Acta Adriat., 28 (1—2): 161—198 (1987)

YU ISSN: 0001 - 5113
AADRAY

Original scientific paper
UDC 597.5.1 (262.3)

SPAWNING OF SARDINE, *SARDINA PILCHARDUS* (WALBAUM, 1792), IN THE ADRIATIC UNDER UPWELLING CONDITIONS

MRIJEŠĆENJE SRDELE, *SARDINA PILCHARDUS* (WALBAUM, 1792), U UVJETIMA POJAVE »UPWELLINGA« U JADRANU

Slobodan Regner, Dubravka Regner, Ivona Marasović
and Frano Kršinić*

Institute of Oceanography and Fisheries, Split, Yugoslavia
**Institute of Oceanography and Fisheries, Split, Biological Laboratory, Dubrovnik, Yugoslavia*

Data on numbers of eggs and larval stages of sardine in the plankton were collected from the eastern half of the northern, middle and a part of southern Adriatic in March-April, 1982. Temperature, salinity, chlorophyll *a* quantity and numbers of phytoplankton were sampled simultaneously as well as the quantity of micro, meso and macrozooplankton.

Spatial distribution of the number of sardine eggs produced under a square metre per day showed that two spawning centres may be clearly distinguished in the Adriatic — one in the middle and other in the northern Adriatic.

The analysis of temperature and salinity data showed that two upwelling zones were formed during the period of our study. Higher quantities of phyto and zooplankton were recorded at the boundaries of upwelling zones. Spawning centres were located also at the edges of these zones. This is indicative of the fact that during a period of the spawning season when the data were collected, the upwelling zones offered most favourable conditions for sardine reproduction.

Data on survival of sardine plankton stages are also presented as well as a preliminary scheme of their transport by currents.

INTRODUCTION

A rather large number of papers on position of sardine spawning areas in the Adriatic has been published. Gamulin (1948, 1954, 1964) and Gamulin et Hure (1955) established that sardine spawned everywhere down to the isobath of 150 m. However, this author pointed to the fact that three spawning centres should be distinguished:

i) in the open northern part of the middle Adriatic, west of the island Dugi otok,

ii) out of the exterior edges of the mid — Dalmatian islands and,

iii) in the area of Palagruža.

Gamulin and Karlovac (1956) found the open sea area at the level of mid-Dalmatian islands to be a very imporatant spawing place for these fish.

Karlovac (1958, 1965, 1967, 1969) carried out egg and larval surveys in the same area studying their abundance and transport of larvae and postlarvae by currents. Hure (1961) studied in detail the spawning in the Palagruža area. Gamulin and Zavodnik (1961), and Zavodnik (1970), concluded that western Istrian waters could not be the area of sardine reproduction since their eggs were recorded therefrom only at the beginning and at the and of spawning seasons. Studies of Rakaj (1962) in the coastal waters of Albania led to the suggestion that sardine spawning centre was situated between the Gulf of Vlora and te Sazana Island. Štirn (1969) and Štirn and Kubik (1974) reported the northern Adriatic spawning area to extend in the open sea out of the island Dugi otok. Škrivanić and Zavodnik (1973) tried to explain the effects of hydrographic conditions on the position of spawning centres. Regular cruises across a grid of stations covering northern, middle and a part of southern Adriatic have been performed since 1979. These egg and larval surveys are carried out within the frame of Yugoslav-Italian co-operative investigations in fisheries with the principal goal of the estimation of spawning sardine stock size in the Adriatic. The results of these surveys pointed to only two clearly distinguished spawning areas of sardine in the Adriatic — in the wider area of the island Dugi otok and Palagruža (Piccinetti *et al.*, 1980 and 1981; Regner *et al.*, 1981). Gamulin and Hure (1983) came to the similar conclusions analysing planktonic material collected during r/v ANDRIJA MOHOROVIČIĆ cruises from 1974 through 1976.

Up to the present time no researches have dealt with all the parameters relevant to the positions of sardine spawning areas in the Adriatic. Spatial distribution of the eggs has been most frequenty the only parameter studied in detail. If spatial distribution was associated with hydrographic parameters no account was taken of biological factors and vice versa. Distribution and transport of larval stages of sardine were studied on only one occasion not taking into consideration their age.

Being aware of the fact that much of the work that has been done has not yest yielded enough evidence, we have tried to throw more light on the problem of sardine spawning areas including as many factors as possible. A serious shortcoming of this study is that it presents the data collected in the course of only one cruise performed during the second half of sardine spawning season, which extends in the Adriatic from October to April and even to May. Therefore it is not to be expected that this paper will account for the general patterns of formation and displacement of sardine spawning centres in the Adriatic nevertheless considerably greater number of factors were considered.

This work is in fact only an introduction into further investigations during which at least three to four cruises should be performed during one or more spawning seasons. In this way the number of collected data will be higher and include, if possible, also a higher number of parameters than that analysed in the present paper.

STUDY AREA

These studies have been carried out within the frame of Yugoslav-Italian joint project for the stock assessment of small pelagic fish (sardine and anchovy) which began in 1976. Cruises covering northern, middle and a part of southern Adriatic, from the Gulf od Trieste to the line connecting Monte Gargano and Oštra Cape at the entrance to the bay Boka Kotorska, are performed once to twice during each sardine and anchovy spawing season. The area covered extends over approximatively 101 700 km^2, which makes about 73% of the total surface of the Adriatic. Material is collected simultaneously by Yugoslav and Italian vessels, each of them operating on its side of the Adriatic.

The cruise the results of which are presented in this paper was performed from March 9 to April 8, 1982. Material vas collected from a total of 75 stations, of which 38 stations along 9 profiles on the Yugoslav side and 37 stations along 10 profiles on the Italian side (Fig. 1).

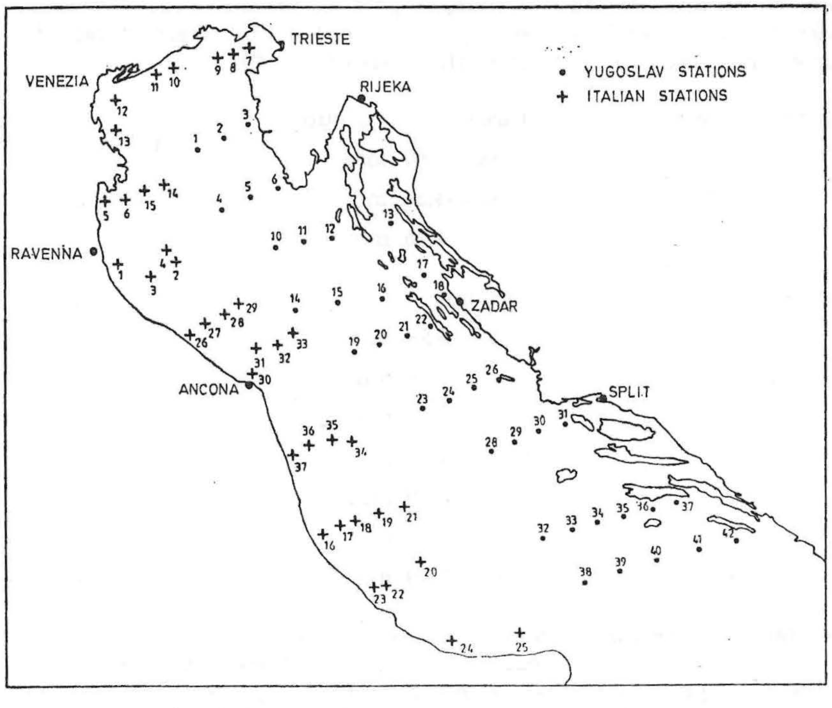

Fig. 1. Distribution of stations over the surveyed area

MATERIALS AND METHODS

Material for the sardine stock assessment was collected by Bongo — 20 net consisting of two cylinders of 20 cm diameters each with its own plankton net. Both nets were of 0.250 μm meshes. Net was provided with flowmeter and depth recorder. At each station net was towed double obliquely at a vessel speed of 1.5 to 2.0 knots. At stations where depth did not exceed 60 m net was lowered to about 5 meters above the sea bottom and at stations with greater water depth to 60 metres. Plankton material from both nets was preserved in the same container in $2^{0}/_{0}$ solution of neutralized formol in the sea water.

Sardine eggs were classified into five developmental stages, A, B, C, D, and E, on the basis of the stage of embryonic development. Abbreviated classification of embryonic stages of sardine eggs proposed by General Fisheries Council for the Mediterranean (GFCM Studies and Reviews, No. 1, 1957) was used on this occasion. Eggs collected by both Italian and Yugoslav vessels were classified in this way. Data on egg numbers by individual stages were used for the calculation of instantaneous mortality rates. In addition to the number of eggs under a square metre and temperature at 1 m depth, these are the only data used in to this paper from the area surveyed by Italian vessel. They were to get information on sardine spawning intensity throughout the study area during the time of cruise.

All the other parameters that will be analysed here refer exclusively to the area covered by 38 stations along 9 profiles on the Yugoslav side.

Sardine larvae and postlarvae were counted and their standard length measured, from the top of snout to the basis of tail fin.

Larvae were separated in three length groups:

L_1	3.00—3.67 mm
L_2	3.68—4.34 mm
L_3	> 4.35 mm

and postlarvae in seven length groups

P_1	4— 5.99 mm
P_2	6— 7.99 mm
P_3	8— 9.99 mm
P_4	10—11.99 mm
P_5	12—13.99 mm
P_6	14—15.99 mm
P_7	16—17.99 mm

Postlarvae exceeding 18 mm in length were not caught during this cruise.

The numbers of sardine eggs, larvae and postlarvae by individual length groups were expressed as their number under a square metre per day. The numbers of egg and larval stages were calculated first by the equation:

$$Y = \frac{X}{A \cdot \frac{L}{d}} \qquad (1).$$

where Y is the number of eggs or larval stages under a square metre, X the number of eggs or larval stages in the sample, A the mouth area of the net (for Bongo-20 it is 0.06498 m^2 for both cylinders), L is the distance towed and d maximum depth reached.

The number of eggs under a square metre per day was calculated by the equation:

$$N = \frac{Y}{\frac{1}{m}(1-e^{-mD})} \quad \text{(Tanaka, 1973)} \qquad (2).$$

where N is the number of eggs under a square metre per day, Y the number of eggs under a square metre from the equation (1), m coefficient of instantaneous mortality rate, D duration of total embryonic development from fertilization to hatching expressed in days.

The number of larvae and postlarvae under a square metre per day was calculated by lenght groups using the equation:

$$N_{gi} = \frac{Y_{gi}}{\Delta t_{gi}} \qquad (3).$$

where N_{gi} is the number of larvae or postlarvae from the length group gi under a square metre per day, Y_{gi} is the number from the length group gi under a square metre (equation 1), Δt_{gi} the time in days required for larvae and postlarvae to grow in length from the initial to the final length of the i^{th} length group.

It follows from the equations (2) and (3) that it was necessary to know the rate of sardine egg development at different temperatures as well as the growth rate of larvae and postlarvae. No separate experiments were performed to obtain these data. We simply made used of the data presented in the papers by Gamulin and Hure (1955) and Blaxter (1969) for the calculations of parameters of equations of egg development as a function of temperature and larval stage growth rates.

On the basis of the data on egg developmental time at different temperatures, at 13 and 18°C (Gamulin and Hure, 1955) and at 10, 15, 16, 17 and 17,3°C (Blaxter, 1969) it was calculated that the developmental time may be estimated by the equation:

$$D = 163.4012\, T^{-1.5018} \qquad (4),$$

where D is the developmental time in days, T temperature in °C. The coefficient of correlation between developmental time and temperature was:

$$r = -0.9151;\ P < 0.001$$

It is of importance to emphasize here, that the data on egg developmental time, as affected by temperature refering to sardine populations far apart from each other, one being from the Adriatic and the other from British waters, show very high and statistically significant correlation. This is indicative of the fact that embryological processes are very likely either the same or very similar in all sardine populations throughout the area of their geographical distribution.

It was calculated on the basis of the same data that the time of individual stage (Δt), as well as mean age of individual stage ($\bar{t}$) may be estimated multiplying the value D for each individual temperature by the following correction factors:

Stage	A + B	C	D	E
Δt	0.28	0.42	0.20	0.10
$\bar{t}$	0.14	0.49	0.80	0.95

It was possible in this way to calculate sardine egg mortality observing the decrease of the number of eggs in individual stages in function of time.

Characteristics of sardine larval and postlarval growth were calculated after graphical presentations of growth proposed by Blaxter (op. cit.). The data on larval growth at 14.5°C temperature and postlarval growth at mean temperature of 16°C were used for these calculations.

It was found that the growth of larval stages could be best approximated by Gompertz function of the form:

$$l_t = a\, e^{-b\, e^{-ct}} \qquad (5),$$

where l_t is the length in time t in days, a asymptote and b and c constants. Function parameters were determined by earlier described iterative procedure (Regner, 1980).

The calculations gave the parameters of function (5) for larval growth at 14°C as follows:

$$l_t = 5.17 e^{-0.3898 e^{-0.4199t}} \qquad (6),$$

where correlation coefficient was:

$$r = -0.99999;\ P < 0.001$$

while the postlarval growth was obtained by the function:

$$l_t = 47.00e^{-2.1985e^{-0.0169t}} \qquad (7).$$

with the correlation coefficient

$$r = -0.991;\ P < 0.001$$

As shown, the equations (6) and (7) are significant at high significance levels. However, since larval growth is affected by temperature up to the point of transition to active feeding, and postlarval growth by temperature and food quantity, these equations may be used only for a rough age estimate due to the fact that they refer to the growth at one temperature only.

The time which larvae or postlarve spend in a given length group (Δt) may be estimated on the basis of equation (5) as follows:

$$\Delta t = -\frac{1}{c}\ln\left[\left(\frac{1}{b}\ln\frac{a}{l_{t_{i+1}}}\right) - \ln\left(\frac{1}{b}\ln\frac{a}{l_{t_i}}\right)\right] \qquad (8).$$

where l_{t_i} and $l_{t_{i+1}}$ are the initial and ultimate lengths respectively od i^{th} length group. Mean age of a length group on the basis of which instantaneous mortality rate was calculated, was taken as $\Delta t/2$ for every group of values.

At each station the data on temperature and salinity from the surface to the greatest depth of 60 m, at 5 m intervals, were collected in addition to the ichthyoplankton material. Measurements were performed by the »Inter Ocean« probe with ± 0.01°C and ± 0.01 S‰ accuracy.

Information on phytoplankton, that is the number of cells and chlorophyll *a* quantities, were obtained by simultaneous sampling as well as the data on micro- meso- and macrozooplankton. As distinct from ichthyoplankton, temprature and salinity, data on other parameters were not collected from all stations. The stations wherefrom individual parameters were sampled are presented in Table 1.

Table 1. Stations at which the data on phytoplankton, micro- meso- and macrozooplankton were collected

Parameter	Stations
Phytoplankton	1, 3, 6, 12, 15, 16, 18, 19, 22, 23, 26, 29, 31, 34, 36, 38, 40, 42
Microzooplankton	4, 6, 10, 12, 14, 16, 17, 18, 19, 22, 23, 26, 29, 31, 32, 34, 36, 38, 40, 41, 42
Meso- and macrozooplankton	1, 3, 6, 12, 14, 16, 18, 19, 22, 23, 26, 29, 31, 32, 36, 38, 41

Phytoplankton was sampled by »Nansen« botles of 1.25 l volume. Samples were collected from 0, 10, 20 m and immediately above the sea bottom. Material for quantitative-qualitative analyses was fixed in 2.5% solution of neutralized formol in the sea water. Numbers and composition of cells were determined on the reversing UTHERMŐHL microscope. Phytoplankton quantity was expressed as the number of cells per liter. Biomass was estimated by chlorophyll *a* quantity measuring fluorescence on a TURNER III fluorometer. Quantity was expressed in mg/m^3.

Microzooplantkton was sampled by a »Nansen« type net 45 cm in diameter at the mouth, with mesh diameter 53 μm. Net was provided with a closing system. Net was towed in the layers 0—50 m and from the bottom to 50 m. Material was preserved in 2% formol solution in the sea water. Microzooplankton quantity was expressed as the number of specimens per cubic metre.

Meso- and macrozooplankton were collected by »Hensen« net, 0.42 m^2 mouth surace, mesh size 333 μm. The net was towed at a speed of 0.5 m/sec from bottom to surface. Maximum sampling depth was 170 m at station 38. Material was fixed in 2% formalin. Quantity of this zooplankton fraction was expressed as the number of specimens per cubic metre.

RESULTS

Spatial distribution of the numbers of sardine eggs under a square metre per day showed that two already mentioned saradine spawning centres (Fig. 2) could be clearly distinguished during the survey the results of which are presented here. As shown by Fig. 2, one centre (northern) is situated between the island Dugi otok and Ancona and the other (southern) in the open sea at the level of the Mljet island. The former is separated in two parts with a secondary centre at approximatively an equal distance from Dugi otok and from Ancona (station 19), and the other one along the outer edges of Dugi otok and Žirje islands (stations 22 and 26). A zone of poor and very poor spawning intensity is situated between northern and southern centres, with almost complete absence of eggs over the Jabuka Pit. The quantity of eggs was also very low in the northern Adriatic waters from the level of Kvarner islands, along the western Istrian coast to the Gulf of Trieste. There were no eggs at all along the italian coast from the Gulf of Venice to the Monte Gargano peninsula. This is well evident in Fig. 2.

It was attempted to associate the distribution of sardine eggs with the distribution of abiotic and biotic factors, the data on which were simultaneously collected during the cruise, so as to account for just that pattern of distribution. Fortunately sardine spawning was most intensive in the eastern part of the Adriatic for which the data on temperature, salnity, phyto- and zooplankton were available. Namely, as pointed out earlier, all henceforth analyses will refer to the data collected from stations along the nine profiles in the eastern Adriatic.

Hydrography

Characteristic for winter, tepmerature declined steadily to the shallow northern Adriatic. Thus the highest surface temperature of 15.56°C was recor-

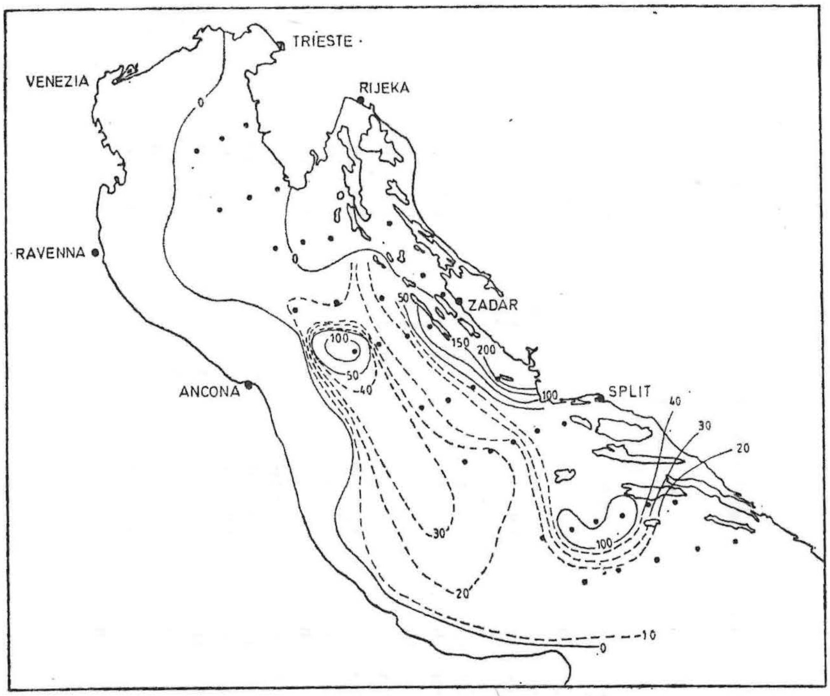

Fig. 2. Distribution of the sardine eggs (N/m^2/day) during the survey

ded at station 40 (profile IX), and lowest of 8.41°C at station 2 (profile I). Mean temperature was as well highest from surface to bottom, that is down to 60 m depth, at station 40, amounting to 14.69°C, while the lowest temperature of 8.55°C vas recorded from station 2.

Salinity, similarly to temperature, showed a decline to the northern Adriatic. The highest surface value of 38.78‰ was found at station 39 (profile IX) and lowest of 37.43‰ at station 2. The lowest mean salinity (37.55‰) of the water column was also recorded from this station.

A simple analysis of extreme temperatures and salinities not applying any detailed spatial analysis, shows a variety of hydrographic conditions in the area surveyed.

To arrive at a detailed information on hydrography of the study area and examine its eventual effects on sardine spawning, temperature, salinity and sea water density distributions were analysed by profiles and depths (Figs. 3, 4 and 5).

As shown by these figures, two areas with clearly distinct characteristics may bez readily distinguished.

The first area is off the western coast of Istria (profiles I and II). It is obviously very cooled and affected by fresh waters from the runoffs of rivers entering the northern Adriatic, the Po River in the first place, nevertheless warmer and more saline waters of the incoming Adriatic current reach the

Table 2. Distribution of the chlorophyll *a* (mg Chl *a*/m^{3}) and the quantity of phytoplankton cells (N/m^{3}) at the investigated area

		Chlorophyll *a*				Number of cells				
		Depth				Depth				
Profile	Station	0 m	10 m	20 m	Bottom	0 m	10 m	20 m	Bottom	m
I	1	1.50	1.49	1.13	0.70	3.3×10^{5}	3.1×10^{5}	4.1×10^{5}	3.0×10^{5}	(30)
	3	0.41	0.58	0.83	—	4.1×10^{5}	—	6.3×10^{5}	—	
II	6	0.34	0.59	0.60	0.60	1.8×10^{5}	2.9×10^{5}	3.3×10^{5}	3.0×10^{5}	(30)
III	12	0.47	0.24	0.44	0.37	1.7×10^{5}	1.4×10^{5}	8.7×10^{4}	—	(40)
IV	15	0.44	0.48	0.55	0.64	1.8×10^{5}	1.4×10^{5}	1.2×10^{5}	1.5×10^{4}	(60)
	16	0.64	0.48	0.59	0.47	3.0×10^{5}	1.3×10^{5}	1.4×10^{5}	1.3×10^{5}	(60)
V	18	0.70	0.58	0.52	0.61	3.7×15^{5}	5.1×10^{5}	2.2×10^{5}	2.3×10^{5}	(40)
	19	0.43	0.49	0.46	0.45	1.5×10^{5}	1.4×10^{5}	2.0×10^{5}	1.1×10^{5}	(70)
	22	0.57	0.75	0.81	0.79	1.8×10^{5}	2.3×10^{5}	—	5.5×10^{4}	(60)
	23	0.57	0.33	0.52	0.83	2.6×10^{5}	1.9×10^{5}	1.8×10^{5}	1.1×10^{5}	(70)
VI	26	0.70	0.92	0.93	1.01	3.2×10^{5}	4.1×10^{5}	4.4×10^{5}	1.7×10^{5}	(60)
VII	29	0.40	0.43	0.50	0.62	1.1×10^{5}	2.5×10^{4}	7.1×10^{4}	7.6×10^{4}	(50)
	31	0.38	0.46	0.49	0.40	2.0×10^{4}	5.5×10^{4}	7.3×10^{4}	2.2×10^{5}	( )
	32	0.52	0.57	0.50	0.45	4.4×10^{4}	6.9×10^{4}	2.6×10^{4}	1.1×10^{5}	(50)
VIII	34	0.50	0.66	0.58	0.61	6.5×10^{4}	8.9×10^{4}	1.2×10^{5}	4.5×10^{4}	(50)
	36	0.35	0.32	0.44	0.41	8.7×10^{4}	4.7×10^{4}	6.1×10^{4}	1.8×10^{5}	(50)
	38	0.33	0.30	—	0.20	—	7.7×10^{4}	5.9×10^{4}	3.1×10^{4}	(100)
IX	40	0.68	0.53	0.68	—	8.7×10^{4}	5.0×10^{4}	8.0×10^{4}	9.8×10^{4}	( )
	42	0.34	0.47	0.39	—	$9,8\times10^{4}$	1.4×10^{5}	2.2×10^{5}	—	( )

northern Adriatic. These are the waters on profiles I and II in the temperature of which exceeds 9°C (Fig. 3), salinity 38‰ (Fig. 4) and density 29.4σt (Fig. 5). The water that overlies this water is colder and less saline, probably originating from the areas affected by the Po River. This area is separated from the southern part by a zone of very intensive mixing (profile III), apparently affected by frequent and strong NE wind, bura, which is particularly intensive in the Bay of Kvarner.

The rest of the surveyed area is obviously affected by the Adriatic inflowing current, with temperatures every where exceeding 11°C (Fig. 3) and salinity 38.50‰ (Fig. 4). However, hydrography of this part is also diverse. The upwelling zones are observed on profiles IV, V, VII and VIII. These zones are in the belt parallel with the coastline direction, 10 to 20 Nm off the most offshore islands of the eastern Adriatic. The upwelling zones are clearly identifiable by temperature (Fig. 3) and density distribution (Fig. 5), cooler and relatively heavy deep water reaching surface at mentioned profiles. Salinity distribution (Fig. 4) is not such a good indicator of upwelling zones. The break of the upwelling belt occurs at profiles VI and IX where, as shown by isothermes, isohalines and isopycnals, water is more intensively mixed. Since, as well shown by Fig. 1, the profile IX is above the edge of Palagruža Sill which separates the South Adriatic Pit from the middle Adriatic, while the profile VI is just above the northwestern sill of the Jabuka Pit, presumably the upwelling is disturbed by the impact of sills on current system in these areas.

Positionss of sardine spawninig centres, as will be shown further in this paper, were associated mostly with zones where the uwpelling was formed.

Biological conditions

The upwelling importance could not be explained without taking into consideration first the biological conditions in the study area. It should be emphasized here that the interpretation of spatial distribution of phytomicro, meso and macrozooplankton is somewhat difficult since these data, as distinct from sardine plankton stages, were not collected from all the stations.

Quantities of phytoplankton cells and chlorophyll *a* are given in Table 2. To show to which extent these two parametres coincide the correlation coefficients were calculated (Table 3).

Table 3. Coefficients of correlation between the number of phytoplankton cells and quantity of chlorophyll *a*

Depth (m)	r	P
0	0.265	n.s.
10	0.597	0.05
20	0.602	0.05
bottom	—0.009	n.s.

As shown by Table 3, relatively high correlation coefficients were obtained for these two parameters for 10 and 20 m depths, significant at 95% levels. Coefficients for surface and particularly those for the bottom are negligible. Relatively good coefficients of correlation between the number of

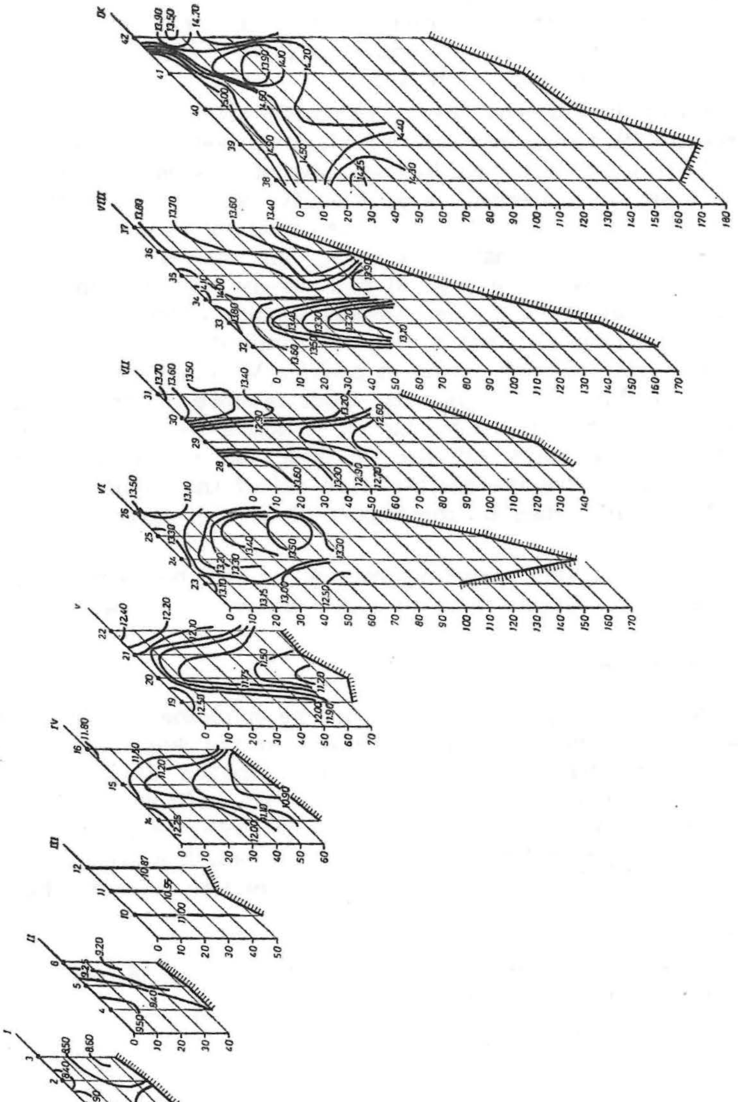

Fig. 3. Distribution of temperature

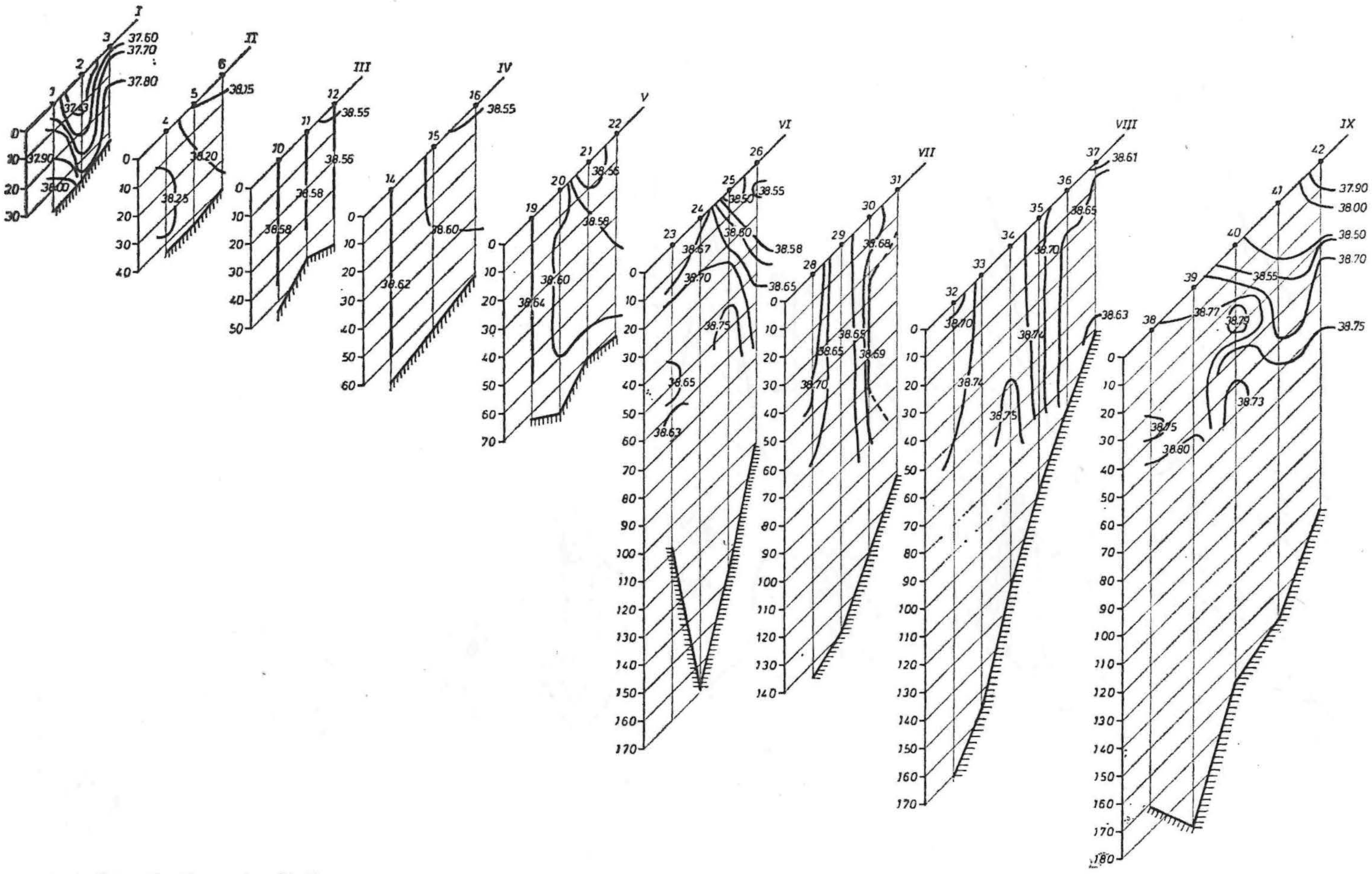

Fig. 4. Distribution of salinity

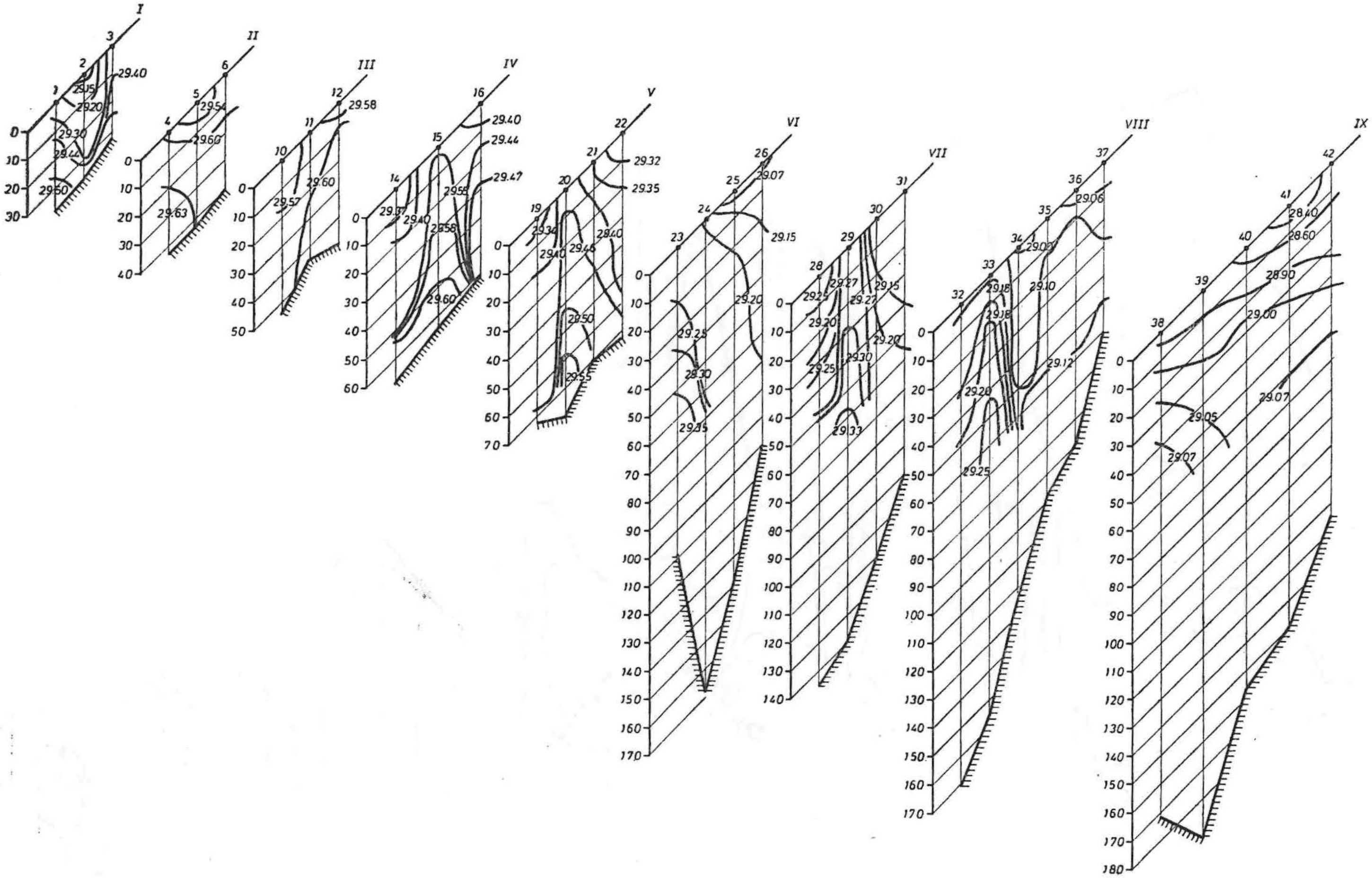

Fig. 5. Distribution of water density

cells and chlorophyll *a* in free water may be indicative of the fact that cell size showed fairly well resemblance throughout the study area.

Largest quantities of both phytoplankton cells and chlorophyll *a* were recorded from the shallow northern Adriatic, profiles I and II. Phytoplankton quantity declines in the frontal zone (profile III), to be increased together with the chlorophyll quantity at profiles IV and V. Thereafter, clorophyll quantity decreases while the number of cells is still pretty high in the mixing zone at profile VI, with the exception for station 26 at this profile at which both values were very high (Table 2). This may be consequent to the mixing of the open sea water with the colder and less saline water from the channel area of the middle Adriatic indicated by the isotherm of 13.10°C and isohaline of 38.55‰ (Figs. 3 and 4). The number of cells is reduced in te southern upwelling zone at profile VII and VIII, while chlorophyll quantity is increased. The number of cells slightly increases and chlorophyll quantity decreases at profile IX in the mixing zone above the Palagurža Sill. To conclude, phytoplankton quantity decreases from the northern towards the southern Adriatic, irrespective of the fact whether it is indicated by the number of cells or by chlorophyll quantity. However, there is a discontinuity in this decrease, since an increase of phytoplankton quantites is observed in the upwelling zones. This increase is much better marked in the northern upwelling zone. Southern zone is in general poorer as to the phytoplankton quantity than the northern one.

The analysis of microzooplankton showed it to consist of Heliozoa, Radiolaria, Tintinnina and copepod nauplii and copepodites (Table 4). Developmental stages of copepods and Tintinnina constitute an important component of sardine postlarval food (Karlovac, 1967).

Heliozoa were found in larger numbers only at stations 41 and 42, affected by coastal waters, in the southern part of the study area. Their numbers in the surface layer considerably exceeded their numbers in deeper layers. They were as well recorded in small numbers from station 38 near Palagruža. Heliozoa were absent at profiles VII and VIII which overlie greater depths, whereas they occurred at all the stations of all the shallower profiles of the northern part of the study area even though their quantities were much lower than at stations 41 and 42. Largest numbers were found at stations 16 and 26 exposed also to the effects of colder and less saline waters from channel areas (Table 4).

The numbers of Radiolaria decreased from the southern towards the northern part of the study area. They were found in somewhat larger numbers ot profiles VII, VIII and IX, if mean numbers are taken, their quantities being equal at the surface and in the layers below 50 m. Their numbers cotinued to decrease thus that they were not recorded from the profiles II and III (Table 4).

Both with respect to the number of individuals and the number of species of Tintinnina showed decrease going from the southern towards the northern Adriatic (Tables 4 and 5). At profiles VIII and IX they were more numerous in deeper layers, from the bottom to 50 m depth than in the surface layer. It was also observed that the number of Tintinnina was considerbly increased at stations at the boundaries of upwelling zones (stations 32, 34, 29, 19 and 14).

Table 4. Distribution of the quantity of microzooplankton (Number of individuals /m^3) at the investigated area

Profile	Station	Layers	HELIOZOA Sticholonche zanclea	RADIOLARIA	TINTINNINA	COPEPODA naupliar	COPEPODA copepodites	COPEPODA adults	»Other Metazoa«	TOTAL
II	4	40—0	10	—	—	18060	753	905	610	20338
	6	30—0	56	—	—	27540	530	1400	1270	30796
III	10	45—0	10	—	66	13140	850	910	160	15136
	12	40—0	20	—	94	11140	790	730	1560	14334
IV	14	50—0	180	—	380	10590	560	770	40	12520
	16	55—0	460	45	305	9950	730	720	153	12363
	17	50—0	80	—	170	11720	420	390	390	13170
	18	40—0	180	—	180	11740	550	570	380	13600
V	19	65—0	160	30	506	8730	466	388	90	10370
	22	65—0	140	—	65	10580	446	330	52	11613
VI	23	60—0	70	42	240	6890	630	490	45	8407
	26	60—0	380	—	330	4500	389	452	140	6191
VII	29	50—0	—	8	785	6320	1090	640	67	9810
		120—50	—	18	473	2980	445	848	20	4784
	31	50—0	—	59	330	6630	650	529	185	8383
		90—50	—	40	300	5120	440	656	100	6656
VIII	32	50—0	—	50	678	7500	890	834	110	10062
		165—50	—	—	1040	4430	890	710	30	7100
	34	50—0	—	60	1050	7380	940	730	142	10302
		115—50	—	65	1275	4500	323	518	117	6798
	36	70—0	—	42	828	3610	142	175	96	4893
	38	50—0	—	67	472	5050	361	420	8	6329
		150—50	20	24	1506	4230	260	315	24	6379
	40	50—0	—	—	499	6010	676	270	91	7546
		150—50	—	55	664	3580	316	412	70	5097
IX	41	50—0	675	—	436	8640	996	645	—	11392
		140—50	277	—	561	1730	225	235	9	3037
	42	50—0	4100	—	507	9290	980	1030	252	16159
		120—0	180	—	577	3480	385	554	168	5386

Table 5. Distribution of Tintinnina species at the ivestigated area

Species	Profile	II		III		IV				V		VI		VII		VIII			IX			
	station	4	6	10	12	14	16	17	18	19	22	23	26	29	31	32	34	36	38	40	41	42
Tintinnopsis radix																					+	+
Tintinnopsis campanula											+						+				+	+
Codonella aspera			+			+			+	+		+		+	+	+	+	+	+	+	+	+
Codonella galea														+		+	+		+	+	+	+
Codonella amphorella														+		+	+		+	+	+	+
Codonella apicata															+							
Codonaria cistellula				+	+	+	+			+	+	+	+	+		+	+	+	+	+	+	+
Stenosemella ventricosa								+	+								+					
Codonellopsis orthoceras																				+		
Codonellopsis schabi																+	+	+			+	+
Cyttarocylis eucecryphalus														+	+	+	+		+	+	+	+
Cyttarocylis cassis						+				+				+	+	+	+		+	+	+	+
Petalotricha ampulla						+							+	+	+	+	+		+	+	+	+
Parundella lohmanni																+	+		+			+
Xystonella treforti														+	+		+	+	+	+		+
Xystonellopsis paradoxa														+		+	+		+	+	+	+
Undella hyalina																+	+	+		+	+	
Undella claparedei					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Undella subcaudata subcaudata																			+			
Amplectella tricollaria																+						
Undellopsis marsupialis															+	+	+		+	+		
Dictyocysta elegans									+										+		+	
Dictyocysta lepida														+	+	+	+	+	+			+
Dictyocysta muelleri																+	+		+		+	
Dictyocysta mitra														+		+	+	+	+			
Steenstrupiella steenstrupii												+	+				+	+		+	+	+
Amphorides quadrilineata						+						+	+		+		+	+	+			+
Amphorides minor				+	+		+										+	+	+	+	+	+
Eutintinnus fraknoi																					+	
Salpingella glockentoegeri																+	+	+	+	+	+	
Number of species			0	4	3	6	3	2	4	4	4	5	5	12	10	18	23	13	21	16	20	18

As distinct from Tintinnina, the fourth component of microzooplankton, copepod nauplii and copepodites, show a continuous increase to the north (Table 4). It is also evident from Table 4 that nauplii and copepodites were much more numerous in the surface layer and down to 50 m depths than in deeper layers at all the stations at which samples were collected by layers.

In addition, even though nauplii and copepodites were most numerous in the waters of the northern Adriatic at transects II and III, the increase of their numbers is well evident also at stations at the boundaries of the upwelling zones (stations 32, 34, 29, 22, 19, 16 and 14).

These studies, as already pointed out, included also qualitative-quantitative composition of meso and macrozoplankton. Of zooplankton organisms Medusae, Siphonophora, Ctenophora, Phyllopoda, Copepoda, Ostracoda, Chaetognatha, Appendicularia and Thaliacea, as well as Decapoda larvae, Mollusca and Echinodermata were observed. The Copepoda group was worked out in detail in view of its quantities (exceeding 96% of total zooplankton) and important part in food chains being the first step of organic matter consumers as well as principal food of commercially important fish species, including the sardine.

Quantities of the total zooplankton, their distribution in north-south direction, and in an offshore direction will be considered first. As shown by Fig. 6. the quantity of total zooplankton is manifold (30—35 times) decreased to the southern Adriatic. The highest values of total zooplankton per 1 m^3 were recorded from the shallow northern Adriatic, on profile I, where depths

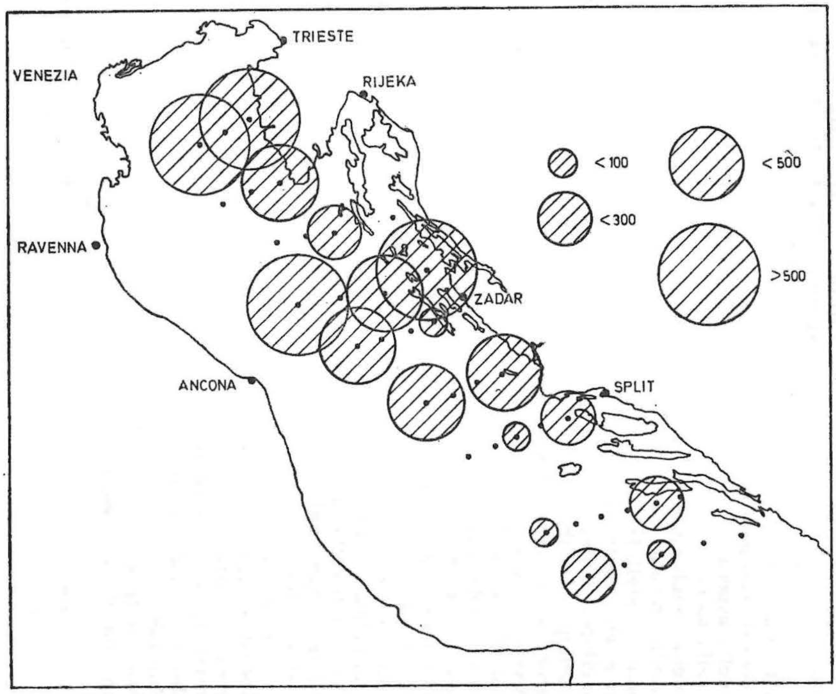

Fig. 6. Distribution of the total zooplankton (N/m^3)

are about 40 m and phytoplankton quantities highest as weel. Next two profiles (II and III) already show 4—6 times lower quantities which are once again increased in the upwelling zone (profile IV). Like in the spatial distribution of phytoplankton quantities, the zooplankton quantities were as well somewhat higher at station 26 (profile VI). This is in agreement with already mentioned assumption that the waters of the open sea are mixed there with the colder and less saline waters of the middle Adriatic channel area. Number of zooplankton organisms continued to decrease in the southern upwelling zone being slightly higher at station 36 (profile VIII), which is in the channel area. On the basis of the data for spring 1982 it may be stated that the number of zooplankton organisms decreases, as does the number of phytoplankton organisms, from the northern towards the southern Adriatic. This has been known for some groups — Copepoda for example- ever since the beginning of this century (Steuer, 1910) and from some later researches (Hure *et al.*, 1980; Regner, D., 1983 and 1985. etc.).

In addition, like for the phytoplankton, an increase in the number of zooplankton organisms is observed in the upwelling zones, much better marked in the northern than in the southern zone.

Studies of zooplankton composition (Table 6) proved Copepoda to be most abundant with the average percentage proportion of about 65%. It may be of interest to mention that their percentage presence is slightly higher in the middle part of the eastern Adriatic than in its southern and northern parts.

Table 6. Variations of mean percentage proportions of some important zooplankton groups in northern Adriatic-southern Adriatic direction

	Copepoda	Siphonophora	Appendicularia	Phyllopoda	Chaetognatha
Northern Adriatic	63	14	19	7	2
Middle Adriatic	67	17	13	3	4
Southern Adriatic	64	20	10	0.2	0.5

As shown by absolute values of the percentage of Copepoda may even reach as high value as 96% particularly at stations 1 and 3 in the shallow northern Adriatic and 82% at stations 26 and 31 in the middle Adriatic.

The Siphonophora group comes next (17%) as to its percentage presence. It may be stated for this group that its percentage value increases regularly from the north southwardly.

This group is followed by Appendicularia both by its number of individuals (Fig. 8) and percentage presence in the total zooplankton (Table 6). Its percentage is 14% throughout the study area with the maximum exceeding 80% at station 12 (profile III). Due to the fact that this group is not uniformly distributed at all the stations, its percentages given in Table 6, decreasing to the south, should be taken only as approximate.

The Phyllopoda group, with mean precentage of 3.4%, decreasing to the south (18% at station 6, profile III) where it is practically absent (Table 6), comes next. Among these is also the group of Chaetognatha with the percentage of 2.2%, being best represented in the middle Adriatic (Table 6).

Upon this short account of the distribution of quantities and composition of zooplankton the Copepoda group will be worked out in more detail owing not only to its dominance in the zooplankton composition, but also for its trophic significance.

The spatial distribution of this group will be considered first. As shown by Fig. 8, Copepoda quantity per cubic metre is highest in the shallow northern Adriatic at profile I, for which was shown that both the phytoplankton quantities, on which most of zooplankton species feed, and total zooplankton quantities, (the numbers of which are determined by phytoplankton quantities) were considerably higher tha nin the other parts of profiles the surveyed area. Copepoda quantity significantly decreases at profiles II and III to be increased in the upwelling zone (profile IV). The values are also decreased at profile V, to increase at profile VI. Thereupon the number of Copepoda continues to decrease being highest at station 36 (profile VIII). In an offshore direction the number of Copepoda is also decreased. Low values recorded from the coastal area (only at station 22) could be due to a momentary weather situation (wind direction, current etc.). Since high sardine production was recorded from that station, the »grazing« effect must not be neglected, since adult sardine feed during spawning, as well.

As shown by everything discussed, it is obvious that the distribution of total zooplankton is dependent on Copepoda quantity. Data obtained agree with the results of studies of some earlier authors and fit into the picture of horizontal distribution of Copepoda in the Adriatic (Hure *et al.*, 1980) who gave mean values for four cruises by seasons.

As to the species composition of Copopoda it should be kept in mind that data may be characteristic of the spring season only. Species composition is rather diverse, and includes neritic and oceanic species, as well as some brackish water species (in the shallow northern Adriatic) in addition to ordinary widely distributed Adriatic species (like *Ctenocalanus vanus* which is with 14% the best represented species). The species *Ctenocalanus vanus* (exceeding 17%), *Paracalanus parvus* (about 14%) *Acartia clausi* (about 13%), *Centropages typicus* (exceeding 9%), that are widely distributed species and ordinary neritic species are most numerous in the northern Adriatic. However, *Clausocalanus pergens,* a typical oceanic species, also occurred with a high percentage of almost 6%, pointing to the strong water mass circulation in this part of Adriatic in spring.

Ctenocalanus vanus (about 15%), *Centropages typicus* (about 10%), *Paracalanus parvus* (about 9%), are best reperesented in the middle Adriatic as well as *Calanus tenuicornis* and *Clausocalanus pergens* which like *Acartia clausi* are present with about 4%.

Ctenocalanus vanus and *Paracalanus parvus* with about 8%, *Calanus tenuicornis* (about 6%), *Clausocalanus pergens* (about 4%) are most numerous in the southern Adriatic. However, markedly oceanic species like *Pleuromamma gracilis, Haloptilus longicornis, Pleuromamma abdominalis* and others were also recorded from this area.

This wide distribution and high percentage proportions of neritic species throughout the eastern Adriatic were established by the researches carried out by Hure et al. (1980).

Sardine plankton stages as affected by environmental factors

Data on temperature and salinity from 20 m depth were used for studies of the relationship between sardine egg distribution and abiotic factors. These data were used since planktonic stages of sardine are found in the surface layer, eggs and larvae immediately beyond the surface and postlarvae from surface to about 20 m (Larraneta, 1960). Furthermore, both temperature and salinity are less liable to short-term variations at a time scale of several days at this depth.

Sardine eggs were recorded at temperatures ranging from 8.43 to 14.78°C and salinity ranging from 37.59 to 38.78‰ (values from 20 m depth). However the most intensive egg production was recorded at temperature ranges of 11.6—13.9°C, with the maximum at 12.1—13.9°C, and at salinity range of 38.57—38.71‰ (Fig. 7). It is of interest that egg production maxima were recorded wihin the same temperature and salinity ranges in both northern and southern spawning centres, nevertheless they are a large distance apart. In addition, it is obvious that small egg quantities are also recorded within, so to say, optimum temperature and salinity ranges (Fig. 7). This is indicative of the fact that the temperature and salinity values are not themselves sufficient and crucial for the formation of spawning centres in the study area, and that besides temperature and salinity some other conditions should be satisfied.

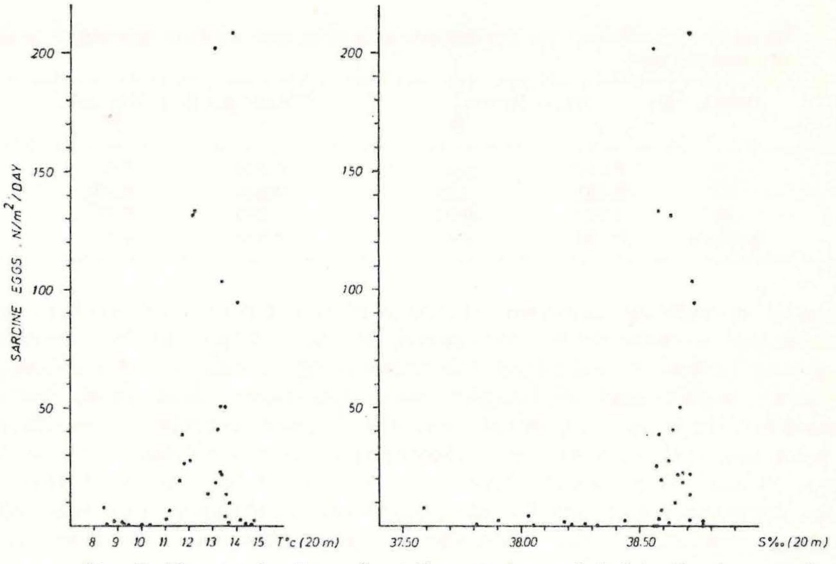

Fig. 7. The production of sardine eggs as related to the temperature and salinity

A comparison of upwelling zones (Figs. 3, 4 and 5) with the spatial distribution of sardine spawning intensity given in Fig. 2, points to the fact that sardine spawned most intensively just along the boundaries of upwelling zones, in the areas of stations 19, 22, 33 and 35. These obviously are the zones of mixing of different water masses caused by upwelling. The effects of zones of mixing on spawning centre formation are also shown by a high number of eggs at station 26 which, as already pointed out, is in the area of mixing of open sea waters with the channel waters.

It is as well apparent that upwelling, or, better to say, the occurrence of frontal zones due to upwelling, considerably affected the formation of sardine spawning centres in the surveyed area, during the time of investigations. In addition, each of mentioned centres seems to be separated in two parts due to this phenomenon: a part along the boundary of the zone turned towards the coast and a part towards the open sea. This is particularly well evident in the northern spawning centre at the level of Dugi otok island (Fig. 2).

Since the phytoplankton anlysis showed that larger quantities of phytoplankton also occurred along the bonudaries of upwelling zones it may be stated that sardine choose for spawning the areas which, within the limits of tolerance of abiotic factors, provide most favourable trophic conditions. To establish to what extent spatial phytoplankton distribution coincides with the spatial distribution of sardine eggs, coefficients of correlation between the number of phytoplankton cells and chlorophyll *a* quantities were calculated on the one side and sardine egg production on the other for all the stations except those in the frontal zone and north of it (profiles I, II and II). Resuts obtained are given in Table 7.

Table 7. Correlation between phytoplankton quantity and sardine spawning intensity (N eggs/m^2/day)

Depth (m)	No cells/m^3		Chlorophyll a (mg/m^3)	
	r	P	r	P
0	0.347	n.s.	0.444	n.s.
10	0.691	0.01	0.805	0.001
20	0.785	0.01	0.693	0.01
bottom	0.193	n.s.	0.555	0.1

Spatial correlation between phytoplankton quantity and sardine spawning intensity is very well pronounced, if the relation to the number of cells on the bottom is neglected. Coefficients of corelation with chlorophyll are slightly higher and statistically more significant than those with the cell numbers. It is also apparent that the highest correlation coefficnents, both with the cell numbers and chlorophyll, were obtained for the layer between 10 and 20 m depth. This is indicative of the fact that this layer provides optimum conditions for phytoplankton development and that sardine is likely to respond to the variations in phytoplankton quantities in that layer.

As distinct from phytoplankton, the coefficients of correlation between zooplankton and sardine eggs were very low and non-significant.

The youngest and oldest larvae from length groups L_1 and L_3 respectively, and the youngest, medium and oldest postlarvae from the P_1, P_3 and P_6 and P_7 (taken together) groups respectively were used for the analysis of spatial distribution of sardine larve and postlarvae. Mean age of larvae and postlarvae from these groups, calculated from fertilization was estimated to be:

	$\bar{t}$ (days)
L_1	4.02
L_3	7.82
P_1	11.78
P_3	26.59
P_{6+7}	51.97

As shown, the age of larval stages is relatively low. Howevrer, the age of oldest postlarvae is estimated to be almost two months. It therefore might be expected that postlarvae will be found far apart from the spawning areas being transported by currents. It may also be assumed that spawning centres may be considerably displaced during this time. Since no more than one cruise was performed, the conclusions drawn by the analysis of the relationship between postlarvae and spawning centres may involve an error due to eventual displacement of the spawning centres.

To show more clearly the spatial relations between sardine larval stages and spawning centres, as well as between larval stages and phyto and zooplankton, distributions of egg production, larvae from L_1 and L_3 groups and postlarvae from P_1, P_3 and P_{6+7} groups, chlorophyll, nauplii, copepodites, copepoda, Tintinnina, Phyllopoda and Appendicularia are presented in Fig. 8. These zooplankton groups were chosen since they are taken by sardine postlarvae as a food.

Sardine larvae occurred in greatest numbers in almost the same areas as eggs, with the greatest shift of about ten miles. However, the effects of currents are observed in oldest larvae for the L_3 group. Their maximum concentration was recorded from profile IV in the northern spawning centre, while egg production was maximum at stations 19 and 22 at profile V. Furthermore, as far as the other part of the northern centre is concerned, that is station 26 at profile VI, larvae were shifted to profile V (Fig. 8). Postlarvae were shifted even further, thus that postlarvae from P_3 and P_{6+7} groups were recorded from profiles I, II and III. The oldest postlarvae were found at stations 13 and 18 in the channel area wherefrom no eggs, larvae and youngest postlarvae were recorded. As shown by these data, larval stages of sardine seem to be drifted northwestwardly of the northern spawning centre. This is the direction of surface current along the eastern Adriatic coast (Zore-Armanda, 1968). Records of oldest postlarvae in the channel area between the north Adriatic islands, N-NW of the spawning ground, leads to the conclusion that they also came from this spawning area, most probably from its part along the boundary of the upwelling zone towards the coast.

As shown by Fig. 8 the situation is quite different in the southern spawning centre. Larvae and younger postlarvae are drifted along the profile VIII, westwardly, while older postlarave from P_3 and P_{6+7} groups were

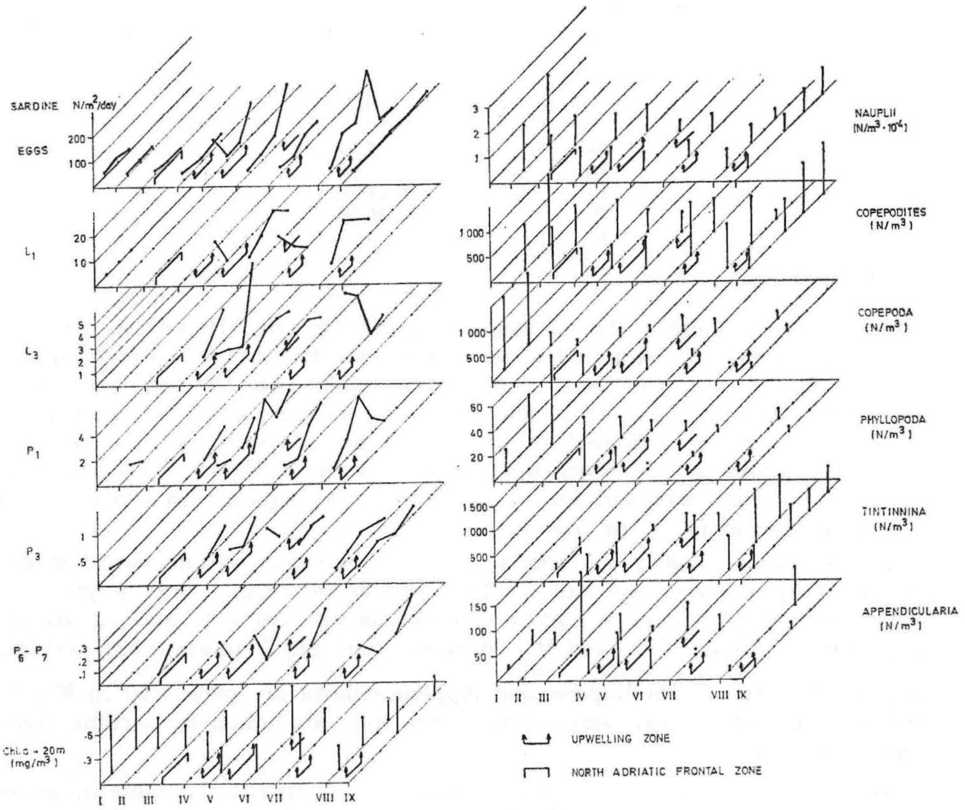

Fig. 8. Distribution of sardine planktonic stages as related to the fito and zooplankton

found at profile IX southwestwardly and southeastwardly of the spawning centre. Such a distribution of postlarvae is indicative of the eddy-like structure of counterclockwise flow in the surface layer.

Since the principal direction of the surface current runs precisely from the southern spawning centre, crossing over the profile VII, postlarvae at this profile may partly come from the southern spawning centre.

Even though the coefficients of correlation between the numbers of postlarvae and zooplankton groups they feed on, were very low and statistically non-significant, nauplii and particularly copepodites and Copepoda as well as Phyllopoda and Appendicularia occurred in higher numbers in areas in which higher numbers of postlarvae were recorded (Fig. 8). Presumably, water masses formed along the upwelling zones, enriched with nutrients and flowing divergently, carry larger quantities of both developmental stages and adult zooplankters providing thus favourable feeding conditions to postlarvae which, leaving the spawning areas, grow gradually.

Possible directions of transport of sardine larval stages are presented in Fig. 9 on the basis of distribution of eggs, larvae and postlarvae. These directions were supposed as likely only on the basis of the material collected from stations in the eastern Adriatic. The picture would have been probably more complete, had the data on larave and postlarvae collected from the western Adriatic part been included.

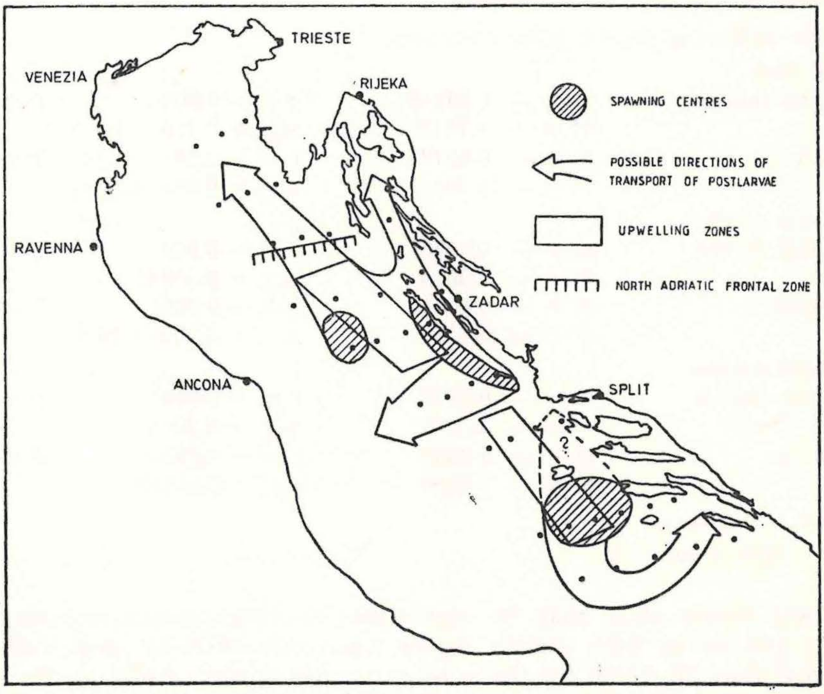

Fig. 9. Supposed patterns of transport of sardine larvae and postlarvae

Survival of sardine plankton stages

Coefficients of instantaneous mortality rates of eggs, larvae and postlarvae were obtained by calculating the coefficient of regression between mean age of individual embryonic stage or length group of larval stages and natural logarithm of the number of individuals under a square metre per day. Thus, in fact, the parameters of mortality were calculated by the equation;

$$N_t = N_o e^{-mt} \qquad (9),$$

where N_t is the number of individuals in time t, N_o the number in time $t = 0$ and *m* coefficient of instantaneous mortality rate.

Since it was observed that logarithms of egg and larval numbers plotted against the time are approximately on the same line, common *m* was calculated for them, and separate one for postlarvae.

In addition, to determine whether the coefficients of instantaneous mortality rate in the northern spawning centre differ from those in the southern one, *m* value was first calculated for the entire surveyed area and thereupon separately for the northern and southern spawning centres. Data on number of eggs, larvae and postlarvae along the assumed vestors of their transport, presented in Fig. 8, were considered.

The following results were obtained:

Entire area			
eggs and larvae	$m = -0.55649$	$r = -0.905$	$P < 0.01$
	$t^* = -4.7614$	$s_{(m)} = 0.116$	
postlarvae	$m = -0.09725$	$r = -0.984$	$P < 0.001$
	$t^* = -11.3946$	$s_{(m)} = 8.535 \times 10^{-3}$	
Northern centre			
eggs and larvae	$m = -0.6545$	$r = -0.944$	$P < 0.01$
	$t^* = -6.3616$	$s_{(m)} = 0.10282$	
postlarvae	$m = -0.0571$	$r = -0.980$	$P < 0.001$
	$t^* = -10.8599$	$s_{(m)} = 5.259 \times 10^{-3}$	
Southern centre			
eggs and larvae	$m = -0.5878$	$r = -0.689$	$P < 0.1$
	$t^* = -2.1267$	$s_{(m)} = 0.2764$	
postlarvae	$m = -0.0559$	$r = -0.892$	$P < 0.05$
	$t^* = -3.9396$	$s_{(m)} = 0.01419$	

---

t^* = t — test value

These results show that the coefficients of instantaneous mortality rate of eggs and larvae were slightly higher when calculated for each individual area, and that the value for the southern centre is statistically at the lowest confidence level. On the contrary, mortality coefficents for postlarvae were lower when calculated by individual areas, with the lowest significance level once again for the southern centre.

Results of estimates of instantaneous mortality rates show considerable lower mortality of eggs and larvae, and slightly lower mortality of postlarvae in the area of southern centre. This is very surprising, particularly when survaival of postalarvae is concerned, since the analyses of phyto- and zooplankton showed their quantities to be higher in the northern centre. It is, however, well known that postlarval survival depends in the first place on the quantity of availabe food. Therefore better survival of postlarvae was expected in the northern spawning centre. However, the relations between confidence limits of 95% (Fig. 10) show these differences not to be statistically significant. As shown by Fig. 10 confidence limits are thus overlapping that no tests of differences between coefficients of instantaneous mortality rates were necessary.

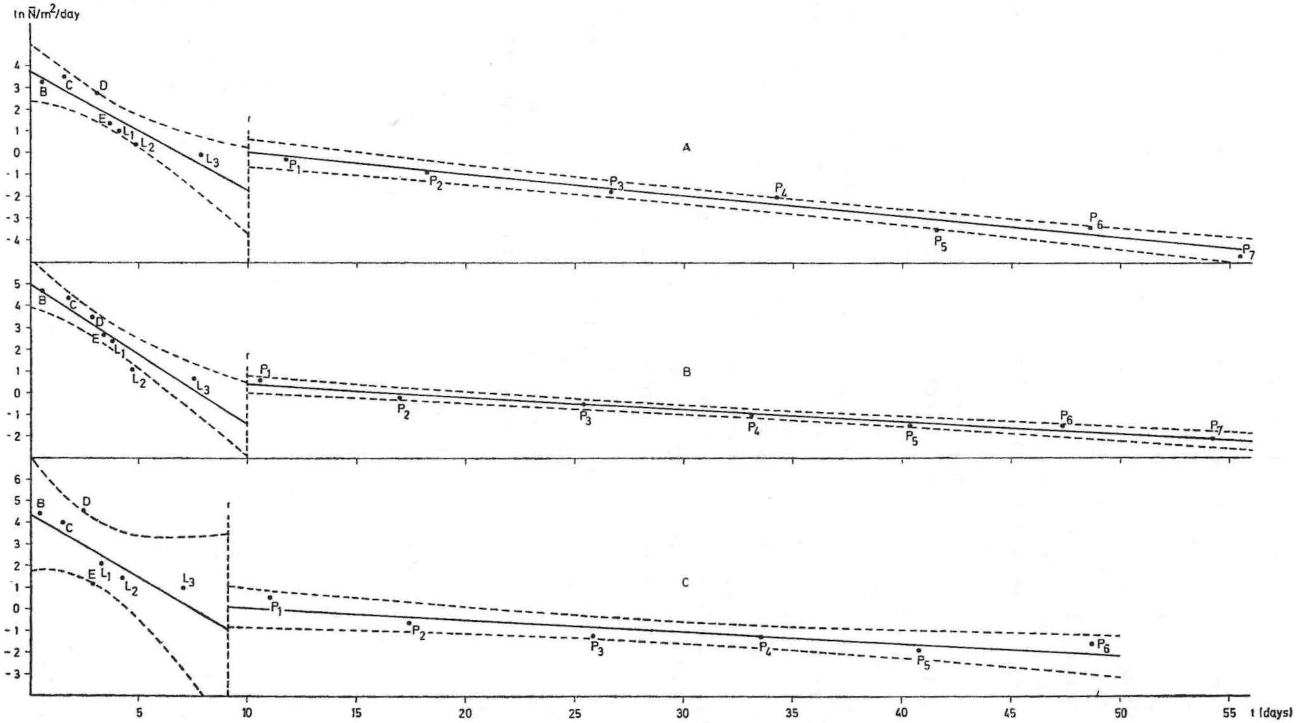

Fig. 10. Martality curves of sardine eggs, larvae and postlarvae (A = total, B = norhern spawning centre, C = southern spawning centre; dashed lines = 95% probability limits; r = the time of yolk sac resorption).

DISCUSSION

The observations of spatial distribution of sardine eggs in the plankton, done during the cruise the results of which are presented, confirm those already mentioned in the introduction which showed that sardine spawned in two areas separated by the Jabuka Pit.

As it was said before, earlier authors held that three spawning centres could be distinguinshed, between the island Dugi otok and Ancona, in the area of middle Adriatic islands (Brač, Vis, Hvar and Korčula), and in the area of Palagruža. The more recent studies (Piccinetti *et al.*,. 1980, 1981; Regner *et al.*, 1981, 1983; Gamulin and Hure, 1983) which covered much wider area of the Adriatic yielded the evidence that only two spawning centres existed, the northern one in a wider area between the island Dugi otok and Ancona and the southern one in the wider area of the Palagruža island. A synthesis of all so far collected data shows that the areas where sardine spawning centres occur are large and that they may be roughly determined by the lines which connect western Adriatic coast at the level of Pesaro with the Susak island on the eastern coast and Pescara with the Žirje island (northern area), then the Penna cape with the northeasternmost end of the Šolta island and peninsula Monte Gargano with the southeastern end of the Mljet island (southern area). Within these limits, sardine spawning centres may be everywhere between the Italian coast and most offshore points of the islands along the Yugoslav coast, dependently on the year, beginning, middlle or termination of spawning season, and on a series of other factors. At the same time, a number of spawning centres may be formed within these limits extending over a wider or narrower area (Regner, manuscript). In addition, in some years southern and northern spawning centres may be joined (Piccinetti *et al.*, 1981). Even though the data on sardine spawning in the southern Adriatic are scarce, presumably the southern area may spread along the Italian coast as far as Otranto (Gamulin i Hure, 1983).

The Adriatic is divided in four productive zones on the basis of nutrient contents and water depth (Buljan, 1964). The first zone where organic production is lowest, zone A, includes the open waters down to the line ting Ancona and Dugi otok to the Gulf of Venice and Gulf of Trieste as well the isobath 50—70 m, so that it does not include a shallow zone along the Italian coast or the area of islands along the Yugoslav coast. The second zone, zone B, includes shallow part of the northern Adriatic, from the line connecting Ancona and Dugi otok to the Gulf of Venice and Gulf of Treiste as well as a part along the Italian coast, approximately to the Monte Gargano peninsula. Salinity is reduced in this zone owing to the freshwater land runoffs (the Po River and other rivers). Owing to the fresh water land runoffs and good vertical mixing due to small depths, nutrient quantities are relatively high and therefore this is the zone of high primary production. The third zone, zone C, includes channel area of the eastern Adriatic coast. It covers smaller area than zones A and B with the production lower than in the B zone but higher than in the A zone. The fourth, smallest zone (D) includes closed bays along the eastern Adriatic and lagoons along the western Adriatic coast. This zone is characterized by high production.

A comparison of the positions of sardine spawning centres and productive zones showed spawning centres to be located for the most part in the zone A where, due to low nutrient contents, production is lowest.

Why are these spawning centres located just in these oligotrophic areas? Temperature distribution during winter seems to be the main reason. After long-term investigations, sardine spawn at temperature range from 11 to 22°C with maxima between 11 and 12.9°C (Karlovac, 1967). Since temperature drops below 10°C in zone B in winter (Buljan and Zore-Armanda, 1976) sardine cannot spawn in this productive zone for the major part of their spawning season. Similar pattern of temperature distribution was recorded during our cruise as well (profiles I and II on Fig. 3).

However, the area of zone A is not ecologically homogeneous, either. Different water masses mix there, due to the presence of different water masses on the one hand and surface current regime on the other.

After Zore-Armanda (1963, 1968), four water types may be distinguished in the Adriatic: S water type, cold and less saline ($T = 11°C$, $S = 38.5‰$) which is formed in the shallow northern Adriatic; M water type ($T = 12°C$ and $S = 38.2‰$) formed in the Jabuka Pit in winters when Adriatic salinity is lower; J water type ($T = 13°$ and $S = 38.6‰$) formed in the area of South Adriatic Pit in winters of lower salnity; A water type ($T = 14°C$ and $S = 38.7‰$), the water of intermediate layer coming from the eastern Mediterranean by advection. On the other hand, gradient current of the surface layer entres the Adriatic through the Otranto Strait, flows along the eastern Adriatic coast, and turns in the northern Adriatic to the western coast along which flows to the Otranto Strait. The inflowing surface current carries A water type in winter, and the outgoing one the water from the northern Adriatic, colder and less saline and therefore lighter, towards the Otranto Strait. Simultaneously S type water flows in the bottom layer towards the middle Adriatic and J water type from the southern Adriatic to the Mediterranean.

Water from the northern Adriatic is considerably richer in nutrients than the A type water originating from the Mediterranean. Flowing along the Italian coast it carries nutrients (Degobbis, 1974).

Flows of incoming and outgoing surface current turn offshore in defined areas due to shore and bottom configurations, forming two gyres where A water type and water from the northern Adriatic are mixed in the middle Adriatic. One gyre is formed in the wider area of Palagruža Sill (Zore-Armanda, 1963, 1968; Buljan and Zore-Armanda, 1976) and the other between the island Dugi otok and Ancona (Artegiani and Azzolini, 1986). Bottom topography, and particularly the sills, seem to affect the formation of gyre system in the Adriatic. It was, namely, shown that Palagruža Sill affects a deflection of the Adriatic incoming current from longitudinal to closed contour pattern (Zore-Armanda and Bone, 1983). Since the northeastern edge of the Jabuka Pit, which extends transversally over the middle Adriatic, is forming a topographic barrier, the cause of formation of a gyre near Dugi otok is likely the same. Apart from topography, some other factors also affect formation of circular motion in the Adriatic. Thus two gyres have recently been discovered in the shallow northern Adriatic in winter-spring, probably generated by NE wind bura

(Zore-Armanda *et al.*, 1983, Zore-Armanda and Gačić, 1986). These gyres do not affect formation of sardine spawning centres since they do not occur in the areas where these fish spawn. However, they might have some influence on the transport of sardine postlarvae.

Accordingly, it is highly likely that the occurrence of gyres in winter-spring (when sardine spawn), where cold and nutrient-rich water from the northern Adriatic is mixed with warmer, but oligotrophic water of the Mediterranean origin, possibly determine the areas where permanent favorable conditions for reproduction of this fish are maintained. Škrivanić and Zavodnik (1973) came to a similar conclusion, establishing that sardine most intensively spawned in the areas of mixing of water masses from the shallow northern Adriatic, which they named the »Alpine« water type, with masses oiginating from the Mediterranean. After these authors, conditions were favourable for sardine spawning. They called these mixing zones the equilibrium areas where temperature ranged from 10—15°C and salinity from 37.5—38.5‰, that is approximatively within the ranges of most intensive sardine spawning after Karlovac (1967).

In general, it seems that the statement of Škrivanić and Zavodnik that the areas of mixing of two water types provide relatively stable ecological conditions for sardine reproducition in the Adriatic, is true. But as it was shown before, the area in which spawning centres are found is very large in view of the Adriatic dimensions. This area is much larger than that suggested by Škrivanić and Zavodnik. Therefore, as suggested by the results of this study, sardine seek favourable, most likely trophic conditions, for spawning. Horizontal mixing seems not to be the only factor providing these favourable conditions. After our findings, vertical rise of water is obviously the other cause of favourable conditions.

As shown by our results, the largest number of eggs and their most intensive production were recorded within 12.10—13.90°C temperature limits and 38.57—38.71‰ salinity limits (Fig. 7), which agrees well with the data of Karlovac (1967). However, very small quantities of eggs were found within the same temperature and salinity limits while the most intensive production was recorded at the boundaries of upwelling zones. This is indicative of the fact that temperature and salinity are, within their broader optimum limits, a factors of secondary importance, trophic factor being probably of primary importance for the formation of spawning centres.

Biological significance of upwelling has been well known for a long time. Upwelling occurs along the coastal boundaries where resultant current directions, wind effects and bottom configuration force deep vater to rise to the surface. The activity of upwelling is evidenced by higher rates of primary production and through trophic chains by reproduction and survival of a number of fish species. The upwelling effects are manifested in two basic ways. First, deep water carries increased nutrient quantities into the better illuminated surface layer. Second, vertical flow rises immobile phytoplankton cells to the surface where conditions for photosynthesis are more favourable (Bakun and Parish, 1980). It was rather early established that rich biological resources off the shores of Chile and Peru (Gunther, 1936), western coasts of Africa (Steeman Nielsen, 1954) and California Sverdrup and Allen, 1939) could be attributed to upwelling. These areas are also the best productive fishing areas of the world (Bakun, 1978; Smith, 1978; Wooster *et al.*, 1976).

The effects of upwelling recorded during this study are also obvious, particularly to primary production since both phytoplankton cell numbers and chlorophyll *a* quantities showed increase in the upwelling zones in spite of their continuous increase to the north. The same is with all zooplankton groups, irrespective of the fact whether their quantities increased or decreased to the north (Fig. 8). It is also obvisous that sardine spawned most intensively in those zones.

Accordingly, sardine, which feed intensively even during spawning (Vučetić, 1964), found favorable conditions of high primary production, within temperature and salinity ranges that suit them best, in the frontal zones at the boundaries of upwelling zones. Since sardine larvae and youngest postlarvae from P_1 group were also found in the vicinity of upwelling zones (Fig. 8), it is apparent that they found there increased food quantities. Namely, the oldest postlarvae not yet having absorbed the yolk sac, but having functional mouth to begin to feed actively, feed, in the first place, on small planktonic organisms, such as nauplii, copepodites and Tintinnina as well as the youngest postlarvae (Karlovac, 1967). As shown earlier, the numbers of these organisms were increased at the boundaries of upwelling zones if compared to the adjacent areas of the southern and northern spawning centres (Fig. 8).

The situation with older postlarave is quite different. As already shown they are drifted out of spawning areas to various directions, to the open sea, to the channel and considerably colder areas of the shallow northern Adriatic (Fig. 9). This transport was to be expected since the upwelling zones are in fact the areas of divergence. These transport directions seem to be permanent in the Adriatic since Karlovac (1967) recorded similar divergence of postlarval onshore and offshore drift out of spawning grounds. How does this transport affect the survival of larvae is not yet known since there have been no data so far on the relationship between quantities and/or mortality rate coefficients of postlarvae and quantities of organisms they feed on. Therefore, no comparison can be done. However, when they are transported off the upwelling zones, postlarvae are presumably in water masses enriched with nutrients due to vertical mixing, which should provide favourable conditions for growth and survival. In addition, with respect to the fact that quantities of nutrients are higher in the northern Adriatic and in the channel areas of the eastern Adriatic where postlarvae are transported, favourable effects on their survival may be assumed.

Of course, trophic basis is not the only crucial factor for a successful surival of postlarvae. Even though the quantity of zooplankton on which postlarvae feed shows a general increase to the northern Adriatic (Figs. 6 and 8), postlarval mortality rate coefficients in the northern Adriatic are sligthy higher than those in the southern Adriatic. Even thought this difference is not statistically significant, it may be assumed as an indicator of the possible influence of predators on this increase of the mortality rate in the northern Adriatic. It is naturally very likely that the number of predators is higher in the northern Adriatic owing to higher primary production.

Analysing mortality of anchovy larvae and postalrave Piccinetti et al. (1982) came to the similar conclusion.

These data show that sardine took the boundaries of upwelling zones for reproduction in March and April 1982. It is, as well, obvious that the forming of upwelling offers favourable spawning conditions to these fish. The question to be answered is, whether the upwelling is a permanent event in the spawning season of sardine in the Adriatic? This is a question of importance, since if upwelling is formed regularly and at defined time, it might be expected that sardine will adapt to these coditions and migrate towards the areas of upwelling.

The upwelling has been recorded from the Adriatic on several occasions up to now. Pollak (1951), from the data of NAJADE Expedition, found homogeneous distribution of high potential density (29.18—29.22 δt) from bottom to surface at station A28, above the South Adriatic Pit in March 1911. This may be indicative of the rise of deep water. After this author no other station of either NAJADE or CICLOPE expedition showed such a homogeneity of the water column. After Županović (1965), the upwelling was recorded from the open waters of the Jabuka Pit, in the area between our profiles VI and VII, in May 1963, June 1964, 1965 and 1966, in September and October 1963, 1965 and 1966. Accordingly, the upwelling occurred in periods when sardine do not spawn or at the very begining of their spawning (end of September, October). The upwelling events were recorded in the close vicinity of the outer shores of Šolta and Vis islands (middle Adriatic) and Mljet island (southern Adriatic) between July and September of the 1932—1934 and 1951—1963 periods (Buljan, 1964, 1965; Buljan and Špan, 1976). Comparing the upwelling data in the vicinity of Mljet island, given by Buljan and Špan, to the data on wind energies and directions in the same period, Gačić (1983) found a very good correlation between the upwelling strength and energy of wind of direction vertical to the coast. Finally, the data of r/v ANDRIJA MOHOROVIČIĆ cruises in 1974—1976 show the upwelling at profiles IV and V which overlie the Jabuka Pit in the area between our profiles VI and VII, in April-May 1975. This upwelling zone is, similarly to the zones we established, in the belt 20—30 nautical miles off the eastern Adriatic coast. An upwelling of considerably lower intensity was observed in the same area in February 1976.

According to the data brought out, the upwelling events have been recorded on only several occasions in periods of the second half of sardine spawning season. The upwelling events have been recorded from the open sea, from relatively limited areas of the Jabuka Pit, and possibly South Adriatic Pit during the colder part of the year. These data cannot suggest upweling to be a regular phenomenon providing conditions to which sardine have been adapted. It should, however, be kept in mind that the late winter and early spring are periods with very unfavourable weather conditinos in the Adriatic. Therefore a small number of field trips have been carried out in the open sea or over a wider areas during that time. Thus the probability to discover the upwelling events has been rather low. Furthermore, since upwelling has not been separately studied in the Adriatic up to now, it is not known whether the resolution of fitting vertical isothermes and isohalines was small enough in the available data to discover this phenomenon. Therefore the question whether this is a regular phenomenon and the extent of the zones it includes, remains open for the time being.

The upwelling zones recorded during our cruise are much larger than expected after earlier findings. Namely, the upwelling zone in the northern spawning centre was 10—20 Nm vide and 60 Nm long, while the zone of the southern centre was slightly narrower (about 10 Nm) but exceeding 50 Nm in length. Both zones together cover the area of about 2 200 square nautical miles, which make up about 10% of the area in which sardine stock has been (Fig. 1).

In addition, the upwelling event in March-April 1982 seems to be of importance not only because of the area it included but also for its duration. Namely, measurements at profiles at which upwelling was formed were performed at 17 day interval (Table 8).

Table 8. Time of measurements at individual profiles during our cruise (+ = upwelling formed, — = no upwelling)

Profile	I	II	III	IV	V	VI	VII	VIII	IX
Date	Mar. 17	Mar. 15	Mar. 15	Mar. 26	Mar. 26	Mar. 27	Mar. 9.	Mar. 10	Apr. 8
Upwelling	—	—	—	+	+	—	+	+	—

Since the upwellings were well formed, and time interval between measurements was 17 days, this phenomenon presumably lasted for about a mont if the time required for formation and disappearance of upwelling is added.

If occurrences of upwelling of such a duration and extent were more frequent, they would probably affect the long-term fluctuations of sardine in the Adriatic. After the available data which are very scarce this question remains open at least for the time being. Županović (1985) suggested that intensified dynamics of bottom water, particularly that from the Jabuka Pit which affects the enhancement of effects of advection of cold water from the northern Adriatic in years of intensified ingressions of the eastern Mediterranean waters into the Adriatic, may be one of the causes of sardine fluctuations in the Adriatic. To what extent would the upwelling, add to the enrichment of surface waters by nutrients in years of intensified dynamics of Adriatic waters could be answered by future researches. At any rate results of our study point to the fact that insufficently studied upwelling phenomenon in the Adriatic should be given more attention in future.

CONCLUSIONS

Two upwelling zones in the open waters of the eastern half of the Adriatic were recorded in the March-April 1982. These upwelling zones are situated along shore 10 to 20 Nm off the eastern Adriatic islands. Increased concentrations of phytoplankton, microzooplankton and meso- and macrozooplankton were found at the boundaries of these upwelling zones. The production of sardine eggs was found to be most intensive there, and sardine larvae and younger postlarvae occurred there in highest numbers. This leads to the conclusion that sardine found favourable conditions for spawning and feeding of both larvae after formation of functional mouth and youngest postlarvae, at the boundaries of the upwelling zones.

With respect to the effect of the upwelling zones on the positions of sardine spawning centres during the time of our study, the upwelling phenomenon insufficiently known in the Adriatic, should be given more attention in future researches.

REFERENCES

Artegiani, A. and R. Azzolini, 1986. Italian advances in hydrological data base for the Adriatic sea. FAO Fish. Rep., 345: 41-52.

Bakun, A. 1978. Guinea Current upwelling. Nature, 271: 147—150.

Bakun, A. and R. Parish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. IOC Workshop Rep., 28: 67—104.

Blaxter, J.H.S. 1969. Experimental rearing of pilchard larvae, *Sardina pilchardus*. J. Mar. Biol. Assoc. U. K., 46:219—234.

Buljan, M. 1964. Ocjena produktivnosti Jadrana dobivena na temelju njegovih hidrografskih svojstava. Acta Adriat., 11: 35—45.

Buljan, M. 1965. Anomalies of temperature and chlorinity of sea water on the station Stončica, Middle Adriatic. Pomorski Zbornik, 3: 949—994.

Buljan, M. i J. Špan, 1976. Hidrografska svojstva Mljetskog jezera i susjednog mora. Aca Adriat., 6 (12), 224. pp.

Buljan, M. and M. Zore-Armanda. 1976. Oceanographical properties of the Adriatic sea. Oceanogr. Mar. Biol. Ann. Rev., 14: 11—98.

Degobbis, D. 1974. Ciklus i bilans dušika u sjevernom Jadranu. MSc. Thesis, Zagreb: 99. pp.

Gačić, M. 1983. Dugoperiodične oscilacije u strujnom polju u Jadranu. Ph. D. Thesis, Beograd, 102. pp.

Gamulin, T. 1948. Quelques observations sur la ponte de la Sardine (*Clupea pilchardus* Walb.) dans la zone insulaire de la Dalmatie moyenne. Acta Adriat., 3 (4), 35 pp.

Gamulin, T. 1954. La ponte et les aires de ponte de la Sardine (*Sardina pilchardus* Valb.) dans l'Adriatique de 1947 à 1950. Reports Exp. »Hvar«, 4 (4C), 66 pp.

Gamulin, T. et Hure. 1955. Contribution à la connaissance de l'ecologie de la sardine (*Sardina pilchardus* Walb.) dans l'Adriatique. Acta Adriat., 7 (8), 23 pp.

Gamulin, I. i J. Hure. 1983. Mriješćenje i mrestilišta pelagičnih riba u Jadranskom moru. Acta Adriat., 24: 97—131.

Gamulin, T. et J. Karlovac. 1956. Etude intensive d'une aire de la ponte de la sardine (*Sardina pilchardus* Walb.) en Adriatique moyenne en 1950——1951. Acta Adriat., 8 (3): 47 pp.

Gamulin, T. and D. Zavodnik, 1961. Spawning of the sardine (*Sardina pilchardus* Walb.) off the west coast of Istria. (northern Adriatic). Proc. Tech. Pap. GFCM, 6: 121—123.

Gunther, E. R. 1936. A report on oceanographical investigations in the Peru coastal current. Discovery Repts., 13: 109—176.

Hure, J. 1961. Contribution à la connaissance de la ponte de la sardine et du maquereau au large de l'Adriatique moyenne. Proc. GFCM, 6: 107—110.

Hure, J., A. Ianora and B. Scotto di Carlo. 1980. Spatial and temporal distribution of copepod communities in the Adriatic Sea. Journ. Plankton Res., 2: 295—316.

Karlovac, J. 1958. Investigations on the larvae and postlarvae of the sardine ((*Sardina pilchardus* Walb.) in the open waters of the Adriatic Sea. Izv. Rep. Rib. — biol. Eksp. »Hvar« 1948—49, 4 (4D), 24 pp.

Karlovac, J. 1964. Mriješćenje srdele (*Sardina pilchardus* Walb.) u srednjem Jadranu u sezoni 1956—1957. Acrta Adriat. 10 (8), 40 pp.

Karlovac, J. 1967. Etude de l'ecologie de la sardine (*Sardina pilchardus* Walb.) dans la phase planctonique de sa vie en Adriatique moyenne. Acta Adriat., 13 (2), 109 pp.

Karlovac, J. 1969. La ponte de la sardine (*Sardina pilchardus* Walb.) en Adriatique moyenne, à l'epoque de son maximum, au cours de quatre saisons de reserches. Thalassia Jugoslavica, 5: 149—157.

Larraneta, M. G. 1960. Synopsis of biological data on *Sardina pilchardus* of the Mediterranean and adjacent seas. FAO Fish. Biol. Synopsis, 9, 37 pp.

Piccinetti C., S. Regner et M. Specchi. 1980. Etat des stocks d'anchois et de sardine en Adriatique. FAO Fish. Rep., 239: 43—52.

Piccinetti, C., S. Regner et M. Specchi. 1981. Distribution des oeufs de sardine en Adriatique. Rapp. Comm. int. Mer Medit., 27 (5): 167—170.

Piccinetti, C., S. Regner and M. Specchi. 1982. Preliminary data on larval and postlarval mortality of anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), in the northern and central Adriatic. Acta Adriat., 23: 449—456.

Pollak, M. J. 1951. The sources of the deep water of the eastern Mediterranean. J. Mar. Res., 19: 128—152.

Rakaj, N. 1962. Reproduction des sardines dans les eaux du littoral de l'Albanie. Bull. trav. scient. économ. pêche, 1 (2):

Regner, D. 1983. The relative importance of copepods in the net zooplankton of the Adriatic sea. Rapp. Comm. int. Mer Médit., 28 (9), 155—157.

Regner, D., M. Specchi and S. Fonda-Umani. 1985. The composition of net zooplankton of the Adriatic sea. Rapp. Comm. int. Mer Médit., 29 (9): 301—302.

Regner, S. 1980. On semigraphic estimation of parameters of Gompertz function and its application on fish growth. Acta Adriat., 21: 227—236.

Regner, S., C. Piccinetti, M. Specchi and G. Sinovčić. 1981. Preliminary statistical analysis of sardine stock estimation from data obtained by egg surveys. FAO Fish. Rep., 253: 143—154.

Regner, S., C. Piccinetti and M. Specchi. 1983. Estimate of spawning biomass of sardine in the northern and central Adriatic from 1979 to 1982 by means of egg surveys. FAO Fish. Rep., 290: 223—232.

Smith, P. E. 1978. Biological effects of ocean variability; Time and space scales of biological response. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 173: 117—127.

Steeman Nielsen, E. 1954. On organic production in the oceans. J. Cons. int. Explor. Mer, 19: 309—328.

Steuer, A. 1910. Adriatische Planktoncopepoden. Sitzb. K. Akad. Wien, 119 (1): 1005—1035.

Sverdrup, H. V. and W. E. Allen. 1939. Distribution of diatoms in relation to the character of water masses and currents off Southern California in 1938. J. Mar. Res., 2: 131—144.

Škrivanić, A. and D. Zavodnik, 1973. Migrations of the sardine (*Sardina pilchardus*) in relation to hydrographical conditions of the Adriatic sea. Netherlands Journ. Sea Res., 7:7—18.

Štirn, J. 1969. Pelagial severnega Jadrana. Dissertationes, 12, 92. pp.

Štirn, J. and L. Kubik. 1974. Contributions to the knowledge of migrations and the volume of the pilchard and anchovy populations in the northern Adriatic. Acta Adriat., 16 (24): 401—422.

Tanaka, S. 1973. Stock assessment by means of ichthyoplankton surveys. In: Hempel, G. (ed.): Fish egg and larval surveys (Contribution to the manual). FAO Fish. Techn. Paper, 122, 82. pp.

Vučetić, T. 1964. O odnosu srdele (*Sardina pilchardus* Walb.) prema bitoskim faktorima sredine — zooplanktonu. Acta Adriat., 11 (37): 269—276.

Wooster, W. S., A. Bakun and D. R. Mc Lain. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. J. Mar. Res., 34: 131—141.

Zavodnik, D. 1970. Comparative data on the spawing of sardine (*Sardina pilchardus* Walb.) sprat (*Sprattus sprattus* L.) and anchovy (*Engraulis encraicolus* L.) in the north Adriatic. Ichthyologia, 2: 171—178.

Zore-Armanda, M. 1963. Les masses d'eau de la mer Adriatique. Acta Adriat., 10 (3), 92 pp.

Zore-Armanda, M. 1968. The system of currents in the Adriatic sea. Stud. Rev. gen. Fish. Coun. Medit., 34, 48 pp.

Zore-Armanda, M. and M. Bone, 1983. Topographic characteristics and current system in the Adriatic. Rapp. Comm. int. Mer Medit., 28 (2): 65—66.

Zore-Armanda, M. *et al.*, 1983. MEDALPEX in the north Adriatic. Bilj. Inst. Oceanogr. Ribar., Split, 50, 8 pp.

Zore-Armanda, M. and M. Gačić. 1986. Effects of bura on the circulation in the north Adriatic. Annales Geophysicae (in press).

Županović, Š. 1964. Ispitivanje koncentracija srdele (*Sardina pilchardus* Walb.) upotrebom termometrijske metode. Pomorski zbornik, 2: 923—983.

Županović, Š. 1985. Biological effects of hydroclimatic changes. Acta Adriat., 26: 165—189.

Accepted: September 16, 1987

MRIJEŠĆENJE SRDELE, *SARDINA PILCHARDUS* (WALBAUM, 1792), U UVJETIMA POJAVE »UPWELLINGA« U JADRANU

Slobodan Regner, Dubravka Regner, Ivana Marasović i Frano Kršinić*

Institut za oceanografiju i ribarstvo, Split, Jugoslavija
** Institut za oceanografiju i ribarstvo, Split, Biološki zavod, Dubrovnik, Jugoslavija*

KRATKI SADRŽAJ

Do sada je objavljen priličan broj radova koji su se odnosili na problem položaja mriještilišta srdele u Jadranu. Analiza svih dosadašnjih rezultata pokazuje da se srdela, u periodu maksimuma sezone mriješćenja koji traje od decembra do marta, mrijesti na dva razdvojena područja koja, za uvjete Jadrana, pokrivaju relativno veliku površinu. Prvo područje zahvaća dio sjevernog i srednjeg Jadrana i može se omeđiti spojnicama Pesaro — otok Susak i Pescara — otok Žirje, dok je drugo približno omeđeno spojnicama rt Penna — rt Maslinica na otoku Šolti i Monte Gargano — rt Gruj na otoku Mljetu, tako

da ono pokriva južni dio srednjeg i dio južnog Jadrana. Centri mriješćenja se na tim područjima mogu formirati na bilo kojemu njihovom dijelu.

O uvjetima koji utječu na položaje centara mriješćenja zna se veoma malo, budući da je najveći broj do sada objavljenih radova uglavnom samo opisivao prostornu raspodjelu jaja sredle. Isto tako, ukoliko su centri mriješćenja uspoređivani sa hidrografskim parametrima, nisu sa biološkim i obratno.

U ovome se radu stoga pokušalo prići problemu formiranja centara mriješćenja tako da se obuhvati što veći broj parametara za koje se smatra da bi mogli imati utjecaja na mriješćenje srdele. Nedostatak ovoga rada je, međutim, to što se odnosi na analizu podataka koji su prikupljeni tokom samo jednog krstarenja, te se od njega ne može očekivati da bi mogao dati odgovore na opće zakonitosti koji utječu na formiranje centara mriješćenja. Sa te strane, ovaj rad predstavlja uvod u daljnja, još detaljnija, istraživanja koja bi morala obuhvatiti čitav period sezone mriješćenja srdele u Jadranu.

Materijal za ovaj rad je sakupljan u periodu od 09. 03. do 08. 04. 1982., u sklopu bilateralne Jugoslavensko-Talijanske suradnje na procjeni biomase srdele i brgljuna u Jadranu ihtioplanktonskim metodama. Radilo se na ukupno 75 postaja, raspoređenih na deset profila, od Tršćanskog zaljeva do spojnice Monte Gargano—Boka Kotarska. Na jugoslavenskoj strani se radilo na 38 postaja na devet, a na talijanskoj na 37 postaja na deset profila (Sl. 1). Na jugoslavenskim postajama uzimani su podaci o temperaturi i salinitetu na svakih pet metara od površine do maksimalne dubine od 60 m, zatim o količini stanica fitoplanktona i klorofila *a*, jajima, larvama i postlarvama srdele, te o mikro i mezozooplanktonu (Tab. 1). Sa postaja na kojima je radio talijanski brod iskorišteni su podaci o količini jaja srdele.

Analiza raspodjele temperature, saliniteta i gustoće vode je pokazala da su, u vrijeme kada je krstarenje bilo izvršeno, bile formirane dvije zone upwellinga, koje su se pružale paralelno sa jugoslavenskom obalom na uadljenosti od 10 do 20 Nm od rubova vanjskih otoka. Također se može zapaziti da je plitki sjeverni Jadran, u kojemu je temperatura bila ispod 10°C, bio odvojen od ostalog dijela frontalnom zonom koja se nalazila u visini Kvarnera (Sl. 3—5).

Istraživanje raspodjele bioloških parametara pokazala su slijedeće karakteristike. Količine stanica fitoplanktona, kao i količina klorofila *a*, pokazivali su porast od južnog ka sjevernom Jadranu, tako da su količine fitoplanktona bile znatno više u plitkom sjevernom Jadranu, iza frontalne zone. Taj porast nije, međutim, bio ravnomjeran, jer su se uz rubove zona upwellinga nalazile relativno povećane količine fitoplanktona (Sl. 8). Zooplankton je, bez obzira da li je količina pojedinih njegovih grupa rasla ili opadala od južnog ka sjevernom Jadranu, pokazivao slične karakteristike u raspodjeli. Tako su neke od komponenti mikrozooplanktona, Heliozoa, Radiolaria i Tintinnina, količinski opadale od južnog ka sjevernom Jadranu (Tab. 4 i 5, Sl. 8), ali im je brojnost bila povećana uzduž zona upwellinga. Četvrta ispitivana komponenta mikrozooplanktiona, nauplii i kopepoditi, je, kao i ukupni mezo i makrozooplankton, pokazivala porast od južnog ka sjevernom Jadranu, ali opet sa relativnim povećanjem brojnosti uz zone upwellinga (Sl. 6 i 8, Tab. 6).

Slične je karakteristike pokazivala i raspodjela brojnosti jaja i larvi srdele. Opaža se da su centri mriješćenja bili formirani uzduž obaju zona upwellinga (Sl. 2), te da su i larve srdele tu bile najbrojnije (Sl. 8). Formiranje centara mriješćenja upravo na tim područjima može se objasniti zajedničkim djelovanjem abiotskih i biotskih faktora. Naime, ustanovljeno je da se srdela intenzivnije mrijestila u rasponu temperature od 11.6 do 13.9°C i saliniteta od 37.59 do 38.78‰, sa maksimumima u rasponu temperature od 12.1 do 13.9°C i saliniteta od 38.57 do 38.71‰ (Sl. 7). Ovi se podaci vrlo dobro poklapaju sa podacima ranijih autora. Pri tome se čini da je granična temperatura za iole intenzivnije mriješćenje srdele 10°C, tako da se ona u maksimumu sezone mriješćenja ne može mrijestiti u najproduktivnijim zonama Jadrana koje se nalaze u plitkom sjevernom Jadranu i uzduž talijanske obale, otprilike do poluotoka Gargano. Stoga je srdela prinuđena mrijestiti se u relativno oligotrofnim vodama srednjeg i južnog Jadrana, gdje su vrijednosti abiotskih faktora, u prvom redu temperature, za nju povoljne. Rezultati ovoga istraživanja pokazuju da ona unutar ovih područja traži zone sa relativno povišenom organskom produkcijom, koje joj mogu osigurati uvjete za ishranu, rast i preživljavanje postlarwi. U periodu kada su ova istraživanja vršena to su, očito, bile zone upwellinga, za koje je i inače poznato da povoljno utječu na organsku produkciju. U ovome je slučaju nađena relativno visoka i statistički signifikantna korelacija između proizvodnje jaja srdele i količine fitoplanktona (Tab. 7), dok je korelacija sa zooplanktonom bila nesignifikantna, iako se vidi da su i njegove količine bile povišene uz rubove zona upwellinga (Sl. 8). Ovo bi ukazivalo da su za formiranje centara mriješćenja, unutar širih granica optimuma za abiotske faktore, od presudnog značaja trofički uvjeti sredine.

Na osnovi ovih istraživanja se može zaključiti da je, u vrijeme kada su ona izvršena, pojava upwellinga imala odlučujuću ulogu za formiranje centara mriješćenja srdele. Budući da je pojava upwellinga u Jadranu još nedovoljno istražena, može se zaukljućiti da bi joj u budućim istraživanjima trebalo posvetiti više pažnje. Naime, ako se on u određenim periodima sezone mriješćenja srdele javlja učestalije, eventualne promjene njegovog intenziteta ili pak potpuna otsutnost bi mogle imati utjecaja na fluktuacije populacije ove ribe u Jadranu.