were found between the growth rates at concentrations of 8 nauplii/ml and that at the concentration of 14 nauplii/ml. Even though we studied the postlarval growth at only three different temperatures, our results seem to agree with the conclusions of Blaxter (1969) that temperature and available food quantity have the greatest influence on the growth of postlarvae.

According to the results obtained, growth of anchovy postlarvae up to the length to which they were reared in our experiments, may be aproximated by the equation (4.1.14) and their age may be estimated by the equation (4.1.17) taking into account the temperature of the environment. However, the time at which postlarvae begin their metamorphosis into the juvenile fish cannot be calculated by these equations even though it is known (Kornilova, 1955; Pavlovskaya, 1955) that the metamorphosis starts when a postlarvae attain a length of about 24—26 mm. It seems, however, as Kramer and Zweifel (1970) found, that approaching the metamorphosis, growth is deccelerated and that the time calculated by the equation (4.1.17) would be shorter than it actually is. Since the postlarvae we found in the plankton did not exceed 10 mm in length the equation (4.1.17) may satisfactorily give the age estimation.

Since the principal aim of the experiments with eggs, larvae and postlarvae was to come to the data which would render possible an estimation of the time of the egg development and the age of larvae and postlarvae caught by plankton net, the factors which considerably effect the error in these estimates should be observed.

It is well known that, in addition to temperature and food quantity the time of egg development and larval and postlarval growth may, as well, be affected by salinity and oxygen quantity (Blaxter, 1969; Holliday, 1969). Therefore, we shall discuss here each of these factors. According to the results obtained, the effects of temperature on the development speed and growth of anchovy larvae seem to be the principal ones. Therefore, it may be assumed that temperature changes within short time interval may have the greatest influence on the errors in these estimates. It is not easy to say the extent of this influence since no experiments with varying temperatures have been carried out. Since the investigations of Alderdice and Velsen (1978) showed that salmon eggs development under natural conditions at varying temperatures was somewhat faster than that under the experimental conditions, similar may be applicable to anchovy eggs.

After some earlier data, anchovy eggs were recorded from the Adriatic within 11.6°C—25.5°C temperature range (Zavodnik, 1970). This range may also cover the occurrence of larvae. After the equations (4.1.5) and (4.1.8) the egg development would last from 6.5 to 0.9 days within that temperature

range, and the development of larvae from 23.8 to 0.89 days. Relatively long period of anchovy egg and larval development at lower temperatures may, owing to the higher liability of temperature to change in the sea, cause rather considerable error in egg and larval age estimates. However, we held that at higher temperature at which both the larger number of eggs and larvae occur in plankton (Regner, 1972) the probability of error is lower, since within shorter time intervals temperature may be, to a certain extent a conservative factor (Buljan, 1976).

Salinity is the second factor known to affect the time of fish egg and larval development by accelerating or deccelerating it (Holliday, 1969). It seems, however, that this factor's influence is indirect through a reduction in oxygen content (Kinne, 1964) after Holliday (1969). We held, however, that these two factors could not affect considerably the anchovy egg and larval age estimates in our study area since salinity is a factor even more conservative than temperature whereas on the other hand, the Adriatic is rich in dissolved oxygen (Buljan and Zore-Armanda, 1971).

Food quantity, as well, affects the growth of postlarvae. This is another factor which makes the error in estimating their age on the basis of their length, more probable than in larvae. Unfortunately, there is no method available to calculate the extent of this error. Further, the development of postlarvae takes much more time than the development of larvae. Using the equations (4.1.15) and (4.1.17) it was calculated that anchovy postlarvae attain a 10 mm length by 24 days after hatching at temperature of 13°C, and by 11 days at temperature of 24°C if the influence of food quantity is neglected. It is quite sure that the temperature is likely to change considerably within these time intervals. In addition, as distinct from eggs and larvae which keep close to the surface, postlarvae seem to have nycto-hemeral migrations within the 20 m to surface layer (Regner, 1972). Thus they are exposed to the considerable temperature changes. On this basis it may be concluded that the errors in age estimates of postlarvae are more probable than those of larvae and eggs.

Further, there are still two factors more which may cause greater errors in age estimates of larvae and postlarvae on the basis of their length. They should be pointed out since it was found that errors due to their effects might be either determined mathematically or minimized by a special method. First of these two factors is a relatively wide range of lengths of larvae and postlarvae of the same age, and the second is the decrease in the initial length of larvae from the beginning to the end of the spawning season.

4.1.4. *Infuence of length range of larvae and postlarvae of the same age on age estimates based on length*

Blaxter (1969a) reports the estimates of age of fish postlarvae on the basis of the experimental data to be problematic due, among the others, to the fact that a large number of experiments showed the differences in length between postlarvae of the same age to be considerable. For instance, as this author reported, after Shelbourne (1963) had undertook a series of experiments with the plaice postlarvae he found that the length of plaice postlarvae of the same age might vary between 7.5 and 37.5 mm and that

the number of small postlarvae was larger in dense experimental populations. Magnuson (1962) arrived at similar results, studying the influence of food on the *Oryzias* genus postlarvae. According to this author if sufficient food was provided there occurred no great differences in length nor its reduction, what would mean that competition for food causes an increase in length differences. From the graphical representations of the growth of fish postlarvae reared under experimental conditions (Lasker *et al.*, 1970; Kramer and Zweifel, 1970; Ehrlich *et al.*, 1976; Kuo and Shehadeh, 1972) it may be seen that the difference in length is constantly increasing with age. This was also recorded both for anchovy larvae and postlarvae (Figs. 6 and 8). To examine whether the growth rates of large and small larvae and postlarvae differ among themselves, *A*, *B* and *c* values were calculated for the extremely small larvae ($l_{t\ min}$) and extremely large larvae ($l_{t\ max}$) for the experiments at all the temperatures at which the sufficent number of specimens were measured for length range. Growth rate coefficients (c) were calculated for the largest and smallest postlarvae of the same age. The results obtained are given in Table 4.1.10. Mean values were given in Table 5.1.7 and in the postlarval growth equations.

Table 4.1.10 *A* and *B* values and growth rate coefficients *(c)* for the largest ($l_{t\ max}$) and smallest ($l_{t\ min}$) anchovy larvae and postlarvae

				Larvae		
	A		B		c	
T°C	l_{min}	l_{max}	l_{min}	l_{max}	l_{min}	l_{max}
16.77	3.43	3.71	1.07	1.16	—1.16944	—1.56949
19.02	3.34	3.49	1.04	0.94	—2.40266	—2.54253
21.30	3.37	3.63	0.98	0.95	—3.66041	—2.3065
21.88	3.43	3.72	1.07	1.17	—2.547281	—1.6717
24.05	3.34	3.60	1.01	0.95	—4.3018	—5.2003
				Postlarvae		
16.02					0.0683224	0.0795599
21.30					0.088657	0.111192
24.05					0.068584	0.09271

On the basis of the data given in Table 4.1.10 standard error of the difference between the mean values of c of l_{max} and l_{min} was calculated both for larvae and postlarvae. It was obtained that:

$$\bar{x}_1 - \bar{x}_2 = 0.158214; \quad S_{x_1 - x_2} = 0.855396; \quad t = 0.1849599$$

for larvae and:

$$\bar{x}_1 - \bar{x}_2 = 0.0192995; \quad S_{x_1 - x_2} = 0.0131406; \quad t = 1.46869$$

for postlarvae.

Since the critical value of t-test for $P < 0.1$ is 1.86 for larvae and 2.13 for postlarvae, it appears that the differences between the growth rate coefficients are not statistically significant. Therefore it may be concluded that both the large and small larval and postlarval specimens have approximately equal growth rate. Thus, according to the equations (4.1.10) and (4.1.14), by which anchovy larval and postlarval growths were described, the difference in length between the individuals of the same age is likely to be dependent on the length range for the time $t = o$. This would be the length range of the newly hatched larvae and the length range of postlarvae at the complete yolk sac resoption. This dependence may be given for larvae by the equation:

$$|\delta l_t| = l_t \{\frac{\delta l_o}{\bar{l}_o} + \frac{\delta B}{\bar{B}} (1 - e^{-ct})\} \qquad (4.1.21),$$

where $\delta l_t = l_{t\,max} - l_{t\,min}$, $\delta l_o = l_{o\,max} - l_{o\,min}$, $\delta B = Bmax - Bmin$, and for postlarvae by the equation:

$$|\delta l_t| = l_t \frac{\delta l_o}{\bar{l}_o} \qquad (4.1.22).$$

However, it appears from the equations (4.1.21) and (4.1.22) that greater the difference in length at the beginning of the growth, larval and postlarval length range (δl_t) is greater at any time provided the growth rate coefficients, as shown by t-test results, are equal for the extremely small and extremely large individuals. This assumption being correct, the error in age estimates of larvae and postlarvae on the basis of length by means of the equations (4.1.13) and (4.1.17) may be expressed by a relative time error where:

$$|\frac{\delta t}{\bar{t}}| \leqslant \frac{1}{\bar{c}\,\bar{t}} \{|\frac{\delta B}{\bar{B}}| + \frac{\delta B}{\left(1 - \frac{l_t}{\bar{A}}\right)} |\frac{\delta A}{\bar{A}}|\} \qquad 4.1.23),$$

for larvae, and:

$$|\frac{\delta t}{\bar{t}}| \leqslant \frac{1}{\bar{c}\,\bar{t}} \left(|\frac{\delta l_o}{\bar{l}_o}|\right) \qquad (4.1.24),$$

for postlarvae, where $\delta t = t\,max - t\,min$, and $\delta A = A_{max} - A_{min}$.

To test how do the experimental data on length range agree with the assumption brought out, δl_t values were calculated for anchovy larvae and postlarvae. The δl_o value was used for larvae of each individual experiment from Table 4.1.6. Since the number of measured larvae at the transformation to postlarvae, the length range of which was the same as δl_o for postlarvae, was far lesser than that of newly hatched larvae, the δl_o value for postlarvae for the time of the complete yolk sac resorption was calculated from the equation (4.1.21). On the other hand the common value (l_o comm.) was calculated on the basis of the data from Table 4.1.7. Values of relative error in time

estimates (δ t/t) were also calculated from both larvae and postlarvae.

Extreme larval lengths during the growth showed to be in good agreement with the mathematically calculated limits of δl_t (Fig. 9), which is another proof that the width of the length range depends, to a larger extent, on the length of larvae at hatching. Distribution of relative time error ($\delta t/t$) shows that the age of larvae may be almost precisely estimated on the basis of length up to, approximately, the time of the beginning of growth decceleration.

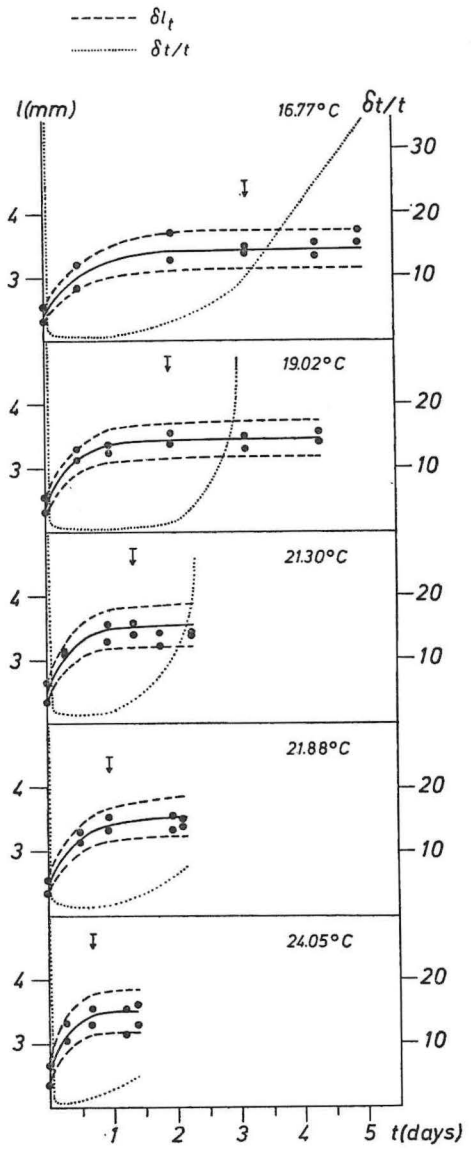

Fig. 9. Relation of lengths calculated from the δl_0 value and extreme length of anchovy larvae to relative error (δ t/t) in age estimates

Thereupon the $\delta t/t$ tends to infinity, thus that the age estimates after the mouth opening and eye pigmentation are not reliable.

As it may be seen from Fig. 10 extreme lengths of postlarvae of the same age also agree well with the calculated l_t limits, particularly with the values calculated on the basis of common δl_0 value from Table 4.1.7. However, as distinct from larvae, the extreme postlarval lengths particularly those of the oldest ones, do not »enter« within the mathematically obtained limits. This is quite in agreement with the fact that food considerably affects the growth of postlarvae. It may, however, be expected that for the smaller postlarvae of the same age which, after Blaxter (1969) are poorer swimmers, it will be difficult to catch food under the conditions of no sufficient food available. Their growth will be more and more delayed and consequently they will reach food with more and more difficulties, whereas the growth of larger postlarvae will be faster and faster owing to minimized competition. It may, therefore, be assumed that, under the conditions of abundant food, differences in length will be due to the initial differences in length as shown by the equation (4.1.22), and that under the conditions of poor food availability these differences will be increased. In any case, it seems that the differences in length between the postlarvae of the same age may be rather accurately calculated by the equation (4.1.22). Distribution of $\delta t/t$ values shows (Fig. 10) that relative error in age estimates is more and more minimized with age. Otherwise, on the basis of the equation (4.1.24) the time error (δt) is constant in postlarvae. In our experiments it ranged from 2.74 days at 19.02°C to 2.06 days at 21.30°C, irrespective of the length of postlarvae.

4.1.2. *Age estimates of larvae as influenced by decrease in their initial lengths from the beginning to the end of spawning season*

Some of the available data show that the length of fish larvae at hatching depends on egg size. Namely, studies of the relation of herring egg size and larval length at hatching showed that longer larvae were hatched from larger eggs and that they, as well, attained greater lengths at the yolk sac resorption (Blaxter and Hempel, 1963). Similar was observed in anchovy from the central Adriatic. It was found that the mean egg size and mean lengths of anchovy larvae decreased as the end of spawning season was coming closer (Regner, 1972). Since a small number of eggs and larvae were measured on that occasion, we examined once again the relation between the egg size and length of larvae on the basis of measurements of the material collected throughout the period of this investigation (9305 eggs and 3020 larvae) comparing the monthly means of the longer diameter of the egg and mean larval lengths (Table 4.1.11).

As it may be seen from Table 4.1.11, length of larvae depends on the mean egg size and may be given by the following relation:

$$l = 0.6358 + 1.7784 \cdot v;\ r = 0.735,\ p < 0.001,$$

where l is mean length of larvae and v mean length of longer egg diameter.

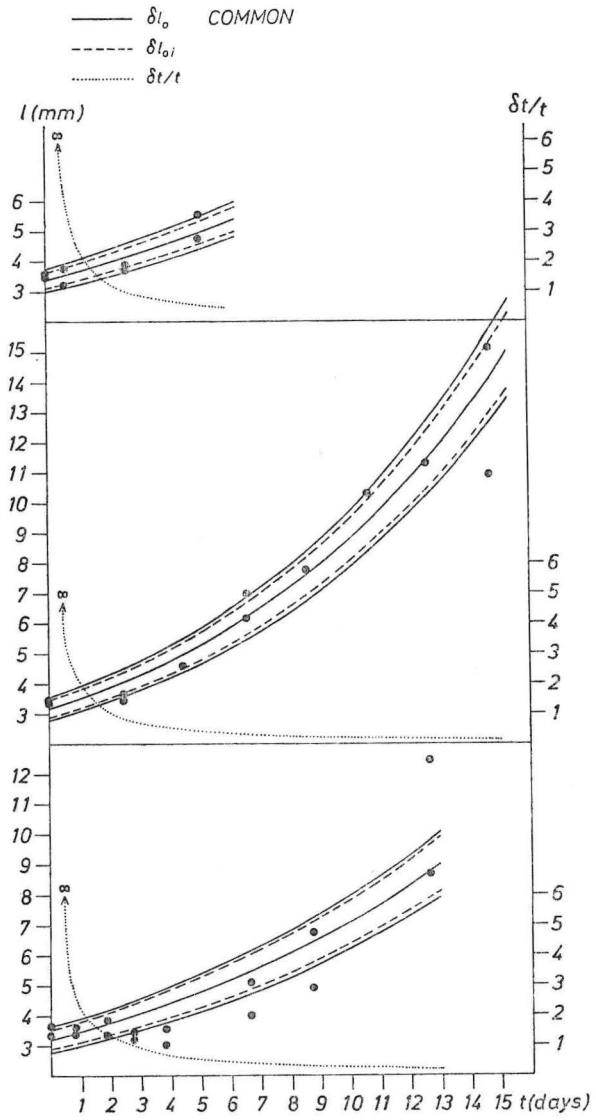

Fig. 10. Relation of length ranges calculated from the δl_0 value and extreme length of anchovy postlarvae to relative σt/t eror

Accordingly, even though the egg size was not separately measured in the course of these experiments it may be concluded that the length of newly hatched larvae depends on egg size. This means that wider the range of egg size the length range of newly hatched larvae (δl_0) is wider and that in this case, according to the equations (4.1.21) and (4.1.24) the error in estimates of larval and postlarval age will be greater.

Table 4.1.11 Mean size of anchovy eggs and larvae in the study area by months (for the 1962—1976 period)

Station	III		IV		V		VI		VII	
	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$
Stončica										
eggs	1.54—1.69	1.57	1.35—1.84	1.56	1.24—1.76	1.51	1.13—1.65	1.40	0.98—1.54	1.31
larvae	—	—	2.63—3.83	2.50	2.36—3.93	3.29	2.06—3.86	3.09	1.88—3.60	2.86
Pelegrin										
eggs	—	1.58	1.43—1.88	1.59	1.20—1.80	1.54	1.13—1.65	1.37	1.09—1.58	1.31
larvae	—	—	3.60—3.71	3.66	2.70—3.93	3.48	2.10—3.75	3.10	1.99—3.64	2.99
Kaštel. zaljev										
eggs	—	1.69	1.28—1.84	1.60	1.28—1.69	1.53	1.16—1.69	1.37	1.13—1.50	1.29
larvae	—	—	2.82—3.53	3.28	2.40—3.86	3.33	2.25—3.68	3.05	2.02—3.49	2.90
All stations										
eggs	1.54—1.69	1.61	1.28—1.88	1.58	1.20—1.80	1.53	1.13—1.69	1.38	0.98—1.58	1.30
larvae	—	—	2.63—3.83	3.48	2.36—3.93	3.37	2.06—3.86	3.08	1.88—3.64	2.92

Station	VIII		IX		X		XI	
	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$
Stončica								
eggs	1.05—1.30	1.27	0.79—1.54	1.30	1.20—1.43	1.31	1.24—1.39	1.30
larve	2.17—3.56	2.89	2.14—3.45	2.92	1.88—3.64	3.05	2.36—3.34	3.30
Pelegrin								
eggs	1.13—1.43	1.29	1.13—1.46	1.32	1.16—1.43	1.30	—	—
larvae	2.33—3.68	3.05	2.29—3.56	2.97	2.66—3.68	2.34	—	—
Kaštel. zaljev								
eggs	1.09—1.50	1.26	1.01—1.41	1.32	1.28—1.43	1.33	1.24—1.35	1.30
larvae	1.95—3.56	2.84	1.73—3.56	2.78	2.44—3.23	3.02	3.04—3.34	3.37
All stations								
eggs	1.05—1.50	1.27	0.79—1.54	1.31	1.16—1.43	1.31	1.24—1.39	1.30
larvae	1.95—3.68	2.93	1.73—3.56	2.89	1.88—3.68	3.00	2.36—3.34	3.34

Further, the measurements of the length of anchovy larvae (Table 4.1.11) collected from the study area and preserved in 2% formol showed that the greatest length range (from the length of newly hatched larvae to that at the transformation to postlarvae) was 1.88—3.93 mm, what, according to the equation (4.1.18) would correspond to the lengths of 2.04 and 4.15 mm respectively of living individuals. This, however, considerably exceeds the maximum range of larvae, 2.18—3.90 mm, measured during the experiments (Table 4.1.7). Undoubtely this might have been expected since it is quite normal that larvae collected throughout the period of investigations and all over the study area showed length variability which exceeded that of the larvae experimentally reared. It was also found that larvae from the period of April—May were considerably longer (2.36—3.93 mm) than those from June—November (1.73——3.68 mm). However, their length range was somevhat lesser. Therefore, if the mean values A and B for preserved individuals obtained by measurements in the course of experiments (equation 4.1.19) are taken as the basis of estimates, the age of larvae will be overestimated, particularly of those from period of April—May. To avoid this the following A and B values were taken:

	April-May	June-November
Range of larvae	2.36—3.93	1.73—3.68
A	3.94	3.69
B	1.58	1.96

Thus the age of larvae found in the plankton from April—May may be estimated by the equation:

$$t = \frac{1}{c} \cdot \ln \frac{1.58}{3.94 - l_t} \qquad (4.1.25),$$

and the those found from June—November by the equation:

$$t = \frac{1}{c} \cdot \ln \frac{1.96}{3.69 - l_t} \qquad (4.1.26).$$

The $B/3$ interval was used in sorting the larvae into the length groups for the later estimates of mortality. The following groups were obtained:

	April-May	June-November
L_1	2.36—2.88	1.73—2.38
L_2	2.89—3.40	2.39—3.03
L_3	3.41—3.93	3.04—3.68

Changing the A and B values is possible since these values in the growth equation (4.1.10) do not significantly affect the assessment of the total develop-

mental time from hatching to transformation to postlarvae. This total developmental time depends largerly on the magnitude of value of exponent (*c*), which, as shown, varied with temperature. This may be illustrated by the following example. The developmental time of larvae at mean temperatures in April ($\bar{x}$ for 0—20 m = 13.99°C) and June ($\bar{x}$ for 0—20 m = 20.68°C) was calculated on the basis of developmental time up to the complete yolk sac resorption as influenced by temperature as well as on the basis of growth equation taking the mean *A* and *B* values for both the preserved individuals experimentally obtained (equation 4.1.19), and those obtained by measurements of the collected material (equations 4.1.25 and 4.1.26). The time at which larvae attain a length of $A - 0.001$ was taken as a criterion by which to judge the termination of larval stage. It was shown that larvae attained this length after the same time (at 10.5 days at temperature of 13.99°C, and at 2.64 days at temperature of 20.68°C) irrespective of the changed *A* and *B* values. Further, the obtained developmental time is in agreement with the developmental time calculated by the equation (4.1.8). According to this equation the development takes 11.7 days at 13.99°C and 2.64 days at 20.68°C (Fig. 11). Mean length range of larvae at hatching ($\delta l_0 = 0.25$ mm) was also calculated on the basis of Table 4.1.6. It provided the basis for calculation of δl_t values for the growth curve obtained from the equation (4.1.19). This rendered possible a comparison of the aberrations in the age estimates by means of the *A* and *B* values calculated by measurements of both the material collected in situ and that reared experimentally. The difference in time estimate for April (Δt) showed to be only slightly higher than the error resulting from the initial length range (δt), while in June this difference was considerably smaller than the above mentioned error (Fig. 11). Larval lengths of *B*/2 for April—May and June—November respectively were used for this comparison. This shows that the adjustment of the *A* and *B* values on the basis of measurements of larvae collected *in situ* is possible and justified and that the equations (4.1.25) and (4.1.26) will probbably give better age estimates than the equation (4.1.19) with respect to the difference in size between the larvae of spring period of spawning season and those from the summer one.

It is quite certain that the error will also occur in the age estimates of postlarvae by the equation (4.1.20), the coefficients of which were calculated on the basis of observations of growth under experimental conditions, since postlarvae from the spring period developed from larvae which, on an average, were longer than those from the summer period. We, however, believe this error in postlarvae to be negligible, in the first place, owing to the fact that the growth rate is influenced by the quantity of available food which, as distinct from temperature, could not be determined. Therefore, postlarvae were separated in four length groups irrespectively of the time they were found at:

P_1 3.34—3.99
P_2 4.00—5.99
P_3 6.00—7.99
P_4 8.00—9.99

The first group includes all postlarvae from the value of *a* in the equation (4.1.20) up to the 3.99 mm length, while the others were separated into 1.99 mm length ranges.

In taking into account the combined influence of temperature and food on the growth of postlarvae, as well as the dependence of larval and postlarval growth on their initial lengths, we may accept the statement of Blaxter (1969a) that age estimates on the basis of larval and postlarval lengths may include the possibility of considerable error. We held, however, that the possibility of error may be minimized if larvae and postlarvae are separated into convenient length groups.

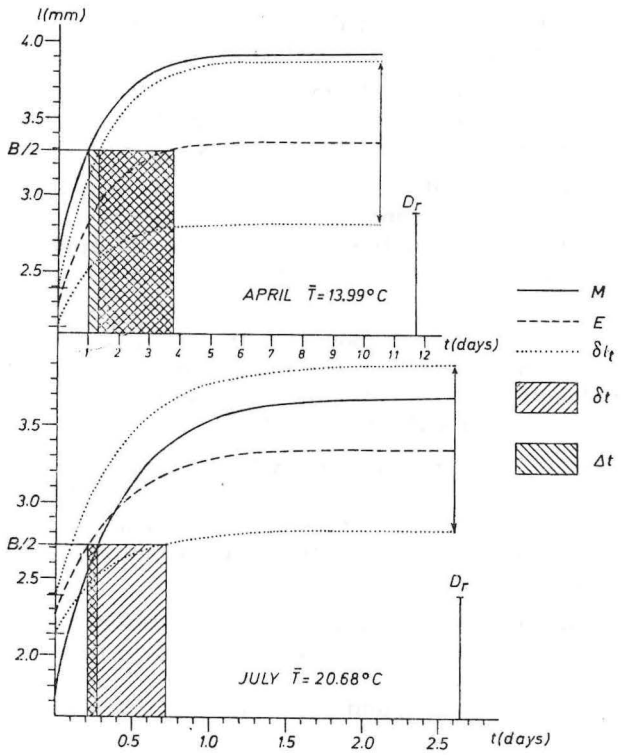

Fig. 11. Growth curves of anchovy larvae calculated from the experimental data and the data obtained by measurements of the material collected *in situ*

M = growth curve calculated from the material collected *in situ*
E = growth curve calculated from the experimental data
δl_t = mathematically defined length range from experimental data
Δt = time error of difference between the *in situ* and experimentally estimated A and B values
δt = time error due to the initial length range
Dr = the yolk sac resorption according to the (4.1.8) equation

Conclusions

1. Under experimental conditions mortality of anchovy eggs was highest in earlier embryonic stages up to the closing of blastopore. It is mainly due to mechanical damages.

2. Under experimental conditions mortality rate of anchovy larvae was approximately constant. It also seems to be mainly due to mechanical damages.

3. Mortality of postlarvae was highest immediately upon the transition to exclusively active feeding. In older postlarvae it was almost negligible.

4. The experiments of artificial »dry fertilization method« of anchovy eggs showed that fertilized eggs averaged 87.71%.

5. Anchovy egg developmental time as influenced by temperature may be approximated by the equation $D = CT^{-b}$, where D = developmental time in days, T temperature in °C and C and b constants.

6. Developmental time of each of the embryonic stages may be calculated by the same equation, multiplying the C or D values by corresponding coefficient characteristic for each of the stages. This is not applicable only to the first stage which takes very short time in relation to the total developmental time of anchovy eggs.

7. Results of the experiment show that the mean length of newly hatched anchovy larvae is 2.46 mm $\pm$ 0.11 s, that mouth opening and eye pigmentation begin at mean length of 3.50 $\pm$ 0.43 s, and that the yolk sac is completely resorbed at mean length of 3.54 mm $\pm$ 0.319 s.

8. The developmental time between hatching and mouth opening and eye pigmentation in larvae, and that between hatching and transformation to postlarvae is also dependent on temperature and may be calculated by the application of the equation by which the relation between egg developmental time and temperature is expressed.

9. Growth of anchovy larvae up to the yolk sac resorption may be approximated by the equation $l_t = A - Be^{-ct}$, where l_t is length in time t, and t is time in days, A is the asymptote while B and c are constants. Growth speed of anchovy larvae depends on temperature, and the relation of growth rate coefficients c to temperature may be calculated by the equation $c = -2.9767 \times 0.26433T$, where T is temperature in °C. This relation is statistically significant for the high significance level.

10. Growth of anchovy postlarvae may be given by the equation $l_t = ae^{ct}$, where l_t is length in time t, and a and c constants. Growth rate coefficient c is, like in larvae, dependent on temperature, and this relation may be calculated by the equation $c = 0.018522 \times 0.004813T$, where T is temperature in °C. However, it is not statistically significant.

11. Growth of anchovy postlarvae is, in addition to temperature, also considerably affected by the available food quantity.

12. Difference in length of either larve or postlarvae of the same age increases with time. This difference is to a larger extent dependent on the initial length range. This difference, as well as the error in age estimates resulting from it, may be mathematically defined.

13. Length of larvae from the study area decreases from the beginning to the end of spawning season, together with the decrease in egg size. This may cause significant errors in age estimates based on length. However, this cause of error may be minimized to a certain extent by calculating the *A* and *B* values separately for larger larvae from the spring period and separately for the smaller ones from the summer period.

14. Shrinkage of anchovy larvae and postlarvae preserved in 2% formol solution averaged 10.9%.

4.2. MORTALITY OF ANCHOVY EGGS, LARVAE AND POSTLARVAE IN THE PLANKTON

Results

Throughout the period of investigations, a total of 65 489 fish eggs were collected from the Kaštela Bay, Pelegrin and Stončica stations. Of this quantity 9 305 eggs belonged to anchovy; 3020 anchovy larvae and 2815 postlarvae were extracted from a total of 24 673 fish larvae and postlarvae caught from the plankton. To calculate mortality coefficients anchovy eggs were separated into embryonic stage groups, couting living and dead eggs together. Larvae and postlarvae were sorted into length groups as shown in the chapter 4.1. Thus it was possible to observe the reduction in the number of eggs from younger to older stages, as well as the reduction in the number of larvae and postlarvae from younger to older length groups. Global, monthly and annual mortality coefficent means were calculated on the basis of thus prepared data.

Mortality was calculated assuming that the number of eggs, larvae and postlarvae decreases exponentially with time and that it may be expressed by the equation:

$$N_t = N_0 e^{-mt} \qquad (4.2.1),$$

where N_t is the number of individuals in time t, N_o number of individuals in time $t = 0$ and m mortality coefficient. Time was expressed in days.

Mortality coefficent (m) was calculated from the linearized form of the equation (4.2.1) by the method of linear regression:

$$m = \frac{\sum_{i=1}^{n} (t_i - \bar{t})(\ln Nt_i - \ln \bar{N}t)}{\sum_{i=1}^{n} (t_i - \bar{t})^2} \qquad (4.2.2),$$

where Nt_i is the number of individuals by each of the embryonic stages or length groups and t_i age in days.

The analysis of the collected material showed some shortcomings due to the very nature of the material and method of collection. They made mortality calculations considerably difficult, particularly those for eggs and larvae. Namely the subsequent daily samplings, carried out over longer or shorter periods dependently on developmental rate, are best suitable for the mortality studies of planktonic stages since they render possible the observations of their elimination from the moment the eggs are spawned. To our regret our collections were made on monthly basis. Therefore the distribution of the number of individuals by stages and length groups showed the following properties:

— the number of eggs of the first and tenth stages was considerably lower than that of other stages. This is due to the fact that these two stages, as already shown in the chapter 4.1., take very little time. Thus it is far less probable that the eggs of these two stages will be caught from the plankton than those of other stages.

— anchovy eggs showed a tendency of grouping in several consecutive developmental stages; most frequently, depending on temperature, in the II, III, IV and VI, VII, VIII or II, III, IV and VIII and IX groups. The number of older stges frequently exceeded the number of younger stages in a group. This is probably the result of that anchovy may spawn over a relatively long period during the day, from 6 in the alternoon to 4 in the morning, after Demir (1965).

— eggs of older stages (VII, VIII and IX) were more numerous than eggs of younger stages in a large number of samples. This is indicative of the fact that the spawning intensity varies from one day to another. It also indicates the possibility of egg immigration in the area of sampling stations, being probably transported by currents from the adjacent areas. This transport by currents may be expected particularly at lower temperatures at which the development lasts longer.

— the number of larvae of the first length group was frequently smaller than that of the second group, what is probably caused by the accumulation of larvae of the second group in the plankton due to their longer development. The same phenomenon is frequent in the relation between the number of the oldest larvae and that of the youngest postlarvae.

To avoid, to a certain extent, the effect of the occurrence of ten successive egg developmental stages on mortality estimates, the number of ten (I—X) stages was reduced to five (A—E) in the following manner:

A — I
B — II, III, IV
C — V, VI, VII
D — VIII, X
E — X

The stage *A*, however, was not taken into account in the mortality coefficient calculations, since its actual developmental time could not be established in the course of the studies of the relationship between egg developmental rate and temperature.

To eliminate, to a certain extent, the effect of accumulation of eggs and larval anchovy stages in the plankton caused by different developmental times of stages and length groups, and therefore different probability to catch them from the plankton, the number of eggs of each of the stages and the number of larvae or postlarvae of each of the length groups were divided by the stage or length group developmental time (*dt*). The time of reaching the middle of the egg developmental stage or the middle of length group was used as the respective stage or length group age (N a k a i and H a t t o r i, 1962).

Developmental time of each of the egg stages was calculated on the basis of the equations (4.1.5) and (4.1.6) by the following expression:

$$dt = Dst_{i+1} - Dst_i,$$

where dt is the developmental time of a stage, Dst_i the time of the beginning of the i^{th} stage and Dst_{i+1} the time of its end.

The mean age of a stage was calculated by the expression:

$$\bar{t} = \frac{Dst_{i+1} - Dst_i}{2} + Dst_i$$

where, to calculate the total egg developmental time (equation 4.1.5) the temperature at 0 m was taken and time was calculated in days.

Age of larvae was calculated by the equations (4.1.25) and (4.1.26), and that of postlarvae by the equation (4.1.29). The values of growth rate coeffi cents (*c*) were calculated by means of the equations (4.1.11) and (4.1.15) by which its relation to temperature was approximated. Mean temperatures for the 0—20 m layer were used for growth rate coefficient calculation.

Developmental time of each of the larval length groups was calculated by the equation:

$$dt = \frac{1}{c} \ln \frac{A - l_{t_i}}{A - l_{t_{i+1}}} \qquad (4.2.3),$$

and that of the each of the postlarval length groups by the equation:

$$dt = \frac{1}{c} \ln \frac{l_{t_{i+1}}}{l_{t_i}} \qquad (4.2.4),$$

where l_{t_i} and $l_{t_{i+1}}$ are the initial and final lengths respectively of i^{th} length group.

Mean age of a group was calculated by the following expression:

$$\bar{t} = \frac{dt_i}{2} + t_i,$$

where t_i is the time of attainment of the initial length of i^{th} length group.

To estimate whether the anchovy planktonic stages mortality may be approximated by the exponential function (4.2.1) the mortality coefficients *(m)* were, in the first place, calculated for the mean number of eggs, larvae and postlarvae below 1000 square meter separately for each of the sampling stations and for the through period of investigations. Number of individuals below a square metre calculated according to the equation (3.2.) was multiplied by 1000 in order to evade the negative values of natural logarithms in cases when N/m^2 was lower than 1. Firstly, the mortality coefficients were calculated separately for eggs, larvae and postlarvae. Since these calculations showed that eggs and larvae had the same mortality coefficients it was calculated then separately for eggs and larvae and separately for postlarvae. The coefficients of correlation (*r*) between natural logarithm of the number of individuals in a stage or length group and time were also calculated to establish by the t-test whether this corelation was statistically significant. The results obtained are given in Table 4.2.1.

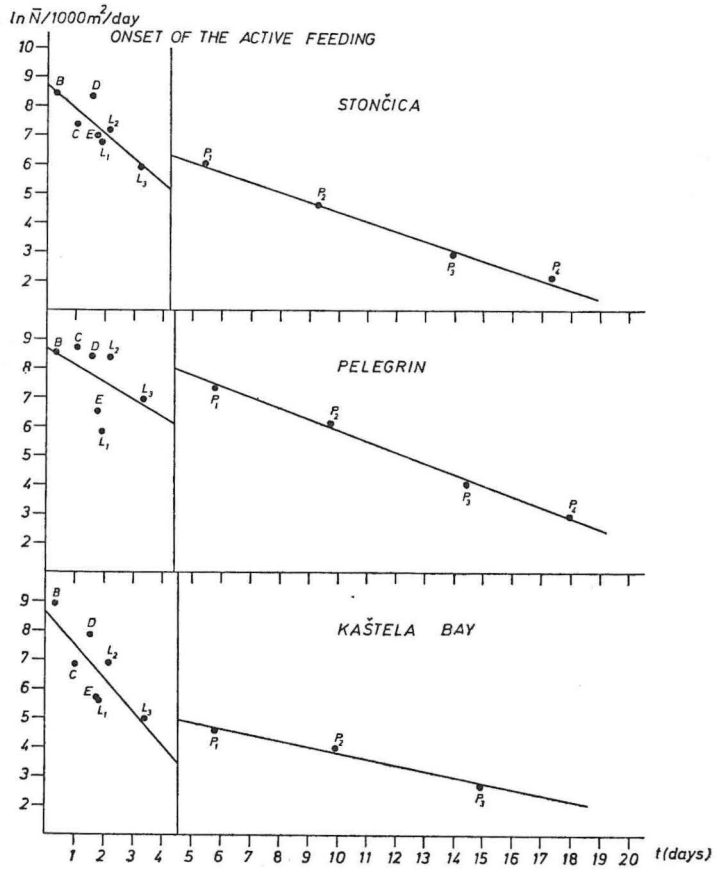

Fig. 12. Curves of mean mortality of anchovy planktonic stages in the study area

Table 4.2.1. Mean mortality coefficients (m) of anchovy eggs, larvae and postlarvae in the study area
* $\ln \bar{N} = \ln \{(\bar{N}/m^2/dt) \cdot 1000\}$

	Stončica $\bar{T}$ (0m) = 20.57°C $\bar{T}$ (0—20) = 19.42°C				Pelegrin $\bar{T}$ (0m) = 20.37°C $\bar{T}$ (0—20) = 19.07°C				Kaštela Bay $\bar{T}$ (0m) = 20.60°C $\bar{T}$ (0—20) = 18.41°C			
	$\bar{t}$	dt	$\bar{N}/m^2$	ln N*	$\bar{t}$	dt	$\bar{N}/m^2$	ln N*	$\bar{t}$	dt	$\bar{N}/m^2$	ln N*
Eggs and larvae												
B	0.35	0.70	3.34	8.47	0.36	0.72	3.65	8.53	0.35	0.69	5.21	8.93
C	1.05	0.70	1.14	7.39	1.08	0.72	4.37	8.71	1.04	0.69	0.65	6.84
D	1.54	0.29	1.21	8.34	1.59	0.30	1.36	8.42	1.52	0.29	0.75	7.85
E	1.73	0.08	0.10	6.98	1.79	0.09	0.06	6.52	1.71	0.08	0.02	5.70
L_1	1.87	0.19	0.16	6.71	1.93	0.20	0.07	5.84	1.86	0.21	0.06	5.60
L_2	2.12	0.32	0.42	7.18	2.20	0.33	1.47	8.40	2.15	0.37	0.38	6.92
L_3	3.25	1.94	0.70	5.89	3.38	2.03	2.16	6.97	3.44	2.21	0.33	4.99
	$m = 0.8505$ $r = -0.848$ $P < 0.02$				$m = 0.6033$ $r = -0.489$ $P-$				$m = 1.1495$ $r = -0.798$ $P < 0.05$			
Postlarvae												
P_1	1.18	2.37	0.99	6.03	1.22	2.43	3.85	7.37	1.27	2.54	0.26	4.61
P_2	5.08	5.42	0.54	4.60	5.20	5.54	2.65	6.17	5.44	5.79	0.32	4.00
P_3	9.72	3.85	0.07	2.93	9.94	3.94	0.23	4.07	10.39	4.11	0.06	2.74
P_4	13.13	2.98	0.02	2.1	13.44	3.05	0.06	2.91	14.04	3.19	0.0	0.0
	$m = 0.3336$ $r = 0.997$ $P < 0.01$				$m = 0.3750$ $r = -0.997$ $P < 0.01$				$m = 0.2066$ $r = -0.989$ $P < 0.1$			

All mortality coefficient means are statistically significant for the high significance levels. The only exceptions are the coefficients for eggs and larvae from Pelegrin and those for postlarvae from the Kaštela Bay. This shows that anchovy planktonic stages mortality may be estimated by the equation (4.2.1).

Egg and larval mortality was found to be highest at the Kaštela Bay Station and lowest at Pelegrin. Postlarval mortality, however, was highest at Pelegrin and lowest in the Kaštela Bay. Mortality coefficient of eggs and larvae is 2.8 times that of postlarvae.

Two periods of specific mortality may be clearly distinguished in the planktonic stages of anchovy from the study area. The first period of high mortality takes the time from egg fertilization to the complete yolk sac resorption, that is transformation of larvae to postlarvae. The second period takes the time from the transition to exclusively active feeding, up to attainment of the maximum length of postlarvae caught from the plankton (10 mm). It may be assumed that this second period last up to the transformation of pastlarvae to juvenile fish. Mortality of the first period considerably exceeds that of the second one (Fig. 12).

Some characteristics common to all of the sampling stations were observed. The deviations from the calculated mortality curve found in eggs and larvae exceeded considerably those found in postlarvae. Namely, C and E stages, as well as larvae from the L_1 length group showed considerable reductions in number if compared with other eggs stages and larval length groups (Fig. 12). Subsequently, as it may be seen from Fig. 12, at all of the stations the N_0 value for postlarvae is higher that the N_t value of the transformation of larvae to postlarvae (termination of the yolk feeding). This may be accounted for by the following: the E stages and L_1 length group take very little time if compared with other stages and length groups. According to Table 4.2.1., at mean temperatures they are present in the plankton not longer than 0.08 days (two hours) and 0.20 days (4.8 hours) respectively. Thus the probability to sample them was very low. This, naturally, led us to an underestimate of their number. The number of C stage at Stončica and Kaštela Bay stations was underestimated from quite different reasons. Namely, at mean environmental temperatures, this stage takes as much time as the B stages, that is about 0.70 day (Table 4.2.1) or 17 hours. Anchovy spawn during the evening and night hours (from 6 p. m. to 4 a. m.) and since all the samplings, throughout the period of investigations, were carried out between 07 and 11 a.m. most sampled eggs belonged to the B stages. This was once more proved by the fact that the number of eggs in the C stages exceeded the number of eggs in the B stages at Pelegrin Station (Fig. 12) at which all of the samplings were carried out in the afternoon, between 12 and 5 p.m. Relatively higher proportions of postlarvae than those of eggs and larvae (Fig. 12) indicate that probably a part of eggs and larvae passed through the plankton net meshes. Subsequently, approximately the same number of eggs and larvae seemed to pass through the meshes thus that their ratio remained unchanged. This is proved by the fact that the relation between the decrease in number of eggs and larvae and time showed high correlation coefficients, significant for the high significance levels (Table 4.2.1). Therefore, it may be concluded that the recorded loss of eggs and larvae through net meshes did not seriously affect their mortality estimates.

On the basis of the knowledge of m coefficient means and mean developmental time between egg fertilization and postlarvae of 9.99 mm in length, it was possible to calculate the mean percentage survival of eggs up to the end of embryonic development, of larvae up to the transformation to postlarvae and of postlarvae up to 9.99 mm in length taking that N_0 is 100 like in the (4.2.1) equation (Table 4.2.2).

Table 4.2.2. Mean percentage of survived anchovy individuals by different development stages

	Stončica	Pelegrin	Kaštela Bay
Hatching	22.19	33.15	13.38
Yolk resorption	2.76	7.08	0.54
Postlarvae 9.99 mm LS	0.02	0.04	0.02

According to the results given in Table 4.2.2, mortality of anchovy planktonic stages was lowest at Pelegrin. Mortality of eggs and larvae was highest at the Kaštela Bay Station. Thus, in the study area the percentage survival of eggs averaged 22.91% of the total number of fertilized eggs up to the termination of embryonic development. This percentage in larvae up to the transformation to postlarvae averaged 3.46% and in postlarvae up to 9.99 mm in length only 0.03%.

Mean mortality coefficients were also calculated for all the months in which planktonic stages were recorded (March-November). They were calculated separately for each of the stations (Table 4.2.3). Linear regression between

Table 4.2.3. Mean mortality coefficients (m) for Pelegrin and Stončica stations in 1962—1976 and the Kaštela Bay in 1968—1976. (* insignificant for $P<0.05$; ~ the number was increased for older stages)

	Months								
	III	IV	V	VI	VII	VIII	IX	X	XI
Stončica									
eggs + larvae	1.5283*	0.6756	0.8906	1.0221*	0.8886*	0.9743*	0.8935*	~	1.7449*
postlarvae	—	0.0456*	0.3157	0.3955	0.3976	0.3488	0.3582*	0.3707	—
Pelegrin									
eggs + larvae	—	0.5114	0.5407*	1.7043*	0.5119*	~	0.0429*	1.1983*	—
postlarvae	—	0.1736*	0.2615	0.4096	0.3917	0.3468	0.3523	0.2875	—
Kaštela Bay									
eggs + larvae	—	0.5171	0.8064	0.9894*	0.8455*	1.2610*	0.7303*	0.5886	0.6089
postlarvae	—	—	0.0122*	0.4425	0.4851	0.4471	0.4971*	0.2261*	—

the mean number of individuals below 1000 square metres recorded in individual months throughout the period of investigations and mean age of each of the stages or length groups obtained on the basis of mean temperatures in the respective months was calculated.

Mortality coefficients were found to vary considerably from one month to another as well as from one station to another. The highest mortality of eggs and larvae was recorded from Stončica in March, June, August and

November, from Pelegrin in June and October, and from the Kaštela Bay in June and August. The highest postlarval mortality occured at Stončica in June, July and October, at Pelegrin in June and July, and in the Kaštela Bay in June and September (Table 4.2.3).

To establish at which of the stations the mortality coefficients vary most, variability coefficients were calculated according to the equation:

$$V = \frac{s \cdot 100}{X} \qquad (4.2.5),$$

where V is the variability coefficient, s standard deviation and X mean value. Results obtained are given in Table 4.2.4.

Table 4.2.4. Variability coefficients of monthly mean mortality coefficients in the study area

	V (eggs and larvae)	V (postlarvae)
Stončica	33.81	36.86
Pelegrin	79.14	25.97
Kaštela Bay	30.74	55.40

Mortality coefficients of eggs and larvae varied most at Pelegrin and mortality coefficients of postlarvae in the Kaštela Bay (Table 4.2.4).

On the basis of known mortality coefficients and mean water temperatures as well as mean developmental time in individual months, percentages of survived eggs at the end of embryonic development, larvae at transformation to postlarvae and postlarvae which attained 9.99 mm in length were calculated (Table 4.2.5).

Table 4.2.5. Monthly mean percentage of survived anchovy planktonic stages in the study area given by individual developmental phases

	III	IV	V	VII	VIII	IX	X	XI	XII
Stončica									
Hatching	0.21	7.42	10.32	17.24	29.60	30.46	29.14	10.07	4.33
L/PL	—	0.10	0.34	1.40	4.87	4.74	3.90	0.55	0.007
PL 9.99	—	0.04	0.001	0.005	0.03	0.06	0.03	0.004	0.00005
Pelegrin									
Hatching	—	12.22	24.92	5.24	48.59	68.96	93.93	12.14	—
LP/PL	—	0.27	3.13	0.08	15.84	38.62	86.28	1.12	—
PL 9.99	—	0.05	0.03	0.0002	0.08	0.39	0.93	0.02	—
Kaštela Bay									
Hatching	—	11.16	14.32	18.97	31.67	19.41	32.24	27.23	—
L/PL	—	—	0.50	1.19	4.57	1.15	7.16	5.93	—
PL 9.99	—	—	0.40	0.001	0.005	0.002	0.01	0.20	—

According to the results shown in Table 4.2.5. percentages of survived anchovy planktonic stages at Stončica and Pelegrin were highest in July—September. The highest percentage survival of eggs and larvae was recorded in the Kaštela Bay in July and September and of postlarvae in May and October.

Calculated monthly mean coefficients provided the basis for calculations of egg mortality correction (K) which, in addition to egg developmental time, is needed for the calculation of egg production per unit time and area (equation 3.3.). The K values were calculated according to the equation:

$$K = \frac{1}{mD}(1 - e^{-mD}) \qquad \text{(Tanaka, 1973)} \qquad (4.2.6),$$

where m is the mortality coefficient and D egg developmental time in days. The K values are shown in Table 4.2.6. They are used for the later calculations of the anchovy egg production.

Table 4.2.6. Monthly mean K values in the study area

	III	IV	V	VI	VII	VIII	IX	X	XI
Stončica	0.1616	0.3559	0.7063	0.4708	0.5783	0.5850	0.5747	—	0.3046
Pelegrin	—	0.4176	0.5403	0.3214	0.7123	—	0.9693	0.4166	—
Kaštela Bay	—	0.4052	0.4409	0.4875	0.5943	0.4916	0.5986	0.5594	0.5768

Annual mean mortality coefficients for eggs, larvae and postlarvae (Table 4.2.7) were calculated on the basis of mean temperatures of anchovy spawning season and distribution of annual egg number by individual embryonic stages and distribution of larval and postlarval numbers by length groups.

Table 4.2.7. Annual mortality coefficient (m) means in the study area (* insignificant for $P < 0.05$; ~ = the number was increased for older stages)

	1962	1963	1964	1965	1966	1967	1968	1969
Stončica								
eggs + larvae	1.4775	1.1571	1.2637*	1.3574	1.0780*	0.7646*	0.7467*	0.9209*
postlarvae	0.4781*	0.3594	0.6530*	0.2295*	0.1994*	0.2254	0.3369	0.2595
Pelegrin								
eggs + larvae	1.1856	0.6949*	0.5707	0.2960*	0.4999	1.3014	0.3489*	~
postlarvae	0.2923	0.3183	0.3660*	0.3749	0.2227*	0.2304	0.2915	0.2516
Kaštela Bay								
eggs + larvae							0.6437*	0.2553*
postlarvae							0.2984*	0.4507*

	1970	1971	1972	1973	1974	1975	1976
Stončica							
eggs + larvae	0.6418*	0.8350*	0.3181*	1.1830	0.9433*	0.9067	0.7187
postlarvae	0.3164	0.2484*	0.3863*	0.3751	0.3744	0.4550*	0.3084
Pelegrin							
eggs + larvae	~	~	~	~	0.8982*	0.3504*	0.7968*
postlarvae	0.2785	0.3544	0.0376*	0.3221	0.3648	0.0553*	0.3443
Kaštela Bay							
eggs + larvae	0.8235	0.8992	0.9361*	1.3898	1.4141	1.0284	2.3865
postlarvae	0.4648	0.4239*	0.6199*	0.0315*	0.3680*	0.5472	~

It is apparent that annual as well as monthly mean mortality coefficients vary considerably. Therefore, variatbility coefficients were also calculated for them (Table 4.2.8).

Table 4.2.8. Coefficients of variability of annual mean mortality coefficients in the study area

	V (eggs and larvae)	V (postlarvae)
Stončica	31.88	34.09
Pelegrin	50.61	38.09
Kaštela Bay	55.49	44.71

As distinct from monthly means, annual means show an increase of variability going from the open sea (Stončica Station) onshore (Kaštela Bay Station) in eggs as well as in larvae and postlarvae (Table 4.2.8). The reason is that variations of environmental factors are less marked in the open sea than in the coastal area what is well known for all seas.

Discussion

Statistical analysis of the decrease of monthly and annual mean numbers of eggs from the initial to final embryonic stages and those of larvae and postlarvae from younger to older length groups showed that their mortality could be approximated as a function of time by the exponential equation (4.2.1). Subsequently, two periods of specific mortality may be distinguished in anchovy planktonic stages. The first period includes eggs and larvae, i.e. the thorough period of the yolk feeding. It is characterized by high mortality. The second period of considerably lower mortality includes the postlarval stage and initiates with the transition to active feeding (Fig. 12). The results obtained are very similar to the results on mortality observations under experimental conditions (chapter 4.1.), with the only difference in that during the experiments an almost dramatical drop in number was observed in postlarvae after transformation from larvae (Fig. 3).

The period of high mortality during the yolk feeding and the period of decreased mortality in postlarval stage was recorded in the planktonic stages of many fishes, such as in Californian sardine *Sardinops caerulea* (Ahlstrom, 1954), japanese pilchard *Sardinops melanostica* (Nakai and Hattori, 1962), horse mackerel, *Trachurus symmetricus* (Farris, 1960), Black Sea anchovy, *Engraulis encrasicolus ponticus* (Dehnik, 1963) and mackerel, *Scomber scombrus* (Sette, 1943).

We may simply distinguish biotic and abiotic causes of mortality of fish planktonic stages. After Nikolskii (1969) principal abiotic mortality causes are sudden changes of temperature, salinity and oxygen insufficiency. The ultraviolet radiation may be an additional factor affecting mortality increase of fish eggs and, to a certain extent, of fish larvae (Marinaro and Bernard, 1966). Subsequently, mechanical disturbances due to wind and wave

effects may be added (Dehnik, 1961; Pavlovskaya, 1955). It is unlikely that sudden changes of temperature may have lethal effects on anchovy planktonic stages, since these changes were not recorded from the central Adriatic (Buljan and Zore-Armanda, 1966). Temperature may probably affect mortality of planktonic stages indirectly through the duration of development, since, it is held that a rather long exposure of the fish planktonic stages to mortality causes may at lower temperatures result in lower survival (Lasker, 1964; Hempel, 1965). There are some reasons why we probably may apply this assumption to eggs and larvae from the study area. However low the mortality coefficients were in April and May, with an exception of Stončica (Table 4.2.3), the calculated percentage of survived eggs and larvae was considerably lower than in the warmer months (Table 4.2.5). This may be the result of a prolongated exposure due to the longer developmental time.

The lethal effects of ultraviolet radiation on anchovy eggs are fully unknown. This radiation may only be assumed to affect somehow the egg survival since it has been established that a large number of eggs are concentrated close to the surface (Specchi, 1968).

Results obtained by the experiments (Chapter 4.1) may, at first sight, support the assumption that wind and waves add considerably to an increase in anchovy egg mortality particularly prior to blastopore closing. In the experiment with pacific halibut eggs Forrester and Alderdice (1973) arrived at similar results. However, they believe that under experimental conditions eggs are more exposed to mechanical damages than in nature where the accelarations due to current flows are lower and where there is no mechanical obstructions such as the rearing tank walls, air pipes and other. Wind and wave effects on anchovy egg survival was studied in the Black Sea on the basis of the ratio of living eggs to the dead ones in each of the embryonic stages at different sea states (Pavlovskaya, 1955). Eggs with the yolk irregular in shape, spilt in the perivitelline space and of small granulation structure, with no cleavage due to broken vesicles were taken as dead eggs. An increased number of dead eggs, particularly in the first and third embryonic stages was found at sea exceeding 3 of the Beaufort's scale. Mortality assessment of eggs in individual stages was attempted on the basis of the ratio of living eggs to the dead ones in the central Adriatic too. Mortality was found to be highest in the earliest stages (Regner, 1972). However, during fishing for living anchovy eggs for experimental rearing of postlarvae (Chapter 3) a large number of fully transparent eggs, particularly of the earlier embryonic stages, were noticed floating on the surface of the jar where the eggs for experiments were taken from. However they had damaged yolks and deformed embryos. Upon preservation in formol these eggs showed all the properties of dead eggs. Therefore, in an ordinary planktonic catch, preserved on board immediately upon the planktonic net lifting, such eggs would have been classified as dead. Since the experiments showed that dead eggs sunk rapidly to the bottom, losing their transparency, it may be concluded that eggs in question were fully undamaged and that they were damaged while hauled by the net. Therefore, it seems very difficult to estimate the survival on the basis of the relationship between dead and alive eggs in the planktonic catches. That is why we believe that the increased number of dead eggs reported by Pavlovskaya to be caused by strong waves, was more likely

the result of jerking of the planktonic net due to the pitching and rolling of ship rather than a result of wave impact on eggs.

It may be concluded from the above, that abiotic factors probably do not have any crucial effect on anchovy planktonic stages mortality.

Biotic causes of fish egg and larval mortality include in the first place, predators and diseases. In postlarvae these two causes may be added the starvation due to the lack of appropriate food (Hempel, 1965; Nikolskii, 1969).

Predators and diseases of anchovy planktonic stages are for the time being very little known. After Demir (1965) all organisms feeding on the plankton are predators of anchovy planktonic stages. Studies of the survival of anchovy postlarvae as influenced by food quantity are somewhat more numerous. This, however, would be discussed in more detail in the two subsequent chapters. Nevertheless, for the time being, we may say that since the intensity of effects of separate causes of mortality of anchovy planktonic stages are very little known, the calculated mortality curves should be held only as a result of a larger number of factors.

Calculated percentages of survived eggs (Tables 4.2.2 and 4.2.5) broadly conform with the data for anchovy from the Azov Sea given by Dehnik (1967) After this author, the number of survived eggs up to the end of embryonic stage averaged 18.4% of a total number of the eggs spawned. However, percentage of survived postlarvae given by Dehnik in the cited paper is far in excess of the percentage of survival we recorded. Since this author reported that in the Azov Sea the survival up to the end of postlarval stage averaged 0.15% it may be understood that the conditions for survival more favourable in the Azov Sea than in the Adriatic. This may be due to the quantity of available food since Duka (1963) reported 11—19000 of organisms per anchovy postlarva. In the Adriatic this number does not exceed 6000.

Further, it has also been shown that anchovy egg mortality in the Adriatic is considerably lower than it was held. Namely, in comparing the number of eggs in the first developmental stage with that in the last one, with no correction for the developmental time of each of the stages, Piccinetti *et al.* (1979) found the survival of only 2% which is far less than shown by our results.

An error in mortality estimates may seriously affect the fish egg production assessment (Tanaka, 1943), and therefore it is essential to know the mortality coefficients. Some of the properties of the material from which the error in mortality coefficient estimates may result have already been mentioned within the introductory remarks of this chapter. The error resulting from the grouping of individual stages due to the longer duration of daily spawning period may be avoided, to a certain extent, by further concentrating them in one group like we did. At the same time, the error resulting from the difference in developmental times between indivdual stages and individual length groups respectively, may be efficiently diminished by dividing the number of individuals of developmental stages and/or length groups by the respective developmental time if it is long enough. It was shown that in cases of very short developmental time, such as in E stage in eggs and L_1 group in larvae, their liabilty to capture was very low and their number underestimated even though the number of found individuals was divided by the

time of their presence in the plankton. We held that it would be better to omit these stages and length groups from mortality coefficient calculations. Subsequently, the relation of the time of plankton sampling to the spawning time and developmental time may seriously affect the estimates of the number of specimens in individual stages, like it was shown for the C stage (Fig. 12).

According to the available data, escapement of a part of eggs, larvae and postlarvae through the plankton net meshes, net avoidance peculiar to postlarvae as well as the immigrations and emigrations of planktonic fish stages due to the escapement of a part of larvae through net meshes. Our results estimates.

Thus, after Farris (1960), Ahlstrom (1954) believed that mortality of early stages of californian sardine *Sardinops caerulea,* was overestimated due to the escapement of a part of larvae through net meshes. Our results have also shown that a part of eggs and larvae passed through net meches. We, however, held that this loss may affect an assessment of the total quantity of eggs and larvae in the plankton, which was not the object of this study, but not the mortality estimates and comparability of data. Namely, the numbers of eggs and larvae as a function of time were found to conform well with the calculated curve (Fig. 12) and the relation between their numbers and time to be stastically significant in a large number of cases for the significance levels exceeding $P < 0.05$ (Tables 4.2.1; 4.2.3 and 4.2.7). Therefore, it may be concluded that the number of eggs and larvae not captured by the net was proportionally the same. Thus the loss is unlikely to exert any significant influence on their mortality estimates.

Postlarval mortality estimates, besides being affected by an eventual loss through meshes, may also be affected by their capability to avoid the approaching net, since their perception abilities and swimming speed are far better than those of larvae. A larger number of authors reported that numbers of postlarvae captured during the night exceeded those captured during the day (Silliman, 1943; Ahlstrom, 1954; Bridger, 1958; Ahlstrom, 1959; Colton *et al.,* 1961; Pearcy and Laurs, 1966). This indicates that the net avoidance is, to a larger extent, dependent on visual perception. It was also found that the number of postlarvae which succeeded to avoid the net was decreased with the greater towing speed and mouth aperture diameter (Ahlstrom, 1948; Arnold, 1958; Colton *et al.,* 1961; Kinzer, 1966; Dicenta *et al.,* 1976). If the percentage of net avoidance was higher in older postlarvae than in the younger ones, a negative deviation of their number from the calculated mortality curve could be expected, like in the E egg stage and L_1 larval length group. According to the results obtained, however, there is no such deviation recorded in anchovy postlarvae (Fig. 12). On this basis it may be concluded that if the net avoidance takes place, the percentage of postlarvae which avoid it sucessfully is the same irrespective of their age or length. Therefore it appears that net avoidance by anchovy postlarvae does not cause any significant error in their mortality estimates, at least up to the length of 10 mm, that is the length up to which we caught them from the plankton. This is probably affected by the large aperture of the net used, the diameter of which was 143 cm. It may also be assumed that »Helgoland« net with 0.516 mesh size used in this study retains almost all anchovy postlarvae, since Lenarz (1972) showed that a net of 0.505 mm mesh size

retained all postlarvae of californian anchovy *(Engraulis mordax)*, the size of which is very similar to that of the Adriatic anchovy.

Karlovac (1967), Watanabe (1970) and Smith (1972) showed that mortality estimates of planktonic stages of sardine (*Sardina pilchardus* Walb.), pacific mackerel (*Scomber japonicus* Houttuyn) and northern anchovy *(Engraulis mordax)* might be seriously affected by drift caused by currents. This seems applicable to the Adriatic anchovy planktonic stages, as well. Namely, the lowest mean egg and larval mortality coefficients were recorded for Pelegrin Station, and the highest for the Kaštela Bay (Table 4.2.1). It was also observed that at the Pelegrin Station, at which the egg production was, as it will be shown in the subsequent chapter, considerably lower that at two remaining stations, eggs from the C and D stages, as well as L_2 group larvae, were represented almost as well as the youngest eggs from the B stage (Fig. 12). One possible explanation is that eggs and larvae were carried by currents from the adjacent areas to the area of Pelegrin. Current measurements at Stončica Station showed that during the spawning months the resultant surface current is to the north, that is onshore. On the contrary, in summer the resultant directions are prevalently to the southeast, that is offshore (Zore-Armanda, 1968). On this basis it may be concluded that anchovy eggs and larvae are drifted to the Pelegrin area from the open sea in spring and from the coastal areas in summer. The outgoing current direction prevails in the Kaštela Bay during the warmer part of the year (Gačić and Smirčić, 1971; Zore-Armanda, 1975) and therefore anchovy planktonic stages immigration to the Bay is excluded. However, the emigration is probable, particularly that of postlarvae since no larvae exceeding 7.99 (P_4 group) in length were recorded from the Kaštela Bay throughout the period of investigations. On the basis of everything aforementioned it may be concluded that mortality of anchovy planktonic stages was probably underestimated at Pelegrin Station and overestimated at the Kaštela Bay Station. However, since the data we had available did not cover a net of stations, the extent of error could not be established. In any case transport of anchovy planktonic stages from one area to another seems to have the highest effects on possible errors in their mortality estimates.

Hjort (1914) postulated a theory that a short period of high mortality occurred in early life stages of fish, that is after the yolk sac resorption at transition to active feeding. He explained this in terms of food insufficiency. This, after Hjort called »critical period« was recorded in many fishes reared under experimental conditions. It was as well noted in anchovy from our experiments, as it already has been brought out in chapter 4.1. Hjort attribued great significance to »critical period« believing that the insufficiency of food for postlarvae in that short time interval had crucial importance for the strength of the brood produced from them. However, in analysing the earlier data on planktonic fish mortality Marr (1956) already criticised Hjort's theory stating that »critical period« could not be established with certainty but that a small number of available proofs was indicative of a constant rate of continuous mortality rather than of the mass mortality in a short time. Farris (1960) arrived to a similar conclusion. The data obtained in this study showed that there was no »critical period« in anchovy in natural environment but to the opposite that mortality rate was considerably reduced after

transition to active feeding. It should be mentioned that during some earlier investigations in the central Adriatic »critical period« was recorded both in sardine (K a r l o v a c, 1967) and anchovy (R e g n e r, 1972). However, on these occassions larval and postlarval mortality was estimated on the basis of the difference in numbers between individual length groups. However, that method is not so good an indicator as observations of the decrease in numbers in relation to time.

C o n c l u s i o n s

1. Mortality of anchovy planktonic stages in the investigated area may be expressed by the equation:

$$N_t = N_0 e^{-mt}$$

where N_t is the number of anchovy planktonic stages in time t, N_0 number in time $t = 0$ and m mortality coefficient.

2. Two periods of specific mortality were recorded in anchovy planktonic stages from the central Adriatic. The first period, characterised by high mortality rate, includes eggs and larvae up to the complete yolk sac resorption. The second period of considerably lower mortality includes postlarvae after transition to exclusively active feeding.

3. The percentage of larvae which attain a 10 mm length averages 0.03% of the total number of spawned eggs in the investigated area.

4. Transport of anchovy planktonic stages by currents seems to have the highest influence on the possible error in mortality estimates.

5. »Critical period« was not established in the planktonic stages on anchovy from the central Adriatic.

4.3. DISTRIBUTION OF ANCHOVY PLANKTONIC STAGES DURING THE SPAWNING SEASON

On the basis of data on anchovy egg developmental time and larval and postlarval growth rates in relation to temperature, as well as on the basis of calculated mortality coefficients, anchovy egg production and the numbers of larvae and postlarvae in individual length groups under an unit area of surface per unit time were calculated separately for each of the samples from which anchovy planktonic stages were taken. Egg production was calculated on the basis of the equations (3.2) and (3.3) and (D) developmental time was calculated for the temperature recorded at 0 m depth at the time of sampling. The K value from the equation (3.3) was taken for each month from Table 4.2.6. Numbers of larvae and postlarvae were calculated for each of the samples thus that the number of individuals in each of the length groups was divided by developmental time (dt) of a respective group obtained on the basis of the equations (4.2.3) and (4.2.4). The c value was calculated for the tempe-

rature of 0—20 m layer at the time of sampling. Egg production and the number of larval stages were calculated as a number of individuals under a square metre per day.

Results

Anchovy eggs were recorded from the Stončica (open sea) and Kaštela Bay stations (coastal area) in April—October and only exceptionally in March and November. At Pelegrin (channel area) eggs were also found in April—October, and only once in March (1972) whereas no eggs at all were found in November. Larvae and postlarvae were recorded from all the stations in April—October. At Stončica larvae were found as well in November 1969 and postlarvae in November 1969 and 1974. Postlarvae were recorded from Pelegrin in November 1974. Accordingly, the conclusion may be drawn that the period in which anchovy larval stages may be found in the plankton is somewhat shorter than that in which eggs occur.

Calculated total mean egg production showed the ratio 1 : 0.42 : 0.99 at Stončica — Pelegrin — Kaštela Bay station. Accordingly, during the spawning season an almost equal number of eggs is produced in the open sea and coastal area. In the channel area, however, the production is considerably lower. It may, therefore, be concluded that the conditions in the channel area are probably not favourable for anchovy spawning. The ratio of larval mean number is similar to that of eggs, 1 : 0.66 : 0.91. However, mean postlarval number is 1 : 0.86 : 0.57. It is apparent that, with respect to the small number of eggs produced at Pelegrin, postlarvae found there had not developed from the eggs produced there.

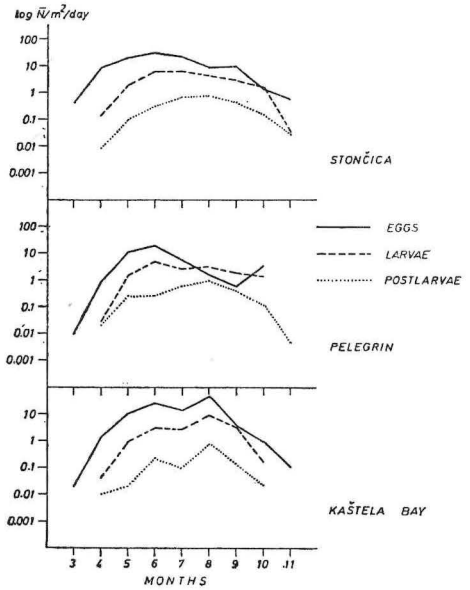

Fig. 13. Distribution of production and numbers of anchovy planktonic stages during spawning season

Long-term means (15-year ones for Stončica and Pelegrin and 9-year ones for the Kaštela Bay) show that egg production reaches an absolute maximum at Stončica and Pelegrin in June and a relative maximum at Stončica in September and at Pelegrin in October. At the Kaštela Bay Station a relative maximum occurs in June and absolute one in August (Fig. 13). Accordingly, the spawning intensity variations in the Kaštela Bay differ from those at Stončica and Pelegrin. Subsequently, it was found that the mean number of anchovy larvae agrees best with the variations in the spawning intensity in the Kaštela Bay. Somewhat poorer agreement was established for two other stations. At the same time, maximum numbers of postlarvae are in good agreement with the maxima of egg production only at the Kaštela Bay Station. At Stončica and Pelegrin the largest numbers of postlarvae occur in August whereas their numbers are relatively low in June (Fig. 13), when egg production is highest. This relatioship is even better shown by the coefficients of correlation between egg production and larval number on the one hand and the number of postlarvae on the other, calculated separately for each of the stations (Table 4.3.1.).

Table 4.3.1. Coefficients of correlation between monthly mean production of anchovy eggs under a square metre per day and monthly mean numbers of larvae and postlarvae under a square metre per day.

Station	r (eggs, larvae)	P<	r (eggs, postlarvae)	P<
Stončica	0.795	0.02	0.379	—
Pelegrin	0.715	0.05	0.888	—
Kaštela Bay	0.909	0.001	0.926	0.001

Distribution of correlation coefficients shows that at the Kaštela Bay the numbers of larvae and postlarvae agree almost completely with the egg production. At Stončica and Pelegrin the number of larvae is in agreement with egg production to a limited extent only, whereas egg production and the number of postlarvae show disagreement.

This is probably a consequence of the system of currents in the surface layer of the study area which affects emigration and immigration of larvae and postlarvae, as shown in the chapter 4.2. Particularly good agreement of anchovy egg production intensity and the numbers of larvae and postlarvae in the Kaštela Bay in which, as shown in the preceding chapter, the outgoing current, which excludes any immigration, prevails, shows that the numbers of larvae and postlarvae are in fact dependent on the egg production intensity. The deviations from this relationship at Stončica and Pelegrin area obviously due to current transport. Postlarvae recorded in maximum numbers at Stončica and Pelegrin in August, when maximum egg production occurs in the Kaštela Bay, probably came from the coastal area. This is supported by the fact that the resultant current direction in the surface layer in summer is to the south—east and south—west, that is offshore (Z o r e - A r m a n d a, 1968). Mean resultant current speed at Stončica is 14 cm/sec in summer, that is about 6.5 NM per day. The developmental time of postlarvae, from the yolk sac resorption to the length of about 10 mm, calculated on the basis of mean

temperature for the 0—20 m layer in June—September in the study area, takes about 13 days in the summer. Therefore it is quite possible that larvae hatched in the coastal area are transported to the channel area and open sea, the distance of which from the coast does not exceed 20 and 30 NM respectively.

Taking into account that the number of postlarvae is highest in summer (July, August and September) it may be concluded that, irrespective of the relatively high postlarval mortality coefficients (Table 4.2.3), the largest part of the new recruits is generated in the study area just during these months.

As to the abiotic factors, the relationship of anchovy planktonic stages to temperature and salinity was studied. The relation between eggs and temperature and salinity means for 0—20 m column was also observed, irrespective of that eggs keep close to the surface and that the temperatures at 0 m were used for their developmental time calculations. It was, however, established that anchovy spawning was affected by hydrographic conditions of the surface layer in their broader sense (F a g e, 1920). The 0—20 m depth column corresponds to the mean depth of thermocline in the Adriatic (B u l j a n and Z o r e - A r m a n d a, 1971).

Temperature and salinity ranges within which anchovy planktonic stages were recorded throughout the period of investigations are shown in Table 4.3.2.

Table 4.3.2. Temperature and salinity ranges within which anchovy planktonic stages were recorded from the study area. Marginal values for 0 m depth are given for eggs.

	Temperature (°C)		Salinity (S‰)	
Station	0 m	$\bar{X}$ (0—20 m)	0 m	$\bar{X}$ (0—20 m)
Stončica				
eggs	13.12—27.32	13.15—23.75	37.03—38.90	37.52—38.90
larvae		14.08—23.85		37.52—38.90
postlarvae		14.08—23.85		37.52—38.90
Pelegrin				
eggs	13.33—25.71	13.20—23.90	35.41—38.64	36.57—38.67
larvae		13.90—23.29		36.83—38.70
postlarvae		13.90—23.29		36.83—38.70
Kaštela Bay				
eggs	13.17—25.62	23.18—22.78	31.60—38.86	34.91—38.09
larvae		13.18—22.78		35.16—38.09
postlarvae		14.93—22.78		35.86—38.09

As it may be seen from Table 4.3.2, anchovy planktonic stages occur within the same temperature ranges at all of the stations. However, salinity ranges are considerably lower in the coastal area than in the open sea.

The distribution of percentages of the total numbers of eggs, larvae and postlarvae ($\sum_{i=1}^{n} \bar{N}/m^2/day_i$) in relation to temperature and salinity showed that

a rather large number of anchovy planktonic stages occurred within wider temperature and salinity ranges (Figs. 14 and 15).

The highest egg production was found to occur at Stončica at 17 and 19C, at Pelegrin at 17—18°C and at the Kaštela Bay Station at 17, 19 and 21°C.

Increased numbers of larvae and postlarvae were recorded from Stončica and Pelegrin at the same temperature at which increased number of eggs was recorded. However, larvae and postlarvae reached an absolute maximum at 22°C temperature, at which egg production was very low at both stations. On the contrary, the increases in numbers of larvae and postlarvae at the Kaštela Bay Station occur at exactly the same temperatures at which maximum egg production occurred (Fig. 14).

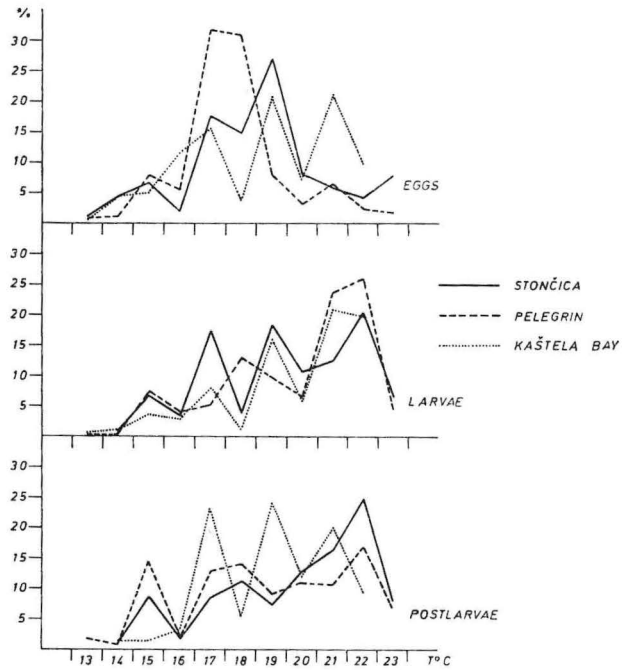

Fig. 14. Distribution of anchovy planktonic stages during spawning season in relation to temperature

Increased numbers of anchovy planktonic stages were also found within very wide salinity ranges. Thus egg, larval and postlarval maxima were recorded from Stončica within 37.80—38.20‰ and 38.60—38.99‰ salinity ranges. At Pelegrin these figures were 37.00—37.20‰, 37.80—38.00‰ and 38.20—38.40‰ for eggs and 37.20—37.40‰ and 38.00—38.20‰ for larvae. Higher number of postlarvae was recorded from this station within 38.00—38.40‰ salnity range and their absolute maximum within 38.60—38.80‰ salinity range. At the Kaštela Bay Station larger numbers of eggs, larvae and postlarvae were recorded within 35.80—36.00‰, 37.00—37.20‰ and 37.40—37.60‰ salinity ranges; an increased egg production was recorded within 37.80—38.00‰ salinity range as well (Fig. 15).

This occurrence of maximum anchovy egg production and maximum numbers of larvae and postlarvae within very wide temperature and salinity ranges show that neither the 17—22°C temperature range nor the 35.8—38.00‰ salinity range affect significantly the anchovy spawning intensity or the numbers of larvae and postlarvae. This is indicative of the fact that temperature and salinity ranges which may be taken as optimum for the reproduction of this fish, are very wide.

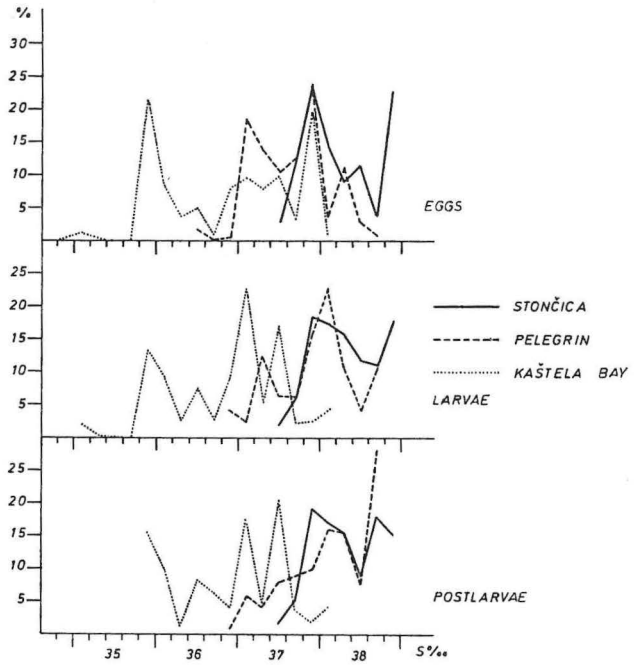

Fig. 15. Distribution of anchovy planktonic stages during spawning season in relation to salinity

It was found that maximum numbers of all of the anchovy planktonic stages occur at the Kaštela Bay Station at the same temperature values and at almost the same salinity values. On the contrary, at Stončica and Pelegrin temperatures at which larval and postlarval maxima occur are mainly higher than those at which egg maxima occur. The same may be applied to salinity at Pelegrin Station (Figs. 14 and 15). This also indicates that a large part of larvae and postlarvae recorded from these stations are not autochthonous.

The relationship between anchovy egg production and larval and postlarval numbers and primary organic production in the study area was also studied. Continuous phytoplankton production measurements were carried out at Stončica and Kaštela Bay stations from 1962—1975 by Steeman-Nielsen C^{14} radioactive carbon method.* The 14-year monthly primary production

* Data on primary production were obtained by courtesy of Dr Tereza Pucher-Petković.

means (mg/c/m^{2}day) at Stončica and Kaštela Bay stations were compared to the long-term monthly means of anchovy egg production and larval and postlarval numbers. It was found that curves of monthly primary production means for both stations had essentially the same form as the anchovy egg production curves, but that egg production maxima showed a phase lag of two months in relation to primary production maxima. Monthly mean numbers of larvae at Stončica as well as those of larvae and postlarvae in the Kaštela Bay showed similar distribution in relation to primary production (Fig. 16). Coefficients of correlation between monthly means of egg production and larval and postlarval numbers and respective primary production values with the negative phase lag of two months showed the following values:

	Eggs	Larvae	Postlarvae
Stončica	r 0.606	0.577	0.143
	P <0.1	n.s.	n.s.
Kaštela Bay	r 0.629	0.578	0.489
	P <0.1	n.s.	n.s.

According to the usual interpretation of correlation coefficients all the obtained values, except those for postlarvae from Stončica, showed an actual significant correlation. However, only the relationship between egg production and primary production is statistically significant for relatively low probability level of not more than 90%. Yet, this probability level shows that the established relationship can not be accidental.

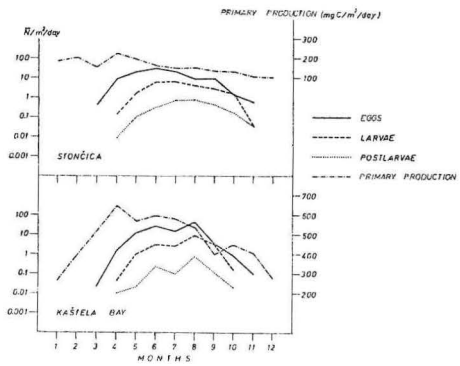

Fig. 16. Relationship between anchovy planktonic stages and primary production

Anchovy planktonic stages show similar relation to the long-term mean zooplankton volume values obtained by sedimentation of each of the planktonic catches throughout the period of investigations (Chapter 3). Seasonal egg production and larval stage numbers distribution curves were found to be

similar to the zooplankton volume distribution curves with a phase lag of two months. Postlarvae from Stončica and Pelegrin, however, showed a three month lag (Fig. 17). Calculation of correlation coefficients with two month lag, with the exception of the aforementioned larvae from the aforementioned stations gave the following results:

		Eggs	Larvae	Postlarvae
Stončica	r	0.672	0.718	—
	P	<0.1	0.1	—
Pelegrin	r	0.864	0.654	—
	P	<0.01	n.s.	—
Kaštela Bay	r	0.202	0.262	0.256
	P	n.s.	n.s.	n.s.

Relatively high correlation coefficients were obtained in eggs and larvae both in the open sea (Stončica) and in the channel area (Pelegrin). The coefficient of correlation between anchovy egg production and zooplankton quantity at Pelegrin is statistically significant for very high significance level of 99.0%. On the contrary, the correlation coefficients calculated for the Kaštela Bay station show no correlation at all.

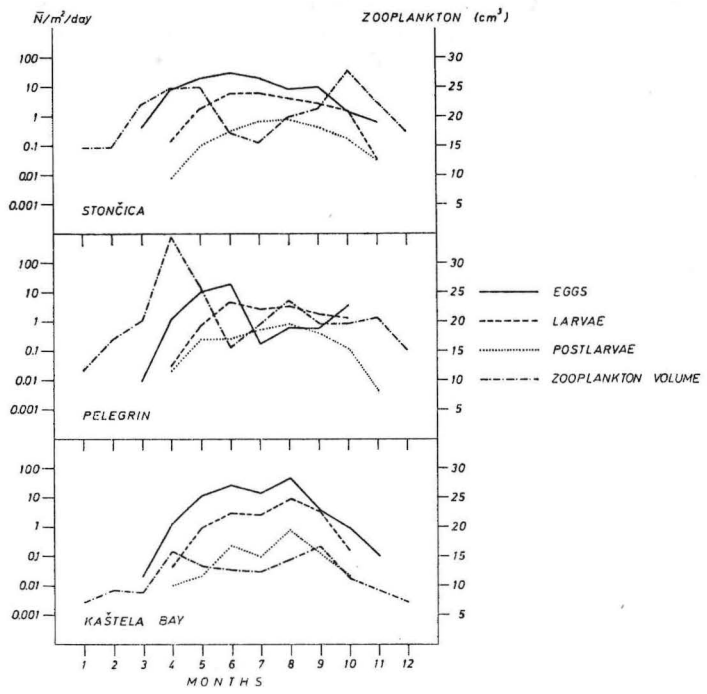

Fig. 17. Relationship between anchovy planktonic stages and zooplankton volume

Relatively high and mostly statistically significant positive coefficents of correlation between egg production and the number of anchovy larvae on the one hand and primary production and zooplankton volume on the other, show that the anchovy spawning intensity is closely connected with general productivity conditions in the study area. A phase lag of two month shows that an intensive spawning probably follows and intensive feeding of adult anchovy during gonad maturation, which coincides with the most intensive organic production.

The number of postlarvae, however, showed to coincide neither with the primary production nor with the net zooplankton volume. It may be assumed hat their number is also affected by the quantity of available food. However, it will be later shown that they feed on neither the phytoplankton nor the net plankton.

Finally, monthly mean egg production was also compared to the monthly mean catch of the anchovy in the study area. It was attempted to examine to what extent may the egg production be an indicator of adult fish presence.

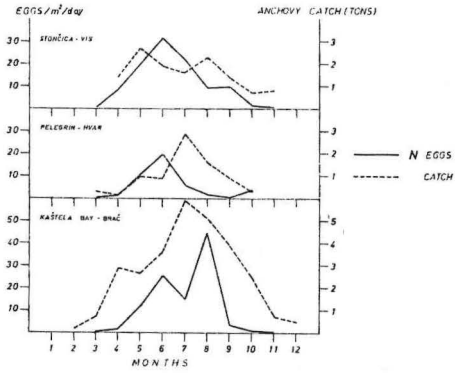

Fig. 18. Relationship between anchovy egg production and catch in the study area

Data on anchovy catches were taken from the STATISTIČKI BILTEN SFRJ (Statistical Bulletin SFRY-u for cattle-breeding and fisheries) for the 1976 period. Egg production at Stončica was compared to the data on catches from the area of Vis; that at Pelegrin to the data on catches from Hvar; and that from the Kaštela Bay to these from the Brač area (see Fig. 1).*

* Data on anchovy catches from the Split area were useless since our statistical bulletins do not comprise the records on fish catches from the areas in which they were actually caught. The records refer to the areas of the vessel's mother port. Vessels of the principal fishing enterprise in the Split area operate (fishing of the small pelagic fish) mainly in the northern part of the central Adriatic — around the island Dugi otok (A. Krstulović, »Jadran« fishing and processing fish enterprise, Split — personal comunication). Fishermen from the Vis Island fish mainly south from Vis and Biševo (M. Kučić — personal communication) and fishermen from the Hvar Island around the Hvar Island and somewhat less around Vis (F. Grubišić — personal communication). Vessels of the »Sardina« factory from Postira, Brač Island fish mainly in the coastal area — Makarska, Brač Channel and in the vicinity of Čiovo Island thus that their fishing records may be compared to the egg production in the Kaštela Bay.

It was found that anchovy catch maxima from the Vis and Brač areas preceded the maxima of egg production at Stončica and Kaštela Bay for about a month. Maxima of catches from the Hvar area, however, occur a month later than the maximum egg production (Fig. 18). Calculated correlation coefficents (Stončica — Vis/ a lag of a month in advance/ $r = 0.723$, $P < 0.1$; Pelegrin — Hvar/ a lag of a month retard/ $r = 0.868$; $P < 0.2$; Kaštela Bay — Brač/ a lag of a month in advance/ $r = 0.570$; $P < 0.1$) show that catch distribution curves, which may be indicators of the presence of larger adult anchovy schools, and the egg production curves, which are indicators of the spawning intensity, coincide. Judging, however, from the correlation between maximum catch and egg production it seems that anchovy catch decreases with an increase in the spawning intensity. This could mean that at the time of the most intensive reproductive activity a change in the behaviour of this fish takes place, which is likely to affect the reduction of catch even though fish are present in rather high quantities.

Discussion

Data on seasonal distribution of anchovy eggs production in the open sea (Stončica) and channel area (Pelegrin) do not esentially differ from the earlier findings (Vučetić, 1971; Regner, 1972), after which the largest numbers of anchovy eggs were also recorded from these stations in June. In the coastal area (Kaštela Bay), however, absolute maximum of egg production was found to occur in August whereas the earlier papers for the 1959—1969 period (Vučetić, 1971) and 1968 and 1969, (Regner, 1972) showed that the largest number of eggs were also recorded from this station in June. Some ecological changes, recently observed in the Kaštela Bay, may be the reason for these differences in the time of occurrence of maxima. It was found, however, that up to the year 1967, seasonal phytoplankton cycle on this station showed the phases of winter and spring bloom and summer-autumn stagnation, similar to those at the open sea. In the 1968—1972 period, however and additional summer phytoplankton maximum was recorded in August as well as a considerable increase in phytoplankton density at this station (Pucher-Petković, 1975). Pucher-Petković held this phenomenon to be the result of the intensified nutrient inflows, particularly those of phosphates, due to the increased organic pollution in the Split area. Thus it is possible that these changes caused the change in the anchovy spawning dynamics in this area which was found to coincide with the phytoplankton primary production (Fig. 16).

On the other hand, later occurrence of egg production maxima in the Kaštela Bay may be due to the fact that younger anchovy are present there. It is well known, however, that younger fish spawn later that the older ones and that, as a rule, produce smaller eggs (Nikolskii, 1963). Mužinić (1956 and 1972) reported anchovy from the open sea to exceed in size the anchovy from the coastal area. On the basis of this author findings and the fact that the eggs from the Kaštela Bay were smaller than those from the open sea plankton it was assumed (Regner, 1973) that prevalenty smaller and younger anchovy inhabited the Kaštela Bay. This assumption was supp-

orted by Sinovčić (1978) who found that the length of anchovy from around this Vas and Biševo islands ranged from 14.9—16.8 cm and that of the anchovy from the Kaštela Bay from 11.0—15.1 cm.

Studies of the correlation between anchovy egg production and larval and postlarval numbers, and temperature and salinity showed that anchovy spawned within very wide ranges of both of these factors. This supports the Demir's report (1965) that neither salinity nor temperature are the factors limiting anchovy distribution in the Mediterranean.

The occurrence of high anchovy egg production and high numbers of their larvae at different temperature and salinity values (Figs. 14 and 15) on the one hand and very good agreement of egg production and larval numbers and seasonal variations of phytoplankton primary production and zooplankton volume (Figs. 16 and 17) on the other hand, have led us to conclude that the anchovy spawning intensity in the study area is affected more by the biotic environmental factors than by the abiotic ones.

Gonad development in many fishes is known to be connected with the quantity of available food. It is, as well, known that the spawning time and area are the result of an adaptation which should provide as favourable environmental conditions as possible for egg and larval stages development (Nikolskii, 1963). Accordingly, good agreement of anchovy egg production and larval number with primary production and zooplankton volume is one of these adaptations. The beginning of maturation is very likely connected with the intensive anchovy feeding during maximum organic production in this area. Andreu and Rodrigez-Roda (1951) reported that the beginning of gonad maturation in anchovy from the western Mediterranean fell in March, whereas a larger number of individuals with ripe gonads occurred in June. This coincides with the phase lag of two months we recorded in our study area. The fact that coefficients of correlation between anchovy egg production and volume of zooplankton, on which adult anchovy feed, exceed the coefficients of correlation between egg production and primary production indicates that the spawning intensity dynamics is closely connected with the adult anchovy feeding. Low coefficients of correlation between egg production and larval number and zooplankton volume were obtained for the Kaštela Bay Station. One possible explanation are monthly differences in planktonic community composition between the coastal area and more offshore areas. Namely, while in August and September copepods are responsible for the high zooplankton numbers at Stončica and Pelegrin, *Pyllopoda* are most numeros in the Kaštela Bay (Regner, D., personal communication).

Relationship between anchovy egg quantity in the plankton and zooplankton dry weight and number of phytoplankton cells respectively were studied by Vučetić (1975) in the same area. This author as well found that anchovy egg quantity fairly agreed with the mentioned parameters. In observing the relationship between anchovy egg quantity in the plankton and individual zooplankton groups, this author found best agreement with the quantities of copepod *Euchaeta hebes* and decapod developmental stages. According to Demir (1965), Fage (1911) found that adult anchovy fed on copepods, mysids and crustacean developmental stages from coastal areas.

Subsequently, the results obtained broadly agree with some earlier records which show that in the study area seasonal distribution of echo trace abun-

dance of small pelagic fish on echograms coincides with the seasonal zooplankton biomass distribution (Vučetić and Kačić, 1973).

As distinct from anchovy egg production and larval number, which in fact reflect the reproductive activity of sexually mature anchovy, it is apparent and shown by Figs. 16 and 17, as well as by calculated correlation coefficients, that postlarval number coincides with neither the primary production nor zooplankton volume.

Feeding of anchovy postlarvae, from the yolk sac absorption to the length of 12 mm, have already been rather intensively studied. It was established that, dependently on length, postlarvae fed on copepod eggs, nauplii, metanauplii and copepodites, that is mainly on copepod developmental stages (Duka 1961, and 1963; Pavloskaya, 1964; Regner, 1971). Phytoplankton was rarely found in the guts of anchovy postlarvae (Duka, 1961; Regner, 1971). It is held that anchovy postlarvae feed only occasionally on phytoplankton. Subsequently, food composition was found to be constant even though the number of respective food constituents was decreasing. On this basis its was concluded that their feeding selectivity was low (Pavlovskaya, 1964). It may, therefore, be concluded that, if predators are excluded, anchovy postlarval numbers and survival are to the largest extent affected by the availability of copepod developmental stages. Quantitative variations of the youngest developmental stages of copepods in the central Adriatic are for the time being practically unknown. Therefore, the collection of data on this matter should be one of the principal aims of further investigations.

A comparison of the distribution of anchovy egg production by months to anchovy catches in the study area showed that the catch curves and egg production curves were very similar in form (Fig. 18). On this basis it may be concluded that egg production is, to a considerable extent, a reflection of the presence of anchovy schools in the study area. Andreu and Rodrigez-Roda (1951) arrived at a similar conclusion studying anchovy spawning in the western Mediterranean. Judging from the maximum catch preceding egg production maxima at Stončica and Kaštela Bay stations and/or lagging behind them at Pelegrin, it appears that a change in fish behaviour takes place, which affects the reduction of catch at that time. After Merker and Vujošević (1972), Rijavec (1966) reported similar phenomenon studying anchovy spawning in the Bay of Boka Kotorska. According to this author's data anchovy maximum catch comes about a month later than maximum number of eggs occurs in the plankton. Anyhow, the cause of this phenomenon should be examined in more detail.

Conclusions

1. The anchovy spawning in the study area is accepted as occupying the period (March) April to October (November). Larvae and postlarvae were, as a rule, recorded from the plankton over a shorter period.

2. Egg production reaches the maximum at the open sea (Stončica) and in the channel area (Pelegrin) in June, and in the coastal area (Kaštela Bay) in June and August.

3. An approximately the same egg quantity is produced in the open sea and in the coastal area during the spawning season. Egg quantity produced

in the channel area is half that in these two areas. The conditions in the channel area seem to be somewhat less favourable for spawning.

4. The time when anchovy larvae and postlarvae reach maximum numbers in the plankton, in fact coincides with the time of the most intensive egg production. The deviations from this relationship recorded at Stončica and Pelegrin are indicative of the immigration of particularly postlarvae, to these areas due to current transport.

5. Absolute maxima of anchovy postlarvae were recorded from all of the stations in August. Judging from the resultant current directions in the summer months it may be concluded that a large proportion of postlarvae recorded from Stončica and Pelegrin at that time came from the coastal area.

6. Anchovy planktonic stages occur in the plankton of the study area within 13.15—23.85°C temperature range. As distinct from temperature, anchovy planktonic stages occur at considerably higher salinity values (35.41—38.90‰) in the open sea and the channel area than in the coastal area (34.91—38.09‰). It seems, however, that within the mentioned ranges, neither temperature nor salinity affect significantly the anchovy spawning intensity.

7. Anchovy egg production intensity, and therefore also anchovy larvae, are indirectly affected by annual variations of phytoplankton primary production, probably through the quantity of zooplankton on which adult anchovy feed. Anchovy egg production and larval number maxima occur up to about two months later than primary production and zooplankton volume maxima.

8. The seasonal distribution of postlarvae is not in agreement with the seasonal variations of examined biotic factors. It may be assumed that the number of postlarvae could be dependent on the quantity of developmental stages of copepods, which after the available data, are principal constituent of the food of anchovy postlarvae.

9. Judging from the relationship between anchovy catch variations in the study area and their egg production, the egg production intensity is a good indicator of the adulit fish presence. It seems, however, that during the most intensive reproductive activity, anchovy are difficultly caught, rather inacessible.

4.4. LONG-TERM FLUCTUATIONS OF ANCHOVY PLANKTONIC STAGES

Annual means of anchovy egg production, common mean numbers of the oldest postlarvae of P_3 and P_4 length groups and annual means of postlarval mortality coefficents (Table 4.2.7) were used for the analysis of long-term fluctuations of anchovy planktonic stages. Annual mean numbers of postlarvae of two oldest length groups from the Kaštela Bay were not considered since postlarvae of P_4 group were never recorded there. Therefore, annual means of postlarvae of all of the length groups were used for the analysis of fluctuations in the numbers of postlarvae at this station. Accordingly, the data on postlarvae from the Kaštela Bay are not full comparable with those from Stončica and Pelegrin stations.

In choosing the parameters for the analysis of long-term fluctuations of anchovy planktonic stages it was assumed that annual mean egg

production was a reflection of the presence, quantity, and reproductive potential of adult fish, that the number of older postlarvae was, to a larger extent, an indicator of the »success« of reproduction, and that calculated mortality coefficients might be taken as a result of a number of fastors affecting survival. Variations in larval numbers were not taken into account since it was shown in the preceding chapter that their number were directly proportional to egg production.

Fefteen-year series of data (1962—1976) on fluctuations of these parameters were available for Stončica and Pelegrin and the nine year ones for the Kaštela Bay. Long-term fluctuations of some abiotic and biotic factors were also observed. Observations of abiotic factors included the variations in mean annual temperature and salinity values for through water column from surface to bottom at all of the studied stations. The following biotic factors were observed: long term variations in primary gross phytoplankton production at Stončica and Kaštela Bay stations expressed as grams of produced carbon under a square metre* per year and variations of annual mean values of zooplankton volume expressed in cubic centimetres per square metre for all three stations. In addition, variations in mean annual catches of anchovy from the areas of Vis, Hvar and Brač islands were also observed.

Table 4.4.1. Standard deviation and variability coefficients of annual mean egg production, numbers and mortality coefficients of postlarvae as well as for some abiotic and biotic factors in the study area ($\overline{X}$ = mean value; $\pm$ s = standard deviation; V = variability coefficient)

Parameter	Station	$\overline{X}$	$\pm$s	V
$\overline{N}$ eggs/m²/day	Stončica	15.59	6.75	43.3
	Pelegrin	7.65	6.33	82.7
	Kaštela Bay	17.37	13.34	76.8
$\overline{N}$ postlarvae/m²/day	Stončica	0.039	0.0338	85.93
	Pelegrin	0.059	0.0451	75.65
	Kaštela Bay	0.19	0.223	114.57
$\overline{m}$	Stončica	0.3470	0.1183	34.10
	Pelegrin	0.2736	0.1042	38.08
	Kaštela Bay	0.4006	0.1791	44.71
Temperature	Stončica	16.22	0.27	1.65
	Pelegrin	16.15	0.34	2.13
	Kaštela Bay	15.95	0.31	1.92
Salinity	Stončica	38.42	0.12	0.31
	Pelegrin	38.20	0.14	0.35
	Kaštela Bay	36.97	0.28	0.76
Primary production	Stončica	57.59	12.84	22.29
	Kaštela Bay	165.14	47.31	28.65
Volume of zooplankton	Stončica	20.32	3.46	17.04
	Pelegrin	20.23	5.89	29.10
	Kaštela Bay	11.62	3.02	25.96

* Data on annual gross phytoplankton primary production for the 1962—1970 period were taken from the paper by Zore-Armanda, Pucher-Petković and Kačić (1970) and for the 1971—1975 period were obtained by courtesy of Dr Tereza Pucher-Petković.

Annual means of anchovy egg production, numbers of older postlarvae and mortality coefficients were found to vary considerably at all of the stations (Figs. 19—21a). Obviously, as shown by the figures, variation ranges of the **observed parameters differ from one station to another.** Standard deviations and variability coefficients of analysed anchovy parameters were calculated to establish at which of the station these variations were highest. For the sake of comparison the same was calculated for all abiotic and biotic factors we had available (Table 4.4.1).

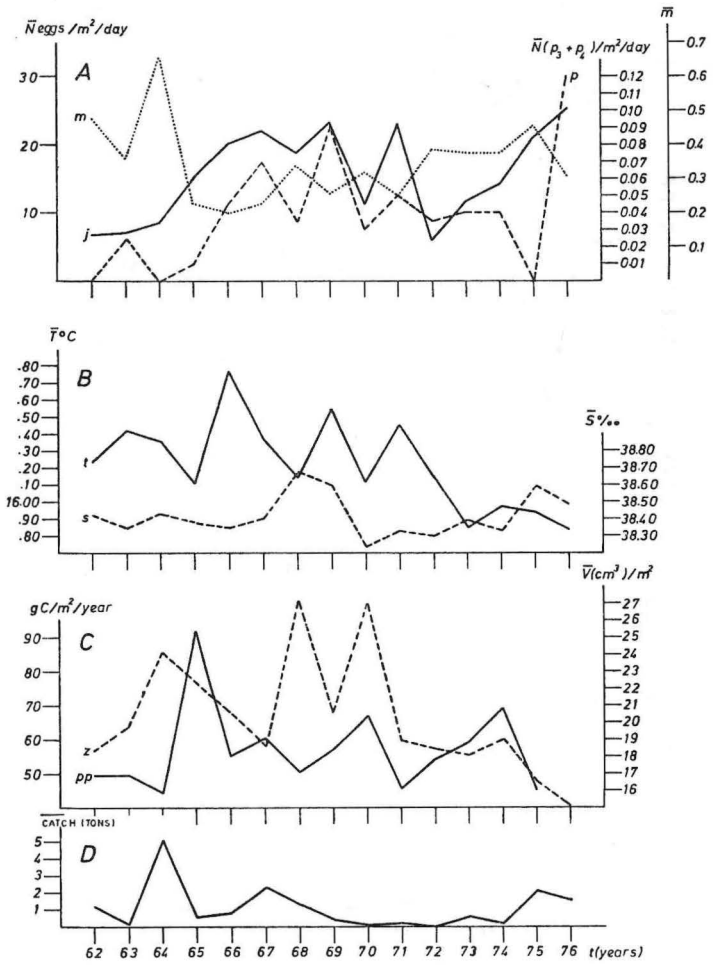

Fig. 19. Long-term fluctuations of anchovy planktonic stages, environmental factors and anchovy catch at Stončica station
(j = egg production; p = numbers of postlarvae, m = postlarval mortality coefficient; t = temperature; s = salinity; pp = primary production; z = zooplankton volume).

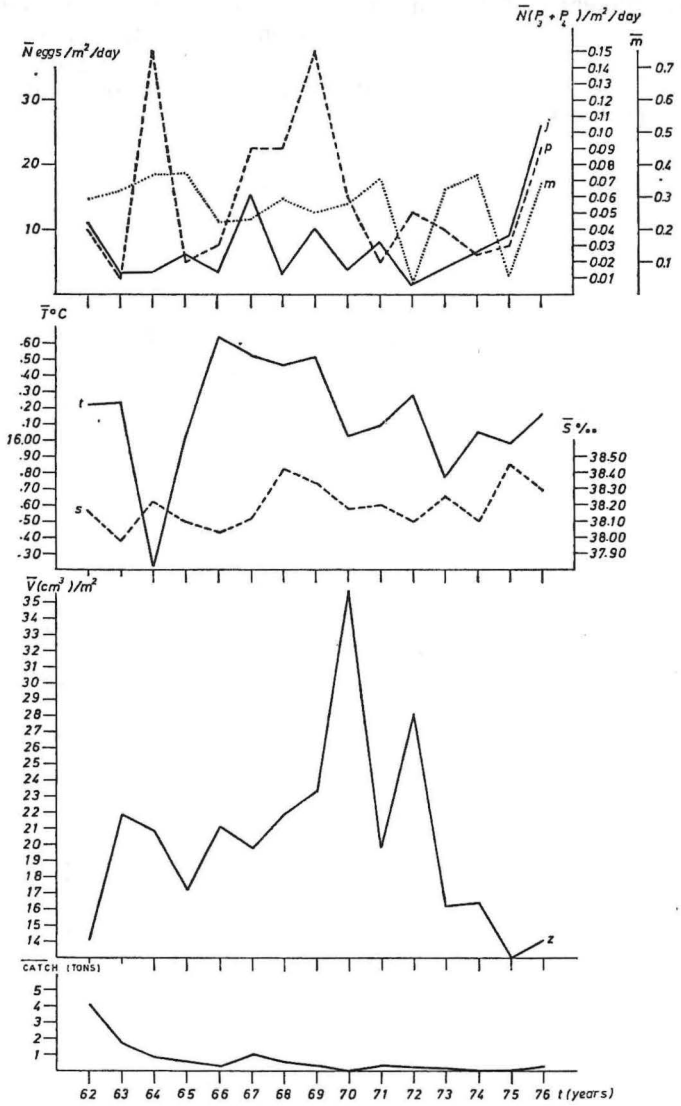

Fig. 20. Long-term fluctuations of anchovy planktonic stages, environmental factors and anchovy catch at Pelegrin station
(j = egg production; p = numbers of postlarvae;
m = postlarval mortality coeficient;
t = temperature; s = salinity; pp = primary production;
z = zooplankton volume).

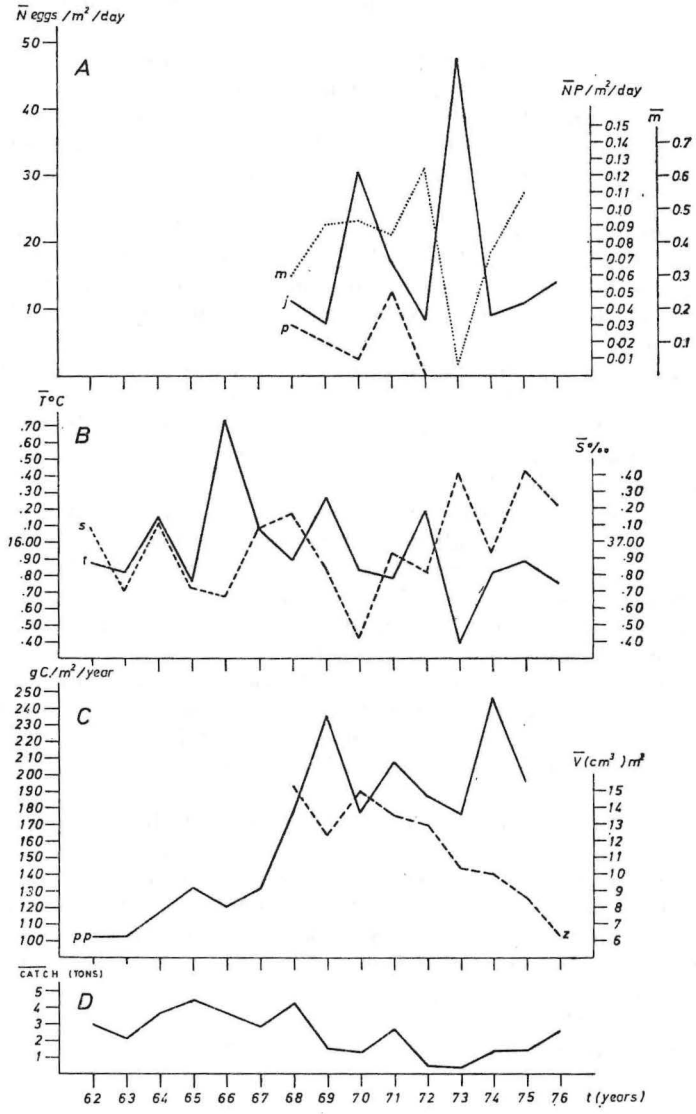

Fig. 21. Long-term fluctuations of anchovy planktonic stages, environmental factors and anchovy catch at the Kaštela Bay station
(j = egg production; p = numbers of postlarvae;
m = postlarval mortality coefficient;
t = temperature; s = salinity; pp = primary production;
z = zooplankton volume).

Judging from the calculated standard deviations and variability coefficients, ranges of long-term variations in numbers of anchovy planktonic stages and postlarval mortality coefficients show rather regular increase going from the open sea onshore (Table 4.4.1). Similar regularity was recorded in temperature, salinity, primary production and zooplankton volume variations. On this basis it may be concluded that long-term variations in egg production on the one hand and the numbers and survival of postlarvae on the other, are, to a larger extent, dependent on the fluctuations of abiotic and biotic environmental factors which are more pronounced in the coastal area than in the open sea.

Subsequently, to establish whether long-term fluctuations of egg production, postlarval numbers and mortality coefficients coincide (in time) or show a phase lag, the method of cross-correlation was applied. This method consists of lagging one data series in relation to another one and of calculating the correlation coefficients for every lag. In this case the series of data on postlarval numbers and mortality coefficients were lagged in relation to the series of data on egg production for $p = \pm 3$ years.

Mortality coefficient data were lagged the same way in relation to the postlarval numbers data. Cross-correlations were calculated separately for each of the station (Table 4.4.2).

Calculated cross-correlation values showed that in the open sea (Stončica) variations of all of the studied parameters of anchovy planktonic stages coincided, since the highest and statistically significant correlation coefficients were obtained for the lag $p = 0$ (Table 4.4.2). Positive coefficient of correlation between anchovy egg production and numbers of postlarvae at Stončica shows that environmenal conditions favourable for an intensive anchovy reproduction are at the same time favourable for postlarval survival. This was proved by negative coefficient of correlation obtained between egg production and postlarval numbers on the one hand and mortality coefficients on the other, which showed that during rather intensive anchovy reproduction postlarval mortality was decreased.

It was found in the channel area (Pelegrin) that fluctuations of postlarvae number lagged behind egg production fluctuations for two years while mortality coefficient variations preceded egg production variations for one year, their correlation, however, being positive (Table 4.4.2). No statistically significant correlation coefficients were obtained between numbers of postlarvae and their mortality coefficients at Pelegrin. The one possible explanation of the disparity between anchovy egg production variations and indicators of postlarval survival at this stations may be, that, as shown in the chapters on mortality and seasonal distribution, the postlarvae are not autochtonous in the channel area but probably transported there by currents from either the coastal area or open sea.

Fluctuations of anchovy egg production and postlarval mortality coefficients in the coastal area (Kaštela Bay) were found to coincide. It was also found that during a rather intensive egg production postlarval mortality decreased. It was, however, shown that variations in numbers of postlarvae preceded egg production variations at this station for two years. No statistically significant correlation coefficients were obtained between the postlarval number fluctuations and mortality coefficients. Data on postlarvae from the Kaštela Bay are not comparable to those from Stončica and Pelegrin.

Table 4.4.2. Cross correlations of studied parameters of anchovy from the study area

Station	Parameter		lag (years) −3	−2	−1	0	+1	+2	+3
Stončica	eggs: postlarvae	r	−0.518	0.367	−0.129	0.654	0.466	0.386	0.140
		P <	—	—	—	0.01	—	—	—
	eggs: $\bar{m}$	r	0.312	−0.127	−0.113	−0.573	−0.312	−0.302	0.216
		P <	—	—	—	0.05	—	—	—
	postlarvae: $\bar{m}$	r	0.031	−0.243	−0.152	−0.556	0.099	−0.247	0.476
		P <	—	—	—	0.05	—	—	—
Pelegrin	eggs: postlarvae	r	0.017	−0.273	−0.156	0.239	−0.065	0.653	−0.163
		P <	—	—	—	—	—	0.05	—
	eggs: $\bar{m}$	r	0.118	−0.436	0.510	0.146	−0.147	0.223	0.116
		P <	—	—	0.1	—	—	—	—
	postlarvae: $\bar{m}$	r	0.110	−0.056	−0.188	−0.197	0.307	−0.072	−0.413
		P <	—	—	—	—	—	—	—
Kaštela Bay	eggs: postlarvae	r	0.019	0.714	−0.047	−0.051	0.187	−0.386	−0.388
		P <	—	0.1	—	—	—	—	—
	eggs: $\bar{m}$	r	0.019	0.720	0.617	−0.719	0.019	0.428	−0.981
		P <	—	—	0.1	0.05	—	—	0.05
	postlarvae: $\bar{m}$	r	−0.163	0.141	0.042	0.222	0.471	0.719	−0.273
		P <	—	—	—	—	—	—	—

The fact that the largest number of correlation coefficients significant for the significance levels exceeding 95% were obtained for the lag p = 0 may indicate that simultaneous occurrences of the long-term variations in egg production, numbers of postlarvae and their mortality coefficients occur simultaneously if smaller areas are considered. Phase lag recorded for Pelegrin is probably due to the immigration of postlarvae. Low correlation coefficients obtained for the postlarvae from the Kaštela Bay Station may be, to a certain extent, accounted for by the fact that their numbers recorded there were always small. This may probably be the result of the emigration of postlarvae due to the prevailing outgoing current in this area.

Long-term fluctuations of anchovy egg production were found to coincide at Stončica and Pelegrin ($r = 0.558$; $P < 0.05$). On the contrary, negative and not statisticaly significant correlation ($r = -0.336$) was obtained between long-term fluctuations of egg production at Stončica and those in the Kaštela Bay. Accordingly, egg production in the open sea seems to alternate with that in the coastal area, since production maxima in the open sea coincide with the minima in the coastal area and opposite. To test this, the cross-correlation between the data on egg production in these two areas was also calculated for the lags $p = \pm 3$ (Table 4.4.3).

Table 4.4.3. Cross-correlation between annual mean egg production at Stončica Station (open sea) and Kaštela Bay (coastal area)

p (years)	—3	—2	—1	0	+1	+2	+3
r	0.389	—0.120	—0.043	—0.336	—0.448	0.501	0.228
P<	—	—	—	—	—	0.1	—

The highest correlation coefficient, significant for the 90% level, was obtained for the lag $p = +2$ (Table 4.4.3). This shows that periodical variations in anchovy egg production in the Kaštela Bay lag behind those at Stončica for two years. To examine whether this was due to some phase differences in ecological factor variations, cross-correlations of long-term variations in temperature, salinity, primary production and zooplankton volume between Stončica and Kaštela Bay were calculated as well as cross-correlations of annaul mean anchovy catches between Vis and Brač islands areas for lags $p = \pm 3$ years (Table 4.4.4).

As shown by the Table 4.4.4. all examined abiotic and biotic factors, with the exception of primary production, show the highest and statistically significant correlation coefficients for the lag $p = 0$. This means that their variations coincide at both stations. Accordingly, phase difference in anchovy egg production established between coastal area and open sea are held not be due to variations of these factors. As distinct from them, annual mean anchovy catches in the coastal area show a phase lag of one year in relation to those in the open sea. On this basis it may be assumed that a phase lag of egg production intensity is due to the peculiarity of adult anchovy distribution in the study area. Namely, as it has already been brought out in the preceding chapter it seems that smaller and younger anchovy predominate in the coastal area. Older and larger anchovy, however, are

dominant in the open sea. Therefore, it is quite possible that in the years of more intensive and more successful spawning of the anchovy in the open sea, more numerous postlarvae are generated which after metamorphosis come to the coastal area. Increased egg production in the coastal area with the two year phase lag may be the result of spawning of these stronger generations of recruit-spawners. Two-year phase lag found for anchovy egg production in the coastal area agree broadly with the phase lag showed by numbers of postlarvae in relation to egg production at Pelegrin (Table 4.4.2). Obviously, fluctuations of postlarvae at Pelegrin coincide with the variations in egg production intensity at the Kaštela Bay Station (r = 0.410, non significant). This is another proof that at least a part of postlarvae recorded from Pelegrin originate from the coastal area.

Table 4.4.4. Cross correlations between annual means of some abiotic and biotic factors as well as between annual mean anchovy catches in the open sea and those in the coastal area

p (years)		— 3	—2	—1	0	+1	+2	+3
Temperature	r	0.402	0.336	—0.001	0.761	0.153	—0.042	0.590
	P <	—	—	—	0.01	—	—	0.05
Salinity	r	—0.248	0.200	0.294	0.600	—0.357	—0.458	—0.357
	P <	—	—	—	0.02	—	—	—
Primary production	r	—0.328	—0.191	—0.001	0.067	0.049	0.026	0.042
	P <	—	—	—	—	—	—	—
Volume of zooplankton	r	0.760	0.747	0.401	0.844	0.435	0.587	0.316
	P <	—	—	—	0.01	—	—	—
Anchovy catch	r	—0.200	0.165	0.007	0.365	0.579	0.248	0.159
	P <	—	—	—	—	0.05	—	—

The regularity of increase of standard deviations and variability coefficients of analysed parameters going from the open sea onshore (Table 4.4.1.) shows that long-term fluctuations in anchovy plaktonic stages and those in abiotic and biotic environmental factors are correlated. At the same time curves of long-term variations of all the parameters show similarity (Figs. 19—21; A—D). They, however, show neither any regular overlapping nor regular phase lag. Therefore the method of spectral analysis was applied to examine precisely whether there is any causality between them. This method consists of decomposing of time series variance into the components of basic frequencies.

After Ralston and Wilf (1960) if the data in a time series are given as the deviations around their mean expressed as a series of positive and negative deviations from zero, the function of their autocovariance may be calculated according to the equation:

$$W_{(p)} = \frac{1}{N-p} \sum_{i=1}^{N-p} X_i \cdot X_{i+p} \qquad (4.4.1),$$

where $W_{(p)}$ is the autocovariance, N total number of data and p time lag.

To make the plotting easier, autocorrelation functions were calculated from the autocovariance function according to the equation:

$$r_{(p)} = \frac{W_{(p)}}{S_x^2} \qquad (4.4.2),$$

where $r_{(p)}$ is the autocorrelation function and S_x^2 variance. The variance for $p = 0$ was used in this paper to calculate the autocorrelation values for any of the p values.

Further, from the autocovariance function and on the basis of Fourier transformation for a limited time interval it is possible to calculate statistical evaluation of spectral density after the equation:

$$L_p = W_o + 2 \sum_{q=1}^{M-1} W_q \cos \frac{qp\pi}{M} + W_M \cos p\pi \qquad (4.4.3),$$

where L_p is the spectral density, W_0, $W_1 \ldots . W_m$ the autocovariance values calculated from the equation (4.4.1) and M maximum p time lag.

Spectral density values calculated on the basis of the equation (4.4.3) were filtered by the Hamming's filter, thus that:

$$U_p = 0.23\, L_{p-1} + 0.54\, L_p + 0.23\, L_{p+1} \qquad (4.4.4).$$

Period to which the determined values of spectral density belong is calculated on the basis of the equation (4.4.3) by the expression:

$$t = \frac{2M}{p} \qquad (4.4.5),$$

where t is the time in years.

For the analysis of our time series maximum lag (M) was defined as:

$$M = N-3 \qquad (4.4.6),$$

where N is the total number of data.

Time series of anchovy egg production, postlarval numbers, annual mean mortality coefficients, temperature, salinity, zooplankton volume, primary production and achovy catches were analysed in the above mentioned manner. A series of fifteen data was available for each of the parameters (from 1962—1976) except for primary production for which we had a series of fourteen data (from 1962—1975). After the criterion (4.4.6) M is 11 years for primary

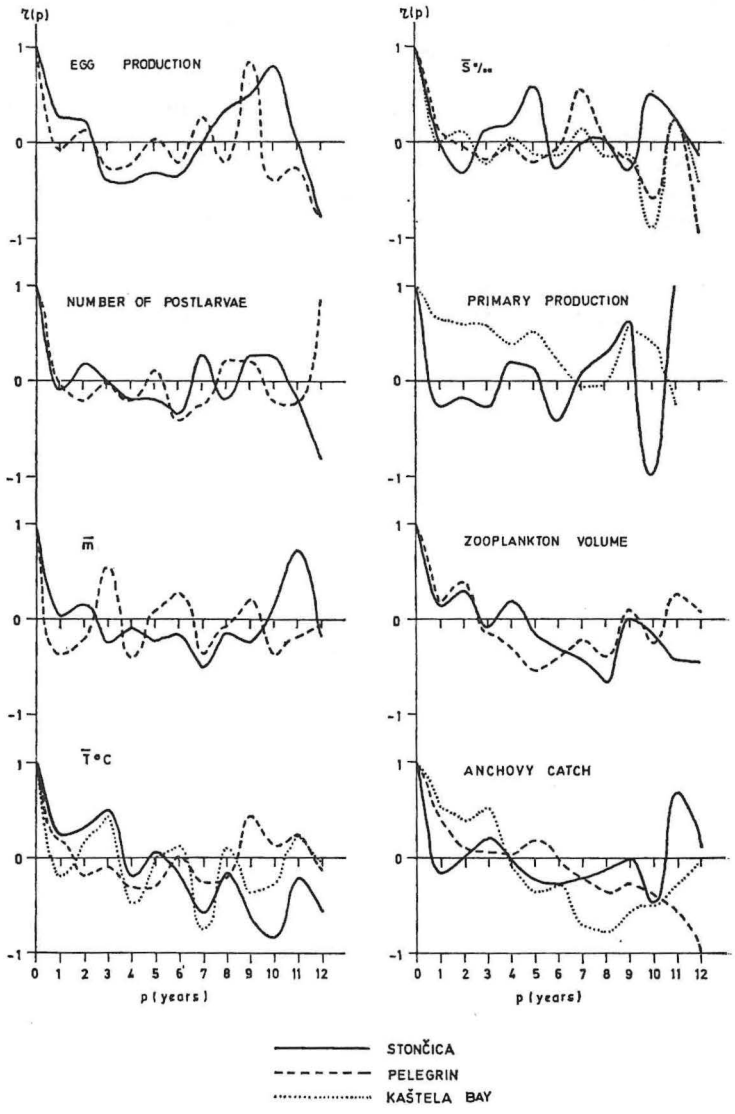

Fig. 22. Autocorrelation functions

production and 12 years for other parameters. We should, however, emphasize, that the results obtained are not statistically significant owing to relatively small number of data and high M values. Data on parameters of anchovy planktonic stages and zooplankton volume could not be analysed by this method for the Kaštela Bay Station since they comprised a series not exceeding nine years (1968—1976).

As indicated by the calculated autocorrelation function all of the analysed parameters show the periods of 2—3, 5—7 and 9—11 years (Fig. 22). It is also apparent that the same parameters in different areas as well as different parameters in the same areas show the differences in periods of 1—2 years as well as the differences in prominence of individual periods. However, owing to the too small number of analysed data it is difficult to say whether these differences are the real ones, or due to the metodical error. In any case, nevertheless the number of analysed data was rather small, it may be concluded that periods obtained for all of the parameters show surprisingly good agreement.

Distribution of density spectra, given in Fig. 23, shows that, as a rule, the amplitudes of short (2—3 year) and long (8—12 year) periods exceed those

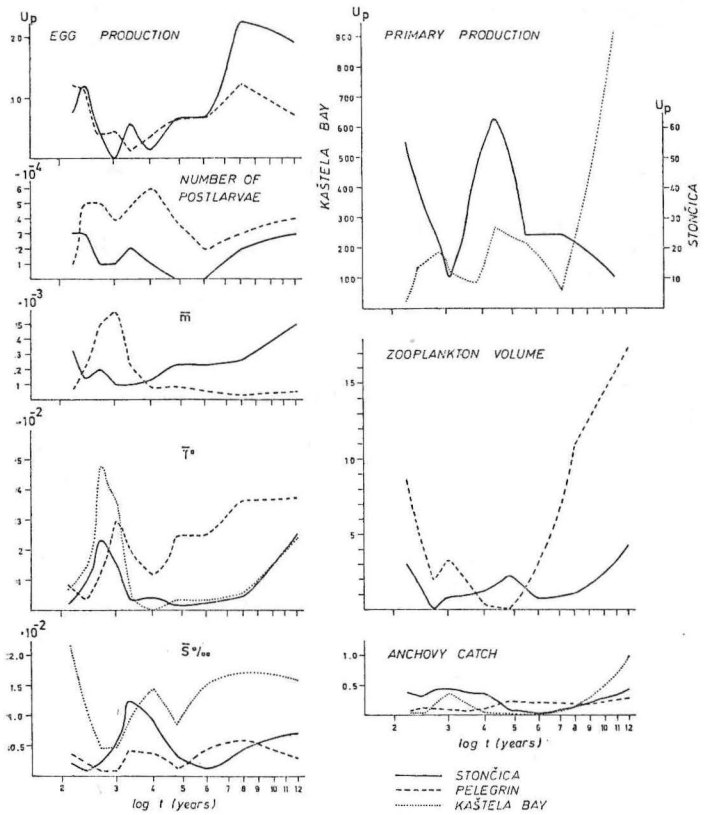

Fig. 23. Spectral density functions

of the medium ones (5—7 years). Subsequently it was shown that the curves of spectral distribution of all of the parameters were similar in form.

After the results obtained, long-term variations of all the observed parameters are in fact the resultant of superimposed periods, both the short-term ones with 2—3 year frequency and the long-term ones with the most probable frequency of 9—11 years. The prominence of these periods depends on the ratio of their amplitudes and their mutual superposition. Similarity between autocorrelation functions and spectral density of all the parameters is indicative of the fact that they show causality, that is, that periodical variations in anchovy egg production, postlarval numbers and mortality in the study area are either directly or indirectly dependent on the periodical changes of abiotic and biotic environmental factors.

Spectral analysis could give neither the numerical representation of the correlation between individual parameters nor show whether they coincided or differed in phase. To examine this, cross-correlations between data series on anchovy planktonic stages and temperature, salinity, primary production and zooplankton volume for the lags $p = \pm 3$ years were calculated for each separate station. However, these calculations gave low and non significant correlation coefficients for all the parameters at all the stations. Accordingly, the results obtained by the cross-correlation method do not, at the first sight, prove the correlation between the variations of ecological factors in the sea and anchovy planktonic stages fluctuations obtained by spectral analysis.

It may, however, be assumed that the correlation between anchovy egg production and postlarval numbers and survival, and variations of environmetal factors is very complex. Data on primary production and zooplankton volume were obtained by the measurements of the total production of organic matter, that is of the total volume of a large number of ecologically different species. Therefore it may be assumed that phyto- and zooplankton groups or species would respond differently to annual variations of abiotic and biotic environmental factors. Since anchovy egg production is in close connection with the feeding conditions and age structure of adult fish, and numbers and survival of anchovy postlarvae with the availability of adequate food and presence of predators, it may be expected that some peculiar changes in individual groups or species of phyto- and zooplankton will cause peculiar changes in production and survival of anchovy planktonic stages. This may result in that planktonic stages maxima sometimes occur earlier, sometimes later, and sometimes coincide with the maxima of ecological and biotic factors as shown by Figs. 19—22, (A—C). This seems to be particularly marked if short-term periods of 2—3 years are taken into account in correlation calculations. Therefore, to examine whether this correlation is better marked in medium and long-term periods as shown by spectral analysis (5—7 and 9—11 years) it was necessary to find a way out to eliminate short periods. This was done by »running mean« method.

By this method every value of any of the parameters (X_s) is given as a mean value of three successive years according to the expression:

$$X_s = \frac{X_{i-1} + X_i + X_{i+1}}{3} \qquad (4.4.7),$$

where X_i is the actual value for i^{th} year.

Running means were calculated for all data series and their correlation calculated taking into account only medium and long-term periods. Cross-correlations were recalculated giving only those lags for which the highest correlation coefficients were obtained. Comparisons carried out by this method gave considerably better results.

Thus the results obtained showed that anchovy egg production increased with the increase in temperature, salinity and phytoplankton primary production, both in the open sea and channel area (Table 4.4.5). The only exception was recorded for the correlation between egg production and zooplankton volume at Pelegrin for which the calculated correlation coefficient was negative.

Table 4.4.5. Correlation between long-term fluctuations of anchovy egg production and long-term variations of abiotic and biotic environmental factors (*Egg production at Pelegrin was compared to primary production at Stončica)

Parameter	Station	r	P	p	Y = a + bX
Temperature	Stončica	0.525	0.1	+1	Y = —21.001 + 2.329 T
	Pelegrin	0.384	—	0	—
	Kaštela Bay	0.410	—	+1	—
Salinity	Stončica	0.613	0.05	0	Y = —1422.977 + 37.452 S
	Pelegrin	0.486	0.1	0	Y = —641.976 + 16.983 S
	Kaštela Bay	—0.564	—	0	—
Primary production	Stončica	0.577	0.05	+1	Y = —6.933 + 0.397 P_p
	Pelegrin*	0.661	0.05	+1	Y = —12.301 + 0.328 P_p
	Kaštela Bay	—0.087	—	0	—
Volume of zooplankton	Stončica	0.231	—	+1	—
	Pelegrin	—0.512	—	+1	—
	Kaštela Bay	0.544	—	+1	—

Subsequently, anchovy egg production showed a phase lag behind all the parameters except salinity. In the coastal area, however, the correlation between anchovy egg production and environmental changes is not so regular. Namely, it was found that in the Kaštela Bay egg production increased with temperature and zooplankton volume increase, and decreased with salinity and primary production increase, irrespective of the fact that non of the negative correlation coefficients was statistically significant.

Similar characteristics were recorded for the correlation between numbers of the oldest postlarvae and abiotic factors. Thus postlarval numbers were found to increase with the increase of all the abiotic and biotic environmental factors both in the open sea and channel area, with the only exception of primary production at Pelegrin (Table 4.4.6). Variations in postlarval numbers were also found either to coincide or to lag a year behing environmental changes.

Table 4.4.6. Correlation between long-term fluctuations of anchovy postlarval numbers and biotic and abiotic environmental factors (*Numbers of postlarvae at Pelegrin were compared to primary production at Stončica)

Parameter	Station	r	P	p	Y = a + bX
Temperature	Stončica	0.187	—	+1	—
	Pelegrin	0.723	0.01	+1	Y = —1.189 + 0.077 T
	Kaštela Bay	0.953	0.01	+1	Y = —24.159 + 1.536 T
Salinity	Stončica	0.499	0.01	+1	Y = —4.082 + 0.107 S
	Pelegrin	0.413	—	0	—
	Kaštela Bay	—0.926	0.01	0	Y = 27.685 — 0.743 S
Primary production	Stončica	0.210	—	+1	—
	Pelegrin*	—0.239	—	0	—
	Kaštela Bay	—0.333	—	0	—
Volume of zooplankton	Stončica	0.108	—	0	—
	Pelegrin	0.419	—	0	—
	Kaštela Bay	0.889	0.01	0	$Y = 0.600 + 0.069\ V_z$

In the coastal area, the dependence between numbers of postlarvae and environmental changes was not so regular as in the open sea and channel area. Namely, whereas numbers of postlarvae in the Kaštela Bay were directly proportional to temperature and zooplankton volume they showed negative correlation with salinity and primary production. However, correlation coefficient calculated for salinity is significant for the high probability level.

Investigations of the correlation between mortality coefficients and environmental changes showed that postlarval mortality decreased with the increase in values of abiotic and biotic environmental factors both in the open sea and channel area. In the coastal area, however, it decreased in relation to all the factors except salinity (Table 4.4.7). Mortality variations mainly showed a phase lag of one year behind environmental changes.

Table 4.4.7. Correlation between long-term fluctuations of mortality coefficients and abiotic and biotic environmental factors (*Mortality coefficients of postlarvae at Pelegrin were compared to the primary production at Stončica)

Parameter	Station	r	P	p	Y = a + bX
Temperature	Stončica	—0.689	0.05	+1	Y = 4.497 —0.256 T
	Pelegrin	—0.370	—	0	—
	Kaštela Bay	0.814	0.05	+1	Y = —10.212 +0.667 T
Salinity	Stončica	—0.328	—	+1	—
	Pelegrin	—0.410	—	0	—
	Kaštela Bay	—0.932	0.01	0	Y = 11.727 —0.307 S
Primary production	Stončica	—0.481	0.1	+1	$Y = 0.644 - 0.005\ P_p$
	Pelegrin*	—0.310	—	+1	—
	Kaštela Bay	0.512	—	+1	—
Volume of zooplankton	Stončica	—0.628	0.05	+1	$Y = 0.739 - 0.02\ V_z$
	Pelegrin	—0.270	—	+1	—
	Kaštela Bay	0.834	0.05	0	$Y = -0.018 + 0.033\ V_z$

Since a large number of calculated correlation coefficients were statistically significant, even for the high significance levels of 99% (Tables 4.4.5.—4.4.7), it may be concluded that periodical environmental changes in the study area affect intensity and success of the spawning of anchovy. Accordingly, this supports the results obtained by spectral analysis.

Further, periodical increases in organic production, that is trophical basis, positively affect anchovy egg production intensity and survival of their postlarvae both in the open sea and channel area. In the coastal area, however, it seems that positive effects of increased food production on postlarval mortality is hidden by the effects of some other factors. It is possible that increase of production is not so marked the coastal area since it is there three times that in the open sea (Table 4.4.1). Therefore, it may be assumed that periodical organic production increase affect an increase in concentration and reproduction of predators thus that their effects are felt more strongly than the effects of available food, superimposing on their emigration due to current transport. But, there are no proofs available than would support these assumptions.

It was shown that correlation between anchovy planktonic stages and environmental changes was linear. Therefore, the correlation between anchovy egg production,, numbers of postlarvae and mortality coefficients, and abiotic and biotic factors available for analysis could be calculated by the linear regression method in all cases of significant correlation coefficients (Tables 4.4.5.—4.4.7). Since higher and significant coefficients of correlation between abiotic and biotic factors and anchovy planktonic stages were obtained only after short periods were eliminated, it is impossible to forecast the intensity and success of anchovy reproduction on the basis of short-term environmentl changes. With respect to the linearity of the correlation established between smoothed sets of data it seems that the analysis of environmental changes trends renders possible, however partial, a forecast of variations in production and survival of anchovy planktonic stages over longer periods.

Spectral analysis showed that analysed parameters of anchovy planktonic stages and adult anchovy catches in the respective areas had the same periodicity (Figs. 22 and 23). Accordingly, it may be concluded that fluctuations of planktonic stages and anchovy catches are correlated. To examine the nature of their correlation, and whether there is a phase lag between them, cross-correlation between egg production, numbers of postlarvae and mortality coefficients at individual stations and anchovy catches in the respective areas were calculated. However, neither the comparison of absolute time series nor of those smoothed by the running means gave higher and significant correlation coefficients for any of the time lags of $\pm$ 3 years at any of the stations.

Since it may be assumed that anchovy schools migrate during spawning season, a comparison was made between egg production and anchovy planktonic stages mortality at individual stations and anchovy catches in different areas but no better results were obtained. And finally, mean egg production, postlarval numbers and mortality were calculated for the through study area for the 1968—1976 period and compared to the total means of anchovy catches from the areas of Vis, Hvar and Brač. This calculation gave the highest correlation coefficients for the lag $p = 0$. Thus, the correlation between egg production and number of postlarvae and anchovy catches was positive ($r = 0.451$ and $r = 0.103$ respectively) in the study area, whereas postlarval

mortality was found to decrease with the increase in annual anchovy catches. Only the coefficient of correlation between postlarval mortality and anchovy catch was statistically significant for $P < 0.05$. The correlation between annual mean anchovy egg production and anchovy catches in the study area may be approximated by the linear equation:

$$U = 0.354 + 0.045\, P_j,$$

and correlation between catches and postlarval mortality coefficient by the equation:

$$U = 8.106 - 21.158\, \bar{m},$$

where U is the annual mean anchovy catches, P_j annual mean egg production and $\bar{m}$ annual postlarval mortality coefficient mean.

The results obtained show that long-term fluctuations in intensity and success of anchovy reproduction in the study area coincide with catch fluctuations and therefore probably with the biomass of sexually mature fish.

Discussion

On the basis of a large number of studies of both adult fish and their developmental stages it was found that out of all environmental factors food availability had the predominant influence on fish population dynamics (Hempel, 1965; Nikolskii, 1969). At the same time quantity of food is equally important for both the adult fish and their postlarvae. After Nikolskii, effect of food quantity on population dynamics through the sexually mature population part is either direct or indirect. Indirect influence is manifested thus that the proportion of fish being well or poorly fed affects the variations of individual growth rate on which the influence of predators is subsequently directly dependent. Further, poorly fed fish are less resistant to abiotic factor changes and more susceptible to diseases and parasites. Food quantity directly affects fecundity through metabolism, since better fed fish attain greater weight than less fed fish of the same age. Better fed fish produce larger number of bigger eggs which contain more yolk and they frequently affect an increases in the number of annual spawnings. After Hempel and Nikolskii food quantity also affects postlarval survival both directly and indirectly; directly in case of food absence an intraspecific competition is intensified which may lead to the starvation to death of a large number of larvae. An indirect influence is manifested through the better growth of well fed larvae as already discussed in the chapter 4.1., which therefore are less exposed to predators and more motile thus that they avoid predator and reach food much easier.

Results of spectral analysis and cross-correlation of a series of data showed that in the open sea and channel area production of eggs is increased and postlarval mortality decreased with an increase in phytoplankton primary production and zooplankton quantity. Thus, it may be concluded that the influence of changes of organic production on the central Adriatic anchovy

population, that is of the available food quantity, is, as well, predominant.

It was shown, however, that fluctuation of anchovy planktonic stages coincided with temperature and salinity variations. However, their effect on anchovy planktonic stages is unlikely to be the direct one. Namely, adult anchovy are known to be the eurythermal and euryhaline species. After Demir (1965) they tolerate 6—29°C temperatures and are adaptable to salinities ranging between 5 and 41.55‰. Therefore it may be assumed that the influence of annual mean temperature and salinity variations of relatively narrow ranges (Table 4.4.1) on age structure of adult anchovy, as well as on fluctuations of its biomass and fecundity, is not significant. Egg production is, subsequently, not affected by them either. It was also shown in the chapter 4.3 that increased numbers of anchovy eggs, larvae and postlarvae occur within wide temperature and salinity ranges (Figs. 15 and 16). Therefore variations of their annual means are unlikely to affect considerably their number and survival in the plankton. It is more probable, however, that particularly good agrement between fluctuations of planktonic stages and multiannual variations of temperature and salinity is due to the fact that temperature and salinity variations are indicators of periodical changes of hydrographic properties of the Adriatic to which fluctuations of organic production are due.

It may also be assumed that fluctuations of primary production do not affect fluctuations of anchovy planktonic stages directly, either, since neither the adult anchovy nor their postlarvae feed on phytoplankton as shown in the chapter 4.3. Since anchovy are markedly zooplanktonphageous (Fage, 1911; Slastetenko, 1956; Nikolskii, 1957), an increase in zooplankton quantity is probably of the greatest importance for them and affects them directly. At the same time anchovy postlarvae feed on developmental stages of zooplankton, predominantly of copepods (Duka, 1961 and 1963; Pavlovskaya, 1964; Regner, 1971) and therefore an increase in zooplankton quantity affects their survival indirectly through the more intensive reproduction of copepods in the first place.

The phenomenon which causes a temporary increases of the Adriatic organic production has already been explained in detail. After Buljan (1953) the ingressions of large water masses from the eastern Mediterranean intermediate layer into the Adriatic take place from time to time. They cause an increase in salinity and temperature of the open southern and coastal Adriatic waters in winter and a decrease of annual temperature amplitudes (Buljan, 1957). These waters carry large quantities of nutrients, phosphorus and nitrogen salts in the first place, which positively affect an increase in organic production and the catches of fish in the Adriatic (Buljan, 1968). It was also found that temporary increases of sardine catches in the Adriatic coincided with cold winters and increased salinity (Županović, 1968).

Later investigations (Zore-Armanda, 1970; Zore-Armanda *et al.*, 1971; Pucher-Petković and Zore-Armanda, 1973; Karlovac, *et al.*, 1974) showed that these temporary inflows of the eastern Mediteranean waters into the Adriatic, called ingressions, were caused by the changes of air pressure gradients over the eastern Mediterranean and penetrations of dry polar air due to the displacements of locations of large baric centres, Islandic cyclone and Sibirian anticyclone. These climatic changes cause an increase of primary production and zooplankton biomass through

the water exchange in the Adriatic. This is reflected three years later as an increase of small pelagic fish catches. Vučetić (1971) suggested that fluctuations in numbers of sardine and achovy eggs in the central Adriatic were dependent on the Mediterranean water ingressions. Since, as shown by our results, anchovy planktonic stages showed broad agreement with the fluctuations of analysed biotic and abiotic factors, a conclusion may be drawn that they fully reflect the already mentioned changes of ecological conditions in the Adriatic.

A phase lag of one year mainly shown by anchovy planktonic stages in relation to environmental factors variations, with the exception of salinity (Tables 4.4.5—4.4.7), should not be taken for granted. Since this was calculated by a comparison of smoothed time series, they may actually be either higher or even lower. Nevertheless, they show that anchovy population requires some time to adapt to environmental changes. A phase lag of one year of egg production may be due to the fact that sexually mature anchovy of a first age class are predominant with the percentage of 30—80% (Fage, 1911; Majorova and Čugunova, 1954; Stoianov, 1961; Padoan, 1963; Dragesund, 1964). Accordingly, a phase lag recorded corresponds to the time required by the newly produced recruits to become reproductive. It is far more difficult to account for the phase lag of the fluctuations of quantity and mortality coefficients of postlarvae since either an increase or decrease in organic production might be expected to affect them directly. Namely, after Nikolskii (1969), Pavlovskaya (1963) showed that long-term fluctuations in numbers of anchovy postlarvae in the Black Sea were directly dependent on annual variations in the number of organisms they fed on. As it has already been shown in the chapter 4.3., anchovy postlarvae predominantly feed on nauplii, metanauplii and copepodites of copepods. Since, owing to their size, these organisms count among the microzooplankton, zooplankton volume calculated from the »Helgoland« net catches cannot be an indicator of their numbers. To our regret, neither the data on variations in copepod developmental stages nor on their correlation to primary production are available for the Adriatic. The only data available are those on *Calanus helgolandicus* given by Vučetić, (1964a) for the area of the Lake Veliko jezero on the Mljet Island. This author assumes that fecundity of this copepod is affected by phytoplankton concentration. This is quite in agreement with the records of Gaudy (1962), who studied the variations in the number of nauplii and copepodites and showed that the number of generations and the number of individuals of a generation of some copepod species from the western Mediterranean were, to a large extent, dependent on the variations in phytoplankton biomass. This may also account for the phase lag of fluctuations in numbers and mortality coefficients of anchovy postlarvae. Namely, some earlier investigations at Stončica and Kaštela Bay stations showed that phytoplankton biomass fluctuations lagged behind the primary production fluctuations for about a year (Pucher-Petković *et al.*, 1971). At any rate, the future investigations should be directed not only to the fluctuations of anchovy planktonic stages but to the fluctuations of copepodites and nauplii as well.

As distinct from the open sea and channel area, positive influence of increased organic production on anchovy reproduction is not so regularly marked in the coastal area. It is even negatively related to postlarval survival

what, as already mentioned, may be due to increased concentrations of predators. It is, however, usually held that survival of postlarvae is less effected by predators than by food availability since the postlarval stage takes little time, not more than few weeks, and therefore could not affect the increase in predator numbers. Therefore, mortality rate due to predators is not dependent on the quantity of postlarvae but on the number of predators, their feeding intensity and capability of postlarvae to avoid them (H e m p e l, 1965). After the same author, however, years when conditions are those as providing sufficient food for postlarvae are also favourable for an increase in the number of predators, and mortality rate due to predators may exceed mortality rate due to a food scarcity. This could be expected to happen in the Kaštela Bay, as well. In the first place, according to the division of the Adriatic to productive zones (B u l j a n, 1964), the Kaštela Bay belongs to the productive zone (D), which owing to the influence of land and shallowness is characterized by high organic production. As distinct from the Kaštela Bay Stončica Station belongs to the zone of low production (A) and Pelegrin to the zone of medium production (C). On this basis it may be assumed that the effects of organic production increase are considerably less felt in the Kaštela Bay than in the open sea and channel area. Subsequently, it is quite certain that neritic species of zooplankton, some of which are predators of fish postlarvae, such as hydromedusae (L e b o u r, 1922) and species of genus *Podon* (R e g n e r, unpublished data) are far better represented in the Kaštela Bay than in other two areas. Their numbers, and therefore the intensity of their activity, might be expected to increase during the increased production what may have some implications to postlarval mortality. After the data by V u č e t i ć (1963), sardine (*Sardina pilchardus* Walb.) guts contained anchovy postlarvae, thus that these fish may be established as predator of anchovy postlarvae. Small sardine constantly inhabit the Kaštela Bay and larger and probably older sardine were recorded here, owing to their feeding onshore migrations in spring and late summer (M u ž i n i ć, 1973a). Since these migrations as well as small sardine quantities are affected by changes of ecological factors (M u ž i n i ć, op. cit.), larger numbers of small and big sardine may be expected to be present in the Kaštela Bay during increased organic production. This may also adversely affect survival of anchovy postlarvae. Thus M u ž i n i ć reports particularly rich catches of adult sardine in the coastal area in the years 1971 and 1972. In addition, the highest mean coefficient mortality of anchovy postlarvae was recorded from the Kaštela Bay in 1972 (Table 4.2.7).

According to the results of spectral analysis, the fluctuations of all of the environmental factors, anchovy catches, intensity of egg production, numbers and mortality coefficients of postlarvae, three basic periods of oscillations, 2—3, 5—7 and 9—11 years, may be distinguished. These data broadly agree with those of Ž u p a n o v i ć (1968) who found that fluctuations of sardine catch in the Adriatic showed 3 and 8 year periods. Our results of spectral analysis even better agree with the results of spectral analysis of a hundred-year series of data on sardine catches (1873—1972), after which it oscilates in periods of 2.3, 3.5, 8 and 11 years (R e g n e r and G a č i ć, 1974). At the same time the distribution of density spectra of all the parameters analysed in this paper are in compliance with distribution of spectral density of sardine catches which also showed that shorter periods (2.3 and 3.5 year ones) and long periods (11 years ones) had higher amplitudes than medium (8 years) ones.

Therefore, our results may be held reliable, nevertheless, due to the too small number of data, are not statistically significant. However, the number of (*M*) lags in spectral analysis of sardine catch was significant for 95% probability level. Further, due to the fact that a poor distinguishing possibilites in the area of low frequencies (after the expression 4.4.5.) and availability of time series of only 15 and 14 years, did not allow an exact calculation of values of amplitudes for the periods in the interval between 8 and 12 years (Fig. 23). However, basing on the similarity between the obtained curves of spectral distribution and sardine spectral distribution curves, the 11 year periods may also be assumed to have the largest amplitude. This is indicated by the calculated autocorrelation functions, which mainly show well marked 11 year periods (Fig. 22). This period, as shown earlier (Regner and Gačić, op. cit.) results from the periodical changes of solar activity. At any rate, our results of spectral analyses lead us to conslude that periodical changes of salinity and temperature in the study area caused the fluctuations of organic production which further affected anchovy and sardine populations with the same periodicity.

Quite similar periods were earlier found for fluctuations of the catch of a large number of fish species from distant geographical regions such as for herring (Jensen, 1927) and cod catches (Hjort, 1914) in Norwegian waters, japanese sardine (Uda, 1959) and species *Onchorhynchus keta* and *O. gorbusha* in the territory of Amur (Birman, 1954, after Nikolskii, 1969). Similar cycles were recorded in the dynamics of the Black Sea phytoplankton (Petrova-Karadžova, 1975). Long-term sea-level variations were found to show the same periodicity in the North Sea (Polli, 1955), Baltic Kowalik and Wroblewski, 1973) and northern Pacific, (Favorite and Ingraham, 1976). It probably may be concluded that periodical variations of hydrographic factors in the sea, which cause organic production to change too, are due to long-term climatic changes of larger extent. This conclusion may be drawn on the basis of the fact that periods recorded for the annual variations of air pressure in Trieste and Venice (Polli, 1955) as well as for the Asian anticyclone (Sorkina and Penjkov, 1973) are quite similar to our ones.

Basing on everything said above, it may be concluded that anchovy population of the central Adriatic responds to the periodical climatic changes of planetary extent. Judging from one year phase lag it responds to them quite quickly.

And finally, it should be pointed out that two somewhat different explanations of the dependence between adult fish biomass and their offsprings may be distinguished. Thus Hempel (1965) holds that egg quantity producted by fish in the course of a year is directly proportional to the biomass and mean age of sexually mature part of the population. However, the size of a newly produced age class is not dependent on quantity of eggs, since this correlation is lost during postlarval and juvenile stages due to their peculiar relation to the environment. On the contrary, Nikolskii (1969) believes that parental biomass and size of newly produced recruits are directly correlated. Results of the analyses of the dependence between egg production, number of postlarvae and their mortality and anchovy catches in the study area speak more in favour of the Nikolskii assumptions, since it was shown that numbers and survival of postlarvae were directly proportional to

anchovy catches, with no phase lag. Non significant correlation coefficients obtained between egg production and numbers of postlarvae and anchovy catches show that catches do not reflect an actual fish biomass in the study area. This is evident from the fact that minimum and maximum anchovy catches and egg production at Stončica coincided with those at Pelegrin (Figs. 20 and 21, A and D). However, absolute numerical values did not coincide and therefore it is impossible to obtain singnificant correlation coefficients. This is most likely due to the preferential sardine catch, what is characteristic for the eastern Adriatic coast (Mužinić, 1974). Namely, in analysing the correlation between sardine catch fluctuations and anchovy catch ones in the central Adriatic in the 1947—1971 period, Mužinić (1974) found negative correlation, what at first sight might appear as if sardine and anchovy biomass alternate. However, by a comparison of the results on anchovy egg production at Stončica for 1963—1970 period with the data on mean number of sardine eggs under a square metre at the same station published by Karlovac *et al.*, (1974), positive and statistically significant correlation coefficient was obtained ($r = 0.638$; $P < 0.05$). This shows that fluctuations of sardine and anchovy biomass probably coincide. It is, therefore, possible that negative correlation between sardine and acnhovy catch results from the fact that fishermen prefer sardine and that anchovy are fished for only when there is not sufficient sardine, nevertheless their biomass is probably reduced then. Therefore, a conclusion may be drawn that, irrespective of the non-signaficant correlation coefficients, egg production intensity and number of postlarvae are likely to be a good indicator of adult anchovy biomass in the study area.

Conclusions

1. Amplitudes of long-term fluctuations in anchovy egg production, numbers and mortality of their postlarvae in the study area increase going from the open sea onshore as well as the amplitudes of fluctuations of analysed abiotic and biotic factors.
2. If limited to smaller areas, fluctuations of annual intensity of anchovy egg production, and of number and mortality of their postlarvae, as a rule, coincide. With an egg production increase, number of postlarvae increases and mortality decreases.
3. Fluctuations of anchovy egg production at the Kaštela Bay Station (coastal area) show a phase lag of two years behind those at Stončica (open sea). This may be due to the spatial distribution of different age classes of sexually mature anchovy.
4. The autocorrelation method makes it possible to establish that the fluctuations of anchovy egg production intensity, number of postlarvae and their mortality coefficients in the study area may be decomposed to the basic periods of oscillations of 2—3, 5—7 and 9—11 years. Since the fluctuations of temperature and salinity, primary production, quantity of zooplankton and anchovy catch may also be decomposed to the same periods, it is apparent that intensity and success of anchovy reproduction are in close connexion with the periodical environmental changes in the study area, what is finally reflected upon the catches.

5. Calculations of spectral density showed that the amplitudes of short, 2—3 years periods, and long, 8—12 year periods, in both anchovy planktonic stages and analysed abiotic and biotic factors, as well as in anchovy catches in the study area, considerably exceed those of the periods of 5—7 years. Accordingly, short and long periods are best marked in superposition.
6. Fluctuations in egg production intensity, numbers and survival of postlarvae lag behind environmental factor variations for about a year. This phase lag is in fact the time required by a new age class to attain sexual maturity.
7. In the open sea (Stončica) and channel area (Pelegrin) fluctuations of anchovy egg production intensity and numbers of postlarvae and variations in mortality coefficients are directly proportional to the variations of abiotic and biotic environmental factors. Periodical changes of food availability in these two areas are probably of crucial importance for the intensity and success of anchovy reproduction, both adult fish and postlarvae being affected by this factor. Food quantity, which is directly proportional to organic production is probably dependent on the periodical variations of the Adriatic hydrographic conditions.
8. Positive influence of organic production increase on anchovy egg production intensity and numbers of their postlarvae in the plankton is less clearly marked in the coastal area than in the open sea and channel area. Further, an increase of organic production here affects an increase of mortality coefficients, what means that increased production adversely affects survival of postlarvae. This may be due to the fact that, during increased organic production, concentrations and numbers of predators are increased and therefore their effect on anchovy postlarvae intensified.
9. In the study area as a whole, increase in annual anchovy catches concides with the increased egg production as well as with the increase in numbers and reduction of mortality of their postlarvae, with no phase lag. This supports the assumption that intensity of reproduction, its success, and biomass of sexually mature part of anchovy population are closely connected.

5. CONCLUSION

This paper is divided in two parts. First part includes the results of studies on anchovy egg development and larval growth at ten constant temperatures, and postlarval growth at three constant temperatures under experimental conditions. The aim of these studies was to obtain the basic elements indispensable for working out the material collected during the field work. The second part is a study of mortality, seasonal distribution and long-term fluctuatiaons of anchovy planktonic stages from the material collected from stations Stončica (open sea) and Pelegrin (channel area) during fifteen years, and from the Kaštela Bay (coastal area) over nine years. In all 65,489 fish eggs were collected of which 9305 belonged to anchovy, and 24,763 fish larvae and postlarvae of which 3,020 were anchovy larvae and 2,815 anchovy postlarvae.

On the basis of the results of experiments it may be concluded that egg developmental rate and larval growth were predominantly affected by temperature while, apart from temperature, the postlarval growth was affected by food quantity. It was, further, established that characteristics of larval growth differed from the postlarval ones, and that these two growth types should be defined by different equations. It was also found that larval and postlarval growth curve exponents showed linear correlation with temperature. Experiments showed that length ranges of larvae and postlarvae of the same age increased with time. Mathematical analysis showed that these ranges were, to a considerable extent, dependent on the initial larval and postlarval length ranges.

In general, it may be concluded that determination of parameters of egg developmental time and larval growth equations as dependent on temperature rendered possible the cauculation of developmental time and age of anchovy plaktonic stages at different environmental temperatures. This, subsequently, made possible the investigations of their mortality in the study area as well as the calculations of corrections by means of which the samples of anchovy planktonic stages, collected by field samplings, were made intercomparable.

On the basis of the analysis of reduction in numbers of anchovy planktonic stages as a function of time, two periods of specific mortality may be distinguished. The first period includes eggs and larvae and ends with the complete yolk sac resorption. The second period occurs at transformation of larvae to postlarvae, that is at transition from passive to active feeding. Since with the transformation from larvae to postlarvae mortality is suddenly reduced, it has been concluded that no »critical period« occurs in anchovy from the study area. This »critical period« is characterized by high mortality at transition from passive to active feeding.

Egg production and numbers of larvae in the open sea were found to be almost equal to those in the coastal area during the spawning season, while they are half as that in the channel area. Therefore, it is likely that the conditions in the channel area are not favourable for anchovy spawning. Subsequently, judging from the fact that the numbers of postlarvae in the channel area considerably exceed those in the coastal area, it has been concluded that during the spawning season postlarvae are transported from the coastal area to the channel area and to a certain extent to the open sea as well.

A comparison of anchovy planktonic stages during the spawning season with temperature, salinity, primary production and zooplankton quantity shows that thier seasonal dynamics is affected more by biotic than by abiotic factors. The analysis of the dependence between egg production and anchovy catches during the spawning season shows these two parameters to be positively correlated, however with a phase lag of about a month. Therefore, the conclusion arrived at is that the number of produced planktonic eggs is a good indicator of the presence and quantity of sexually mature fish but also that anchovy are rather difficultly caught during intensive reproductive activity.

Long-term fluctuations of egg production, numbers and mortality coefficients of anchovy postlarvae were found to concide with the fluctuations of analysed abiotic and biotic environmental factors but with a phase lag of about a year. Since the production and numbers of anchovy planktonic stages increased and postlarval mortality decreased with the increase in organic

production, it may be concluded that fluctuations of planktonic stages of this fish are, for the most part, affected by the variations of food availability. The only exception was the mortality increase with organic production increase in the coastal area. This may be explained by an intensified predator activity in the years of increased organic production. A comparison of anchovy planktonic stages fluctuations with the fluctuations of catcehs of adults shows that egg production in the plankton increases with the increased catches and that postlarval mortality in reduced. This indicates that the fluctuations of sexually mature part of anchovy population and those of their planktonic stages are closely connected.

The spectral analysis method shows that fluctuations of anchovy planktonic stages and catches as well as those of abiotic and biotic environmental factors are the resultants of superposition of several basic oscillation periods. Three different periods may be distinguished in all of the analysed parameters, the short ones (2—3 years), medium (5—7 years) and long (9—12 years). The amplitudes of short and long periods exceed the amplitudes of the medium periods. On the basis of similarity of periods in all analysed parameters it may be concluded that fluctuations of anchovy planktonic stages in the study area fully reflect the environmental changes. Since similar periods have already been established for a series of biological, hydrographic and meteorological parameters from different and distant areas on the Earth, it may finally be concluded that anchovy population in fact responds to the long-term climatic changes of planetary extent. Subsequently, the establishing of these periods provides the basis for eventual long-term forecast of not only the fluctuations of anchovy planktonic stages but of general ecological conditions in the Adriatic.

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EKOLOGIJA PLANKTONSKIH STADIJA BRGLJUNA, *Engraulis encrasicolus* (Linnaeus, 1758), U SREDNJEM JADRANU

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KRATKI SADRŽAJ

Osnovni cilj ove studije je bio da se ispita odnos dinamike planktonskih stadija brgljuna prema nizu abiotskih i biotskih faktora sredine, te da se utvrdi da li postoji veza između količine planktonskih stadija i ulova odraslog brgljuna na području srednjeg Jadrana.

Sa tim je ciljem dugi niz godina sakupljan planktonski materijal na transverzalnom profilu koji se pruža gotovo ravno na jug od Splita. Na tome su profilu raspoređene postaje Kaštelanski zaljev (43°31'N 16°22'E), Pelegrin (43°12'N 16°19'E) i Stončica (43°00'N 16°20'E) (Sl. 1). Ove su postaje raspoređene tako da obuhvaćaju područje pod izrazitim utjecajem kopna (postaja Kaštelanski zaljev), zatim kanalsko područje gdje se miješaju utjecaji kopna i otvorenog mora (postaja Pelegrin) i područje pod izrazitim utjecajem otvorenog mora (postaja Stončica).

Na postajama Stončica i Pelegrin istraživanja su vršena od jaunara 1962. do decembra 1976. godine, a na postaji Kaštelanski zaljev od februara 1968. do decembra 1976. godine. Na svim je postajama materijal sakupljen jednom mjesečno. Uzorci zooplanktona su uzimani dvostrukim vertikalnim potezima planktonske mreže tipa »Helgoland«. Otvor mreže je imao promjer 143 cm (površine otvora je 1.6 m^2), a promjer okašaca planktonske svile je bio 0.516 mm. Mreža je povlačena od dna do površine brzinom od 0.5 m/sec. Tokom ovih istraživanja sakupljeno je ukupno 65489 jaja i 24673 larve i postlarve riba, od čega je 9305 jaja, 3020 larvi i 2815 postlarvi pripadalo brgljunu.

Uz uzorke zooplanktona, uzimani su i podaci o temperaturi i salinitetu na standardnim oceanografskim nivoima, zatim podaci o ukupnoj količini zooplanktona izraženi volumenom sedimentiranog uzorka, a na postajama Kaštelanski zaljev i Stončica mjerena je primarna produkcija fitoplanktona pomoću radioaktivnog ugljika.

Kako je brzina razvitka razvojnih stadija riba upravno srazmjerna temperaturi sredine, u planktonu se, ovisno o temperaturi, akumuliraju jaja izmriještena tokom različitog broja dana, kao i larve i postlarve čiji razvitak traje različito pri različitim temperaturama. Stoga jednostavna usporedba brojnosti planktonskih stadija riba ne može dati pravu sliku intenziteta mriještenja i dinamike brojnosti larvi i postlarvi, ukoliko se ne izvrše korekcije utjecaja temperature sredine.

Da bi podaci o količini jaja, larvi i postlarvi brgljuna bili međusobno usporedljivi bez obzira na mjesto i vrijeme kada su planktonski uzorci uzeti, te da bi se moglo procijeniti njihovu smrtnost u funkciji vremena, ispitani su brzina razvitka jaja i larvi, kao i karakteristike rasta larvi i postlarvi ove ribe u odnosu na temperaturu. Ova su ispitivanja vršena u eksperimentalnim

uvjetima. Brzina razvitka jaja i brzina razvitka i rasta larvi ispitivana je na deset srednjih temperatura unutar raspona od 16.70°C do 24.05°C, a brzina rasta postlarvi do standardne dužine od 15 mm na tri temperature u rasponu od 19.02°C do 24.05°C (Tab. 4.1.2. i 4.1.6.).

Ovim su eksperimentima dobijeni podaci o odnosu dužine ukupnog razvitka jaja brgljuna, od oplodnje do izleganja larvi, te o trajanju svakog pojedinog od deset definiranih embrionalnih stadija u odnosu na temperaturu (Sl. 4), kao i podaci o odnosu temperature i vremena potrebnog da se larvama formiraju funkcionalna usta i da potpuno resorbiraju žumančanu kesicu (Sl. 5). Odnos brzine embrionalnog razvitka jaja i temperature aproksimiran je matematički pomoću četiri različite jednadžbe (jednadžbe 4.1.1. do 4.1.4.), pri čemu su najbolje rezultate dale jednadžbe (4.1.3.) i (4.1.4.). Za daljnja izračunavanja je, zbog svoje jednostavnosti, upotrebljena jednadžba (4.1.4.). Istom je jednadžbom aproksimiran i odnos vremena potrebnog za formiranje funkcionalnih usta i resorpciju žumančane kesice larvi i temperature.

Rast larvi brgljuna u funkciji vremena aproksimiran je izvornim oblikom jednadžbe von Bertalanffyja (4.1.10.) (Sl. 6), postlarvi eksponencijalnom jednadžbom (4.1.14) (Sl. 8). Pri tome je nađeno da eksponenti obiju jednadžbi pokazuju pozitivan linearni odnos prema temperaturi (jednadžbe 4.1.11. i 4.1.15) i slika 7. Ovo je omogućilo izračunavanje starosti larvi i postlarvi brgljuna na osnovi njihove dužine pri bilo kojoj temperaturi sredine (jednadžbe 4.1.19 i 4.1.20.).

Ispitan je i utjecaj pojave srazmjerno velikih raspona dužina larvi i postlarvi iste starosti na pogrešku procjene njihove starosti na osnovi dužine. Nađeno je da ovaj raspon ovisi o početnom rasponu dužina larvi pri izleganju i postlarvi u trenutku potpune resorpcije žumančane kesice, te da je on po svoj prilici genetski uvjetovan. Pogreška procjene starosti, koja može nastati uslijed ovoga raspona, može se matematički procijeniti (jednadžbe 4.1.21. do 4.1.24.; slike 9. i 10. Analiziran je, također, i utjecaj pojave da su jaja i larve brgljuna veći na početku sezone mriještenja (mart-maj), nego u njezinom srednjem i krajnjem periodu (juni-novembar). Ovo uzrokuje potcjenjivanje starosti larvi u proljetnom periodu i precijenjivanje njihove starosti u ostalom dijelu sezone mriještenja ukoliko bi se starost računala na osnovi srednjih vrijednosti parametara jednadžbi rasta. Stoga su izračunati posebni parametri ovih jednadžbi za proljetni period i posebni za ostali dio sezone mriještenja (jednadžbe 4.1.25. i 4.1.26.), kako bi se ova pogreška eliminirala.

Na osnovi ovih analiza, pomoću kojih su dobijeni parametri brzine embrionalnog razvitka jaja i larvi, te stope rasta larvi i postlarvi brgljuna u odnosu na temperaturu, omogućeno je izračunavanje smrtnosti planktonskih stadija brgljuna, kao i potpunija analiza dinamike njihove brojnosti i raspodjele u prostoru i vremenu. Ovo drugo je bilo moguće učiniti jer su podaci o brojnosti planktonskih stadija brgljuna, sakupljani tokom čitavog perioda istraživanja, učinjeni međusobno komparabilnim bez obzira na vrijeme i mjesto kada su prikupljeni, i to uz pomoć korekcija kojima su osnova poznata dužina razvitka u odnosu na temperaturu sredine i stopa smrtnosti (jednadžbe 3.3., 4.2.3. i 4.2.4.).

Smrtnost planktonskih stadija brgljuna je računata polazeći od pretpostavke da brojnost njegovih jaja, larvi i postlarvi eksponencijalno opada sa vremenom (jednadžba 4.2.1.). Ustanovljeno je da se na istraživanom podru-

čju javljaju dva perioda specifičnog mortaliteta. Prvi period obuhvaća fazu jaja i larvi i završava sa prelazom u postlarvu, odnosno sa potpunom resorpcijom žumančane kesice. Drugi period, za koji je karakteristična znatno manja stopa smrtnosti, počinje nakon prelaza larvi u postlarve i traje, po svoj prilici, do metamorfoze (Sl. 12). Utvrđeno je, nadalje, da na moguće pogreške procjene smrtnosti planktonskih stadija brgljuna znatno utječe režim površinskih strujanja koja prenose, u prvom redu postlarve, iz jednog područja u drugo. Tako je nađeno da je smrtnost svih planktonskih stadija najveća u priobalnom području, na postaji Kaštelanski zaljev, a najmanja u kanalskom području, na postaji Pelegrin. Međutim, režim je površinskih struja na istraživanom području takav da se na početku sezone mriještenja brgljuna, u rano proljeće, struje kreću od otvorenog mora ka obali, dok je u ljetnom periodu smjer struja upravo obratan. Stoga se može pretpostaviti da je, uslijed imigracije, mortalitet u kanalskom području potcijenjen, dok je u priobalnom području mortalitet precijenjen uslijed emigracije.

Ispitana je i dinamika brojnosti planktonskih stadija brgljuna na istraživanom području tokom sezone mriještenja. Sezona mriještenja počinje na ovome području u martu, a završava u novembru. Proizvodnja jaja je na području otvorenog mora i u kanalskom području najveća u junu, dok se u priobalnom području javljaju dva maksimuma, relativni u junu i apsolutni u augustu (Sl. 13). Odnos proizvodnje jaja brgljuna prema brojnosti njegovih larvi i postlarvi pokazuje pozitivnu korelaciju samo na postaji Koštelanski zaljev (Tab. 4.3.1.). Na osnovi ovoga se može zaključiti da je ovaj odnos u kanalskom području i na području otvorenog mora poremećen uslijed već spomenutog transporta strujama.

Nađeno je da se planktonski stadiji brgljuna javljaju u planktonu istraživanog područja unutar raspona temperature od 13.15°C do 23.85°C. Za razliku od temperature, planktonski se stadiji brgljuna nalaze na otvorenom moru i u kanalskom području unutar znatno višeg raspona saliniteta (od 35.41 do 38.90‰), nego u priobalnom području (34.91—38.09‰). Unutar tih granica nema nikakve značajne povezanosti između pojave maksimuma planktonskih stadija brgljuna i temperature i saliniteta (Sl. 14 i 15), na osnovi čega je zaključeno da ovi faktori nemaju znatnijeg utjecaja na intenzitet reprodukcije ove ribe.

Analiza odnosa dinamike brojnosti planktonskih stadija brgljuna tokom sezone mriještenja prema dinamici primarne produkcije fitoplanktona i količine zooplanktona pokazala je pozitivnu korelaciju, ali sa faznim pomakom od oko dva mjeseca (Sl. 16 i 17). Ovo je upravo vrijeme koje je potrebno da gonade brgljuna sazriju nakon perioda intenzivnog hranjenja koji prethodi mriještenju. Analiza odnosa proizvodnje jaja prema ulovu odraslog brgljuna tokom sezone mriještenja pokazala je da ova dva parametra stoje u pozitivnoj korelaciji, ali sa faznim pomakom od oko mjesec dana (Sl. 18). Na osnovi toga je zaključeno da je intenzitet proizvodnje jaja dobar pokazatelj prisutnosti i količine spolno zrele ribe, ali i to da je u vrijeme intenzivne reproduktivne aktivnosti brgljun teže dostupan izlovljavanju.

U zadnjem poglavlju ove studije analizirane su dugoročne fluktuacije godišnjih srednjaka proizvodnje jaja, brojnosti i koeficijenata smrtnosti postlarvi brgljuna, pri čemu su one uspoređene sa fluktacijama godišnjih srednjaka temperature, saliniteta, primarne produkcije, količine zooplanktona i

ulova odraslog brgljuna (Sl. 19—21). Nađeno je da se fluktuacije proizvodnje jaja, te brojnosti i koeficijenata mortaliteta postlarvi brgljuna dobro poduda-raju sa fluktuacijama analiziranih abiotskih i biotskih faktora sredine, ali sa faznim zakašnjenjem od godinu dana (Tab. 4.4.5 — 4.4.7.) Na osnovi toga što je nađeno da sa povećanjem organske produkcije rastu proizvodnja i broj-nost planktonskih stadija brgljuna i da se smrtnost postlarvi smanjuje, mo-glo bi se zaključiti da na fluktuaciji planktonskih stadija ove ribe najvećeg utjecaja imaju promjene količine raspoložive hrane. Usporedba fluktuacija planktonskih stadija sa fluktuacijama ulova brgljuna pokazala je da se sa po-većanjem ulova povećava i proizvodnja jaja u planktonu, a da se smrtnost postlarvi smanjuje. Na osnovi toga se može zaključiti da su fluktuacije spolno zrelog dijela populacije brgljuna i njegovih planktonskih stadija tijesno među-sobno povezane.

Metodom spektralne analize (jednadžbe 4.4.1. do 4.4.6.) nađeno je da su fluktuacije planktonskih stadija i ulova brgljuna, kao i fluktuacije abiotskih i biotskih faktora sredine rezultante superpozicije nekoliko osnovnih perioda oscilacija. Ovi se periodi kod svih analiziranih parametara dijele na kratke (2—3 godine), srednje (5—7 godina) i duge (9—12 godina), pri čemu su am-plitude dugih i kratkih veće od amplituda srednjih perioda (Sl. 22 i 23). Na osnovi sličnosti perioda kod svih analiziranih parametara zaključeno je da fluktuacije planktonskih stadija brgljuna u potpunosti odražavaju promjene sredine. Kako su slični periodi već nađeni kod niza bioloških, hidrografskih i meteoroloških parametara na međusobno udaljenim područjima na Zemlji, može se zaključiti da, u krajnjoj liniji, populacija brgljuna reagira na više-godišnje klimatske promjene planetarnih razmjera. Nalaz ovih perioda pred-stavlja osnovu za eventualne dugoročne prognoze ne samo fluktuacija plan-ktonskih stadija i ulova brgljuna, nego i općenito ekoloških prilika na istraživanom području Jadrana.

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