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A STUDY OF THE LIFE HISTORY OF BRAZILIAN SARDINE, *SARDINELLA BRASILIENSIS*. IV. DISTRIBUTION AND ABUNDANCE OF SARDINE LARVAE*

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SYNOPSIS

Data on distribution and abundance of larvae of the Brazilian sardine, *Sardinella brasiliensis*, are presented based on samples collected in waters off southern Brazil during 1969 to 1971. The distribution pattern and relative abundance of sardine larvae during three spawning seasons are discussed. Relative abundance, using regional census estimates, was calculated each year. In general, larval abundance in each subarea coincided with that of eggs, although the area of distribution of larvae was larger than the spawning area. Estimates of larval abundance showed that the 1970-71 spawning season was the poorest, both in larval and egg abundance, despite the enlarged size of the area surveyed. The average temperature at stations where sardine larvae occurred was 23.4°C, ranging from 14.6 to 27.4°C, and the average salinity was 35.6°/oo, ranging from 35.0 to 36.7°/oo. Distribution of the larvae in different depth zones was analysed. Larvae usually were most abundant in the 51-100 m depth zone. No tendency for a unidirectional transport of larvae was observed; apparently they move from the spawning ground in all possible directions, spreading over the continental shelf. An estimate of survival rate of larvae, based on length frequency data pooled from the three years, was calculated. Undersampling of larvae during daytime was observed. The mean night-day catch ratio, based on larvae from all length classes sampled, was 3.93.

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INTRODUCTION

The ichthyoplankton survey of Brazilian sardine began in 1968 and since then information on the early life history has been gathered. The main purpose of this paper is to compare the relative abundance of the larvae from three spawning seasons and to study the relationship between larval distribution and environmental conditions. Results described here on distribution of sardine larvae were obtained from survey cruises of the project SOL with the research vessels "Prof. W. Besnard" and "Emília" of the Instituto Oceanográfico da Universidade de São Paulo.

MATERIAL AND METHODS

ZOOPLANKTON COLLECTION

During the survey cruises, a conical-cylinder plankton net (mesh = 420 micra) was used, according to the recommendations of UNESCO (1968). A small flow meter was attached to the mouth of the net to measure the volume of water strained. The net was towed vertically from a depth of 80 m to the surface at a velocity of 0.8-1.0 m per second. During the cruise of December 1971, vertical and horizontal hauls were conducted at each station. The horizontal hauls were made on the surface layer during 5 minutes by towing velocity of about 1.5 knots. Because no flow meter was used in this cruise, catches of larvae were quantified by calculating the estimated volume filtered:

Estimated water volume = (mouth area) x (towing distance) x (filtration coefficient).

A filtration coefficient was measured in experimental tank and it was 0.9 for our conical-cylinder net.

The plankton samples were preserved in a solution of 10% formalin. Measurements of sardine larvae were made with a micrometer eyepiece under the stereomicroscope. If there were over 500 specimens in a sample, only 500 were randomly selected and measured. In other cases all larvae were measured.

IDENTIFICATION OF THE LARVAE

The larvae of *Sardinella brasiliensis*, *Opisthonema oglinum*, and *Harengula jaguana* (= *H. pensacolae*) are very similar and their identification is puzzling. However, recent papers by Houde & Fore (1973), Houde *et al.* (1974), Richards *et al.* (1974), and Matsuura (1975*b*) enabled an accurate separation.

SURVEY AREA

The station plan of the three spawning seasons is presented in Figure 1. The stations represented are only those actually occupied by the R/V "Prof. W. Besnard". The full area was divided into six subareas: I - region of Cabo de São Tomé; II - region of Rio de Janeiro; III - region of Ilha Grande; IV - region of Santos; V - region of Paranaguá; and VI - region of Santa Catarina.

During the 1969-70 spawning season, four cruises were made in the region of Ilha Grande and Rio de Janeiro. The cruises of September 1969 and March 1970 were made in the region of Ilha Grande and samples were taken only during day-time. The cruises of November 1969 and January 1970 were made in the region from Cabo Frio to São Sebastião (Figs 2-3).

During the 1970-71 spawning season, four cruises were made. The cruise of October 1970 covered the entire region of Ilha Grande. The cruises of November-December 1970 and February-March 1970 covered a larger area which extends from Cabo de São Tomé (22°S) to beyond Cabo de Santa Marta Grande (29°20'S). The cruise of January 1971 covered the region from Rio de Janeiro to Peruíbe (47°W). Results of three of these cruises are presented in Figures 4, 5, and 6.

During the 1971-72 spawning season, a single cruise was conducted in December 1971, in the region which extends from Rio de Janeiro to Paranaguá (48°30'W). Vertical and horizontal hauls were made at each station (Figs 7-8).

In order to illustrate the influence of undersampling during daytime, night hauls are represented by black dots and day hauls by white circles in the figures. The abundance of larvae is represented by different sizes of circles and dots.

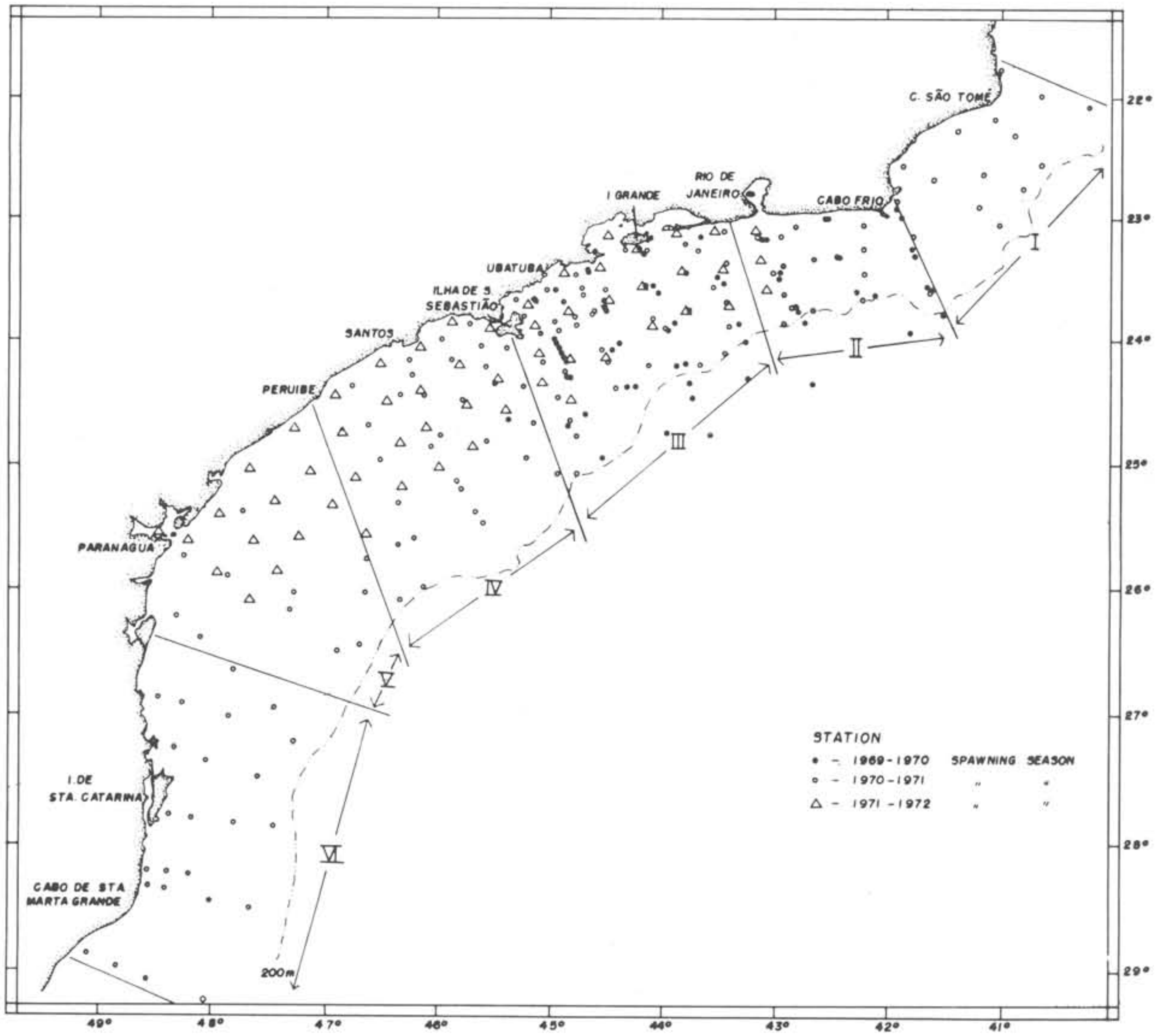


Fig. 1 – Stations occupied by the R/V "Prof. W. Besnard" during survey cruises made in 1969 through 1971.

REGIONAL CENSUS ESTIMATE OF THE LARVAE

Total numbers of larvae were not estimated because of the great influence of gear avoidance by Brazilian sardine larvae observed at the fixed stations, which would make estimation of larval abundance inaccurate. Furthermore, the survey area differed each year making it difficult to compare annual variations in abundance for the whole area.

For this reason we applied the "regional census estimate" described by Smith (1972), who used this method to compare relative abundance of sardine and anchovy larvae. He determined abundance of larvae in a given area "r" from the following formula:

$$C_{k4} = 10\, A_r m^{-1} \sum_{i=1}^{m} (c_i d_i a_i^{-1} b_i^{-1})$$

where

C_{k4} = estimate of abundance of larvae in region "r" in each quarter.

A_r = area of region "r" in number of 10 m^2 areas.

m = number of stations occupied during a three month period.

a_i = area in square meters of mouth of the net used at the "ith" station.

b_i = length of tow in meters estimated from a calibrated flow meter at station "i".

c_i = number of larvae at "ith" station.

d_i = tow depth in meters estimated from the wire angle at maximum wire out at the station "i".

The area of each subarea was measured with a planimeter. At first, the mean number of larvae per unit of sea area (1 m^2) in each subarea was calculated and then it was multiplied by the area of the region in square meters.

RESULTS

1969-70 SPAWNING SEASON

During the cruise of September 1969 no sardine larvae were collected.

During the cruise of November 1969 the occurrence of larvae coincided with the occurrence of eggs (Matsuura, 1971) in the region off Ilha Grande and Cabo Frio-Saquarema (42°30'W), and during January 1970 the overlap of occurrences (eggs and larvae) was still greater (Figs 2-3). During the March 1970 cruise only daytime sampling was conducted in the region of Ilha Grande, and sardine larvae occurred in only two out of 21 stations.

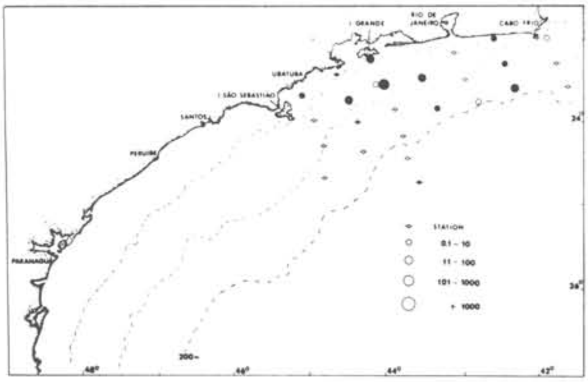


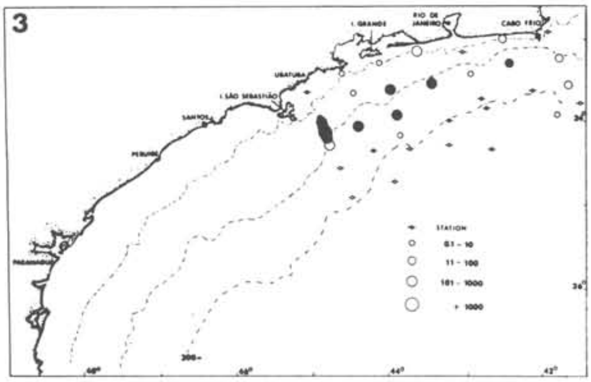
Fig. 2 - Distribution and abundance of sardine larvae in the cruise of November 1969. Number of larvae per square meter of sea area is presented by size of circle (day hauls) and not (night hauls). Negative stations are shown by small circle or dot with transverse bar.

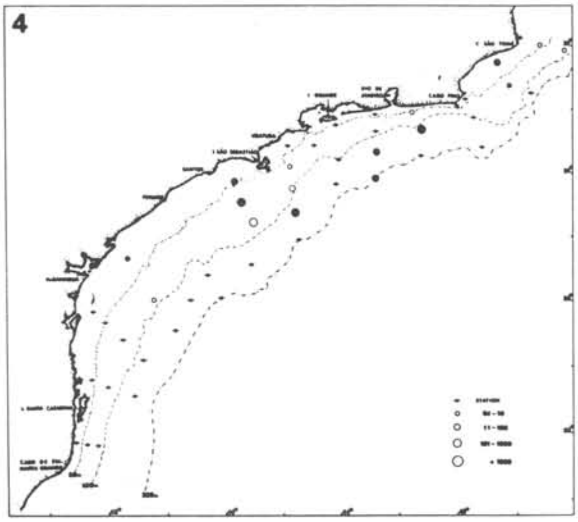
During the 1969-70 season the area sampled on the station line off Rio de Janeiro produced only few sardine larvae. Two concentrations could be visualized: one large group off Ilha Grande and a small one off Cabo Frio-Saquarema. Comparison of areas of distribution of eggs and larvae revealed that the area of the latter was considerably larger than the former.

1970-71 SPAWNING SEASON

Four cruises were carried out in this season. Only in October 1970 no sardine larvae were collected. Figure 4 shows the occurrence of larvae from the cruise of November-December 1970. Two heavy concentrations were observed in the region of Santos-São Sebastião and of Rio de Janeiro. In the region of Cabo de São Tomé larvae were scarce and only a few occurred near Paranaguá. It is surprising that the main spawning ground off Ilha Grande, in which a large concentration of eggs and larvae was observed in the previous season (Matsuura, 1975*a*), had neither larvae nor eggs in this cruise.

During the cruise of January 1971 (Fig. 5), large numbers of larvae were collected all over the surveyed area. The distribution of the larvae seems to be continuous in the coastal zone from Peruíbe to Rio de Janeiro and bounded by the 100 m isobath. Because the nearshore stations off Ilha Grande and Rio de Janeiro produced a large number of larvae, we can assume that distribution of larvae extended to the shallower area where no sampling was done. The offshore stations near the edge of the continental shelf in the region of Ilha Grande and Rio de Janeiro produced no sardine larvae.





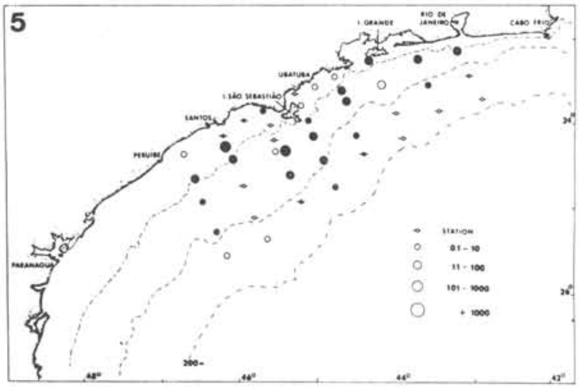


Fig. 3 – Distribution and abundance of sardine larvae in the cruise of January 1970.

Fig. 4 – Distribution and abundance of sardine larvae in the cruise of November-December 1970.

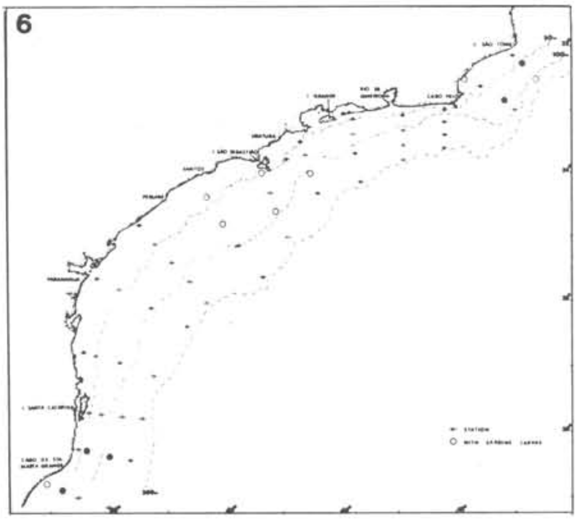
Fig. 5 – Distribution and abundance of sardine larvae in the cruise of January 1971.

During the February-March 1971 cruise (Fig. 6), larvae occurred in three regions: Cabo de São Tomé, Santos-São Sebastião and Cabo de Santa Marta Grande.

Summing up results of the three cruises, we can assume that there is a heavy concentration of larvae in the region of Santos-São Sebastião-Ubatuba and smaller concentrations in the regions of Cabo de São Tomé and Cabo de Santa Marta Grande.

1971-72 SPAWNING SEASON

Only one cruise was made in December 1971. Figure 7 shows the estimated number of larvae per square meter of sea area and Figure 8 shows the number of larvae per 100 cubic meters of sea water.



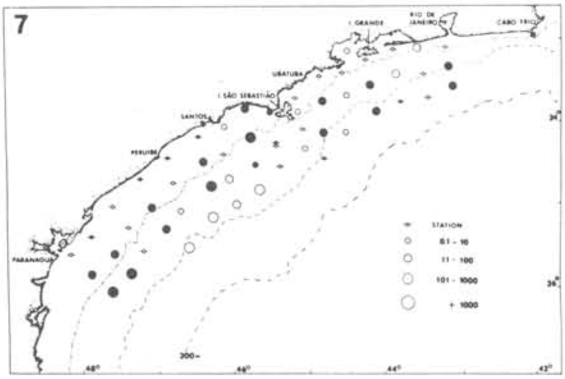


Fig. 6 - Distribution and abundance of sardine larvae in the cruise of February - March 1971.

Fig. 7 - Distribution and abundance of sardine larvae collected in vertical hauls in the cruise of December 1971.

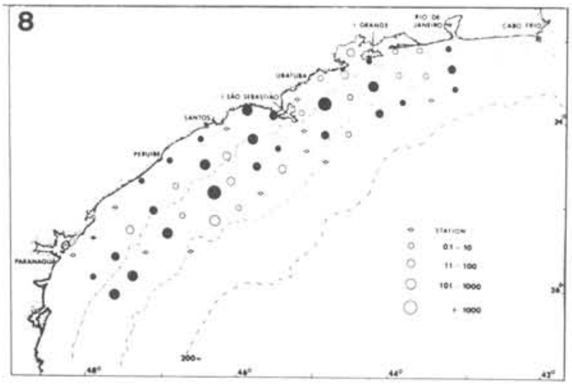


Fig. 8 - Distribution and abundance of sardine larvae collected in horizontal hauls in the cruise of December 1971.

Larvae occurred at all stations in the surveyed area, with the exception of nearshore stations off Paranaguá-Santos and off São Sebastião-Ilha Grande. A heavy concentration was observed in the region of Peruíbe-Santos-São Sebastião in the 51-100 m depth zone. The distribution of larvae in this cruise coincided almost exactly with that of the eggs (Matsuura, 1975*a*) and no significant differences were found on distribution patterns determined by either vertical or horizontal hauls.

RELATIVE ABUNDANCE OF THE LARVAE

The occurrence of larvae during the survey cruises is shown in Table I. Using data from this table it was possible to calculate the mean number of larvae per station. The results are presented in Table II, which contains only data collected during the intensive spawning period: November, December, and January.

TABLE I - Abundance of sardine larvae, by cruise and subarea, in 1969-1971 (Vertical hauls)

Subarea	I			II			III			IV			V			VI			Total		
Cruise	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
September 1969	-	-	-	-	-	-	17	0	0	-	-	-	-	-	-	-	-	-	17	0	0
November 1969	-	-	-	9	5	58	15	5	55	-	-	-	-	-	-	-	-	-	25	11	246
Fixed station							1	1	133+												
January 1970	-	-	-	13	6	96	24	16	4429	-	-	-	-	-	-	-	-	-	37	22	4525
March 1970	-	-	-	-	-	-	21	2	2	-	-	-	-	-	-	-	-	-	21	2	2
October 1970	-	-	-	-	-	-	20	0	0	-	-	-	-	-	-	-	-	-	20	0	0
Nov.-Dec. 1970	8	4	9	4	2	103	13	5	345	6	3	1016	4	2	9	10	0	0	45	16	1482
January 1971	-	-	-	3	1	18	19	14	191	17	10	332	-	-	-	-	-	-	40	26	721
Fixed station										1	1	180+									
Feb.-Mar. 1971++	7	4	18	8	0	0	10	1	1	7	4	7	8	0	0	14	4	34	54	13	60
December 1971	-	-	-	3	2	99	21	11	254	18	13	1360	13	6	486	-	-	-	56	32	2199
Fixed station										1	0	0+									
Total	15	8	27	40	16	374	161	55	5410	50	31	2895	25	8	495	24	4	34	315	122	9235

A = number of stations occupied, B = number of stations at which sardine larvae were collected, C = total number of sardine larvae collected

+ At the fixed station, total number of larvae were divided by number of hauls and mean number of larvae per haul is presented in the table

++ Collected with Hensen plankton net except 12 stations in the subarea VI

Subareas: I = São Tomé, II = Rio de Janeiro, III = Ilha Grande, IV = Santos, V = Paranaguá, VI = Santa Catarina

The ratio of positive stations against all stations ranges from 43 to 68% (all subareas contributed, except the subarea VI in the region of Santa Catarina in which no larvae were taken during this period). The ratio of positive stations against all stations was 41% for daytime and 67% for night-time, suggesting that daytime hauls may not be effective to collect sardine larvae.

Table II shows that larval density varies from year to year. In the 1969-70 spawning season, the values of larval density in subarea III (region of Ilha Grande) are higher than those of subarea II (region of Rio de Janeiro). This coincided with results obtained for egg abundance. In the 1970-71 spawning season, the subarea IV (region of Santos) had the highest value followed by subareas II, III, V, I, and VI in that sequence. In the 1971-72 spawning season, the highest value again was obtained in subarea IV, the values decreasing in subareas V, II, and III.

Using the method of Smith (1972), the regional census estimate of larvae for each subarea in a three month period was calculated. The results are shown in Table III. The subarea estimates of relative abundance of larvae coincided almost entirely with those of the eggs (Matsuura, 1975*a*).

TABLE II - Comparison of mean number of larvae per station

Spawning season \ Subarea	I	II	III	IV	V	VI	Total
1969-70							
(B/A) x 100	-	50%	55%	-	-	-	53%
C/A	-	7	116	-	-	-	77
C/B	-	14	210	-	-	-	145
1970-71							
(B/A) x 100	50%	43%	59%	58%	50%	0%	49%
C/A	1	17	17	64	2	0	26
C/B	2	40	28	109	5	0	52
1971-72							
(B/A) x 100	-	67%	52%	68%	46%	-	57%
C/A	-	33	12	72	37	-	39
C/B	-	50	23	105	81	-	69

A = number of stations occupied, B = number of stations in which sardine larvae were taken (= positive station), C = total number of sardine larvae taken

Note: Only data from cruises of November, December and January were used for calculation of mean number of larvae

During the 1969-70 spawning season relative abundance of larvae in subarea III was greater than in subarea II, and during the 1970-71 spawning season the highest values were obtained in subarea IV, followed by subareas III, IV, V, and I in this sequence. In the 1971-72 spawning season, subarea IV was again first, followed by subarea V, II, and III in this sequence.

TABLE III - Regional census estimate of sardine larvae taken during main spawning period of November-December-January (in billions)

Subarea* / Area** / Spawning season	I	II	III	IV	V	VI	Total
Area**	19.019	13.269	27.683	31.482	28.568	39.815	159.836
1969-70	-	88	3205	-	-	-	3293
1970-71	19	358	545	1263	72	0	2257
1971-72	-	486	372	2504	1186	-	4548

* Subareas: I = São Tomé, II = Rio de Janeiro, III = Ilha Grande, IV = Santos, V = Paranaguá, VI = Santa Catarina

** Area in square meters (x 10^9)

\- No sampling in the subarea

The values obtained for three spawning seasons in subarea II indicate that the highest relative abundance occurred in the 1971-72 spawning season, followed by 1970-71 and then the 1969-70 season. In subarea III the opposite situation was observed, for the heaviest concentration of larvae occurred there in the 1969-70 season.

In subareas V and IV, the 1971-72 season had higher values than those for 1970-71.

DISTRIBUTION OF LARVAE IN DIFFERENT DEPTH ZONES

The mean number of larvae per station in different depth zones is presented in Table IV.

The general tendency for a zonal distribution of the larvae during three spawning seasons can be summarized as follows: heaviest concentration in the 51-100 m depth zone with decreasing values for the 101-200, 15-50 m, and beyond 200 m depth zones in this sequence.

Beyond the continental shelf where no spawning was observed, some larvae were taken. From 17 stations in this depth zone, five positive stations pro-

TABLE IV - Mean number of sardine larvae per station in different depth zones

Spawning season \ Depth zone	15-50 m	51-100 m	101-200 m	+ 200 m
1969-70	22.1	162.3	74.1	4.3
1970-71	12.8	51.7	17.1	9.8
1971-72	12.4	84.0	14.3	0
Total	13.8	91.7	40.3	5.6

Only data from the cruises of November, December and January, were used for calculation of mean number of larvae

vided a total of 95 sardine larvae. It seems reasonable to assume then that at least part of the larvae that originated from spawning in shelf waters may be carried away to off-continental shelf regions in which poor survival could be supposed.

Before this investigation, it was generally accepted that sardine larvae, during their planktonic stage, would be carried to the coastal region by surface currents. This was mainly because of the occurrence of juveniles in estuarine waters during the autumn and winter. To test this supposition, the size frequencies of larvae from different depth zones in different subareas were calculated and the results are shown in Figures 9 and 10.

Comparing the size frequencies of larvae from four depth zones (Fig. 9), we can see that individuals representing early postlarval stages are concentrated mostly in the 51-100 m depth zone. In the remaining three depth zones, larvae of greater mean length occurred. This implies that some of the first larval stages, which were found on the main spawning ground (51-100 m depth zone), apparently are transported to other zones. From Figure 9, it is evident that the movement is not a single direction, either from the spawning ground to the coastal region, or from the spawning ground to the offshore region, but instead the larvae seem to disperse from the spawning

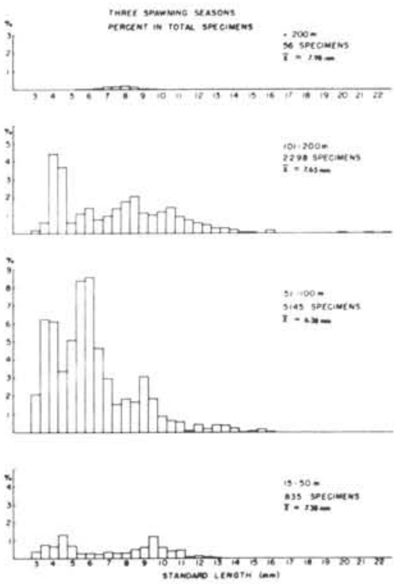


Fig. 9 – Size frequencies of sardine larvae taken in different depth zones.

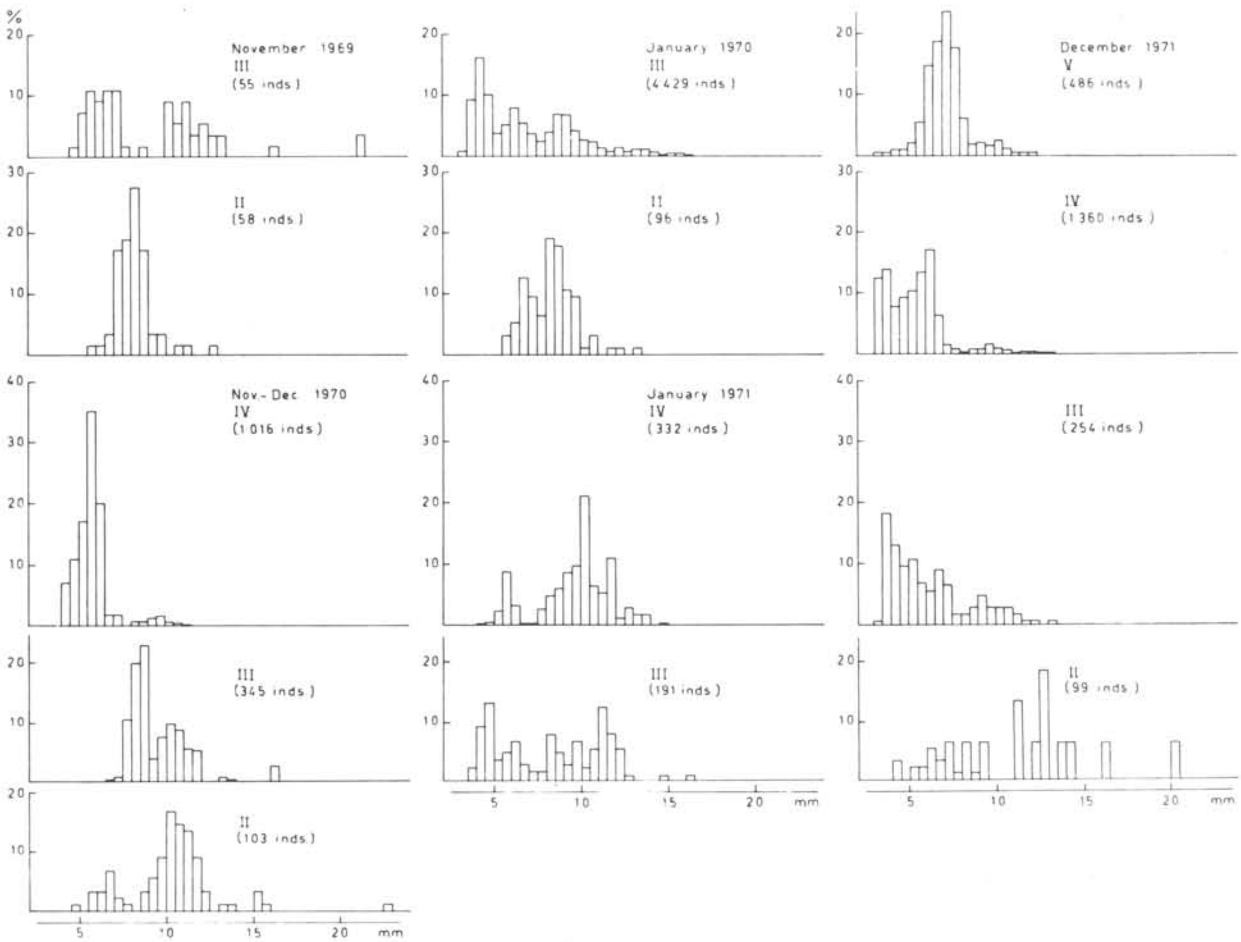


Fig. 10 – Size frequencies of sardine larvae taken in each subarea.

ground in all directions over the continental shelf and occasionally to the off-continental shelf region.

Data on size frequencies of larvae from each subarea show a tendency of increase in mean length from south to north, but the relationship does not always hold.

Figure 10 indicates that there is a polymodal distribution of larvae in some regions and this suggests that successive spawning may have occurred during the spawning season. Or we can also suppose that a schooling tendency of similar-sized larvae may have caused patches in the sea and this caused a polymodal size frequency in the subarea in which only few samplings were made.

NIGHT/DAY CATCH RATIO

With regard to the night/day catch ratio of larvae, results at the fixed stations gave a value of 32 in 1969 and 615 in 1971 (Matsuura, 1977). In this paper we compare those stations with routine station data for three spawning seasons.

The total number of sardine larvae collected during night time exceeded the daytime catch by 4.55 times. To calculate the N/D ratio, the mean numbers of larvae per positive station were used (Tab. V). The N/D ratio in the 1969-70 season was higher than that for the other two seasons. The mean N/D ratio for three spawning seasons was 3.93. If we had used the mean number of larvae from all the stations occupied, the N/D ratio would have increased, because the proportion of positive stations relative to total stations was higher for night hauls than for day hauls (night: 67% and day: 41%).

Comparison of data from the fixed stations with those of the routine stations, shows that the N/D ratio of the former is extremely high. Because the observations at the fixed stations were made only during a 24-hour period, it is possible that we might have sampled an occasional concentration of sardine larvae during the night at the two fixed stations. To clarify this problem, we intend to conduct a 48-hour period of sampling at the fixed station in the near future.

TABLE V - Night-Day catch ratio of the sardine larvae

Spawning season	Day hauls			Night hauls			N/D*
	A	B	C	A	B	C	
1969-70	13	347	26.7	19	4291	225.8	8.46
1970-71	14	485	34.6	27	1538	56.9	1.64
1971-72	14	764	54.6	18	1435	79.7	1.46
Total	41	1596	38.9	64	7264	113.5	3.93

A = numbers of stations, B = numbers of larvae, C = mean numbers of larvae
N/D* = Night-Day catch ratio of sardine larvae
Note: The data from the fixed stations were not included

Table VI and Figure 11 show the N/D ratio for different length classes of larvae collected from all routine stations. Figure 11 shows that the N/D ratio increases exponentially with size. A fitted regression, using the least squares method, was obtained.

$$y = 0.34177\ e^{0.45196x}$$

where y = N/D ratio and x = length in mm. The N/D ratio for large larvae is higher than that observed for Pacific sardine larvae (Ahlstrom, 1965) and others. Furthermore, the small length classes in which little avoidance should occur, also show values two times higher at night than during the day. Because no large larvae (larger than 14 mm) were taken in daytime, a low towing speed in vertical hauls (0.8-1.0 m/sec.) could be the reason for low catches in day hauls, but this does not explain the undersampling of small size larvae.

TEMPERATURE AND SALINITY ON THE NURSERY GROUND

Spawning of the Brazilian sardine occurs in shelf waters when water temperature ranges from 16.8 to 27.2°C and salinity ranges from 35.3 to 36.0°/oo (Matsuura, 1975*a*).

TABLE VI - Night-Day catch ratio for different size classes of larvae

Class	Day	Night	N/D ratio
3.5	237	610	2.57
4.5	461	1160	2.52
5.5	454	865	1.91
6.5	175	1071	6.12
7.5	43	519	12.07
8.5	53	734	13.91
9.5	19	735	38.68
10.5	11	430	39.09
11.5	3	244	81.33
12.5	2	161	80.50
13.5	1	133	133.00
14.5		34	-
15.5		29	-
16.5		19	-
17.5		1	-
18.5		0	-
19.5		0	-
20.5		6	-
21.5		2	-
22.5		2	-
Total	1459	6755	
Note: Only routine station data were used			

Larvae occurred in waters with slightly higher temperatures and salinities (Tab. VII). The mean temperature in the three spawning seasons was 23.4°C, but larvae were present in the range from 14.6 to 27.4°C. In approximately 84% of the positive stations the temperature ranged from 21.0 to 26.9°C. The highest temperature at positive stations was observed in the 1970-71 spawning season. As recently shown (Matsuura, 1975*a*), a warm water mass remained over the continental shelf during this season and spawning was poor compared with the other two seasons. Larval abundance was also poor in 1970-71.

The mean salinity at positive stations was 35.6°/oo, ranging from 35.0 to 36.7°/oo. No salinity data were obtained for the 1970-71 season.

TABLE VII - Mean temperature and salinity at 10 m deep positive stations

	Temperature (°C)	Salinity (°/oo)
November 1969	20.9	35.8
January 1970	21.8	35.6
1969-70 spawning season	21.5	35.7
Nov.-Dec. 1970	22.9	-
January 1971	25.8	-
Feb.-Mar. 1971	25.5	-
1970-71 spawning season	24.8	-
December 1971	22.5	35.6
1971-72 spawning season	22.5	35.6

CATCH FREQUENCY

In order to calculate a survival curve, all sardine larvae were grouped in classes of 2 mm. Factors that affect the size frequency are avoidance by large larvae during daytime (Clutter & Anraku, 1968; Lenarz, 1973) and escapement of small larvae through mesh apertures (Vannucci, 1968; Lenarz, 1972). The number of larvae in each length class was plotted against standard length (Fig. 12). Data from the three spawning seasons were pooled to obtain the plot. The figure shows that the number of larvae longer than 6 mm decreases rapidly with increase in length. The 4 mm class was represented by fewer larvae than the 6 mm class; therefore, the 4 mm class was considered to be reduced by escapement and for this reason was omitted from the calculation of the reduction curve. The curve was fitted by the least squares method:

$$y = 91915\ e^{-0.4962x}$$

where y = number of specimens and x = length class of larvae. From this equation, we can calculate the mean survival of larvae, e.g. from 10,000 larvae in the 6 mm length class, only 4 will survive at the 22 mm class.

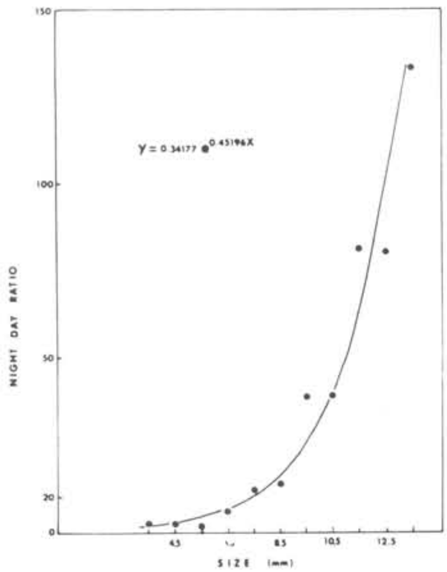


Fig. 11 - Night/day catch ratio of sardine larvae for different size classes. (All samples collected from routine stations).

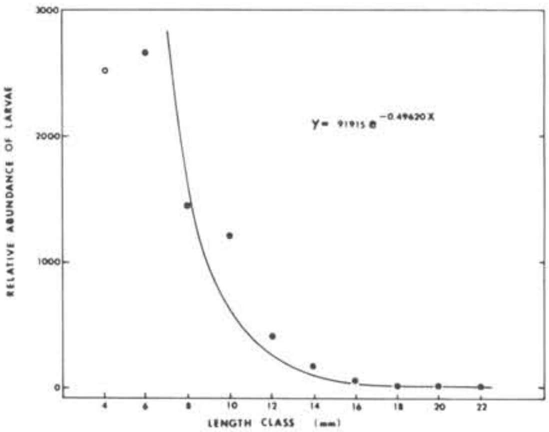


Fig. 12 - Survival curve of sardine larvae.

Obviously, survival obtained from this equation does not consider avoidance of large larvae and efficiency of the sampling gear; hence the survival in nature will be higher than that implied by the mortality coefficient of the equation.

DISCUSSION

When studying the early life history of a fish we must take into consideration that the life history of a species is a result of adaptation to environmental conditions throughout a long historical period. To survive, a species has to seek the best spawning and nursery grounds and to adapt itself to possible variations of the environmental conditions. It is well known that good or bad year-classes of a given stock are determined during the planktonic stages of eggs and larvae (Marr, 1956; Hempel, 1963; 1965; Gulland, 1965; May, 1974; and others). To understand the mechanism of variation of recruitment, it is essential to investigate the relationship between egg and larval stages and environmental conditions.

One factor that could affect recruitment is a change of environmental conditions on the spawning and nursery grounds. The change of the environmental conditions could directly affect survival of eggs and larvae: a) through productivity of planktonic food in the nursery ground (Nakai, 1960); b) by direct physiological influence on the mortality of eggs and larvae (Blaxter, 1969); c) by a change in transportation and/or distribution of the larvae (Nakai, *op. cit.*); d) by favoring spawning of a competing species that occupies the same trophic level in the ecosystem (Ahlstrom, 1965); and e) by favoring small predators such as chaetognaths, carnivorous copepoda etc. (Murphy, 1961). The references cited above have not proved a relationship between these factors and recruitment, but they have pointed out the possible consequences of them.

With this in mind, I hope in this paper to examine some critical problems regarding the early life history of the Brazilian sardine.

The main fishing ground of the sardine extends from Cabo de São Tomé (22°S) to the south of Cabo de Santa Marta Grande ($29^{\circ}20'$S), a range of about 1,075 km (580 nm). The main habitat of the sardine is formed by a half moon-shaped pocket of the continental shelf with its maximum width near Santos (220 km). Purse seiners in this region usually operate in the depth zone less than 50 m, but sometimes they fish in 51-100 m depth zone. We have no reliable information on the distribution of the sardine stock beyond the 100 m isobath, but the result of acoustic surveys on the continental shelf revealed few pelagic fish schools in the offshore region.

Through ichtyoplankton surveys the main spawning grounds have been located in three areas: Ilha Grande; Santos-Santa Catarina; and Cabo de São Tomé-Cabo Frio. Most spawning takes place a few hours prior to mid-night in the 51-100 m depth zone. Spawning occurs in shelf waters where water temperature ranges from 19 to 25°C and salinity from 35.0 to $36.0^{\circ}/oo$, and where the direct influence of the oceanic Brazil current is small. Spawning apparently occurs in an area where there is coastal upwelling of cold water (Matsuura, 1971).

The incubation period of eggs in the sea is short, being of only 24 hours duration (Matsuura, 1975*a*), but the larvae have a longer planktonic period. Dr. E. D. Houde of the University of Miami, succeeded in rearing larvae of *Sardinella anchovia* in the laboratory to 36.8 mm. The larvae required 21 days after hatching to reach 22 mm standard length at a water temperature of 26°C (personal communication).

The estimation of total larval abundance, in general, could not be done successfully because of: 1) avoidance of the larvae from the sampling gear and 2) escapement of small larvae through the mesh aperture. Furthermore, avoidance depends on the size of larvae, type of sampling gear, and time of day. The interaction of these factors makes calculation of larval abundance and mortality very difficult. Consequently, in this paper we calculated relative abundance of the larvae instead of total abundance and compared the relationship with environmental conditions.

The size frequency of the larvae revealed that they tend to disperse from the spawning ground in all directions over the continental shelf and show no tendency to be transported in one direction either from north to south or from the offshore to coastal region. But it is well known that juveniles occur in estuarine regions during autumn and winter and remain there for 6 or 9 months.

In the light of the present results, some questions can be raised. "How do the larvae appear in the coastal estuary region after dispersing all over the continental shelf? What is the transportation system involved?" We might also ask "It is indispensable for juveniles to approach the coastal region in which high productivity of food plankton is apparently present?" If the approach to the coastal region during the juvenile stage is indispensable to their life history, we could then ask "What would be the mortality rate of the larvae in offshore waters near the edge of the continental shelf (more than 200 km from the coast)?"

In order to answer some of these questions, I refer to Kondo's work on the distribution of larvae, juveniles and young stages of the Japanese anchovy (Kondo, 1969; 1974). He showed that there is a close relationship between occurrace of juveniles and the penetration of coastal water mass in to the estuary region. He suggested that not only the anchovy but also the sardine possibly can live in shelf waters during the juvenile stage and that the movement to the estuary is due to a search for food, not to a physiological need (personal communication). In addition, Dr. Houde informed that in his rearing experiments clupeids could tolerate a wide range of temperature and salinity.

As shown in the present results, large larvae were collected not only in the coastal region but also in offshore regions and they did not show any sign of starvation. If there is no active movement of juveniles to the coastal region, then we can assume that juveniles that appear in the estuary are only part of the total juvenile population and that juveniles can survive in shelf waters as well as in coastal waters. We observed a large school of *Euthynnus alletteratus* (Scombridae) preying on sardine juveniles 40-55 mm SL near Laje de Santos (52 km from the coast with 50 m sea depth). This observation supports the hypothesis proposed above.

Hoping to obtain information on these problems, we began the second phase of the ichtyoplankton survey using the Bongos net sampler which enables us to collect large larvae and juveniles. We hope thus to obtain information which will help us to clarify the problems mentioned above and understand the influence of environmental conditions on recruitment.

RESUMO

O presente trabalho apresenta a distribuição e abundância de larvas de sardinha-verdadeira, *Sardinella brasiliensis*, coletadas nas águas do sul do Brasil no período de 1969 a 1971.

A abundância relativa de larvas para três épocas de desova foi calculada usando o método apresentado por Smith (1972). De um modo geral, a abundância de larvas de cada subárea coincidiu com a dos ovos, mas sua distribuição abrangeu uma área um pouco maior do que a dos ovos.

A abundância relativa de larvas na época de desova de 1970-71 foi mais fraca do que as de 1969-70 e de 1971-72. Tal resultado confirma o obtido para a abundância de ovos, e, a razão deste fracasso, poderá ser atribuída ao fato de que massas de água mais quentes cobriram a área de desova na época de 1970-71.

A temperatura média nas estações oceanográficas onde as larvas foram coletadas, foi de 23,4°C, variando de 14,6 a 27,4°C. A salinidade média foi de 35,6°/oo, variando de 35,0 a 36,7°/oo.

A razão de captura noite/dia de larvas foi de 3.93. Foi calculada curva de sobrevivência. Foram analisadas a distribuição da freqüência de comprimentos das larvas e sua distribuição nas diferentes profundidades e subareas. O resultado mostrou que não há deslocamento de larvas em uma direção única, mas sim uma dispersão da área de desova para toda plataforma continental. São discutidos alguns problemas sobre a distribuição e migração de larvas e jovens de sardinha-verdadeira.

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APPENDIX I - Occurrence of sardine larvae

Sample number	Date	Time (h)	Position		Depth (m)	No. of larvae	Volume of water (l)	Towing depth (m)	No. of larvae/m²*
			Lat. (S)	Long. (W)					
Cruise of November 1969									
232	21/11	12:10	23°00'	41°51'	64	3	292	60	0.6
236	21/11	21:45	23°36'5	42°16'	313	49	102	80	38.4
238	22/11	00:35	23°18'5	42°24'	119	1	105	80	0.8
239	22/11	03:20	23°00'	42°33'	52	1	41	45	1.1
240	22/11	08:00	23°46'	42°46'5	224	4	185	80	1.7
244	22/11	19:10	23°28'5	43°29'5	105	23	116	80	15.9
245	23/11	00:00	23°51'5	43°19'	130	2	143	80	1.1
269	24/11	19:10	23°14'	44°12'	43	13	47	70	19.4
271	25/11	02:45	23°43'	44°30'5	74	15	59	70	17.8
279	25/11	23:00	23°39'	45°07'	31	2	38	30	1.6
Cruise of January 1970									
282	06/01	14:05	23°15'	41°45'	120	45	107	80	33.6
283	06/01	16:40	23°34'	41°36'	136	3	23	80	10.4
288	07/01	15:20	23°57'	41°46'	1.000	2	78	90	2.3
291	08/01	03:00	23°19'	42°25'	112	30	59	80	40.7
292	08/01	07:00	23°00'	42°30'	56	15	52	55	15.9
296	10/01	14:45	23°26'	42°55'	114	1	82	80	1.0
309	12/01	03:15	23°32'	43°27'	114	242	112	80	172.9
310	12/01	10:05	23°08'	43°38'	48	155	41	50	189.0
311	12/01	16:30	23°16'	44°09'	50	5	50	50	5.0
312	12/01	23:00	23°35'	44°01'	86	92	62	80	118.7
313	13/01	02:30	23°54'	43°56'	131	1.085	97	80	894.8
314	13/01	06:20	24°10'	43°52'	210	1	83	80	1.0
326	15/01	05:00	24°03'	44°27'	125	243	111	80	175.1
328	15/01	09:40	23°44'	44°30'	70	8	48	60	10.0
330	15/01	15:55	23°25'	44°39'	42	2	32	40	2.5
333	15/01	22:45	23°58'	44°58'	72	6	68	70	6.2
334	16/01	00:45	24°00'	44°57'	72	109	64	70	119.2
335	16/01	01:10	24°01'	44°56'	72	880	121	70	509.1
336	16/01	01:25	24°03'	44°55'	72	956	39	70	1715.9
337	16/01	01:50	24°05'	44°54'5	72	267	56	50	238.4
338	16/01	02:10	24°07'	44°54'	72	275	74	70	260.1
339	16/01	06:15	24°16'	44°49'	108	103	27	80	305.2
Cruise of November-December 1970									
482	28/11	09:50	22°00'	40°35'	44	3	58	40	2.1
483	28/11	16:00	22°04'	40°09'	105	3	147	80	1.6
485	30/11	18:35	22°22'	41°07'	42	1	39	35	0.9
486	30/11	22:15	22°16'	41°20'	22	2	12	20	3.3
491	02/12	03:00	23°20'	42°37'	105	97	48	80	161.7
492	02/12	08:20	23°03'	42°47'	56	6	43	50	7.0
495	02/12	22:35	23°40'	43°25'	120	76	76	80	80.0
496	03/12	04:10	24°05'	43°25'	205	39	71	80	43.9
503	04/12	12:30	23°54'	44°54'	66	2	61	60	2.0
504	04/12	17:30	24°13'	44°51'	92	10	71	80	11.3
505	04/12	20:25	24°38'	44°48'	140	218	63	80	276.8
508	05/12	14:05	24°47'	45°34'	80	403	77	75	392.5
509	05/12	18:30	24°27'	45°46'	64	540	64	60	506.3
510	05/12	23:05	24°07'	46°51'	42	73	39	35	65.5
518	07/12	17:15	25°59'	47°15'	81	4	66	75	4.5
520	08/12	01:35	25°20'	47°42'	75	5	20	20	5.0

* $y = \frac{d.x}{v}$

y = number of sardine larvae per square meter
d = towing depth
x = number of larvae collected
v = volume of water filtered

APPENDIX I - Occurrence of sardine larvae (cont.)

Sample number	Date	Time (h)	Position Lat. (S)	Position Long. (W)	Depth (m)	No. of larvae	Volume of water (l)	Towing depth (m)	No. of larvae/m²*
Cruise of January 1971									
531	16/01	05:00	23°07'	43°09'	58	18	46	50	19.6
535	16/01	18:50	23°32'	43°32'	114	3	65	80	3.7
536	16/01	21:40	23°14'	43°40'	57	19	42	50	22.6
537	17/01	04:55	23°13'	44°17'	43	19	27	38	26.7
538	17/01	11:10	23°32'	44°08'	69	12	62	70	13.5
542	17/01	22:15	24°07'	44°28'	133	4	82	80	3.9
543	18/01	01:00	23°44'	44°36'	70	21	59	65	23.1
544	18/01	03:10	23°35'	44°40'	51	47	41	42	48.1
545	18/01	06:30	23°26'	44°45'	40	3	25	35	4.2
546	18/01	09:15	23°33'	45°00'	36	2	27	30	2.2
548	18/01	13:35	23°46'	45°11'	35	7	49	30	4.3
549	18/01	18:25	23°57'	45°06'	58	5	45	55	6.1
550	18/01	19:40	24°07'	45°02'	74	15	56	70	18.8
551	18/01	22:30	24°25'	44°54'	112	33	73	80	36.2
552	19/01	01:00	24°44'	44°44'	154	1	69	80	1.2
554	19/01	05:50	24°36'	45°20'	86	49	70	80	56.0
604	20/01	20:15	23°50'	45°40'	21	1	13	15	1.2
607	21/01	03:00	24°14'	46°10'	39	129	38	35	118.8
608	21/01	04:55	24°24'	46°05'	50	87	46	45	85.1
611	21/01	15:00	25°19'	45°41'	116	25	153	60	9.8
612	21/01	17:45	25°32'	46°10'	128	1	69	80	1.2
613	21/01	21:10	25°14'	46°19'	81	2	89	80	1.8
614	22/01	00:40	24°55'	46°27'	62	7	73	55	5.3
615	22/01	03:30	24°37'	46°35'	45	27	62	39	17.0
616	22/01	09:00	24°18'	46°44'	22	4	27	15	2.2
Cruise of February-March 1971									
617	27/02	08:45	28°49'5	49°07'5	34	4	39	30	3.1
618	28/02	01:15	28°56'	48°51'	60	23	64	55	19.8
622	28/02	22:25	28°25'	48°01'	105	4	107	80	3.0
623	01/03	01:40	28°20'	48°26'	79	3	73	75	3.1
641	05/03	10:05	24°24'	46°18'	45	4	-	40	-
642	05/03	15:00	24°49'	46°01'	66	1	-	60	-
646	06/03	13:00	24°38'	45°05'	102	1	-	80	-
647	06/03	16:50	24°20'	45°12'	78	1	-	75	-
651	07/03	13:45	23°44'	44°36'	65	1	-	60	-
666	10/03	15:30	22°31'	41°48'	32	8	-	25	-
668	11/03	01:35	22°53'	41°08'5	87	7	-	80	-
670	11/03	15:30	22°30'	41°35'	120	1	-	80	-
671	11/03	20:00	22°16'	40°50'	60	2	-	55	-

* $y = \frac{d.x}{v}$

y = number of sardine larvae per square meter
d = towing depth
x = number of larvae collected
v = volume of water filtered

APPENDIX I - Occurrence of sardine larvae (cont.)

Cruise of December 1971 (Vertical haul)								
Sample number	Date	Time (h)	Position		Depth (m)	No. of larvae	Towing depth (m)	No. of larvae/m^2
			Lat. (S)	Long. (W)				
680	11/12	19:00	25°49'	47°58'	37	10	32	11.1
682	11/12	20:00	26°02'5	47°41'5	58	237	50	263.3
684	11/12	22:15	25°49'	47°26'	61	137	56	152.2
686	12/12	00:45	25°35'	47°39'	45	16	40	17.8
696	12/12	19:15	25°18'	46°58'	60	59	55	65.6
698	12/12	21:30	25°01'	47°08'	42	27	37	30.0
706	13/12	11:00	25°04'	46°44'	60	6	60	6.7
708	13/12	14:15	25°32'	46°38'	100	206	95	228.9
710	13/12	17:25	25°09'	46°19'	76	136	80	151.1
712	13/12	20:05	24°49'	46°20'	62	436	55	484.4
714	13/12	22:30	24°29'	46°26'	47	31	42	34.4
718	14/12	06:30	24°02'	46°10'	17	3	12	3.3
722	14/12	12:15	24°41'	46°04'	63	14	60	15.6
724	14/12	14:50	25°00'	46°00'	82	65	80	72.2
726	14/12	17:15	24°50'	45°41'	80	244	75	271.1
727	14/12	19:10	24°30'	45°45'	67	9	42	10.0
729	14/12	21:30	24°10'	45°48'	50	120	45	133.3
731	15/12	00:25	23°50'	45°52'	23	86	20	95.6
733	15/12	03:25	23°54'	45°31'	33	4	28	4.4
761	16/12	09:15	24°18'	45°05'	82	2	77	2.2
765	16/12	12:50	23°52'	45°10'	39	8	36	8.9
771	16/12	20:30	23°46'	44°51'	55	65	50	72.2
773	17/12	01:50	24°07'	44°49'	92	44	80	48.9
777	17/12	07:20	24°08'	44°31'	130	1	80	1.1
779	17/12	10:25	23°42'	44°30'	72	4	70	4.4
783	17/12	15:40	23°08'	44°28'	31	6	26	6.7
787	17/12	20:55	23°33'	44°11'	72	45	65	50.0
789	18/12	01:05	23°53'	44°07'	56	10	115	11.1
793	18/12	06:50	23°26'	43°51'	82	45	77	50.0
797	18/12	12:50	23°06'	43°32'	37	24	35	26.7
803	18/12	20:30	23°35'	43°05'	122	77	115	85.6
805	18/12	22:35	23°20'	43°08'	104	22	80	24.4

Note: Filtration coefficient = 0.9

APPENDIX I - Occurrence of sardine larvae (cont.)

Cruise of December 1971 (Horizontal haul)

Sample number	Date	Time (h)	Position		Depth (m)	No. of larvae	Volume** of filtered water (m^3)	No. of larvae/100 m^3
			Lat. (S)	Long. (W)				
681	11/12	19:15	25°49'	47°58'	35	6	(232)	2.6
683	11/12	20:17	26°02'5	47°41'5	58	272	(232)	117.2
685	11/12	22:45	25°49'	47°26'	61	248	(232)	106.9
687	12/12	01:45	25°35'	47°39'	45	48	(232)	20.7
693	12/12	13:54	25°16'	47°26'	38	30	(232)	12.9
697	12/12	19:32	25°18'	46°58'	60	1845	(232)	795.3
699	12/12	22:03	25°01'	47°08'	42	35	(232)	15.1
701	13/12	01:37	24°40'	47°16'	19	10	(232)	4.3
703	13/12	05:30	24°26'	46°54'	24	10	(232)	4.3
705	13/12	08:21	24°45'	46°50'	42	1	(232)	0.4
707	13/12	11:10	25°04'	46°44'	60	2	(232)	0.9
711	13/12	17:45	25°09'	46°19'	76	292	(232)	125.9
713	13/12	20:12	24°49'	46°20'	62	3186	(232)	1373.3
715	13/12	22:45	24°29'	46°26'	47	649	(232)	279.7
717	14/12	03:55	24°10'	46°30'	22	7	(232)	3.0
721	14/12	09:37	24°22'	46°08'	45	41	(232)	17.7
723	14/12	12:40	24°41'	46°04'	63	89	(232)	38.4
725	14/12	15:05	25°00'	46°00'	82	20	(232)	8.6
728	14/12	19:26	24°30'	45°45'	67	149	(232)	64.2
730	14/12	21:40	24°10'	45°48'	50	1784	(232)	769.0
732	15/12	00:34	23°50'	45°52'	23	402	(232)	173.3
734	15/12	03:41	23°54'	45°31'	33	24	(232)	10.3
760	16/12	07:02	24°33'	45°24'	77	127	(232)	54.7
766	16/12	13:00	23°52'	45°10'	39	23	(232)	9.9
770	16/12	17:55	23°26'	44°55'	30	1	(232)	0.4
772	16/12	20:35	23°46'	44°51'	55	2982	(232)	1285.3
774	16/12	01:55	24°07'	44°49'	92	132	(232)	56.9
778	17/12	07:35	24°08'	44°31'	130	2	(232)	0.9
780	17/12	10:40	23°42'	44°30'	72	3	(232)	1.3
782	17/12	13:15	23°24'	44°34'	40	26	(232)	11.2
784	17/12	15:50	23°08'	44°28'	31	55	(232)	23.7
786	17/12	18:07	23°13'	44°15'	42	2	(232)	0.9
788	17/12	21:05	23°33'	44°11'	72	284	(232)	122.4
790	18/12	01:32	23°53'	44°07'	117	83	(232)	35.8
792	18/12	04:25	23°46'	43°47'	118	15	(232)	6.5
794	18/12	07:16	23°26'	43°51'	82	13	(232)	5.6
796	18/12	10:26	23°06'	43°55'	30	2	(232)	0.9
798	18/12	13:02	23°06'	43°32'	37	22	(232)	9.5
800	18/12	15:45	23°25'	43°28'	100	1	(232)	0.4
804	18/12	20:52	23°35'	43°05'	122	21	(232)	9.1
806	18/12	23:02	23°20'	43°08'	104	187	(232)	80.6
808	19/12	00:39	23°06'	43°11'	56	14	(232)	6.0

** Estimated volume

APPENDIX II - Occurrence of sardine larvae at fixed stations (Vertical hauls)

Cruise	Day	Time	Position		Depth (m)	Mean no. of larv./haul	Number hauls	Mean water vol. (m^3)	Towing depth (m)	Mean no. of larv./m^2
			Lat. (S)	Long. (W)						
Nov. '69	23.24	Night	23°32'	44°04'	78	257	6	137	70	134
	24	Day				9	6	115	70	5
Jan. '71	19.20	Night	24°18'	45°28'	65	392	11	116	60	203
	19.20	Day				0.5	13	68	60	0.4