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A STATISTICAL CONTRIBUTION TO THE STUDY IN ECOLOGY OF SARDINE (*SARDINA PILCHARDUS* WALB.) IN THE CENTRAL ADRIATIC

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A STATISTICAL CONTRIBUTION TO THE STUDY IN ECOLOGY OF SARDINE (*SARDINA PILCHARDUS* WALB.) IN THE CENTRAL ADRIATIC

By

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INTRODUCTION

In the following pages an attempt will be made to examine, by means of statistical analysis, whether there is any coincidence between the results of Sardine migration obtained by tagging and the size of catch. The analysis is limited to the central Dalmatian region only where the migrations have been established owing to intensive tagging.

The question, from what place do Sardine approach the mainland, i.e. where do they withdraw during the spawning time, is another ecologic question which has been answered in several ways. According to Krafft (1887), Krisch (1900), Lorini (1903), and Gast (1922, 1925), Sardine remain in deeper water during the winter.

Basing upon statistical data on catches, Kotthaus (1938) supposed that Sardine retreat to the two large Adriatic pits (Jabuka and Bari Pits) in winter and that from there they migrate in the direction of the mainland in spring. By analyzing the amount of Sardine eggs caught in various places, Gamulin (1940, 1948, 1949, 1954 a, and 1954 b) established that the spawning of Sardine in the central Dalmatian region occurred neither in larger depths nor at a considerable distance from the mainland.

Comparisons will be made in this paper between the data of the 1949 Sardine catches taken in the regions of the islands of Biševo, Svetac, Vis, and Hvar (along the south coast) and the results arrived at by means of tagging. The same data, i.e. on catches and tagging, will be considered to estimate the size of the population and to calculate the extent of its exploitation. The catches which are the subject of this analysis were taken in places shown in Fig. 1. Roman numerals indicate the size of each of the fishing areas.

Beside the migration of Sardine during the summer fishing season, we shall try, in this paper, to touch briefly the question of their

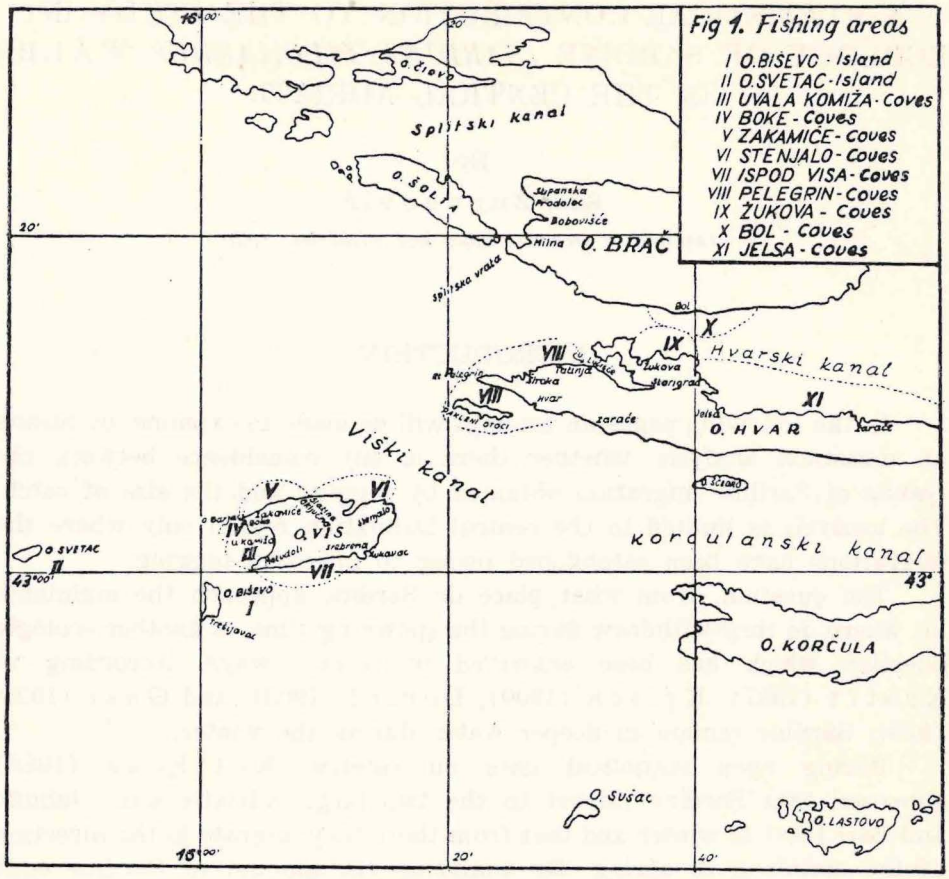

Fig. 1. Fishing areas

hibernation. In what direction, to what place, and how far, do Sardine migrate — these are still unanswered questions, although the investigations into their spawning grounds helped us to draw our first picture giving general information on the Sardine spawning and spawning grounds in the Adriatic (G a m u l i n, 1954 b).

THE MATERIAL

The 1949 material was collected in the field by the author himself. The catches taken in the regions of Biševo and Vis islands during the first two darks of the moon (April, May), are not complete with regard to particular fishing localities and dates, since they refer to results

obtained by means of only 5 out of 13 purse seines applied in those regions (Fig. 3).

The catches referring to Pelegrin region (i.e. the northwest coast of Hvar Island including Pakleni Islets) are represented by data obtained from fresh fish sales. These data, as well as those referring to Žukova (the north coast of Hvar Island) and Bol (the south coast of Brač Island) were entered according to dates and fishing regions only, unlike the data on the catches taken in the vicinity of Biševo, Svetac and Vis islands and along the northeast part of Hvar Island, which were entered according to particular fishing localities.

STATISTICAL ANALYSIS OF 1949 SARDINE CATCH

TABLE I

Showing Monthly Catches For Each Fishing Region (in Kg)

Sardine Fishing Region	Month							Total
	IV	V	VI	VII	VIII	IX	X	
Komiža	166820	692280	271500	209360	25510	31420	8240	1405130
Hvar	72450	143350	44200	93480	21680	18140	430	393730
Starigrad	42500	73500	16470	10800	1400	19400	—	164070
Bol	1410	39070	26560	15180	1380	4700	180	88480
Jelsa	44500	135010	19810	39790	6910	12700	9780	268500
Total	237680	1083210	378540	368610	56880	86360	18630	2339910

It is evident from the above table that Sardine were more intensively caught at the beginning of the fishing season, i.e. during the first darks of the moon than in the later stages when a gradual decline is noticeable. This more od less general phenomenon in the central Dalmatian region, consisting in the occurrence of smaller quantities of Sardine in summer, after May/June maximum, and in regular appearance of larger quantities in September, was already noticed by Kotthaus (1938) also.

The 1949 Sardine catch in the central Dalmatian region was really a remarkable one. Similar catches, although of somewhat smaller size, owing to the use of fishing gear of a more primitive kind, were recorded in Dalmatia in 1835/1837, 1875, 1876, and 1909.[1]) The causes of these periodical abundance of Sardine catches are unknown.

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[1]) ...»Doch scheinen so zahlreiche Einwanderungen in das Adriatische Meer wie in den Jahren 1875/76 und 1876/77 nur selten vorzukommen; denn nach den zollämtlichen Ausfuhrlisten Dalmatien's zu schliessen, nach welchen im Durchschnitte der Jahre 1835—1837 jährliche 27531 metrische Centner zubereiteter Fische, worunter 80 bis 90 Percente Sardellen, zur Ausfuhr gelangten und diese Ausfuhr bis zum Solarjahre 1873 beinahe successive auf 8800 metrische Centner sank, schwang sich die Fischausfuhr Dalmatien's erst wieder in den Solarjahren 1875 und 1876 (25339 und beziehungsweise 26475 metrische Centner), also erst wieder nach 38 Jahren zur Höhe der Ausfuhr der Jahre 1835 bis 1837 auf« (Krafft, 1878).

Buljan (1953) attempted to find a causal connection between the abundant catch in 1949 and the ingressions into the Adriatic of Mediterranean waters, enriched with salts and nutrient matter, contributing to the productivity of organic matter in sea water.

We find, however, a different situation when the ingressive water retires and a prolonged phase of declining salinity sets in. We have then a series of years yielding considerably poorer catches, notwithstanding the fact that the fishing gear remained almost the same.

Similar coincidences of catches with the phenomena of ingressions/regressions happend before also. A support of this statement is provided by the comparison of ingressions which occurred in 1875/76 and 1948/49, i.e. during a period of 73 years, with the corresponding Sardine catches in the region of Vis and Biševo islands over a succession of years. We have the following ratio:

VIS ISLAND

Year	Catch		Year	Catch	
	(q)	(%)		(q)	(%)
1876	*11500*	*33,14*	*1949*	*18712*	*38,45*
1877	*9673*	*27,87*	*1950*	*11997*	*24,65*
1878	5937	17,14	1951	5330	10,95
1879	2680	7,72	1952	5562	11,42
1880	2460	7,09	1953	5077	10,45
1881	2446	7,04	1954	1989	4,09

The inrush of the ingressive water in 1875/76 and 1948/49 coincides with maximum Sardine catches. The coeficient of correlation between the data of catches amounts to $r = 0{,}93 \pm 0{,}06$.[2]) This correlation coeficient is decidedly significant.

A positive correlation of such an extent, although obtained from a small number of variants, is another reason for the need of the carrying on of examinations of the said mutual connections, which are of utmost importance not only for the estimation of the production of a fishing region, but for the examination of the ecology of Sardine in the Adriatic as well.

[2]) This coeficient of correlation, as well as its mean error, have been calculated by means of the formula for a small number of variants.

RELATIVE FLUCTUATIONS OF ABUNDANCE OF THE 1949 SARDINE CATCHES

The 1949 Sardine fishing season had an early beginning. So the first catches of Trešijavac, in the south part of Biševo Island, occurred early in April. A fortnightly fluctuation of Sardine catches in various regions is graphically shown in Fig. 2. Relative rises and falls of catches evident from Fig. 2., are proportional for all fishing regions almost until the beginning of August, i.e. up to the end of IV dark of the moon. It is only

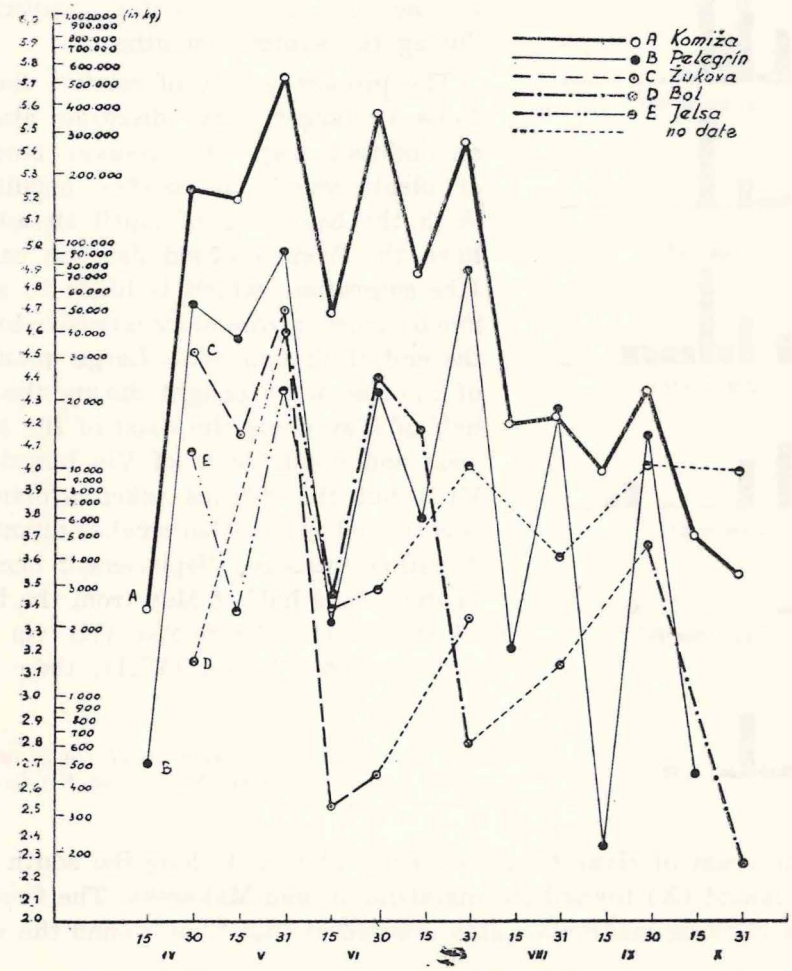
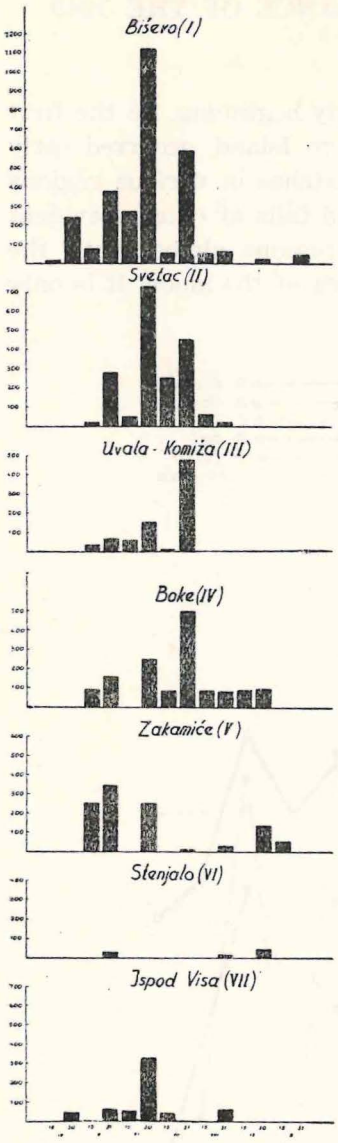


Fig. 2. — *Semi-logarithmic scale showing the 1949 Sardine catches taken in various fishing areas*



then that we find certain disturbances in the displacement of Sardine, manifesting themselves also in the considerable decrease of catches in August. We ignore the cause of these fluctuations. Do hydrologic factors, perhaps, intensify their influence upon the migration and behaviour of Sardine? This phenomenon of decreasing catches is considered by Kotthaus (1938) also a consequence of the rise of sea water temperature during the summer months.

The proportionality of relative fluctuations in larger areas discloses also, in an indirect way, the general tendency of displacements of Sardine population. With the beginning of April already we have the first recorded data on catches (the migration, which is likely to set in much earlier, grows more intensive toward the end of that month). Large quantities of Sardine were caught during the first half of May along the coast of the northwest and north parts of Vis Island (IV, V),[3]) but the catches taken around Biševo Island (I) yielded smaller quantities. A rather intensive displacement occurred in the second half of May from the island of Biševo (I) and Svetac (II) via Pelegrin — Hvar Island (VIII), then along

Fig. 3. — The 1949 Sardine catch (in q) taken in the regions of Biševo, Svetac, and Vis Islands

the north coast of Hvar Island (Žukova, IX), and along the south coast of Brač Island (X) toward the mainland around Makarska. The first and the most striking maximum catch occured at that time around the island

[3]) Roman numerals in brackets refer to fishing localities in Fig. I.

of Biševo and Vis (Komiža) and the maximum displacement of Sardine in the direction of the inner channels and mainland is evident from catches taken in the other fishing regions. A secondary maximum, about the end of June, was attained by the catches taken in the region of Vis Island (Komiža) and around Bol in Hvar Channel, while there was a decrease in the size of catches taken at Pelegrin and along the north and northeast coast of Hvar Island. A tertiary maximum appeared in Komiža Cove in they disappear from those localities. Catches of smaller size are taken and Jelsa. There is a gradual decrease in the size of catches at Biševo (I) during the following darks of the moon, while larger or smaller numbers of fish remain at Pelegrin (VIII) until the beginning of October, when they disappear from those localaties. Catches of smaller size are taken during the last darks of the moon along the southeast coast of Brač Island (X), along the northeast coast of Hvar Island (XI), along the north coast of Vis Island (V), in the vicinity of Slatina, and along the south coast of Biševo Island, not far from Trešijavac (I).

Figure 3, besides containing an analysis of the relative changes in the dynamics of Sardine population, i.e. a comparison of relative changes of single parts of a whole, expressed in graphical way by means of a semi-logarithmic curve, enables us to follow its course by means of absolute indices throughout the fishing season in the regions of the islands of Biševo, Svetac, and Vis. These absolute indices completely agree with the above relative changes of the c o n v e r g e n t direction of Sardine displacement from the high Adriatic toward the inner channels and the coast of the mainland.

CONGRUENCE BETWEEN THE DATA ON CATCHES AND TAGGING RESULTS

Before we attempt to make an analysis of the congruence between the data on catches and the tagging results, we are going to give here some interesting experiences of practical fishermen, all concerning the 1949 and the foregoing Sardine catches in various fishing regions, as well as their opinion on Sardine displacements.

The first 1949 Sardine appeared in the vicinity of Trešijavac (Biševo Island) and in Komiža Cove. Catches were taken in this place through all the fishing season. This locality was always the first to record the presence of Sardine in the course of the last four years (1946, 1947, 1948, 1949), but not so in the other years (Komiža).

In 1949, Sardine were caught in all localities of the Pelegrin region from Cape Pelegrin to Cape Tatinja, in April and throughout the summer. In June, July, and August Sardine were caught not only in the Pelegrin region, but also around Pakleni Islets and along the south coast of Hvar Island as far as Zaraće. Fish arrive every year from the west (from the high Adriatic) and are caught in large quantities in April and May. The individuals coming from the open sea are usually larger in size than those coming from the channels (Hvar).

Large Sardine shoals were noticed to appear from Pelegrin eastward beginning with April and onwards. While there were no Sardine in the Starigrad region in June and July 1949, they were caught in the Jelsa region. These belonged to the shoals migrating from Pelegrin. According to the fishermen from Rudina (north coast of Hvar Island), the first Sardine always appear in March and April coming from Pelegrin toward their fishing grounds (Žukova, IX). A reverse Sardine displacement, i.e. from the littoral around Makarska in the direction of Hvar Channel, is of infrequent occurrence, noticed mostly in August and September (Rudine, Žukova).

Since no Sardine tagging was carried out before the beginning of May, we were unable to follow the Sardine displacement which occurred in April i.e. during the first dark of the moon. These missing data on movements at the beginning of the fishing season can be completed to some degree by the available data on catches for 7 days' periods. This 7 days' unit was obtained by adding all the days that elapsed between the release of tagged specimens and their recapture, and by dividing the total by the number of localities of recovery. By applying the above method we found that the average displacement period of Sardine, judging from the results of tagging, lasted for 7 days throughout the fishing season, if the exceptional catch taken at Široka on July 23 rd, i.e. after 59 days, is left unconsidered.

An analysis of Sardine catches by means of the above 7 days' unit, given in Table II, enables us to establish the following migrations:

TABLE II.

SARDINE CATCHES IN VARIOUS FISHING LOCALITIES SHOWN IN 7 DAYS' PERIODS (IN KG)

Time Interval	Biševo Island (I)	Svetac Island (II)	Komiža Coves (III)	Boke Coves (IV)	Zakamiće Coves (V)	Stenjalo Coves (VI)	Ispod Visa Coves (VII)	Pelegrin Coves (VIII)	Žukova Coves ((IY)	Bol Coves (X)	Jelsa Coves (XI)
April											
17—23	11886	—	—	—	—	—	3689	12380	14024	160	7798
24—30	12011	—	—	—	—	—	—	36606	18489	1250	3902
May											
1—7	6749	705	2363	7503	24072	—	6005	30305	12942	—	—
18—14	308	300	—	1709	—	—	—	5922	2200	—	—
15—21	10662	6339	—	1236	14779	2231	2604	41936	19495	22650	22707
22—28	15664	6377	6773	2022	16532	—	—	32373	9155	10860	2355
29—4/VI	21804	16078	—	13404	2674	—	—	15930	19807	6795	2500
June											
5—11	—	2174	—	—	—	—	—	756	—	1020	—
12—18	51335	15100	6077	—	24200	—	9000	4326	—	1020	—
19—25	51681	21988	1400	3436	—	—	23300	6948	—	720	5400
26—2/VII	11500	40682	13100	21801	—	—	6263	10344	445	13660	—
July											
3—9	900	—	—	6500	—	—	4800	5510	—	13120	—
10—16	1515	24900	4900	2400	3900	—	—	5200	—	1600	—
17—23	38500	35243	40867	31918	—	—	—	25343	534	—	5847
24—30	21389	10168	2081	17900	—	—	300	41906	1582	300	4319
31—6/VIII	6800	6400	—	6600	300	—	—	4250	—	—	—
August											
7—13	—	—	—	—	—	—	—	—	—	—	—
14—25	3097	200	—	—	—	—	—	—	—	—	—
21—27	2212	1200	—	8276	1200	1500	200	15006	—	970	1720
28—3/IX	2500	800	—	1400	827	—	6078	3502	—	615	2300
Sept.											
—10	—	—	—	—	—	4000	—	—	—	—	—
1—17	—	—	—	17625	—	—	—	753	—	250	200
8—24	600	—	—	800	1189	—	—	2166	—	1600	10158
5—1/X	600	—	—	—	16749	—	—	11311	—	2850	2000
Octob.											
—8	—	—	—	—	—	—	—	432	—	—	—
—15	—	—	—	—	—	—	—	—	—	—	—
—22	3300	—	—	—	—	—	—	—	—	150	6540
—29	—	—	—	—	—	—	—	—	—	30	3282

The April and May data are incomplete as far as the islands of Biševo and Vis are ıcerned. The 7 days' totals of Sardine catches in various fishing localities have been ained by the addition of daily catches.

There was an intensive Sardine movement during the first half of April (until April 30th) from Biševo Island (I) in the direction of the northwest and north coast of Vis Island (IV, V), where catches of considerable size were taken in the beginning of May. The displacement of Sardine shoals, starting from the north coast of Vis Island (V), went on toward Pelegrin region (VIII) to proceed in the direction of Hvar Channel (IX, X, XI).

The migration was particularly intensive in May, i.e. during the second dark of the moon. It occurred toward the end of May and at the beginning of June from Biševo Island (I) along the northeast coast of Vis Island (Boke, IV) and along its north coast (V), probably joining the movement coming from the Svetac region (II), to proceed in the direction of the northwest coast of Hvar Island (VIII).

The displacements were less intensive in June, i.e. during the third dark of the moon than in the preceding month. In their majority, they were concentrated in the adjacent localities. More intensive displacements of local character occurred from Biševo Island (I) toward the end of June and at the beginning of July. This movement was a heterogeneous one. The direction of the performed movements can be inferred on the ground of maxima attained in various localities. So the trend of the movements at the beginning of July was partly toward Svetac Island (II), partly toward Komiža Cove (III), and partly toward the northwest coast of Vis Island (IV). Sardine stopped here in large numbers, it seems, during this dark of the moon, producing high concentrations. But displacements were noticed to occur along the south coast of Vis Island (VII) also, in the direction of Stiniva and Rukavac. The displacements occurring along the north coast of Vis Island (V) toward Hvar Island are of an insignificant extent. Some other movements, however, were found to occur in Hvar Channel during this dark of the moon. Mužinić, R. (1950) has inferred, from two recoveries of tagged specimens, that a retrograde east-west displacement via Hvar Channel occurs in that month. This displacement, in spite of its earlier occurrence, is in agreement with the fishermen's experience. By comparing the maxima of catches taken along the south coast of Brač Island (X) with the Pelegrin maxima VIII) which took place during the same dark of the moon, we shall find that these maxima have a reverse course, i.e. to a maximum occurring in the vicinity of Bol, on the south coast of Brač (X), corresponds a minimum in the Pelegrin region (VIII), and vice versa.

Fig. 4. — Comparison between the movements of Sardine resulting from catches and from the tagging perfomed in various areas during each dark of the moon. The movements assumed on the basis of catches only, as no tags were recovered, are marked thus ——

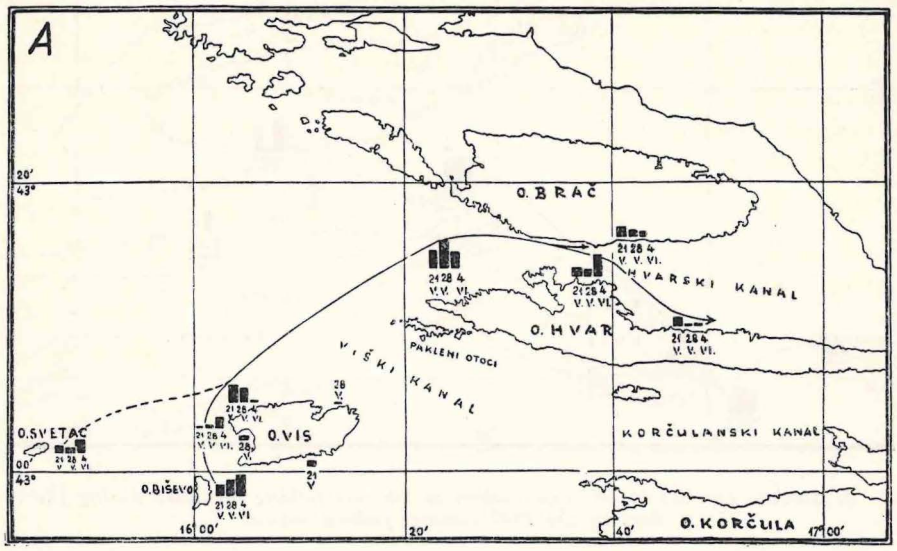


Chart A. Sardine catches in per cent. taken in various fishing localities during the second dark of the 1949 summer fishing season

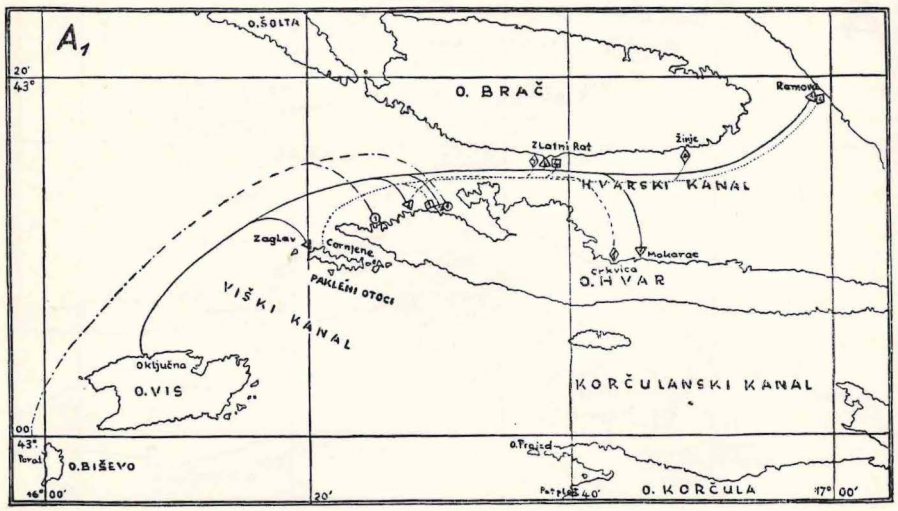


Chart A_1. Movements of sardine shown by recoveries from the taggings carried out during the second dark of the moon of the 1949 fishing season

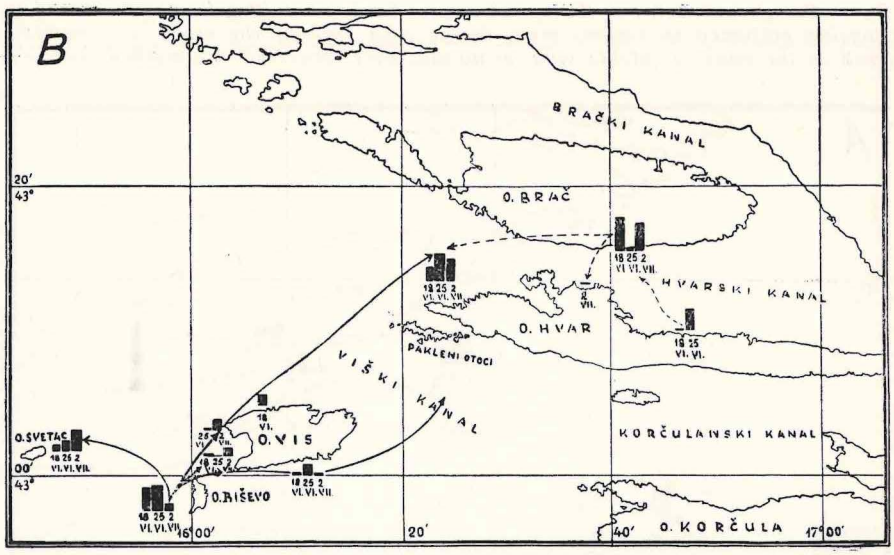


Chart B. Sardine catches in per cent. taken in various fishing localities during the third dark of the 1949 summer fishing season

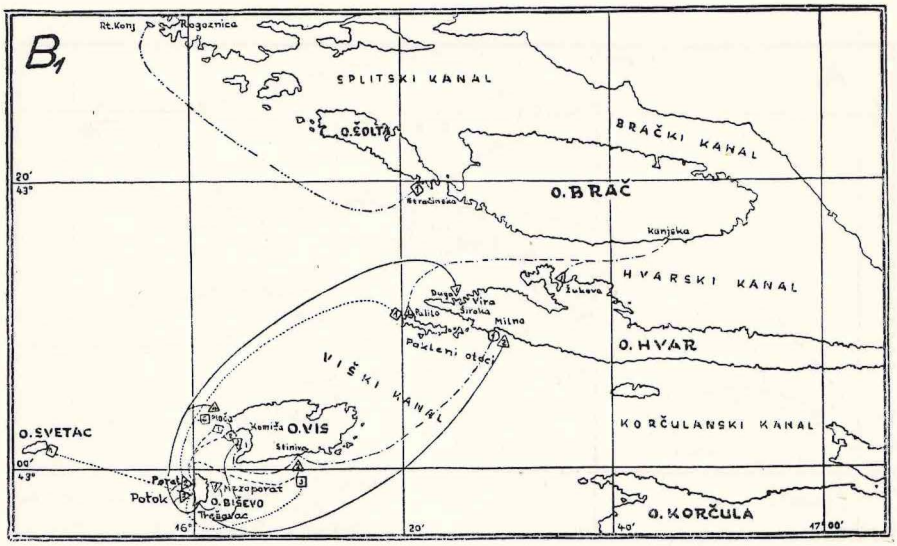


Chart B_1. Movements of sardine shown by recoveries from the taggings carried out during the third dark of the moon of the 1949 fishing season

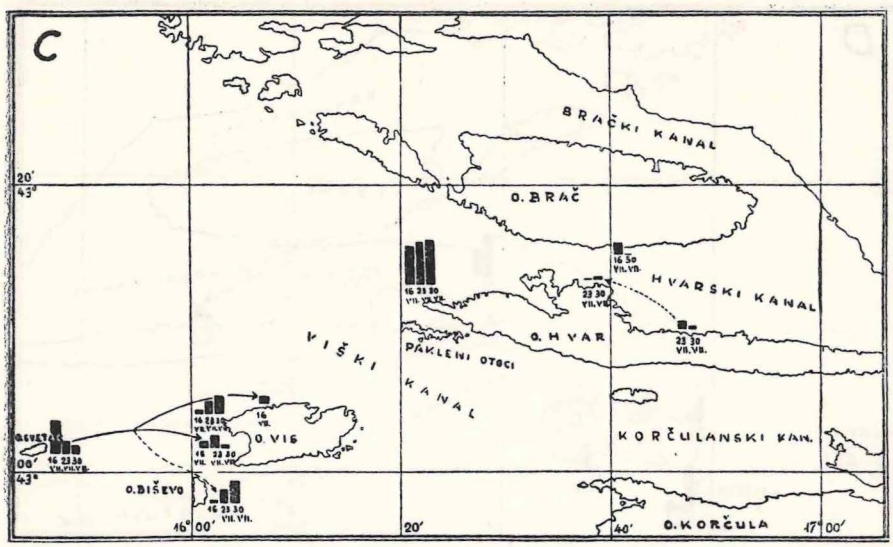


Chart C. Sardine catches in per cent. taken in various fishing localities during the fourth dark of the 1949 summer fishing season

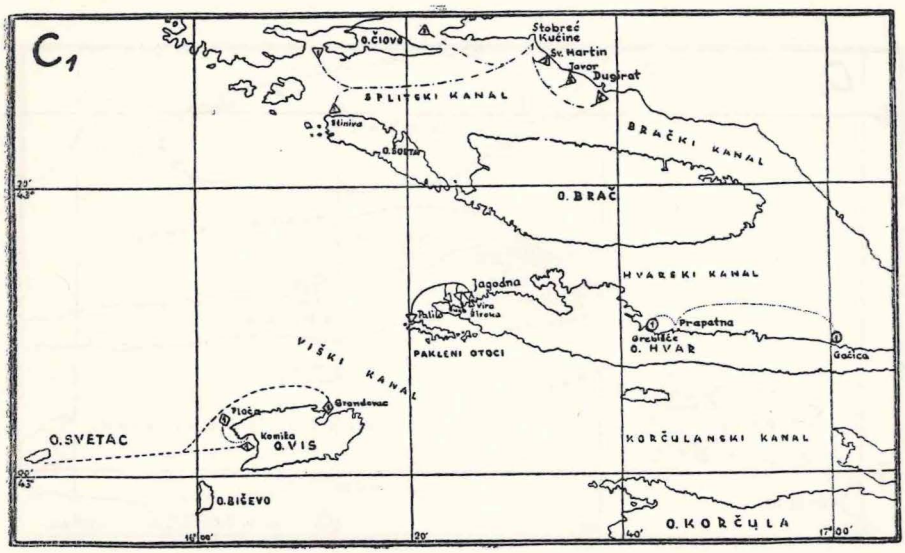
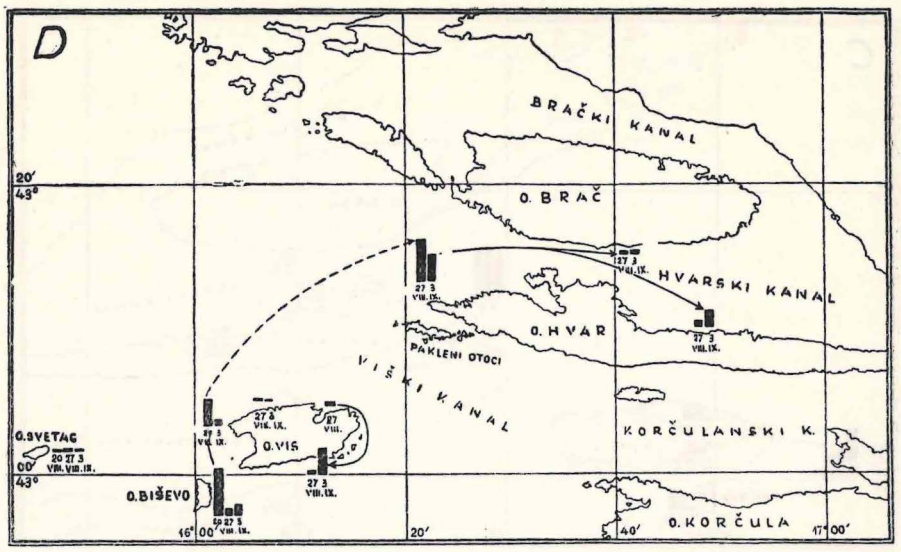


Chart C_1. Movements of sardine shown by recoveries from the taggings carried out during the fourth dark of the moon of the 1949 fishing season



Coart D. Sardine catches in per cent. taken in various fishing localities during the fifth dark of the 1949 summer fishing season

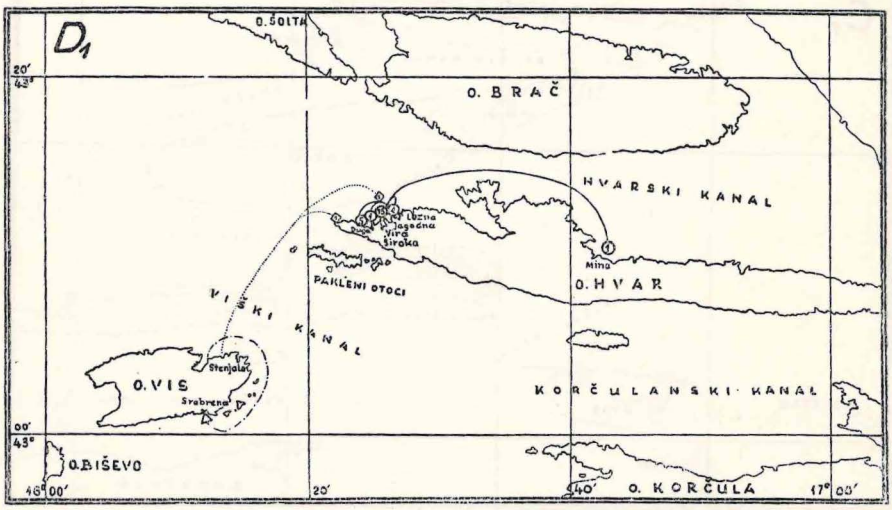


Chart D_1. Movements of sardine shown by recoveries from the taggings carried out during the fifth dark of the moon of the 1949 fishing season

There was no intensity in the displacement that occurred during the second half of July, i.e. during the fourth dark of the moon. It went from Svetac Island (II) in the direction of Komiža Cove (III) and the northwest coast of Vis Island (IV), likely also toward Biševo Island (I), judging from the identical maxima of catches taken near Biševo Island and along the northwest coast of Vis Island. A movement of no intensity took place along the north coast of Vis Island (V). Concentrations of Sardine were noticed in the Pelegrin region (VIII) toward the end of this month. A movement of some importance was noticed in the direction of the northwest coast of Hvar Island.

Toward the end of August, i.e. during the fifth dark of the moon, the displacement occurred along the northwest (IV), north (V), and northeast (VI) coasts of Vis Island in the direction of its south coast (VII) where a maximum was attained at the beginning of September. Unimportant movements result from the size of catches taken during the following darks of the moon. The course of these movements has been already given — in outline — on the foregoing pages.

These, then, are the displacements resulting from the statistical data on the 1949 catches.

The question arises here whether there is a congruity between the data on catches and the results of tagging.

An intensive tagging of Sardine was carried out by Mužinić, R. (1950) during the fishing season lasting from May 6th to October 1st 1949.

»The noticed Sardine movements had a small amplitude. The most significant migration was noticed at the end of May and during the first half of June, going from the region of Vis and Biševo Island in the direction of the mainland (the littoral around Makarska). Sardine approached the coast of the mainland via Hvar Channel. By the end of June and at the beginning of July Sardine movements were noticed to occur from the region of Biševo and Vis Islands in the direction of the west coast of Hvar Island, where they joined the movements coming through Hvar Channel in the east-west direction. In the second half of July a Sardine movement occurred from Svetac Island toward Vis Island and a concentration of tagged individuals was found at the tagging locality along the northwest coast of Hvar Island. Toward the end of August a movement of Sardine was noticed to occur from the northeast coast of Vis Island in the direction of the northwest coast of Hvar Island.

A lesser concentration of tagged individuals at the above mentioned tagging locality was also found in the course of September.«

It is in the above way that the recoveries of the tagged specimens in the central Dalmatian region were recorded in 1949, which region coincides with the area covered by our statistical data on catches.

Fig. 4 shows the convergent course of Sardine displacements obtained from the data on catches and the tagging results (AA_1, BB_1, CC_1 and DD_1). The dates found under each column on the charts A,B,C,D of Fig. 4 stand for the last day of each week. The catches are given in per cent., showing, in proportion to the total catch, the results obtained in various fishing regions for consecutive periods of seven days. This was done separately for the region of Biševo, Svetac, and Vis islands, and separately for the Pelegrin and Hvar Channel Region. On the same pages (Fig. 4, charts A_1 B_1 C_1 D_1) we find the Sardine displacements which took place during the same dark of the moon according to the tagging results. The number of recoveries of tagged specimens is given for each place of recovery.

A comparison between the results contained on both the left and right hand sides of Fig. 4 enables us to conclude that the compared data show a considerable coincidence. They coincide not only in their general course, but also in the dates of recovery and catch respectively which took place in the fishing region under analysis, during the period of time when the 7 days' unit was applied.

ESTIMATE OF THE SIZE OF THE SARDINE TOTAL POPULATION BY MEANS OF SCHNABEL'S METHOD

Tagging of fish species, beside providing data on movements, migrations, etc., can also be usefully applied for the estimation of the size of population of a species and for the computation of the intensity of its exploitation. There are several methods serving this purpose. One of them was used by Schnabel (1938) to ascertain by computation the size of population by means of an uninterrupted tagging going alongside with intensive fishing operations over a shorter period of time. When applying this method, each space of time is covered by a separate estimate of populations. The method is applied on the presumption that the fish caught during the experiment are all returned to the water unharmed (Ricker, 1948).

This method has a shortcoming consisting therein that both the recruitment and the natural mortality are disregarded during the expriment as they are considered constants.

Several systematic errors, among various others, are the outcome of the disregarding of the above mentioned factors. The author, however, made no attempt at correcting these systematic errors in the course of his approximate estimation of the size of population.

Four darks of the moon, II, III, IV, and V, were taken for the purpose of the estimate. (Average duration of a dark of the moon in the central Dalmatian region amounts to about 20 fishing days). Each of these darks was divided into spaces of time embracing twice five days. The estimate of the size of population is given in Table III. It is based on repeated sampling of a constant, Sardine population (Mužinić, R. 1954).

TABLE III.

ESTIMATE OF THE SIZE OF POPULATION BY MEANS OF INTENSIVE TAGGING

Space of time (t)	Tagged specimens released at the end of the space time T (t)	Caught specimens (in 000) C (t)	Number of recovered tags R (t)	T(t-1) C (t) (in 000)	T (t 1) C (t) (in 000) R (t)	Cumulative E (in 000)	Cumulative D	G/H (in 000)
A	B	C	D	E	F	G	H	I
1	2567							
2	4883	11220	2	28801740	14400870	28801740	2	14400870
3	6645	12213	15	59636079	3975738	88437819	17	5202225
4	9119	3134	2	20825430	10412715	109263249	19	5750687
5	10394	6418	19	58525742	3080302	167788991	38	4415500
6	12825	7573	5	78713762	15742752	246502753	43	5736622
7	15425	4256	103	54583200	527992	301085953	146	2062233
8	17396	1164	1	17954700	17954700	319040653	147	2170345
9		1458	2	25363368	12681684	344404021	149	2311436
			149	344404021	2311436			
	Poisson limits of 95 percent confidence						126—175	2733486-1968017
	Population, in thousands, at P of 0,05 = 2311436 (							

The columns in the above table refer as follows: Column A (t) to the short space of time (5 days in our case); Columns B to the number of tagged specimens released at the end of a space of time T (t); Column C to the whole number of specimens caught within each space of time C (t). (The number of specimens for each space of time was ascertained by computation on the basis of the average number of individuals found

in a kilogram, considering each dark of the moon separately); Column D to the numbers of recovered tags during each space of time; Column E to the whole number of specimens caught within a space of time C (t) multiplied by the number of recovered tags at the end of the preceding interval T (t-1); Column F to the values of Column E divided by the values of Column D, R (t); Columns G and H to cumulatives of Columns E and D; Columns I to the values of Column G divided by the values of Column H.

As only a small proportion of the total population was tagged, the numbers of recoveries by intervals were distributed in a Poisson distribution.

An analysis of Table III, Column I, where the catches are less variable, will show that the Sardine population was constantly growing smaller from May 18th to August 31st, i.e. during the space of time chosen for the analysis of catches and tagging results by means of Schnabel's Method. The reduction of population was in keeping with the diminution of Sardine catches at the time when Sardine shoals kept moving from the high Adriatic in the direction of the mainland as already stated. These conclusions are drawn on the presumption that the area over which the tagging of Sardine took place was rather a small one — this probably contributing to a quick distribution of tagged individuals within the population — and that the natural mortality of fish was insignificant.

On the basis of an approximate estimate of the size of population we are able to find out the 1949 exploitation rate of the population concerned. The following formula was used by Ricker (1948) for this purpose:

$$\mu = \frac{\Sigma\ (C)\ \Sigma\ (A)}{\Sigma\ (AD)}$$

(Here C stands for the number of recovered tags; A for the total number of caught individuals; and D for the number of tagged individuals — not corrected for known deaths from fishing).

By applying the above formula, we shall find that the Sardine rate of exploitation (μ) during the 40 fishing days in 1949 amounted to 0,07. If we realise that the central Dalmatian fishing season of average intensity extends over about 100 days hence the annual expectation of capture (fishing mortality) would result then about 0,17.

This exploitation fraction would no doubt be a higher one if we were able to calculate the corrections for recruitment, natural mortality

and other systematic errors involved in the tagging technique, such as loss of tags, the mortality of tagged individuals owning to possible injuries either due to fishing or to tagging itself, the unnoticed tags among the caught fish, etc.

But if we consider this rate of exploitation irrespective of correction, we shall find that the 1949 Sardine catch in the central Dalmatian region, otherwise above average, was still a minimum one in comparison with the estimated size of population. The question arises, therefore, what is going to happen with that insufficiently exploided population during the successive years? It is impossible to give a more substantial answer to this question without the knowledge of the dynamics of population, i.e. without the detailed data on the estimate of the size of total population, obtained by means of vital statistics. This seems to be the more imporant as several questions arose as soon as we attempted to compute the extent of the fishing mortality, viz.:

First, whether there is here also, perhaps, a »causal« connexion between the ingressions/regressions of sea water with a higher salinity ration and the Sardine migrations?

Second, what percentage of the total mortality is shared by natural mortality caused by predation, parasites, disease, or senility? Third, whether there is any longitudinal migration along the eastern shore of the Adriatic, beside the convergent displacement going from the main sea toward the coast of the mainland? These questions concerning the migrations of Sardine and their disappearance respectively, cannot so far be answered by the tagging results available.

The last 1949 Sardine catches in the central Dalmatian region were recorded on several points during the whole of October and amounted as follows: at Splitska vrata (the passage between Brač and Šolta Islands) 450 q; along the northeast coast of Hvar Island, from Zaraće to Pogorila 98 q. In the region of Vis Island the last catches were taken: at the beginning of October in the vicinity of Slatina (on the north coast of island), 49 q, and at the beginning of the second half of that month not far from Biševo Island, 53 q.

These changes of ecologic niches which become manifest in seasonal appearances or disappearances of Sardine, are likely to be closely connected with the problem of their hibernation. While the appearance of Sardine during the fishing season was dealt with on the foregoing pages, when their convergent displacements going from the high sea in

the direction of the mainland coast were examined, particulars of their disappearance from that coast are not sufficiently known.

Certain indications of an inverted movement of Sardine and their possible hibernation are shown by the analysis of phenologic seasonal aspects of Sardine in space which we shall try to dwell upon (hypothetically at least) in the following chapter.

INVERTED SARDINE MIGRATION IN WINTER

The East Adriatic Sardine fishing comes to an end in October. We do not know where Sardine then retreat, since a suitable gear which would enable us to continue the fishing operations is not available. Sporadic Sardine catches taken by means of trawl or winter drift net are too insignificant to justify any substantial conclusion as to their hibernation. Considerable winter catches, however, are not unknown in the Vis Island region, as stated by Krafft (1890): »Lissa ist der einzige Unterbezirk, welcher seit 1873/74, und zwar im Jahre 1878/79 auch für die Winter — Campagne einmal die verhältnissmässig bedeutende Ausbeute von 2600 Metercentner Sardellen zu verzeichnen hatte, ein Beweis, dass man auch in der Winter — Campagne grosse Mengen Sardellen fangen kann, wenn sie zur Laichzeit nur mehr geschont würden.«

The knowledge of Sardine spawning grounds and spawning season could, in absence of detailed data on catches, provide an indirect evidence of the place of their hibernation and their winter-time movement. The investigations into the Sardine spawning season and spawning grounds in the Adriatic have only recently been attempted. The probability of Sardine hibernation, i.e. during the time when they disappear from the inshore and shallow waters, was not analyzed but only suggested by some older authors. Let us, therefore, quote the opinions held by those authors on the one hand and the results attained by the recent investigation into the ecology of the Adriatic Sardine on the other hand.

In Krafft's (1887) opinion, Sardine take to deeper water in winter. We find the same opinion repeated by other authors, e.g. Krisch (1900), Lorini (1903), and Gast (19922, 1925). According to Kotthaus (1938), Sardine retreat to larger depths in order to protect themselves from rough weather. Gamulin (1954 b), basing upon investigations of Sardine spawning grounds and spawning season,

thinks that Sardine do remain some time on more important spawning grounds during the winter, but points out that such spawning grounds are found above the 100—150 m isobath. In our opinion, *there is a winter-time retreat of Sardine from the shore in the direction of the high sea, performed in stages, i.e. an inverted displacements during the fishing season.*

This opinion is confirmed by the results of investigations into the ecology of Sardine displacements in their lifetime and in their adult state as well. According to Mužinić, S. (1936), Sardine withdraw from the inshore region and from less deep water areas during their lifetime to take to the open Adriatic, toward larger depths. Some data on the adult Sardine displacements in the direction contrary to those occurring during the fishing season are given by Mužinić, R. (MS) as a result of her examination of the composition of catches taken from the region of Vis and Biševo Islands.

»..... we can mention the withdrawal of big fish from the coastal region at the very end of the fishing season or even after its termination, and periodical catches of adult individuals by means of towed nets in the channel region or in the main sea.«

What causes this withdrawal of adult Sardine from the inshore region toward the main sea at the end of the fishing season and during the spawning?

Furnestin (1943) observes that some stability of the physical environment, particularly of temperature, is needed by Atlantic Sardine af the time of spawning. When there is a drop of temperature in winter and the atmospheric conditions grow unfavourable, mature individuals leave the inshore region and take to the open sea where they are caught by trawlers by means of towed nets. This phenomenon is confirmed by Planas, A. and F. Vives as far as Mediterranean Sardine are concerned. Sardine are caught in bottom water by means of a gear called »bous« along the east coast of Spain all the winter round. While real migrations of the species depend on physiological changes, the physical factors (such as wind and current) according to these authors, are responsible but for minor displacements of Sardine in the direction of deeper zones and thence, in spring, toward the coast of the mainland. Gamulin (1954 b) considers the stenothermy and stenohalinity of this Adriatic clupeid species to be responsible for the withdrawal of individuals from inshore and shallow waters when their sexual glands reach the stage of maturity, and for their going in search for places of preference with a stable temperature and salinity.

DIVERGENT DISPLACEMENTS OF ADULT SARDINE IN INVERTED STAGES

Nowhere in the central Dalmatian region lasts Sardine fishing as long as in the area lying between Šolta and Brač Islands, i.e. in the vicinity of Bobovišće, Boka od Stipanske, and Prodolac (see Fig. 1). When calm and good fishing conditions prevailed in these localities, the Milna fishermen used to catch a great quantity of matured Sardine in October and November 1949. The last catches of already mature individuals and the first manifestation of spawning provide a basis for our assumptions on Sardine displacements occurring in stages from the coast of the mainland in the direction of the main sea.

The displacement continued over the area extending from Bobovišće to Splitska Vrata (the passage between Brač and Šolta Island), where Sardine eggs were first found (October, November), toward the nort-west coast of Hvar Island (Pelegrin), where the autumnal (early) spawning maximum was reached in November. The divergent displacement proceeded then in the direction of the north coast of Vis Island and toward the main sea of the southeast coast of Hvar Island. The most intensive February spawning occurred in the area lying among Svetac, Vis, and Biševo Islands. This was the so called secondary or winter (late) spawning maximum. Hypothetic directions of that d i v e r g e n t Sardine displacements in the direction of the main sea, assumed on the basis of the number of Sardine eggs found in plankton, are marked by arrows in Fig. 5. The data on quantities of Sardine eggs found in 1947/48 and 1948/49 as well as on the localities concerned, we owe to G a m u l i n (1954 b) whose paper is based on the material caught by means of ring-trawl only.

It results from Fig. 5 that the late autumnal spawning takes place along the coast (in the regions of Splitska vrata and Pelegrin). The integral mean temperature from the surface to the bottom for the mentioned regions amounted to 17,9°C in October, November, and December 1947/48 and 18,1°C in September and December 1948/49. The cooling of inshore waters, caused by abundant rainfalls and influx of streams, »forces« perhaps adult Sardine to retreat gradually toward the main sea, where their secondary or winter maximum takes place in February, at an average water temperature ranging between 14,1°C in 1947/48 and 13,3°C in 1948/49. The quantities of eggs found in March and April are less important. (Each of the localities did not yield the

same quantities during a series of years, and they also vary in proportion to the autumnal and winter spawning maximum).

Generally taken, this is the time when the approach of Sardine to the coast of the mainland begins and when spawning takes place in passing most likely of those individuals whose maturing of gonads had retarded. May this, perhaps, — instead of retardation — be called a belated phase of a discontinued spawning of the later maturing individuals?

What are the causes of these displacements of adult Sardine? Do they consist in the changes of physical conditions of the environment

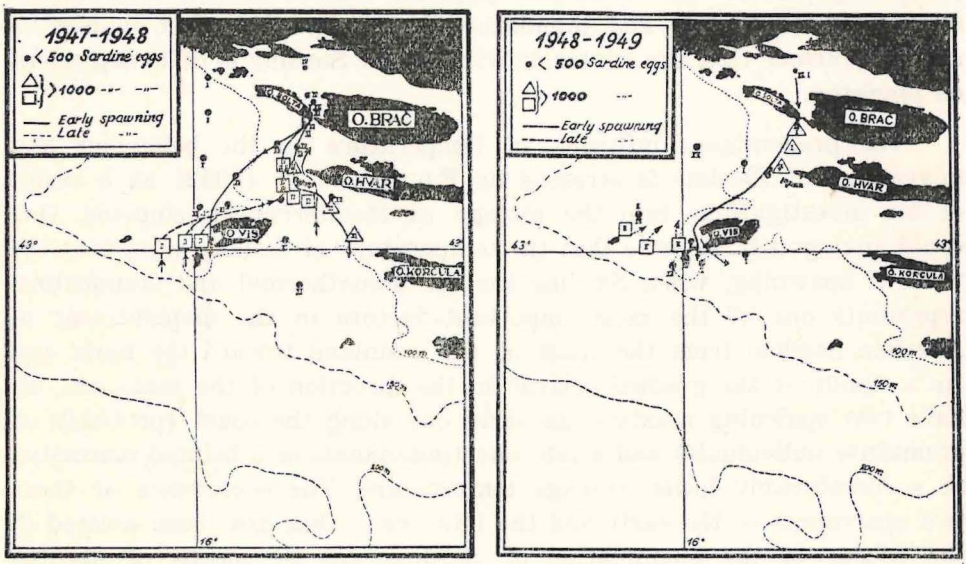


Fig. 5. — Number of Sardine eggs foud during the early and late spawning in 1947—1948 and in 1948—1949. (Figures indicating the months, if situated under the localities, refer to early spawning and above the localities to late spawning.

or in the abundance of plankton of a higher nutrient value? According to Ruivo, M. and K. Wirz (1952), plankton analyses in association with Sardine eggs and larvae are likely to contribute to the explanation of the ecologic conditions of spawning. Basing on his observations made for a term of a year, Gamulin (1954 b) attempted to bring the spawning into a positive correlation with the feeding. This relation feeding/spawning coincides to some extent in the Pelegrin region in November, but not in February when the quantities of zooplankton grow

larger while the number of eggs diminishes in comparison with the November level. A reverse situation is found in the triangle formed by the islands of Svetac, Vis, and Biševo. This region abounds in zooplankton in October, November, and December, with almost no eggs, while a maximum amount of eggs occurs in the region in February, with insignificant quantities of plankton of a higher nutrient value. This phenomenon could hipothetically be explained merely by the fact that sexually mature individuals have not yet »penetrated« in their numbers into the region (or have already »penetrated« but have not yet reached the stage of their sexual maturity), in spite of plankton being abundant, preferring places with favourable physical factors of the environment irrespective of feeding and abundance of plankton. This fact enables us also to conclude that the winter distribution of Sardine is little dependent on plankton.

The predominant influence of temperature on the behaviour and migrations of Sardine is stressed by Furnestin (1952) as a result of his investigations into the biology of Mediterranean clupeids. One could analogously suppose that the temperature of inshore waters at the time of spawning, when Sardine become stenothermal and stenohaline, represents one of the most important factors in the displacement of Adriatic Sardine from the coast of the mainland toward the main sea. As a result of the gradual retreat in the direction of the main sea, we have two spawning maxima, an early one along the coast (probably of premature individuals) and a late one (individuals of a belated maturity) at a considerably lower average temperature. The occurrence of these two spawnings — the early and the late one — has also been noticed in the course of the examination of Sardine age by means of otoliths Mužinić, R. (1952). The time interval between the two spawnings embraces several months. The otoliths found in Sardine individuals belonging to the late spawning are more fragile than those shown by individuals of the early spawning. During the summer fishing season, both kinds of otoliths are found in specimens of the same catches, but intermediary forms occur among them also.

What is responsible for this difference in the consistency of otoliths belonging to the early spawning and the late one? Is the difference of a phenotype or a genotype character? It is rather difficult to answer this question for the time being. According to Mužinić, R. (1952), the difference might be attributed to the seasons in which the individuals happened to hatch, i.e. to conditions which pertain to characteristics of

the season concerned. In the formation of meristic characters of the Adriatic Sardine, however, the influence is perhaps felt not only of conditions prevailing after the spawning season, but of ecologic factors of the environment during the spawning time as well, i.e. of factors pertaining to the closer habitat of the spawning ground. Now, these ecologic factors of the environment, if subject to a detailed examination, could prove most helpful in the analysis of different physiologic reactions of individuals at different temperatures and in different localities during a year. This differentiation becomes manifest during the spawning time only. Johnsen (1936) supposes that the »total effect« of various external factors is in proportion with the eggs and larvae development. This author classifies the external factors influencing the development and determinism of meristic characters into two categories, i.e. »factors which influence the rate of the metabolic processes (temperature, oxygen, hydrogen-ion concentration and other factors)« and »factors which influence the size of the egg (density of the medium). In Ruivo, M. and K. Wirz's (1952) opinion also the knowledge of the dominant hydrologic conditions during the spawning time is indispensable for the explanation of the determinism of meristic characters of Mediterranean Sardine.

When the spawning terminates, Sardine approach the coast of the mainland. They are then less stenothermal and stenohaline. Migrations on physiologic grounds are not likely to occur any longer. This is the opening of the fishing season. At this time Sardine rush to the fishing grounds lying in the inshore waters where a larger biomass of smaller zooplankton was noticed to occur during the warmer part of the year than in the outer areas. (Gamulin, 1954 b).

As Sardine come nearer to the coast of the mainland, the mean integral water temperature along the eastern Adriatic shore amounts to 14°C. This is in agreement with the findings made by Andreu, B. and J. Rodriguez-Roda (1951) along the east coast of Spain, where Sardine reappeared in the inshore waters at a surface temperature of 14°C in 1949-1950, and 13,9°C in March 1951.

SUMMARY

1) A considerable coincidence has been noticed between the data resulting from the analysis of the size of the 1949 Sardine catch and of the outcome of the 1949 Sardine tagging in the waters of the central Dalmatian region where an intensive tagging was carried out. The Sardine displacements were congruous, and in substance they were convergently directed at the inshore channels and the coast of the mainland.

2) The 1949 Sardine catch, in relation to the estimated total size of population, was a minimum one. The corrections for systematic errors were not considered when the size of population was computed.

3) A divergent retreat of Sardine occurring in stages toward the main sea, i.e. in the contrary direction of the displacement during the fishing season, was manifest along the central Adriatic shore when the fishing season came to an end in October. The abiotic factors of the environment, being most important in the occurrence of this movement, have been employed in the attempt to explain the phenomenon of Sardine spawning taking place (in both the inshore and offshore waters) in different seasons.

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STATISTIČKI PRILOG POZNAVANJU EKOLOGIJE SRDELE (*SARDINA PILCHARDUS* WALB.) U SREDNJEM JADRANU

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Kratak sadržaj

Pisac je u ovom radu analizirao mogućnost postojanja koincidencije između rezultata kretanja srdele dobivenih markiranjem i kvantitete ulova 1949. godine na srednjedalmatinskom području. Osim kretanja srdele za vrijeme ljetne sezone lova, dodirnuta su također i pitanja procjene veličine njene populacije, eksploatacije, kao i eventualnog zimovanja. Dobiveni rezultati su slijedeći:

1. Analiza kvantitete ulova i rezultata markiranja srdele 1949. godine na srednjedalmatinskom području, gdje su ta markiranja bila intenzivna, pokazala je, da između obiju podataka postoji znatna koincidencija. Kretanja srdele su se podudarala. Ona su uglavnom bila konvergentno upravljena prema unutrašnjim kanalima i obali kopna.

2. Ulov srdele 1949. godine, u odnosu na ukupno procijenjenu veličinu populacije, bio je minimalan. Kod toga izračunavanja veličine populacije nisu uzete u obzir korekcije sistematskih griješaka.

3. U oktobru mjesecu, nakon završetka sezone ribolova u srednjem Jadranu, srdela se divergentno povlači u etapama prema pučini, t. j. izverzno kretanju za vrijeme sezona lova. Kod toga povlačenja abiotski faktori sredine su veoma važni i pomoću njih je pokušano protumačiti mriještenje srdele (uz obalu i na pučini) u različito doba godine.

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