DISTRIBUTION AND ECOLOGY OF PELAGIC FISHES STUDIED FROM EGGS AND LARVAE IN AN UPWELLING AREA OFF SPANISH SAHARA

MAURICE BLACKBURN[1] AND WALTER NELLEN[2]

ABSTRACT

Fish eggs and larvae were taken in vertical zooplankton hauls in a small upwelling area off Spanish Sahara. Series of hauls were made repetitively from March to May 1974, sometimes with accompanying hydrocasts. About 58% of the eggs and 72% of the larvae belonged to the following pelagic species: *Sardina pilchardus*, *Engraulis encrasicholus*, *Trachurus* spp., and *Maurolicus* sp. It was estimated from contemporaneous current meter data and other information that the eggs of those species were spawned very close in time and space to where they were collected. Thus adult *Sardina* and *Engraulis* appeared to occur typically on the continental shelf, adult *Trachurus* at the edge of the shelf, and adult *Maurolicus* over the continental slope. These distributions were verified for *Sardina* and *Trachurus* from fishing results of Polish vessels. Acoustically detected concentrations of fish were identified by species according to those results.

The area of abundance of *Sardina* was characterized by maxima of phytoplankton and small zooplankton. Abundance of *Sardina* eggs changed with time, because of variations in the size of the adult population in the area (acoustically estimated) and in its production of eggs. The major change in population size coincided with a similar change in the amount of food, especially phytoplankton, available. Variations in egg production may have been associated with the mean temperature in the water column, since eggs were scarce when the mean was below 16.5°C even when adults were abundant.

A multidisciplinary group of U.S. scientists made an oceanographic study off Spanish Sahara from March through May 1974. The program is called Coastal Upwelling Ecosystems Analysis (CUEA) and is part of the International Decade of Ocean Exploration (IDOE). The operation off Spanish Sahara (Figure 1) was called JOINT-I. It made observations of many kinds over an upwelling area which was small enough to be studied synoptically in great detail repetitively under various conditions such as changes in the wind field. Most of the work was done from the coast to long. 18°00′W, between lat. 21°30′ and 21°50′N. The continental shelf in this area is bounded by the 100-m isobath, beyond which there is a steep slope (Figures 2-4).

Pelagic fish are a major component of the animal biomass in the area. They support large fisheries conducted by several nations. It was the task of a small group of CUEA investigators to estimate biomass of pelagic fishes by species and, if possible, by trophic levels during JOINT-I; to show the distributions of these biomasses in space and time;

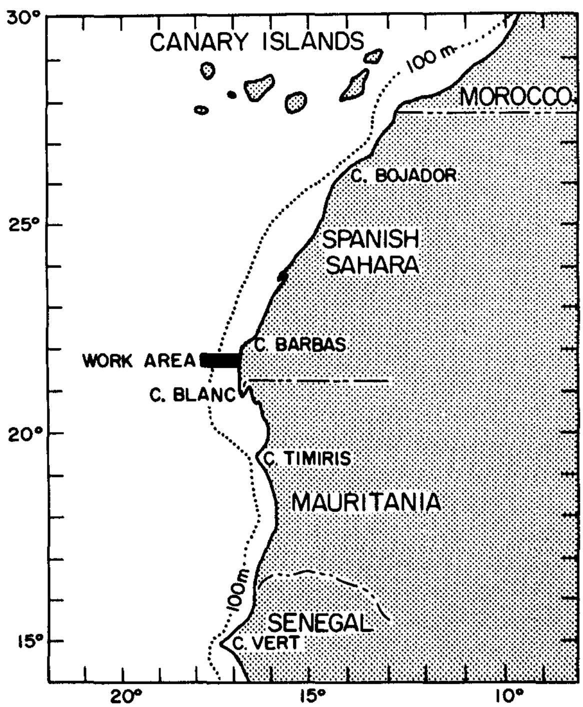

FIGURE 1.—Part of northwest Africa showing the principal area of JOINT-I work.

[1]Institute of Marine Resources, University of California, La Jolla, CA 92093.
[2]Institut für Meereskunde, Universität Kiel, Kiel, West Germany.

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and to explain the distributions in terms of environmental parameters. Biomass of total pelagic fish was estimated acoustically (Thorne et al. in press). Partitioning it by species was to be based on the following: contemporaneous catches by fishing or fishery research vessels, samples of fish taken by the CUEA ships, fish eggs and larvae from the zooplankton catches of the CUEA ships, and the literature. In the outcome, only the fish eggs and larvae (ichthyoplankton) were useful during the cruise. Good information on fish catches by other vessels was not received until many months later, sampling from the CUEA ships was unproductive for adults of epipelagic species, and the literature did not resolve all questions. The ichthyoplankton results and the fish catches agreed as to the principal species present in different parts of the area. Acoustically detected concentrations of fish (Thorne et al. in press) were identified accordingly.

This paper gives the principal results of work on the eggs and larvae. It then uses the egg distributions to estimate contemporaneous distributions of adults of some species and compares those with data from contemporaneous fish catches and the literature. Finally the paper attempts to explain the distributions of an abundant species, *Sardina pilchardus* (Walbaum), according to environmental data collected at the same time as the eggs.

MATERIAL AND METHODS

Zooplankton

The fish eggs and larvae were sorted from the zooplankton catches made during JOINT-I and partly identified by Blackburn. Most of the identifications were made later by Nellen. The zooplankton catches were made and processed, apart from the ichthyoplankton, by R. I. Clutter. Some observations on the zooplankton in general are relevant in this study. A more complete report on JOINT-I zooplankton will appear elsewhere.

The net hauls for zooplankton were made vertically from 200 m or the bottom, whichever was less, to the sea surface. Two cylindro-conical, nonclosing Bongo plankton nets mounted side by side were used. Each net had a mouth diameter of 60 cm and a uniform mesh size of 102 μm. Nets were lowered at 40 m/min and hauled up at 60 m/min. A calibrated digital flowmeter was mounted in the mouth of each net. Volume of water filtered by the two nets ranged from 12 to 158 m^3, depending mainly upon the haul length. Only one net was used in series 1 and 2 (Table 1).

Processing was as follows, with exceptions shown in footnotes to Table 1. The catches from the two nets were immediately combined and suspended in water. The suspension was shaken and four ¼-aliquots were decanted. Each of two aliquots was filtered through a series of sieves (mesh sizes 1,050, 505, 223, and 102 μm) until no more water dripped. This procedure yielded subsamples of zooplankton in four size ranges, approximately 100 to 200, 200 to 500, 500 to 1,000, and > 1,000 μm. The subsamples from one aliquot were scraped from the filters, blotted on paper towels until no more water appeared, and weighed. The subsamples from the other aliquot were washed off the filters and preserved in Formalin.[3] The fish eggs and larvae were sorted from the preserved 500- to 1,000- and >1,000-μm samples and combined. The four wet weights per haul were standardized in grams under 1 m^2 of sea surface. Allowance was made trigonometrically for effects

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

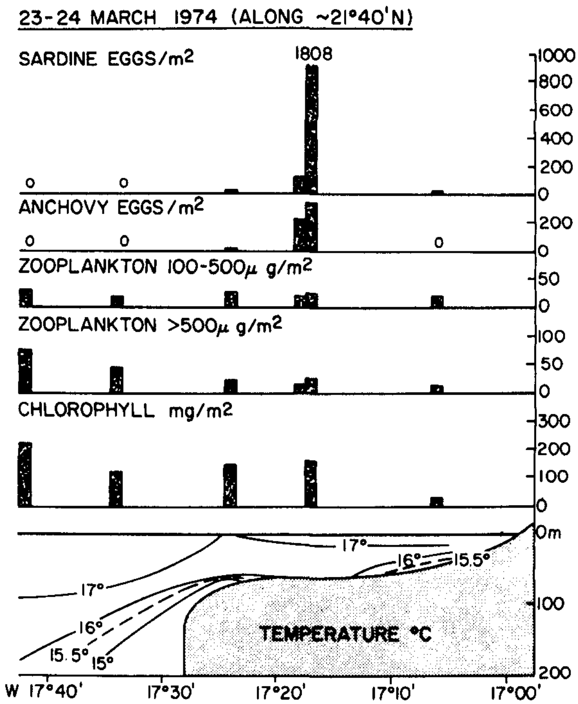

FIGURE 2.–Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40'N on 23-24 March 1974 (series 5 in Table 1).

TABLE 1.—Means of variables for the water column at stations from long. 17°08′ to 17°25′W, in series of stations along lat. 21°40′N together with indications of relative abundance of adult sardines explained in Discussion.

Series	Date 1974	No. of stations	Sardine eggs/m²	Anchovy eggs/m²	Temp. °C	Chlorophyll (mg/m²)	Small zooplankton (g/m²)	Abundance of adult sardines
1	8- 9 Mar.	[1]4	10	1	16.5	115	[2]85	Low
2	10-11 Mar.	[3]4	4	0	16.5	30	[2]90	Low
3	15-17 Mar.	[4]4	0	0	16.0	193	[5]78	([6])
4	18 Mar.	3	5	30	16.0	71	[5]27	([6])
5	23-24 Mar.	3	648	195	16.5	164	20	High
6	1- 2 Apr.	2	0	57	16.5	52	19	Low
7	5 Apr.	3	8	5	15.5	187	24	Medium
8	12-13 Apr.	[7]3	54	36	17.0	147	32	Medium
9	22-23 Apr.	3	7	19	16.0	192	28	Medium
10	9-10 May	4	431	2	16.5	323	53	High

[1]Three stations for eggs and zooplankton.
[2]Estimated from settled volumes at 1 ml = 0.8 g. Not corrected for phytoplankton contamination.
[3]One station for chlorophyll.
[4]Two stations for eggs and zooplankton.
[5]Estimated according to mean ratio of small to total zooplankton at same longitudes in other series, namely 67%. Not corrected for phytoplankton contamination.
[6]Unknown.
[7]Two stations for chlorophyll.

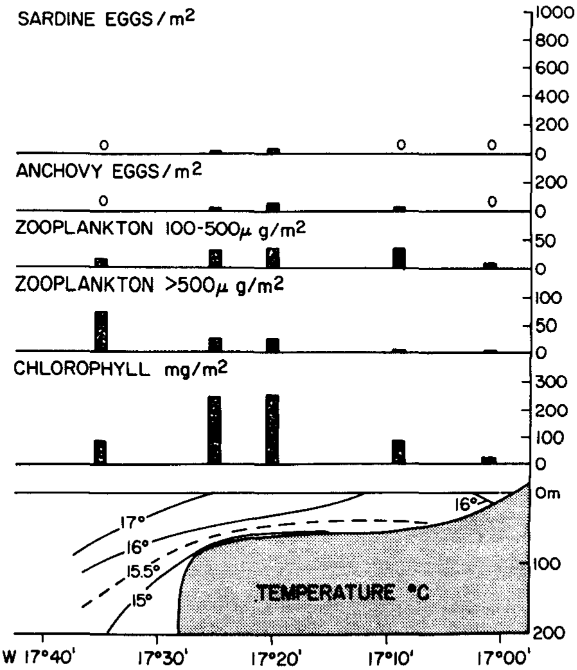

FIGURE 3.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 22-23 April 1974 (series 9 in Table 1).

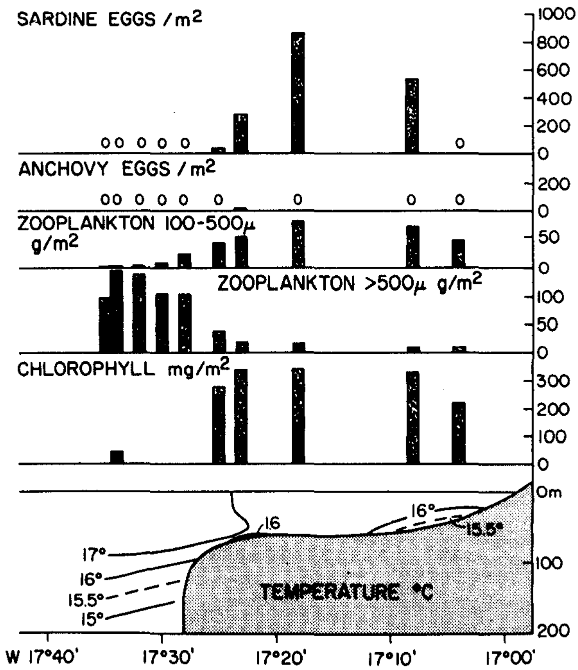

FIGURE 4.—Distribution of sardine eggs, anchovy eggs, and environmental parameters along lat. 21°40′N on 9-10 May 1974 (series 10 in Table 1).

of nonzero wire angles on distance covered by the net. To determine effects of clogging, the expected flow of water through the net was compared with that indicated by the flowmeter revolutions. Counts of various kinds of fish eggs and larvae from each haul were standardized in numbers under 1 m² of sea surface.

In general the spatial distribution of zooplankton biomass was similar for the 100- to 200- and 200- to 500-μm fractions. The two fractions of larger-sized plankton were also distributed similarly, but not like the smaller-sized fractions. Thus we distinguish only zooplankton at 100 to 500 μm and at >500 μm (Figures 2-4). Most of the biomasses given here, but not all (see Table 1), have been corrected for contamination by phytoplankton. The correction was made as follows. The amount of chlorophyll *a* was determined in a ¼-aliquot by SCOR methods (UNESCO 1966) and partitioned among the four subsamples according to inspection of the preserved samples. The inspection indicated approximate relative amounts of phytoplankton in the samples. The chlorophyll weight for each subsample was converted to carbon following Lorenzen (1968) and then to wet weight according to Cushing et al. (1958). The correction generally reduced the original biomass by less than 10% but occasionally up to 30%. All biomasses shown in Figures 2 to 4 have been corrected.

The preserved samples of zooplankton <500 μm were not examined for ichthyoplankton, because few specimens (except some newly hatched larvae) were expected to pass through a 500-μm sieve. For eggs of Engraulidae, which are oval and measured from 500 to 580 μm (mean 570 μm) in transverse diameter in our material, our numbers per haul could have been slightly too low because of losses through the 500-μm sieve. It is unlikely that these losses were high. During a later cruise (AUFTRIEB 1975) in the same area, we counted engraulid eggs in the catches of two Bongo nets of uniform mesh sizes, 300 and 500 μm, but otherwise identical and hauled side by side in the same net assembly. Egg numbers were 122 and 145, so the 300-μm net retained no more than the 500-μm net.

Temperature and Chlorophyll *a*

These properties were measured from hydrographic casts which used plastic 5-liter Niskin bottles with reversing thermometers. Sampling depths in the upper 200 m were usually 0, 3, 10, 20, 30, 50, 75, 100, 150, and 200 m, depending on the bathymetry. Concentrations of chlorophyll *a* were determined by SCOR methods (UNESCO 1966) and integrated in milligrams per square meter. The integration program summed the area of each depth integral using the area formula of a trapezoid. Samples for chlorophyll *a* were generally not taken below 75 or 100 m, because results of other casts showed little chlorophyll below those depths.

Area and Periods of Study

Almost all the zooplankton hauls and hydrographic casts of JOINT-I were made in the area shown in Figures 1 and 5. They were generally made along an east-west line at about lat. 21°40′N, where series of hauls and casts (not always together) were frequently repeated. Figure 5A shows the positions of all zooplankton hauls made in the area. Nine other hauls were scattered in space and time in adjacent areas, and are not used in this paper. No distinction is made here between day and night hauls. Hauls on the shelf were made mostly by day and those on the slope mostly at night. Eggs are of more interest than larvae in this study as explained above and should have been equally available by day and night. Larvae might have avoided the nets more by day than by night.

The total period of JOINT-I in which zooplankton hauls were made was 8 March to 10 May 1974. It was divided by port calls into three parts, Legs 1, 2, and 3 (Table 2). The periods of these legs (first to last zooplankton haul) were 8 to 24 March, 1 to 14 April, and 22 April to 10 May.

Ten series of hauls were made together with hydrographic casts along lat. 21°40′N, each series occupying 1 to 3 days. Figures 2 to 4 show data for some of the series and Table 1 summarizes data for all of them.

TABLE 2.—Principal categories of fish eggs and larvae taken on JOINT-I in the area of Figure 5, showing numbers per square meter averaged for hauls on each leg of the cruise and summed for the cruise.

Category	Leg 1 (41 hauls)	Leg 2 (22 hauls)	Leg 3 (38 hauls)	Cruise total No.	Cruise total %
Eggs:					
Sardina	77.7	10.9	75.9	6,308	35.1
Engraulis	19.0	16.1	14.8	1,695	9.4
Maurolicus	6.2	29.3	15.4	1,487	8.3
Soleidae	9.9	15.0	8.8	1,071	6.0
Carangidae	4.8	0.7	18.1	897	5.0
Others	55.3	56.1	79.8	6,531	36.2
Larvae:					
Clupeoidei	60.5	82.9	84.7	7,522	69.7
Heterosomata	24.1	16.5	5.0	1,541	14.3
Sparidae	6.6	22.6	9.3	1,120	10.4
Maurolicus	1.2	1.3	2.8	185	1.7
Myctophidae	0.9	0.7	1.3	102	0.9
Carangidae	0.4	2.1	0.4	78	0.7
Others	3.5	2.3	1.5	251	2.3

IDENTIFICATION AND ENUMERATION OF EGGS AND LARVAE

The eggs and larvae from all stations in Figure 5A were identifiable in the categories shown in Table 2. Most of the identifications were made at the Institut für Meereskunde from the large collections, literature, and experience of northwest

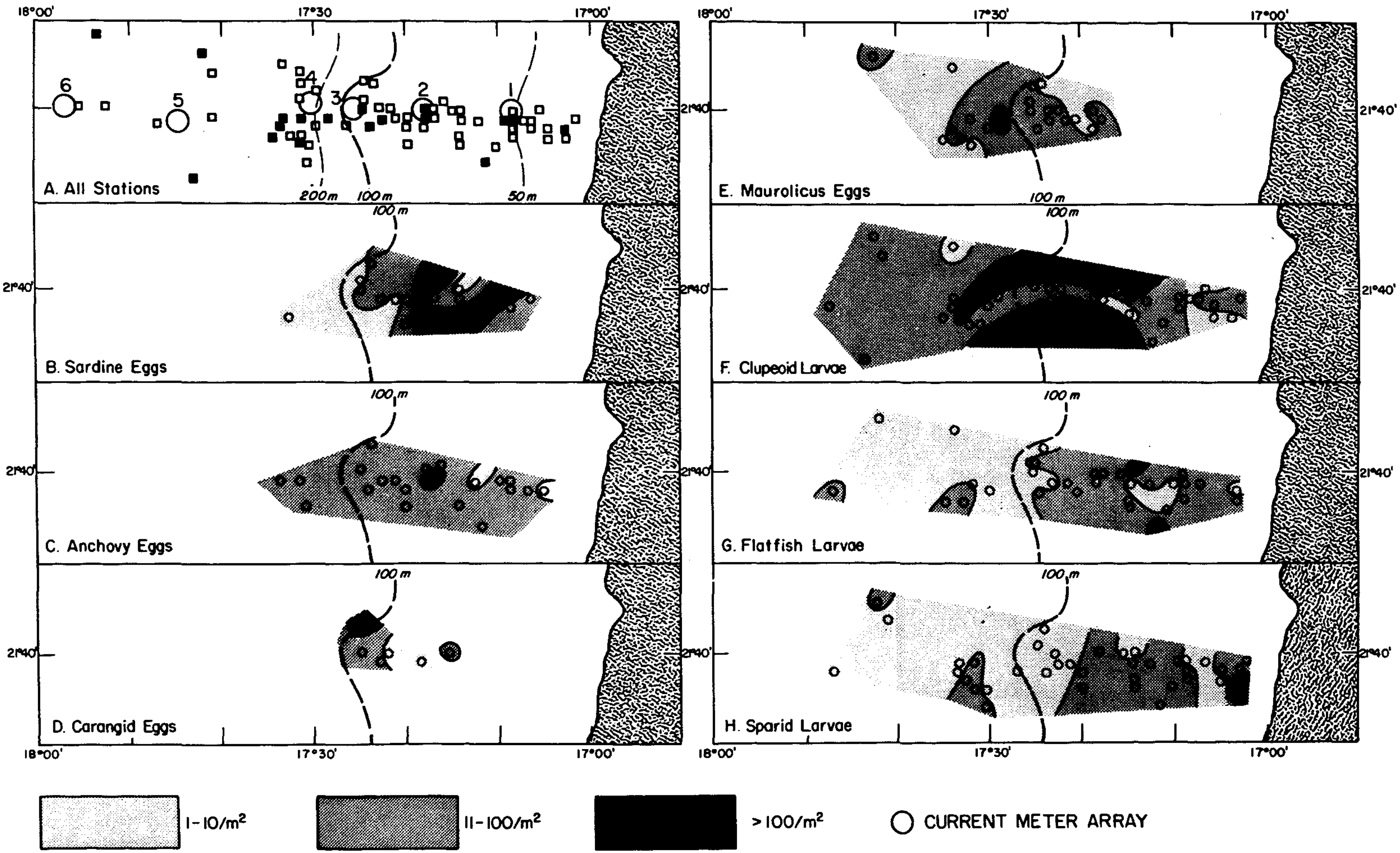

FIGURE 5.—Distributions of fish eggs and larvae from the zooplankton of JOINT-I, between lat. 21°30′ and 21°50′N. A. Positions of all zooplankton hauls. Solid squares show where hauls were repeated. Circles show current meter arrays. B to H. Positions of positive hauls for kinds of eggs and larvae stated, contoured in numbers per square meter.

African ichthyoplankton available there. Identifications of larvae were more complete than those of eggs, as is usual in work of this kind.

Among the eggs the following kinds, which are well known in literature because of conspicuous characters, were easily identified: *Sardina*, *Engraulis*, *Maurolicus*, and Soleidae.

The eggs of *Sardina* and *Sardinops* are alike but the only species of either genus recorded off northwest Africa is *Sardina pilchardus* (Walbaum). *Sardina pilchardus* occurs off southwestern Europe, in the Mediterranean, and on the coast of northwest Africa as far south as lat. 20°N (de Buen 1937; Larrañeta 1960; Maurin 1968; Furnestin and Furnestin 1970). We identify the eggs as that species, which we later call "sardine." Egg diameters in our material range from 1.33 to 1.50 mm (mean 1.46 mm), slightly lower than those of the same species in the Mediterranean (1.40 to 1.70 mm; Larrañeta 1960). However they are considerably larger than those of *Sardinella*, the other clupeid genus that might occur, whose eggs measure 1.1 to 1.3 mm off west Africa (Marchal 1967).

Engraulid eggs were easily recognizable by their oval shape. Two species of Engraulidae have been reported off southern Spanish Sahara, *Engraulis encrasicholus* (Linnaeus) and *Anchoa guineensis* (Rossignol and Blache) (Lozano Cabo 1970; Bravo de Laguna Cabrera and Santaella Alvarez 1973). No adults were obtained during JOINT-I, so identification has been made from the eggs. Eggs of *E. encrasicholus* range from 0.90 to 1.9 mm in length and 0.42 to 1.2 mm in maximum breadth (Demir 1963); corresponding ranges for *A. guineensis* are 1.05 to 1.23 and 0.54 to 0.58 mm, respectively (Marchal 1966), and for our material 1.33 to 1.50 and 0.50 to 0.58 mm, respectively. Our eggs could belong to either species as far as breadth is concerned, but only to *E. encrasicholus* on the basis of length. We refer to this species later as "anchovy." It occurs off western Europe and in the Mediterranean and Black seas, as well as off northwest Africa, where its southern limit is not exactly known (de Buen 1931 and references above).

The eggs of *Maurolicus* (family Gonostomatidae) are those of *M. muelleri* (Gmelin), which has been recorded off southern Morocco and northern Mauritania (Maurin et al. 1970). The eggs of Soleidae could belong to several species recorded off Spanish Sahara (Maurin et al. 1970; Lozano Cabo 1970).

The carangid eggs were identified with help from E. H. Ahlstrom, who noted that some of them resembled *Trachurus*. They measured about 0.9 to 1.0 mm, in the size range reported for *T. trachurus* (Linnaeus) off northwest Africa (Kiliachenkova 1970). Three other species of *Trachurus* have been recorded off northwest Africa, namely *T. picturatus* (Bowdich), *T. trecae* Cadenat, and *T. mediterraneus* Steindachner. *Trachurus picturatus* is not common and *T. mediterraneus* may be a subspecies of *T. trachurus* (Letaconnoux 1951; Maurin et al. 1970; Witzell 1973). The three most common carangids in the area of Figure 1 are *T. trachurus*, *T. trecae*, and *Caranx rhonchus* Geoffroy St. Hilaire. The first two spawn off Spanish Sahara from about November to April, and *C. rhonchus* from about May to August (Boely et al. 1973). Aboussouan (1967) and Conand and Franqueville (1973) described larvae of these species. The distinctions between larvae of *Trachurus* and *C. rhonchus* are slight and the larvae of the two *Trachurus* species cannot be distinguished. Most of our carangid eggs are probably *Trachurus* ("horse mackerel"), which was abundant along the coast of Spanish Sahara between March and June 1974. The most likely species is *T. trachurus*. All specimens of *Trachurus* taken in research trawling during JOINT-I were that species. We took 22 post-larval and juvenile *Trachurus* up to 6 cm long in various hauls of a micronekton net during JOINT-I. All specimens large enough to be identified were *T. trachurus*. We identified carangid eggs conservatively and so may have failed to count some.

The remaining eggs, 36% of the total, were of several kinds not readily identifiable by us. Probably few of them were eggs of pelagic species, except possibly some carangids as suggested above. They lacked segmented yolks and thus were probably not Isospondyli. *Scomber japonicus* Houttuyn is a pelagic species that spawns mostly from December to February in the vicinity of Cap Blanc (references in Blackburn 1975). If *Scomber* eggs occurred in our collections, they were probably not abundant. We found no *Scomber* larvae. Other abundant pelagic species of the JOINT-I area spawn principally in summer (Blackburn 1975). Thus unidentified eggs probably were mostly demersal species, as were 25% of larvae, i.e., Heterosomata and Sparidae, as shown in Table 2. Spatial distribution of unidentified eggs resembled that of the demersal larvae (Figure 5G, H).

All larvae were identified to some taxon. Closer identifications could have been made in some cases but were not needed for this study. Clupeoids predominated. Many clupeoids were small (about 5 to 10 mm) and had lost part of the intestine, probably because of the repeated filtering of the zooplankton. Clupeidae and Engraulidae were not separately counted, but both families were well represented. Preanal myomeres were counted in randomly selected good clupeid specimens. These counts ranged from 41 to 43, which agree with *Sardina pilchardus* (Saville 1964). Comparable ranges in two other west African clupeids, *Sardinella aurita* Valenciennes and *Sardinella eba* (Valenciennes), are respectively 38 to 41 and 35 to 38 (Conand and Fagetti 1971). These species were looked for because Maigret (1972) found *Sardinella* larvae near the area of JOINT-I in May. Evidently they were absent or scarce in our material. They were absent or scarce in the 1974 fish catches reported to us. We conclude that our clupeoid larvae were *Sardina pilchardus* and *Engraulis encrasicholus*, like the clupeoid eggs. Carangid larvae were scarce. Larvae in the last line of Table 2 ("Others") were *Merluccius*, *Callionymus*, Paralepididae, and Anguilliformes (leptocephali).

Table 2 shows that *Sardina* dominated the egg samples. It shows also that abundance of *Sardina* eggs varied greatly during JOINT-I, which is discussed later.

SPATIAL DISTRIBUTION OF EGGS AND LARVAE

Figure 5B-H shows distribution and abundance of the principal kinds of eggs and larvae identified, during the whole period of cruise JOINT-I. All positive hauls for each kind were charted and the observed numbers per square meter were contoured without averaging. The purpose of Figure 5 is to show where maxima and minima occurred, although some of them were more prominent at those locations on some legs of the cruise than on others. For example the midshelf maximum of *Sardina* eggs was not prominent on Leg 2, when eggs were scarce everywhere (cf. Tables 1, 2). We were most interested in the pelagic species and especially in their eggs, whose distributions should be close to those of the adults. Furthermore, the methods employed were more suitable for eggs than larvae. Some larvae could have avoided the nets, especially in daytime.

Sardine and anchovy eggs were absent close inshore, most abundant on the continental shelf between the 50- and 100-m isobaths, and occasionally found just beyond the shelf edge (Figure 5B, C). These eggs occur most abundantly in the uppermost 25 m of the water column (Furnestin and Furnestin 1959; Larrañeta 1960; Demir 1963), where temperatures on JOINT-I were about 16° to 17°C (Figures 2-4). The eggs take about 3 days to hatch at such temperatures (Larrañeta 1960; Demir 1963), so their average age should be about 1.5 days.

Six vertical arrays of current meters were moored during JOINT-I (Figure 5A). No ichthyoplankton were collected near array number 6. The other arrays operated for periods of about 20 days (number 3) to 60 days (number 2). Means of the meridional and zonal components of water movement, v and u, are available for each current meter during the period of operation (Pillsbury et al. 1974). The top meter in each array was about 20 m below the surface. At this depth, mean v was about 20 cm/s on the continental shelf (arrays 1 and 2) and 10 cm/s on the edge and slope (arrays 3, 4, and 5), towards the south. Mean u was about 2 cm/s towards the west, except at array 3 where it had the same velocity towards the east. Thus, from where it was spawned by the parent, a sardine or anchovy egg of average age on the continental shelf could have drifted about 14 nautical miles to the south and 1.4 miles to the west. The movement to the west is negligible for our purpose. The coastline and isobaths run generally north and south along this section of the coast, as do isopleths of surface temperature and surface nitrate concentration (Voituriez et al. 1974; D. W. Stuart and J. J. Walsh, pers. commun.). Thus the parent fish probably occurred over the same bathymetry and under the same environmental conditions as the eggs did, but slightly farther north.

Carangid eggs (Figure 5D) were found on the outer half of the shelf, especially at the edge. Kiliachenkova (1970) found eggs of *Trachurus trachurus* distributed in exactly the same way in the same area in November, December, and May. The literature does not clearly show the vertical distribution of the eggs of *T. trachurus*. Kiliachenkova (1970) found them abundant at the surface. The eggs of the related *T. symmetricus* in the California Current are most common at the surface but fairly abundant down to 30 m, with smaller numbers occurring deeper (Ahlstrom 1959). We, therefore, assume our eggs came mostly from the top 30 m. *Trachurus trachurus* eggs hatch 3 or 4 days after being spawned at temperatures from 15° to 19°C (Letaconnoux 1951), so average age in our material should be 1.5 to 2 days. Then, taking mean v as 10 cm/s we estimate that a *Trachurus* egg collected near the shelf edge was probably spawned near the edge about 7 to 10 miles farther north.

Maurolicus eggs (Figure 5E) were most abundant just outside the shelf edge. Adults are mesopelagic fish of the continental slope (Maurin et al. 1970; Hureau and Tortonese 1973) and presumably spawn there. We frequently found eggs on the outer one-third of the shelf as well as on the slope, which suggests some eastward transport. The current meter data from arrays 3 and 4 show a mean u about 10 cm/s to the east at 60 m. This could account for the observed distribution if *Maurolicus* eggs occur at that depth and hatch in a few days. Eggs of *M. japonicus* off Japan are most abundant at 50 to 60 m (Nishimura 1957). This species is considered synonymous with *M. muelleri* (Hureau and Tortonese 1973).

Clupeoid larvae (Figure 5F) were abundant at midshelf, on the outer shelf, and over the slope. In general their distribution extended about 10 to 15 miles west of the eggs. Their average age probably was 10 to 20 days more than that of the eggs. Larvae of *Sardina pilchardus* and *Engraulis encrasicholus* occur most commonly in the upper 25 m (Fage 1920). Thus the movement of 20-m shelf water towards the west at about 0.9 nautical mile/day generally explains the observed larval distribution. This water movement is presumably the Ekman transport, which provides a mechanism for the coastal upwelling.

Larvae of demersal fish (flatfish and sparids) occurred mostly on the shelf as expected, but occasionally on the slope. They were most common in inshore waters where eggs and larvae of pelagic species were scarce (Figure 5G, H).

VERIFICATION FROM COMMERCIAL FISH CATCHES

From egg and larval evidence, the adult pelagic fishes in the area and period of JOINT-I should have been predominantly *S. pilchardus* and *E. encrasicholus*, especially the former, on the shelf; *Trachurus*, probably *T. trachurus*, at the shelf edge; and the mesopelagic *M. muelleri*, on the continental slope. Differences in fecundity between species could affect these findings, however, and other species could have been present but not spawning. Commercial fish catches provide a useful check on the results of the studies with eggs and larvae. Some useful information of that type was kindly provided by the Sea Fisheries Institute of Gdynia, Poland.

Polish pelagic (mid-water) trawlers of the Odra Deep Sea Fishing Company fished just south of the JOINT-I area at the end of March 1974. They operated from lat. 20°40′ to 21°00′N, between the coast and shelf edge. Reported catches (tons/day) of pelagic species were about 3.3 *Trachurus* spp., 6.5 *Caranx rhonchus*, and 0.2 *Scomber japonicus*. *Caranx rhonchus* was the principal species within the 50-m isobath, *Trachurus* the principal fish in more offshore waters. During April, the trawlers were located far north of the JOINT-I area between lat. 23° and 27° N, where their catches were predominantly *Sardina pilchardus*.

The Polish research vessel *Professor Siedlecki*, equipped for large-scale pelagic trawling, made 77 hauls between 13 May and 24 June, starting just after JOINT-I. The hauls were made between lat. 20°16′ and 25°01′N which includes the area of JOINT-I. Hauls north of lat. 21°00′ were all on the continental shelf between the 35- and 70-m isobaths and caught almost exclusively *Sardina*. Hauls south of lat. 21°00′ were made at the shelf edge (100-m isobath) and caught almost exclusively *Trachurus* or *Sardina*, usually *Trachurus*.

Klimaj (1971, 1973) summarized results of commercial Polish trawling from 1965 to 1971 in a small area (his area 22) which includes the area of JOINT-I. The principal pelagic fishes taken from March to May were *Trachurus* spp., *Caranx rhonchus*, *Scomber japonicus*, and *Pomatomus saltatrix*. *Caranx rhonchus* was common only in March and *P. saltatrix* only in May. The other two were important in all months, with *Trachurus* generally much more abundant than *Scomber*. The *Trachurus* would have been either *T. trachurus* or *T. trecae*, which are not distinguished in the Polish fishery.

It was noted earlier that the principal spawning seasons of *Caranx* and *Scomber* are respectively later and earlier than the period of JOINT-I. The spawning season of *Pomatomus* is also later (references in Blackburn 1975). Thus these forms could have occurred in the area and period of JOINT-I although we did not recognize them in the ichthyoplankton. *Caranx rhonchus* probably did occur in March, especially inshore, and *S. japonicus* may have occurred, although not in great abundance.

The Polish data support our conclusion that *Trachurus* was the principal pelagic fish at the edge of the shelf. Our conclusion that *Sardina pilchardus* was an important species on the shelf is supported by the results of the *Professor Siedlecki* hauls, but not by those from the commercial vessels. Commercial fishing for that species is concentrated farther north, especially between lat. 24° and 26°N (Chabanne and Elwertowski 1973; Odra Company results given above). Sardine catches of the *Professor Siedlecki* were much higher between lat. 22° and 25°N (mean of 62 hauls, 2.37 tons/h) than between lat. 20° and 22°N (mean of 15 hauls, 0.17 ton/h). There appears to be no commercial fishing for *Engraulis* off Spanish Sahara.

SPATIAL AND TEMPORAL DISTRIBUTION OF SARDINE AND ANCHOVY EGGS

In this section we characterize the area in which sardine and anchovy eggs occurred on JOINT-I, and note temporal changes in their abundance. The findings on areal distribution would apply also to adult fish in reproductive condition. We have assembled data on temperature, chlorophyll *a*, small zooplankton (<500 μm), large zooplankton (>500 μm), sardine eggs, and anchovy eggs for the 10 series along lat. 21°40′N. Figures 2 to 4 show the data for three series, including the two series in which sardine eggs were most abundant. Anchovy eggs were most abundant in the 23-24 March series (Figure 2).

Vertical distributions of temperature and density varied as shown by Barton (1974) and L. A. Codispoti (pers. commun.), and are not discussed in detail. Figure 3 shows typical coastal upwelling and Figure 4 a relaxation of upwelling conditions. Figure 2 shows weak coastal upwelling and upwelling at the shelf edge. Other series showed similar variations. It is doubtful if upwelling ever occurred only at the edge.

Chlorophyll *a* in the water column always showed a primary or secondary maximum on the middle or outer part of the shelf, and sometimes another maximum over the slope. The maximum over the slope was found when upwelling occurred at the edge, as in Figure 2, and was probably a result of it. Maxima of small zooplankton were distributed like those of chlorophyll. Both chlorophyll and small zooplankton were relatively low, close inshore in all series, and also beyond the shelf edge in series where second maxima did not occur. Large zooplankton were relatively scarce on the shelf in each series. Their biomass increased sharply at the edge, and generally continued high as far offshore as we sampled.

Sardine and anchovy eggs were virtually confined to the middle and outer parts of the shelf on all series, regardless of their abundance. Their mean abundance there is given in Table 1, together with means of temperature, chlorophyll, and small zooplankton for the water column in the same area, for each series. Temperature means are approximate.

DISCUSSION

Sardine eggs were most abundant on the middle and outer continental shelf during haul series 5 and 10, moderately abundant during series 8, and scarce on other series (Table 1). Figures 2 to 4 show the abundance on series 5, 9, and 10. Low numbers of eggs indicate either a small population of adults in the vicinity, or one that is spawning little. Mean biomass of adult fish was estimated acoustically for the same part of the shelf on the same sampling line, at various dates commencing 31 March (Thorne et al. in press). This biomass showed an irregular increase with time. It was about 8 g/m^2 on 31 March, 40 g/m^2 on 6 to 9 April and 22 to 26 April, and 80 g/m^2 on 1 to 6 May. These four periods were close in time to series 6, 7, 9, and 10, respectively. The predominant species was probably sardine as stated earlier. The egg numbers show that adult sardines were probably abundant on series 5 and moderately so on series 8, but we have no acoustic estimates of biomass for those series or for series 1 to 4.

The low mean egg number on series 6 probably reflected a very small adult population, but it is unlikely that the low numbers on series 7 and 9 did so, in view of the biomass estimates just given. It is more probable that sardine spawning was inhibited during series 7 and 9. The low mean temperatures in the water column during those series, namely, 15.5° and 16.0°C (Table 1), could have been responsible. Furnestin and Furnestin (1959, 1970) stated that spawning of *Sardina* is absent or feeble below 15.5°C and optimal from 16.0° to 18.0°C, especially over 16.5°C, in Moroccan waters. Spawning might, therefore, be low at 15.5° to 16.0°C in waters off Spanish Sahara. The limiting effect of temperature appears to be not on the spawned eggs, which can develop at 10°C

(Larrañeta 1960), but on the adults, as to whether or not they release eggs. The adults occur in most parts of the water column (Furnestin and Furnestin 1970; Thorne et al. in press), which is the reason for considering mean water temperature here. Furnestin and Furnestin (1970) make it clear that spawning depends on the temperatures over most of the water column, not necessarily on those in the upper 25 m where most eggs are found. Thick layers of water below 15.5°C make an area unsuitable for sardine spawning even if there is warm water at the surface, according to those authors. Figure 3 shows such a situation for series 9. From the criteria of Furnestin and Furnestin and the vertical distributions of temperature in our 10 series (examples given in Figures 2-4), it can be said that temperature conditions on series 3, 4, 7, and 9 were unsuitable for sardine spawning on the middle and outer shelf. Conditions on the other series were relatively suitable with mean temperatures for the water column at 16.5° or 17.0°C. It can then be deduced that adult sardines were scarce on series 1 and 2, because few eggs were found. We have no information about relative abundance of adults on series 3 and 4; they could have been present but not spawning. Relative abundance of adult sardines on the other series is given as low, medium, or high in Table 1, according to indications discussed above.

This succession of changes in abundance of adults is too irregular to be attributed to growth of individuals in a stationary population. It must be due largely to movements into and out of the small area studied. In the last major change, the biomass approximately doubled in about 2 wk between series 9 and 10. No pelagic fish species has such a high growth rate for adult individuals. It was noted during April and May that fish on the continental shelf were more abundant north of the sampling line (as far as lat. 22°20′N, which was the limit of the acoustic surveys) than along the sampling line (Thorne et al. in press). The fishing results of the *Professor Siedlecki* also indicated that sardines were more abundant to the north of our area than within it. It is therefore very probable that the biomass increase between series 9 and 10 represented a movement of sardines into the study area from the north.

It is of interest to consider possible causes of the sardine movements. A population of sardines living off the southern part of the coast of Spanish Sahara would be likely to move into a particular area, like our study area, when conditions were suitable to them and move out of the area when conditions became unsuitable. The principal determinants of distribution of pelagic fish are believed to be temperature and food supply. Temperature conditions in the study area were suitable for adult sardines during the whole period of JOINT-I, since they occur in waters from 14° to 18°C off Morocco (Furnestin and Furnestin 1970). Changes in abundance of food might however have caused movements of sardines into and out of the study area. No studies of the diet of *Sardina pilchardus* have been made off Spanish Sahara except for two fish mentioned later. Elsewhere in its range, including waters off Morocco, it feeds on phytoplankton and small zooplankton (Larrañeta 1960; Furnestin and Furnestin 1970). The distribution of sardines along the sampling line was like that of phytoplankton and small zooplankton as shown earlier: all three having maxima on the middle and outer parts of the continental shelf. This suggests that relative abundance of one or both of those kinds of food determines sardine distribution in a spatial sense and might do so in a temporal sense.

Comparison of means of zooplankton concentration with data on sardine abundance (Table 1) shows no relation between them. If means of chlorophyll concentration are used, there is the following relation: sardine abundance is low when chlorophyll values are 115 mg/m^2 or less, and medium or high when chlorophyll values are 147 mg/m^2 or more. This suggests that sardines entered the study area in order to feed on phytoplankton when it was relatively abundant and left the area when phytoplankton was relatively scarce.

No adult sardines were obtained during JOINT-I. On cruise AUFTRIEB 1975 we caught two sardines in the same area in February. M. Elbrächter kindly identified the contents of their stomachs: one contained no organisms except foraminifera, and the other contained phytoplankton in good condition, including 15 species of diatoms, and 2 species of dinoflagellates, and 2 copepods. Thus *S. pilchardus* feeds on phytoplankton and zooplankton off Spanish Sahara, as it does off Morocco and in other parts of its range. Phytoplankton might be an important part of the diet of the Sahara sardine, sufficiently to cause the sardine to move in relation to changes in phytoplankton abundance as suggested by our data, but we cannot be certain. More work on the diet of the sardine off Spanish Sahara is needed. Mauritanian sardines have more gillrakers than Moroccan sardines of the same size (Furnestin 1955). This could signify that the mean size of organisms in the diet of sardines decreases from north to south along the African coast.

Table 1 shows that abundance of anchovy (*Engraulis*) eggs does not run parallel in time with that of sardine eggs. There is a large difference between the ratio of the mean numbers of the two kinds of eggs on series 5 and 10, for instance, although temperatures were about the same (Figures 2, 4). We are unable to draw any conclusions about changes in anchovy abundance and their causes, even in the tentative ways attempted here for the sardine.

The concentration of *Trachurus* at the shelf edge may indicate a feeding aggregation on large zooplankton, such as euphausiids and large copepods, which are more abundant there than on the shelf (Figures 2-4). The high abundance of large zooplankton sometimes extends farther offshore than *Trachurus*, however. Some other factor must help to determine abundance of *Trachurus*. The diet of *T. trachurus* and *T. trecae* off northwest Africa is about 80% euphausiids, 10% copepods, and 10% small fish such as anchovy (Boely et al. 1973). Phytoplankton is sometimes a minor constituent of *Trachurus* stomach contents, however (Letaconnoux 1951; Overko 1964; S. Schulz pers. commun.).

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