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By Buenaventura Andreu

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THE GILL RAKERS IN THE CHARACTERIZATION OF POPULATIONS
OF SARDINA PILCHARDUS (WALB)*

by

Buenaventura Andreu**

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Key to abbreviations used in this work:

LS - Standard length

LT - Total length

LF - Fork length

IC - Head length

MV - Vertebral mean

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II STATEMENT OF THE PROBLEM

The general opinion of fishermen and of some authors is that sardines migrate in large numbers, so much so that their abundance in African and Mediterranean waters and their scarcity along the Atlantic Coast of Spain during the period 1946-56, were attributed to the fact that the schools which normally populate Galician waters had migrated to the African and Mediterranean coasts. The French, influenced by ANDERSON (cit. in LE GALL, 1953), felt that the concentrations of sardines which annually reach the French coasts - from St. Jean de Luz to the western tip of French Finisterre - all formed part of a single bank which was displaced from North to South, later appearing along the coasts of Malay, those of Spain and Portugal, the Bay of Biscay, the coasts of the Vendée and lastly, Brittany. It was believed that with the first colds, this sardine began returning to southern waters. Following this idea, fishing forecasts for the southern coasts of France were made on the basis of catches obtained in Spain, in the belief that a good fishing year in our country would necessarily be a good fishing year in France. However, this hypothesis did not appear fully satisfactory, for it was known that sardines were fished the year round on the Iberian Peninsula and, in the middle of winter, in the Bay of Biscay. In addition, since 1862, French trawlers had been reporting their presence at sea bottom - not far from the coast - in Belle-Ile and off the southern coast of Finisterre - (LE GALL, 1953), and they were and are

still being fished by trawlers, from July to March, at the bottom of the English Channel.

Though at the end of the past century, there was some isolated research on the biology of the sardine, the methodical study of this species, and the establishment of populations or "races", are of relatively recent date. It may be said that they began with the research on the vertebral mean, published by PAGE in 1920, in which this author established different races for the Atlantic and the Mediterranean. In spite of this, later research was much influenced by the idea of grand migrations. Thus DE BUEN (1929a) concluded in a work of 1928, referring to the Southern Atlantic sardine race, that "during spawning time, in winter, it is to be found in two zones: one off our province of Biscay; another off Setubal, in Central Portugal".

FURNESTIN (1943) has suggested that there are two yearly migration directions along the French coasts of the Bay of Biscay, in addition to other small seasonal migrations of lesser importance along the coasts of Les Landes. This same author (1950) believes that, in Tangier Bay and on the western tip of the Strait, Mediterranean sardines meet the Atlantic Moroccan ones, leading to the establishment of a heterogeneous group in which the Atlantic variety predominates. RUIVO (1950) considers the sardine population of Vigo, Leiões, Lisbon and the South of Portugal, which he calls Ibero-Atlantic (west coast), as being definitely homogeneous, from a vertebral point of view, discarding the possibility that stocks of these sardines may migrate

towards the Moroccan coasts, however mentioning that very probably there is an intrusion of Ibero-Atlantic sardines - across the Strait - and considering the Alboran sea as a frontier zone where Mediterranean sardines alternate with those of the Atlantic.

BARDAN & NAVARRO (1962) make a thorough analysis of the hypothesis of FURNESTIN (1950 b) and RUIVO (1950) concerning the immigration to the Alboran sea of sardines of Atlantic origin, coming to the conclusion that on the one hand, sardine researchers are seriously intent on the characterization in limited geographical areas of taxonomic groups (races or populations) differing in somatic or physiological characters which are easily obtainable through observation. However, on the other hand, many of them have recourse to the hypothesis of large migrations, to explain the dynamic biology of the sardine in its totality, or in its local peculiarities. Such migrations could only result in the continuous, accumulated mixing of reproducers and the appearance of a progeny which, in virtue of the laws of heredity, would become very rapidly homogenized. Geographical distinctions and migratory habits - they conclude - are incompatible.

In previous works, we mentioned (ANDREU 1954 a, 1962) that the sub-division of the species into different populations or "races" seems to indicate the existence of definite barriers - geographic or hydrographic - which prevent or hinder the interpenetration of similar populations. For this reason, the hypothesis of large migrations parallel to the coast - we stated - has been discarded, to be replaced by the theory that

such migrations are instead limited, being accompanied by displacements perpendicular to the shore, of approach (trophic migrations) and departure, dispersion and immersion (reproductive migrations).

Even in the case of sardine populations of two fishing areas as close together as those of Matozinhos (North of Portugal) and Vigo, which have no apparent "barrier" separating them, we were able to establish appreciable differences in the length of the head (ANDREU, 1955 a). However, contradicting the theory of the migration of the sardine of northwestern Spain to the Portuguese coasts, so popular in Galicia, are additional factors which we shall consider briefly: a) Monthly fishing curves follow a similar pattern, with largest catches in autumn and equal periods of catches in the sardine of winter origin. b) The composition of the population, by ages, in the sardine of Vigo and the North of Portugal, is expressed in so many similar percentages, which would not occur if the adult sardine was displaced in one direction or other. c) The spawning period of the Galician sardine is much longer than that of the Portuguese one, extending from the end of autumn to the beginning of summer (ANDREU, 1962). The diagram of sardine races set up by FAGE in 1920, with a very limited quantity of material, proved to be excessively restricted as time went on, in the face of new data which authors attempted to somehow adapt to the initial diagram, without there ever having been an exhaustive review of the published material which has been accumulating through the years. On the other hand, the great variability of

the vertebral mean in the sardine of well-defined areas caused authors to gradually lose faith in this character as a means of differentiating populations (NAVARRO, 1947) attitude which was reaffirmed on the basis of the works of RUIVO (1950), RODRIGUEZ-RODA, G. LARRAÑETA, MARGALEF & ANDREU (1951), BARDAN & NAVARRO (1952) and ANDREU, ANADON, ARTE & TOLL (1952), which emphasize the great plasticity of the genotype, in the sense that the number of vertebrae and other meristic characters depend on two determinants: the genotype and external factors which come into play during phenogenesis, which ordinarily occurs during the embryonic and larval stages.

Another character which has come to be generally used, together with the vertebral mean, in the characterization of populations, is the cephalic index, expressed as the percentage of the lateral length of the head in relation to the total body length. In addition to the inevitable mean errors, which in these indices are multiplied by five, BAS (1964) mentions that percentage ratios "have the disadvantage of falsifying the true ratios between the measurements being compared." He adds that the formula proposed by HUXLEY, which is simple and elementary, better represents the ratio between the measurements compared. These indices must be discarded (MARGALEF, 1955). The wide use of regression analysis (of original measurements) - according to MARR (1955) - would be a solid contribution towards the solution of the usual types of problems and, paradoxically - he adds - the use of indices has in the past led to confusion or doubtful conclusions.

The use of serology for differentiating races and populations of fish has received growing attention in the last fifteen years and has been tested on the Clupeidae of the Northwestern Atlantic by MAIRS & SINDERMAN (1962), on the Pacific sardine (ANLSTROM, 1960; VROOMAN, 1964) and on Sardina pilchardus by LEE (1961, 1965 a). This last author, from a hematological point of view, has encountered differences between the Atlantic sardines (St. Jean de Luz) and those of the Mediterranean (Sète) and among these latter - within the narrow limits of the Gulf of Lion - he has been able to distinguish three "forms": Catalán, Langedocian and Provençal. Lastly, as regards the specificity of muscular tissue proteins, FARRIS (1958), in the California sardine has demonstrated by means of chromatographic methods that the variation of free amino acids may be the result of diet, since it is not possible to distinguish between genetically caused differences and those induced by the environment.

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III SCOPE OF THIS WORK

Ever since REGEN (1916), in his synopsis of the family "Clupeidae", separated the sub-species Sardina pilchardus sardina from the type species Sardina pilchardus, depending on whether the lower limb of the first gill arch had more or less than 60 gill rakers, this character has been used in the taxonomy of the clupeids and in the characterization of populations, though in the case of the European sardine

Sardina pilchardus (Walb)]], only the average number of gill-rakers has been taken into account, as if this meristic character were fixed for each particular individual, beginning at a given size, as occurs in many other species. However, in Sardina pilchardus, new gill rakers keep forming throughout the entire lifetime of each fish, initially at a very rapid rate, and later more slowly, since the frequency distribution of the number of gill rakers may conform to the size of the fishes, to a potential function.

The number of gill rakers and the number of vertebrae, as well as other meristic characters, are determined at different times: the number of vertebrae becomes fixed during the initial phases of development of the sardine, so that it can no longer vary, while the first gill rakers - on the other hand - begin appearing much later, during the advanced phases of metamorphosis, when the number of vertebrae has already become definitely established. In the first case, the incidence of the factors which may condition the phenotype, is limited to a few days, while in the second case, it extends over the entire lifetime of the sardine. On the other hand, it must be kept in mind that 433 the embryogenesis and the larval development of this species occur in surface waters, which are those subject to the greatest number of seasonal temperature variations; in a single population having a lengthy spawning period, there will be substantial variations in the vertebral mean depending on whether the generations originated at the beginning or end of the spawning period. Young sardines (following chromogenesis) and adults, on

the contrary, live in sub-surface waters, below the thermocline (MARGALEF, 1963) and in its absence - during winter - they live on the coastal platform near sea-bottom, where seasonal and inter-annual temperature variations are much more moderate than on the surface and also less variable by latitude. The possible effect of temperature on the increase rate of the number of gill-rakers is much more complex and naturally less pronounced than in the case of the number of vertebrae.

The differences encountered in the distribution of the number of gill rakers in relation to body size in the Vigo sardine, as compared with those of Eastern Spain (ANDREU, 1953), encouraged us to continue this line of research, undertaking at a later date the study of the appearance and development of the spines in young forms (ANDREU, 1960) and their filtering function in feeding. We now propose to make a study of the gill-rakers in material taken from the greatest possible number of geographical regions within the area of distribution of the species. We have left a few gaps (sardine of the South of England, Málaga, and other parts of the Mediterranean) which we shall attempt to fill at a later date.

In this work, we propose to attempt the characterization of populations of Sardina pilchardus (Walb) on the basis of the variation in the number of gill rakers in relation to the size of the fishes, however, we felt it was first necessary to collect all literature published on the vertebral mean, adding our own observations on the Galician sardine. We shall also compare the relative growth of the head, using our own

observations. Lastly, we shall report those characters which may throw some light on the affinities or discrepancies between the different groups of populations studied and offer some ecological comments on the different tendencies observed and their possible significance from a point of view of evolution.

IV TAXONOMY

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According to LOZANO REY (1947), the taxonomic description of the species with which we are concerned is as follows:

PHYLUM: Vertebrates
SUPERCLASS: Gnathostomata
CLASS: Fish
SUBCLASS: Teleostomi
SUPERORDER: Teleostei
SERIES: Physostomi
ORDER: Clupeiformae
SUBORDER: Clupeoidea
FAMILY: Clupeidae
GENUS: Sardina, Antipa 1906
SPECIES: pilchardus (Walb.) 1792

The Clupeiformae developed from the Elopidae, through the genus Thrissopater. The Clupeidae begin in the Upper Cretaceous with the genus Histiiothrissa (LE DANOIS, 1943). Almost all species are essentially pelagic, with a certain anadromous tendency, which is complete in the shad fish Pomolobus and Brevoortia.

GUNTER, SULYA & BOX (1961), on the basis of a study of plasma proteins, were able to demonstrate the existence of a series of increasing complexity of less to more specialized fishes. The Clupeidae - they claim - appear as a rare group within the evolutive scale, since on the one hand, they have the

characters of more evolved fishes and on the other, they show similarities with the more primitive groups.

The family Clupeidae is composed of about 70 genera and perhaps 150 or more species (HILDEBRAND, 1963) of which five genera and nine species are found in European waters and in Northwest Africa (LOZANO REY, 1950): Clupea harengus L., C. sprattus [modernly called Sprattus sprattus (L)] ; Sardina pilchardus (Walb) Alosa alosa L, A. fallax (Lac); Sardinella aurita, Val, S. maderensis (Lowe); S. eba, Val; Ethmalosa fimbriata (Brow).

In spite of the fact that the sardine was a well-known, abundant species, LINNEO (1758) inadvertently omitted it from his Systema Naturae, which later gave rise to many errors. To demonstrate this, it is sufficient to observe the synonymies found by DE BUEN (1930) and LOZANO CABO (1965).

The first to note the omission of LINNEO was the Spaniard CORNIDE who, in 1788, designated the sardine as Arengus minor. However, the work of CORNIDE was unknown to the ichthyologists of his time, so that BONNATERRE (1788), RISSO (1810) and others, believed that they should give the sardine the name of Clupea sprattus L. The Spanish naturalist ASSO (1901) was able to distinguish the sprat from the sardine as were CUVIER & VALENCIENNES (1837), however the laws of priority had established Clupea pilchardus (Walbaum, 1792), of which the species name has been preserved, while the generic name Sardina, given it by ANTIPA in 1905, has since been adopted.

To correct the derivations which could result from the priority of CORNIDE (1788), LOZANO CABO (1965) cites the new wording of the International Code of Zoological Nomenclature, which introduces the concept of nomen oblitum, replacing the nomina conservanda, which relegated the name Arengus minor CORNIDE, 1788, to the list of "forgotten names", since it had not been used for more than 50 years. LOZANO CABO (loc. cit.) proposes the name of Sardina pilchardus (Walb) for the sardine.

After it stopped being confused with the sprat, the sardine was considered as an unassailable taxonomic unit by the majority of naturalists (NAVARRO, 1955). Attempts to break it down into distinct species or well-defined sub-species did not meet with success. Thus, the Sardina dobrogica of the Black Sea, created in 1905, by ANTIPA, has not been accepted. However - adds NAVARRO - the hypothesis that the Mediterranean sardine is not exactly identical with the Atlantic one has been making headway.

In his work on the family Clupeidae, REGAN (1916), when referring to the genus Sardina, establishes - within the group having uneven scales - the species S. pilchardus on the one hand and the sub-species S. pilchardus sardina on the other, depending on whether they have more or less than 60 gill rakers, respectively, in the lower limb of the first gill arch. This author situates the type form along the Atlantic coasts of Europe, from Portugal to the British Isles, and the sub-species sardina in the Southwest of the Black Sea, the Mediterranean Sea, the Atlantic coasts of Morocco, Madeira and the Canary Islands.

CHABANAUD (1926), taking as a starting point the research of REGAN, carries out a revision of the genus Sardina based on the anatomy of the hyobranchial skeleton and separates S. sardina (Risso) from S. pilchardus (Walb) since in the first, he encounters a small bone (prosohyal?) in the anterior portion of the glossohyal, which he did not observe in S. pilchardus. DE BUEN (1927 a) feels that CHABANAUD exaggerates in separating two species which he (De Buen) accepts as being two "forms of the same species: the form sardina for the Mediterranean and the form pilchardus for the Atlantic (DE BUEN, 1935-1936). LOZANO REY (1947) in his "Spanish Ichthyology," corroborates the opinion of REGAN. FURNESTIN (1950 b) encounters 64 to 80 gill rakers in the Moroccan sardine, and for this reason he includes it in what he calls the variety S. pilchardus (Walb), while he calls that of the Mediterranean, with 49 to 62 gill rakers, the "variety" S. sardina (Risso); in the sardine of Tangier, this same author encounters a number of gill rakers varying between 52 and 89, which leads him to accept the co-existence, in that zone, of S. sardina and S. pilchardus. /436

The examination of a lot of sardines coming from the Azores leads LETACONNOUX (1954 b) to recognize the presence of Sardina sardina with Mediterranean characteristics in these islands, and in Madeira and the Canaries, since the number of gill rakers - he says - is always lower than 60, while in the S. pilchardus, it is higher than that number. In the same work, he mentions the presence in the Atlantic sardine (Azores and La Rochelle) of the prosohyal, bone which CHABANAUD attributes to the Mediterranean sardine exclusively. We also made this observation during the same period, in the Vigo sardine (ANDREU, 1953) discrediting the

differences established by CHABANAUD when separating the two species in question. As regards the number of gill rakers, BARDAN, NAVARRO & RODRIGUEZ (1949), in the sardines of the Alboran Sea, had already encountered up to 74 gill rakers in those coming from Almería, and up to 78 in those of Estepona; we (ANDREU, loc. cit.)^{encountered} up to 73 in the sardines of Eastern Spain and LEE (1961) up to 70 in those of Sète and Marseilles. Therefore, the individual or average number of gill rakers and the presence or absence of the prosohyal are discarded as valid characters for the separation of the two species of Sardina, as used by some authors up until now.

LEE (1961) has demonstrated that Atlantic sardines (St. Jean de Luz) differ from those of the Mediterranean (Sète) from a hematological viewpoint: the hematids of the former do not agglutinate in the presence of the serum of tuna caught near Sète, while in the latter, agglutinations are produced to the extent of 25%. This leads him to consider the Mediterranean sardine as an independent sub-species of the type form of the Atlantic (Sardina pilchardus sardina) as was proposed by REGAN (1916), criterion which we feel is a bit exaggerated. Subsequently, LEE (1965), by means of serological tests, was able to distinguish three "forms" of sardines in the Gulf of Lion: the Catalan, the Languedocian and the Provençal.

V GEOGRAPHICAL DISTRIBUTION. IMPORTANCE IN FISHING

The area of distribution of Sardina pilchardus (Walb) is very wide (Fig. 1.), extending from the northern tip of Dogger-Bank, off the Danish coasts (FURNESTIN, 1939), where they are caught with other pelagic species, to the Saharan coast of Cabo Blanco and Lévrier Bay, in Mauritania (CADENAT & MOAL, 1955), also including the archipelagos of the Azores, Madeira and the Canaries. It further extends over the Mediterranean Basin and adjacent seas, the Gulf of Gabès excepted, the coasts of Libya and the northern portion of the Black Sea (GOMEZ LARRAÑETA, 1960). According to this author as well, isolated fishes have been encountered along the coasts of Egypt and small schools in Tunisia, Israel, southern Turkey, Rumania, east of the Black Sea, Crete, Syria and Lebanon. /437

The sardine has mainly coastal habits: in the Adriatic (GRUBSIC, 1964) it lives at a maximum depth of 200 meters, however during the fishing season, it rarely descends to more than 100 meters (GOMEZ LARRAÑETA, 1960). French and German trawlers catch it at sea bottom - together with the herring - in the vicinity of Eddystone (ANONYMOUS, Lab. Leaflet, Lowestoft, 1965), some years in great quantities. The same occurs on the Spanish Mediterranean coast where - during winter - they appear in dragging nets, though in small quantities.

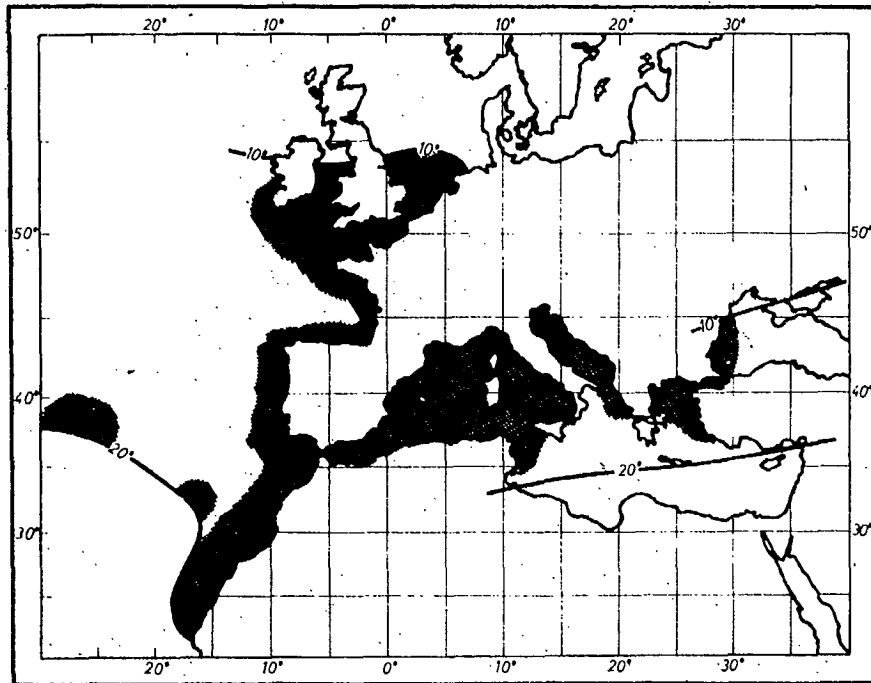


Fig. 1. Geographical distribution of Sardina pilchardus (Walb) according to FURNESTIN (1952).

On the Galician coasts, fishing is carried out within the 100 m. isobath; fishermen use seines for the catching of Scomberesox and Engraulis up to 35 miles from the coast, without any sardines appearing in these catches (ANADON, 1954).

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It may be considered as a temperate zone species: the 10° C isotherm in the North, marks its northern limit approximately and that of 20° C its southern limit; the temperature conditions of the Sahara coast are more similar to those of the Bay of Spain than to those of the tropical Atlantic (FURNESTIN, 1952).

From North to South, the area of distribution extends over about 4,000 km. and from East to West (from the Azores to the Dardanelles), over about 6,000. The diversity of environmental

conditions (physico-chemical and biological), and the coastal and insular geography of such a wide area of distribution, are so many other factors favoring the isolation and the diversification of populations.

The importance of international clupeid fishing, which includes well-known species like herrings, sardines, sprats, sardinellas, shadfish and even anchovies (which are not well-known from a taxonomical viewpoint), increases from year to year. Of the 52.5 million tons of food extracted from the different oceans during the year 1965 (Statistical Annals of Fishing of the FAO, Vol. 20, 1966) 17.5 million were clupeids, representing 33.4% of the total fish landed. In Spain, the total that year amounted to 1.13 million tons, of which 22% were clupeids.

Centering our attention exclusively on catches of Sardina pilchardus in its entire area of distribution, we see that the main area of abundance of the species is to be found off the western coasts of the Iberian Peninsula, and more specifically between the estuaries of La Coruña and Aveiro, with other important areas on the coasts of Morocco and in the South Atlantic region of Spain. The map in Figure 2 gives a fairly good general idea of the importance of the various sardine fisheries throughout the last decade, considered in the light of official statistics.

In order of importance, by countries, the first two positions are occupied by Morocco and Portugal (see Table I) which attain or exceed 160,000 tons yearly. Next come Spain,

with 124,000 tons; France and Italy, up to 35,000; Algeria, up to 14,000; Yugoslavia, up to 11,000; United Kingdom, up to 6,000 tons, followed by Greece, Turkey, Tunisia, Holland, German, the Azores and Madeira, with lower quantities which - in the majority of cases - are not expressed statistically. In the overall averages, the Atlantic sardine represents 80.2% of the catches, the remaining 19.8% being of Mediterranean origin.

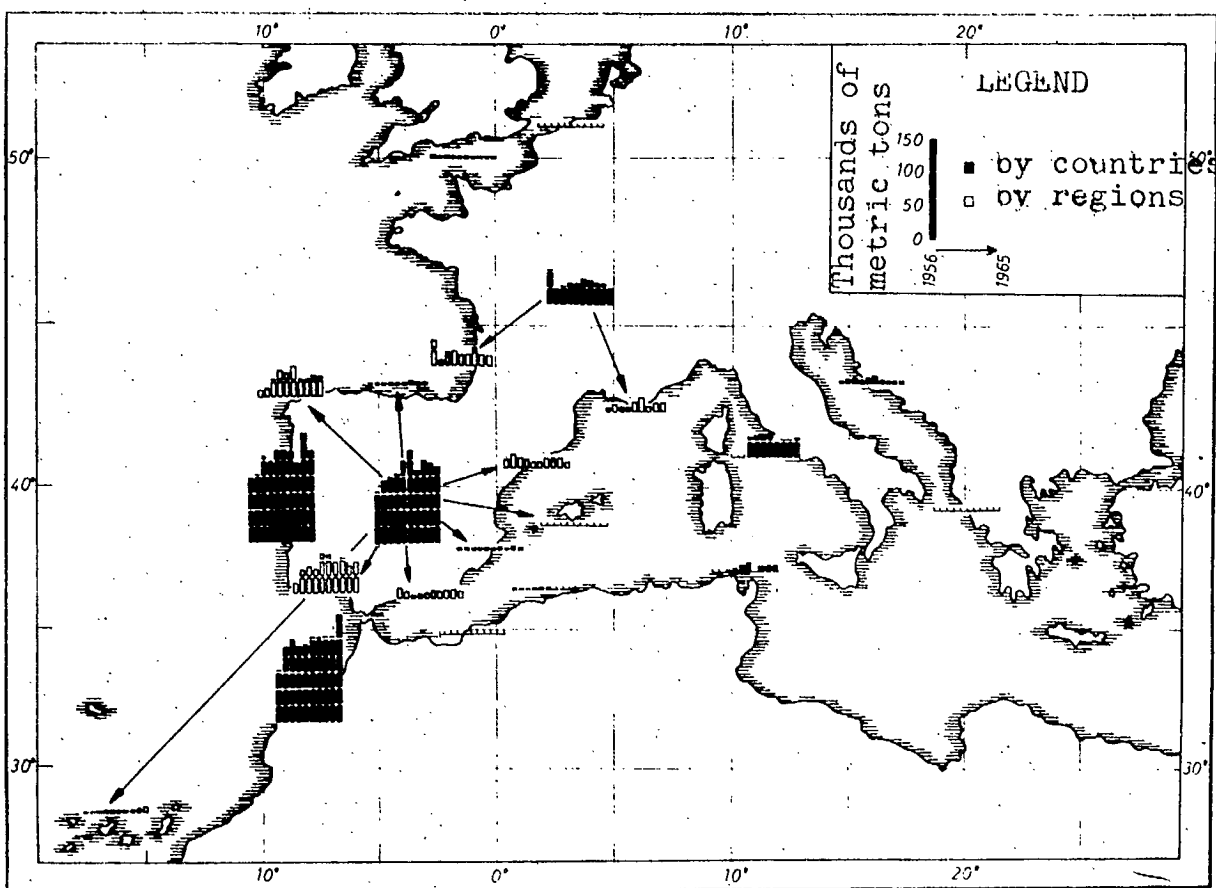


Fig. 2. Importance in fishing of *Sardina pilchardus* (Walb): distribution of landings by countries. Those of Spain are also indicated by fishing regions as are those of France, separating the Atlantic from the Mediterranean ones.

In Spain (Table II, Fig. 2.) the most important sardine region is that of the South Atlantic, followed by those of the Northeast, North, South Mediterranean, Canaries, Eastern Spain, Cantabrian Region and the Balearic Islands, in that order.

Sardine fisheries, because of their immediate dependence on primary production, are very sensitive to its fluctuations, so that the catches show marked and sometimes prolonged ups and downs. MARGALEF (1967) remarks, with a trace of irony, that it is strange how man reacts to similar fluctuations. Positive variations - he says - are considered as a reward for his tenacity and intelligent effort and negative variations are immediately described as catastrophes and crises.

VI DIVERSIFICATION OF THE SPECIES: "RACES"

The question of sub-populations or races, according to AHLSTROM (1960) is one of the principal lines of research on the Pacific sardine Sardinops caerulea (Girard), in that heterogeneity, within the area of distribution of the species, has been clearly demonstrated. In the South African sardine, JAGER (1960) and MATTEWS (1960) have encountered no differences in the vertebral mean, which leads them to suppose that the sardines of Walvis Bay [Sardinops ocellata (Pappe)] belong to the same population. In Australia and New Zealand a certain degree of racial segregation has been noted in Sardinops neopilchardus (Steindachner), with the presence of at least two different groups (BLACKBURN, 1960). In the Japanese

sardine Sardinops melmosticta (Temminck & Schlegel), not only is there clear evidence of fragmentation, but the taxonomic differences between this species and Sardinops caerulea (Tokai Reg. Fish. Res. Lab., 1960), do not seem to be completely clear.

KREFFT (1954) states, with regard to the European herring that, for reasons of nomenclature, we should not use the concept of sub-species and race, terms which he at present considers as being almost synonymous in quantitative differentiation, and believes that the term micro-subspecies is more suitable - and better expresses its purely quantitative character - for designating these lower categories.

We have already mentioned that the expressivity of the heredity of meristic characters in fishes is very much influenced by abiotic environmental factors, which certainly does not prevent these characters, generally speaking, from providing us with very interesting information concerning the fragmentation of populations. These differences, in many cases, have a genetic basis, even if this is not always easy to demonstrate. HEMPEL & BLAXTER (1961) have carried out experimental studies in the laboratory with first stage larvae of herrings of the German coasts (Vertebral mean, 55.4) and of the Clyde area (Vertebral mean, 57.00) kept at different temperatures in two series of separate tanks; in this way, they encountered not only a significant negative correlation between vertebral mean and temperature of incubation, but also a considerable difference between the test vertebral means of both series, thus permitting

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them to demonstrate the existence of a broad genetic difference between the two groups. Something similar is being demonstrated by the serological and biochemical studies under way in different countries.

In the case of Sardina pilchardus, as in the rest of the clupeids, the breaking down into "races" or "populations" has been based essentially on the differences in the vertebral mean and subordinately, in the relative length of the head, characters which, as we already mentioned in a preceding chapter, have posed difficulties in the characterization of "races" or "populations", both in the Atlantic and in the Mediterranean and more especially in the latter. We are not going to repeat here what we have already said concerning the cephalic index.

Strictly for information purposes, we are summarizing here below present knowledge on the establishment of races in Sardina pilchardus:

FAGE (1920), on the basis of the vertebral mean, established the existence of five races;

1. Channel race, which included the population of the English Channel and the North Sea; vertebral mean 52.25 (52.03-52.47).
2. Bay Biscay race, including the area from Santander to Brest; MV* 51.76 (51.66-51.86).

*MV - vertebral mean.

3. South Atlantic race, which includes the area from the Bay of Cadiz to the Galician coasts; MV 51.31 (51.14-51.48)
4. North Mediterranean race, from the Gulf of Naples to the Balearic Islands; MV, 51.63 (51.52-51.74).
5. South Mediterranean race, which extends from Argèles to Almeria; MV, 51.29 (51.15-51.43). He added as a probability the Azores race; MV, 5.95 \pm 0.20.

FURNESTIN (1952) has reviewed the initial diagram of FAGE, adding the cephalic index and reviewing the moduli of the vertebral mean in the establishment of racial differences in the Atlantic sardine, which he breaks down in the following manner:

1. North Atlantic race, between the North Sea and the Cantabrian coast; MV, more than 52; cephalic index 20 (he includes here the Channel race of FAGE).
2. Southern or Spanish race, between the Cantabrian coast and the Strait of Gibraltar, up to the Bay of Malaga; MV, 51.20; cephalic index 21.

He establishes two new races:

3. Morroccan race, between Cape Espartel and Cape Juby; MV, below 51.0; cephalic index, 22.
4. Sahara race, between Cape Juby and Lévrier Bay; MV, below 50.30; cephalic index, above 22.

According to LETACONNOUX (1954), the Mediterranean sardine and that of the Atlantic islands (the Azores, Madeira and the Canaries) are represented by a single phenotype, and this - in

his opinion - could be explained either by the similarity of environmental conditions or by the lesser degree of plasticity of the meristic characters of these sardines. GOMES LARRAÑETA (1960), on the other hand, mentions that the racial composition of the Mediterranean sardine is difficult to determine, since neither the biometric indices nor the vertebral mean give clear evidence of groups, pointing out that the two races established by FAGE have not yet been discarded. The most difficult problem - he adds - is posed by the sardines of the Alborán Sea where, in the opinion of RUIVO (1950) and FURNESTIN (1950 b), mixtures occur due to the arrival of sardines of Atlantic origin, while BARDAN & NAVARRO (1952) claim that the sardines of the Alborán Sea are native. Furthermore, in spite the alleged uniformity of environmental conditions in the Mediterranean, MUZINIC (1954) mentions that the studies carried out up to the present would indicate the existence of a certain gradient in the number of vertebrae: the North Mediterranean sardine - he says - has 52 vertebrae, while that of the South has 51. In another later work, the same author (MUZINIC, 1958 b) suggests the existence of two or more "stocks" of sardines in the Eastern Adriatic; LASKARIDIS (1948) is of the opinion that the sardine of the North of the Aegean Sea is different from that of the South. SUAU (1958) divides the Spanish sardine of the Mediterranean into four "stocks": a) from the French frontier to the Sagunto; b) from Cape Lanao to Cartagena, including Ibiza and Formentera; c) from Cartagena to the Strait of Gibraltar and d) Isle of Mallorca. And lastly LEE (1965 a) encounters three

distinct forms in the Gulf of Lion: the Catalan, the Languedocian and the Provençal, mentioned previously. As we can see, the picture, especially as regards the Mediterranean sardine, seems rather confused.

VII. MATERIAL

In this work, we are studying different aspects of Sardina pilchardus: morphology of the lingual skeleton, of the gill arches and of the gill rakers. Genesis of the gill rakers, lateral length of the head in relation to the total length of the fish, variation in the length of the first gill arch, separation between gill rakers - both characters in relation to the size - and the vertebral mean. /443

The morphological studies were conducted on sardines coming from the Vigo estuary, from Banyuls-sur-mer and from Eastern Spain. The vertebral mean only on Vigo sardines, and studies on gill rakers include localities which cover almost the entire area of distribution of the species (Fig. 3.). Below, we are giving some details concerning the origin and characteristics of the material used in each study.

VERTEBRAL MEAN (MV)

In all, a total of 11,351 sardines were studied, all taken from commercial catches made in the Vigo estuary, during the periods between the month of October 1951 and June of 1955

and in November 1964. These fishes normally form part of lots of 100 individuals, taken at random from the catch of a single vessel. Table IV shows some supplementary characteristics.

LATERAL LENGTH OF HEAD (LH)

Measured in 3,191 fishes: 141 from Maumusson and Sables d'Olonne (France), 325 from Santander, 1,105 from Vigo, 83 from Oporto, 279 from Lisbon, 257 from Sanlucar de Barrameda and Ayamonte, 21 from Casablanca (Morocco), 136 from the Azores, 166 from Madeira, 220 from the Canaries (Isle of Tenerife), 64 from Split (Yugoslavia), 73 from Tunisia, 42 from Castiglione (Algeria), 234 from Castellón and 52 from Alicante. Generally speaking, the size ranges correspond to those indicated under the next heading and are recorded in Table III.

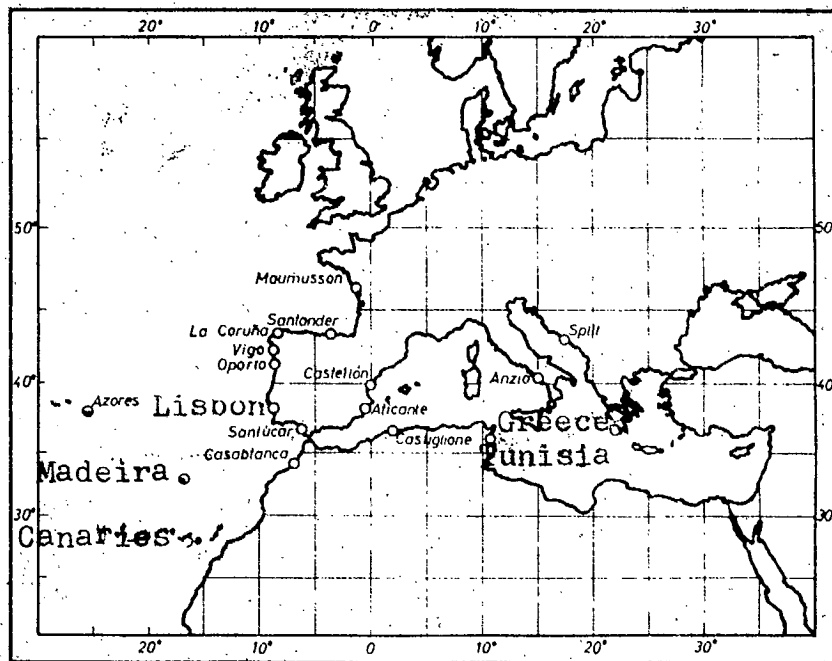


Fig. 3. Map showing the places of origin of the sardine specimens studied in this work.

STUDIES ON GILL RAKERS:

Our original idea was to obtain samples of sardines covering the widest possible size range, preferably between 100 and 200 mm., taken from all the most representative fishing zones within the wide area of distribution of the species. We have been gathering this material for 13 years (1953 to 1965), thanks to the kindness of friends and colleagues from Spain and other countries, who provided us with it. It was studied as it came into our hands. On occasion, as in the case of the Casablanca sardine, we had as few as 21 fishes, although given the variety of size groups and the uniformity of results, they sometimes proved more useful than other more numerous samples /444 from other countries, which had to be discarded since the exact opposite occurred. In all, the number of gill rakers was counted in 3,618 sardines, the length of the lower limb of the first gill arch was measured in 3,345 fishes and the separation between spines in 943 individuals. Below, we are giving some of the most important data on the samples studied, indicating the number of fishes in which the gill rakers were counted. Table III provides information on the second and third aspects mentioned above.

Vendée (Maumusson and Sables d'Olonne, France): material consisting of 145 sardines having a total length of from 85 to 100 mm., caught between July and October of 1963.

Santander: 284 sardines from Santoña and Santander, caught in May of 1954 and August of 1964 respectively, length between 115 and 225 mm.

Vigo: 1184 sardines coming from the Vigo estuary, caught between the month of December 1953 and the month of May 1955. Total length between 85 and 225 mm. Samples from La Coruña and El Ferrol were also studied, however in partial size groups. /445

Oporto (Leixões): 378 sardines caught on the coastal fringe between the Minho River and the Aveiro estuary, in April and December of 1954. Total length between 128 and 216 mm.

Lisbon: 434 sardines caught between the month of January and the month of May and in August of 1955. Total length between 89 and 211 mm.

Sanlúcar de Barrameda: 251 sardines caught in the months of March and September of 1955 and in June of 1957. Total lengths between 101 and 175 mm.

Morocco: 21 sardines from 100 to 190 mm. in length, caught in the month of July 1953 on the coast of Casablanca.

Azores: 131 sardines caught in March and September of 1965; total lengths between 115 and 195 mm.

Madeira: 146 sardines of the months of July and August 1965; total lengths between 100 and 220 mm.

Canary Islands: 205 sardines caught in May of 1954 and August of 1955 on the coast of Tenerife. Total lengths between 90 and 220 mm.

Eastern Adriatic: 64 sardines coming from the coast of Yugoslavia (Split), received in January of 1957. Total lengths between 105 and 165 mm.

Tunisia: 70 sardines caught in September of 1956; total lengths between 120 and 170 mm.

Algeria: 42 sardines from 100 to 175 mm. in length, caught on the coast of Castiglione. Received in February of 1957.

Castellón: 214 sardines caught in July of 1955. Total lengths between 95 and 115 mm.

Alicante: 49 sardines from 130 to 195 mm. in length, caught in May of 1958.

In addition, we studied material coming from Anzio (Italy), Greece, Audierne, La Rochelle, Ile de Ré and Arcachon, which could not be included in this work because the small number of size groups available did not enable us to obtain sufficiently representative regressions.

VIII WORKING METHODS

Except for material used in the calculation of vertebral means, we have not taken into account the criterion normally followed in studies of population dynamics, however we were able to combine fishes of the greatest possible number of size classes from very well-defined fishing areas, thus enabling us to better study the variations in the characters retained and obtain regression curves which were more representative.

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CRITERION OF LENGTH, SIZE CLASSES

Measurements of fishes are carried out to the millimeter on millimeter paper, measuring from the snout to the median line joining the extremities of the lobules of the tail fin extended in a normal position (total length, LT) as shown in Figure 4, inasfar as possible, grouping the material in size classes to the nearest half centimeter. As in the Portuguese sardine, the length of the Galician sardine from the snout to the fork (central radii of the tail fin, LF) represents 90% of the total length. The heads coming from Oporto and Lisbon were referred to size classes taking into account LF, so that it was easy to relate them to LT. The heads of the sardines of Casablanca and the Canary Islands were grouped in size classes (LT) to the nearest centimeter. Those of Castellon were grouped together in size intervals (LT) of between 90-95 mm., 95-100 mm., etc., and those of Yugoslavia between 100-110 mm., 110-120 mm., etc.

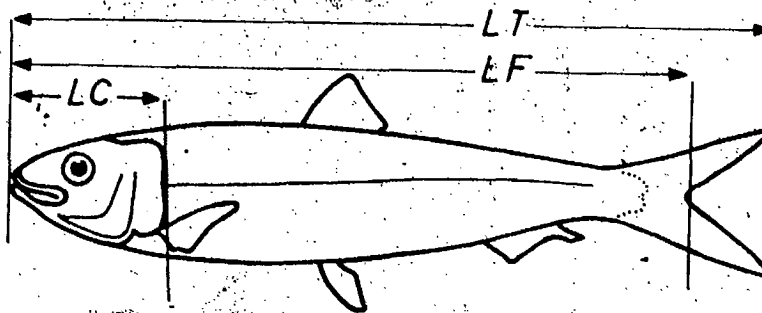


Fig. 4. Diagram showing the method used in taking measurements: LT, total length; LF, fork length; LC, lateral length of head.

LENGTH OF THE HEAD (LC)

Was measured, between perpendicular lines, from the extremity of the snout to the posterior bony margin of the operculum (Fig. 4.).

VERTEBRAL MEAN (MV)

In Vigo sardines, vertebrae were counted from the occipital condyle, not included, to the urostyle, included and considered as a single piece, so that the figure obtained corresponds to the number of intervertebral discs.

NUMBER OF GILL RAKERS (NB)

In our observations, we used only the first gill arch of the left side of each fish. In non-pigmented larvae, dissections were performed under a binocular microscope and under the naked eye, in the more highly developed forms. In sardines of more than 40 mm. LT, we studied only the lower limb of the gill arch which includes the ceratobranchial and the hypobranchial (Fig. 12.). In all cases, with the first gill arch, the edge

of the left side of the tongue was also dissected, so as not to omit from the count the small gill rakers which cover this organ laterally. In the larval and young forms, counting was done /447 from the tail - excluding those of the upper limb (epibranchial) - with a 100 magnification binocular. In adult fishes, the first arch and part of the tongue were separated and, after being carefully washed with the tip of the fingers in running water, they were preserved in formol at 5% up to the time of counting of the gill rakers. The method used in counting, which gave good results in previous works (ANDREU, 1953), is as follows: 1) Under a binocular, using 10 magnifications, we separate the upper limb of the arch (epibranchial) at the point of articulation with the ceratobranchial; as a reference, we use the upright pointed apophysis of the first gill raker of the ceratobranchial, which almost forms a right angle with the transversal apophysis of said gill raker. 2) Using handled needles, we press on the separated end of the ceratobranchial, holding it against the tray, while with the other needle we press and pull, in a direction perpendicular to the bone in question, on the cord of soft tissues which include the apophysis of the gill rakers. With a little experience, it is possible to easily and rapidly separate the entire garland of gill rakers from the lower limb of the gill arch which projects into the lingual mucous. 3) Using a binocular, at between 10 and 20 magnifications, depending on cases - the counts are easy to make and very precise.

To determine whether or not there are sensible differences in the number of gill rakers in the lower limbs of the left and the right arches, we made comparative counts on a lot of 50 fishes coming from the Vigo estuary, having a size interval of between 145 and 175 millimeters. The results were as follows: 50% of the fishes had the same number of spines on both sides, 42% showed a difference of one gill raker, and 8%, 2 gill rakers. The differences are compensated, so that the counts on the left limb give an average of only 0.06% more than the right one, a figure which is far below the margin of error of the counts. In the size class most represented (160 millimeters, with 19 fishes) the averages were equal and in the next (165 mm., with 12 fishes), the average of the left limb was higher than that of the right by 0.3. Something similar, though with a lesser degree of coincidence, occurs with the upper limbs on each side.

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SEPARATION BETWEEN GILL RAKERS

The separation between gill rakers is determined by measuring under a microscope, with an ocular micrometer (1 division - 14 μ), the distance between the middle portion of two adjacent spines, with the gill arch distended. Four measurements were taken for each fish.

LENGTH OF THE LOWER LIMB OF THE FIRST GILL ARCH (li)

The length of the lower limb of the first gill arch has been taken in the broadest sense, since it includes not only the ceratobranchial and hypobranchial bones, but was measured

from the beginning of the former, to the base of the last gill raker located in the latero-lingual mucous. The measurements were taken on the basis of the garland of gill rakers, after they were separated from the lower limb of the arch, placing it over a millimeter tray, under a binocular microscope; in this way, the measurement is more precise - regardless of the curvature of the arch - and the ratio between the number of gill rakers and the separation between spines will be more exact, so that the product of the distances between spines by the number of spines (\pm the accumulated errors) will have to be more or less equal to the length of the lower limb of the arch, since this consists theoretically in the total sum of the distances between all its spines.

* * * * *

The allometric constants were calculated, in each case, by the method of least squares, thus obtaining the corresponding regression formulae.

The calculation of the confidence limits of each of the regressions and very especially the significance of the differences between the allometric constants encountered among different populations, are aspects which we have not touched upon, because of their statistical and mathematical complexity, as may be seen from the work of TAKASHI (1953), in which this

author solves a problem similar to ours, related to variations in natural populations of copepods.

Other authors have also alluded to this problem. For example, BERRY & BARRET (1963) in the separation of species of the clupeid Opisthonema, limit themselves to representing graphically the number of ceratobranchial gill rakers in relation to the length of the fishes and encircling the distribution of points with a continuous line in the guise of a perimeter, which the authors call a profile. Each profile is used in the characterization of the species. KREFFT (1954), in the European herring, used a mathematico-statistical method based on the intergradation averages of populations, however, in the case of the herring, the number of gill rakers soon becomes almost constant, which greatly simplifies the problem of comparing populations.

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We have limited ourselves to using the calculated allometric constants, attempting to find their ecological significance, going only as far as the biological criterion would permit.

IX RESULTS

1. VERTEBRAL MEAN

a) Vertebral Mean of the Vigo Sardine

We owe the first observations on the vertebral mean of the Vigo sardine to DE BUEN (1934), who used material made up of 401 fishes. Subsequently, NAVARRO (1944) published the results corresponding to the years 1940-43, based on observations

of 2,681 sardines. However, the largest number of contributions were made between the years 1947-1952 (LOZANO CABO, 1948; NAVARRO, 1948; OLIVER, 1950; OLIVER & NAVARRO, 1952). In all, the material studied by all the aforementioned authors totals 9,322 fishes, to which must be added 1,397 coming from El Ferrol and La Coruña studied by DE BUEN (1934) and NAVARRO (1944) respectively. Therefore, we have sufficient antecedents on the vertebral mean of the Galician sardine.

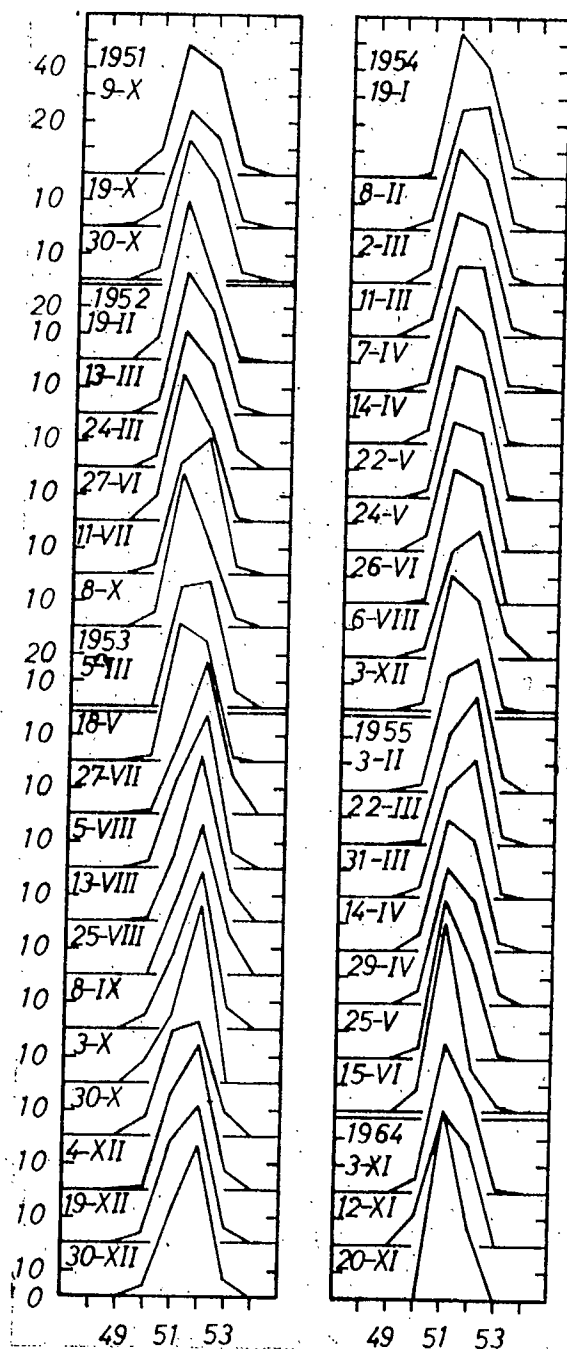
Our observations cover the periods between the months of October 1951 and June 1955; and November of 1964. They refer to a total of 11,351 fishes. In Table IV, we note the results obtained on each one of the lots studied and Table V gives the summarized totals per year.

The vertebral mean obtained from the total of our own observations is 51.36 ± 0.02 , which is slightly higher than that of the other contributions dealing with Galicia.

The number of vertebrae counted in each fish varied between 49 (0.7%) and 54 (0.4%), those having 50, 51, 52 and 53 vertebrae being most represented numerically, especially those having 51 and 52, which constitute 53.12 and 38.42% respectively, /450 of the fishes examined. Those having 50 and 53 vertebrae correspond to 6.27 and 2.08% (Table V).

Apart from the fishes with 54 vertebrae that were allegedly encountered in Vigo, it is strange that in the distribution of vertebral frequencies by lots (Table IV, Fig. 5.), the modal value corresponded to sardines with 52 vertebrae on 16 occasions. OLIVER & NAVARRO (1952), in a lot of January 30, 1952, are

surprised to encounter a modal value of 52 vertebrae, instead of 51, which - they claim - did not occur on more than three occasions in 13 years.



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Fig. 5. Frequency distribution of the number of vertebrae in the Vigo sardine, during the period October 9, 1951 to November 20, 1964.

The vertebral mean per lots varied between 51.13 ± 0.02 (June 15, 1955) and 51.88 ± 0.33 (August 25, 1953). July 27 and August 13 of 1953, gave very high vertebral means: 51.85 ± 0.17 and 51.86 ± 0.24 (Fig. 6.), so the fact in itself cannot be considered exceptional, though there are no precedents in the Galician sardine. However, vertebral means lower than 51.13 had previously been encountered on 11 occasions, the lowest being 51.00 ± 0.38 (NAVARRO, 1944); 51.02 ± 0.20 and 51.05 ± 0.21 (OLIVER, 1950).

In his "Contribution to the biometry of the Spanish sardine" NAVARRO (1944) mentions that the lowest value for the vertebral mean corresponds to Vigo, however - he adds - in its variation it is as high as those of La Coruña and Northern Portugal and even that of Málaga. This brings him to state that if there really is a South Atlantic race, it cannot be separated from that of the South Mediterranean on the basis of the vertebral mean, since in Málaga (1940-1943) he finds a mean of 51.33 ± 0.03 (n - 6,597) and in Galicia and Northern Portugal (1940-1944) it is 51.29 ± 0.03 (n - 4,067).

In 1948, NAVARRO speaks of the great stability of the vertebral mean in the Galician region throughout the years (51.19), however in 1952, OLIVER & NAVARRO mention seeing an increase, beginning in autumn of 1949 (OLIVER, 1950; OLIVER & NAVARRO, 1951), however at the end of March 1952 - these same authors add (OLIVER & NAVARRO, 1952) - the mean value descends and becomes normalized (51.19).

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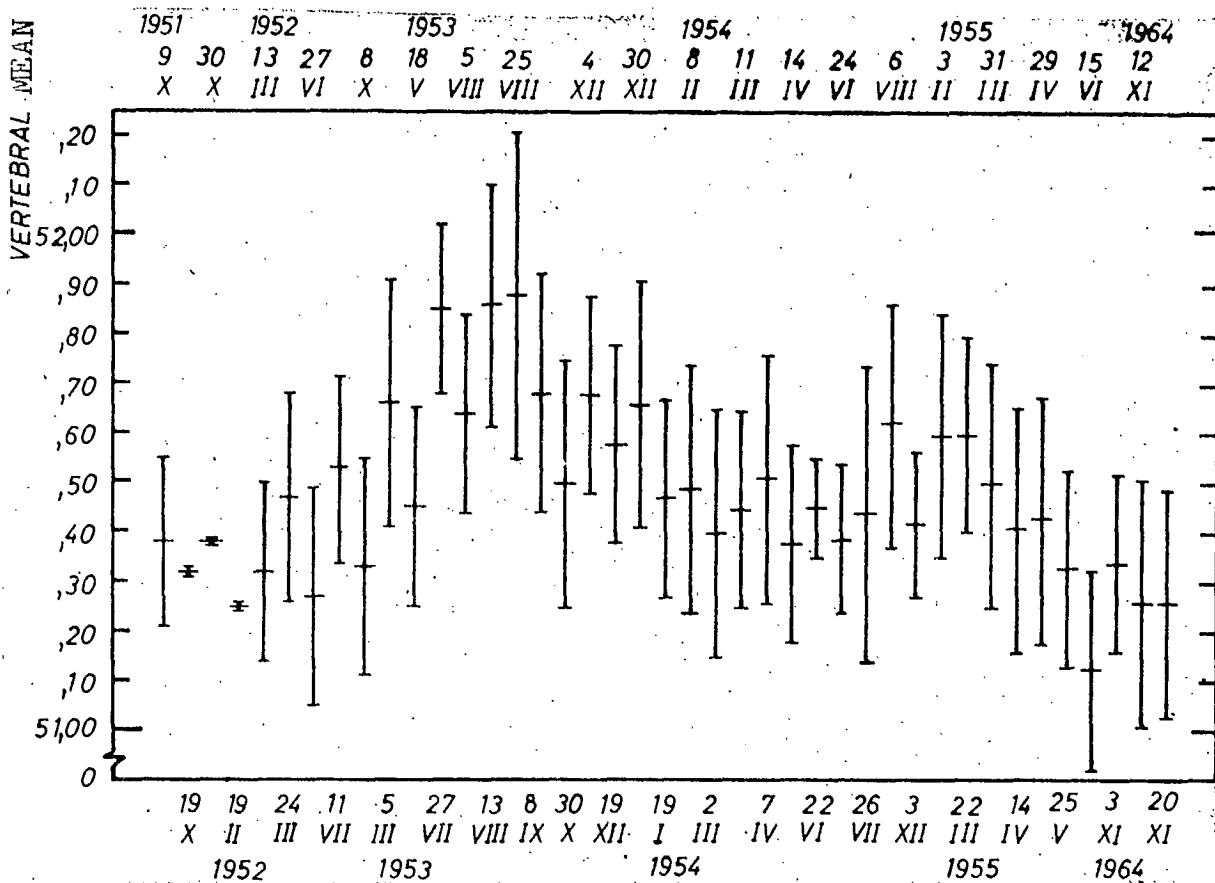


Fig. 6. Variation of the vertebral means of the Vigo sardine and their fluctuations, by lots, years 1952 to 1964.

In Figure 6, we see that during the period considered by us, the vertebral mean varied with a certain regularity, showing two maximums. However, these variations are followed with a certain parallelism by two series of values, which denote the existence of at least two distinct generations, separated phenotypically because of their different period of birth. Grouping together on the one hand all the lots made up exclusively of fishes of the zero class (size between 95 and 150 mm.) which did not have the occasion to mix with other schools of older fishes of the months of October to March, and on the other

hand, lots of fishes having the same characteristics as the preceding ones, but caught between June and August, we find ourselves with two completely different vertebral means:

Fishes of Class 0 caught in winter, MV 51.39 ± 0.05 (n: 1535); /452

Fishes of Class 0 caught in summer, MV 51.57 ± 0.06 (n: 1045).

Calculating the parameter t (YULE & KENDALL, p. 536), for G.I. $-\infty$, the value of t = 3.291 ($P > 0.001$), so that the difference between these means has high statistical significance.

These differences probably have no cause other than the fact that each generation was born in waters having a different temperature, which is explained by the very long reproductive period of the Galician sardine (ANDREU, 1955 c); to the thermal factor must be added the possible influence of the diameter of the egg, salinity and the action of light. However, we cannot completely discard the possibility that there is some influence of a genetic type, perhaps maintained free of hybridization through time because of the lack of coincidence between the spawning periods of each generation; this hypothesis would need to be proven as HEMPEL & BLAXTER (1961) did for the herring.

The continuous renewal of schools of sardines, which was demonstrated by us in the Vigo estuary (ANDREU, 1955 a), is a normal phenomenon in the sardine of the bottom of the Bay of Biscay, where CREAC'H (1950) says that particularly abundant hatchings occur in two seasons, winter-spring and summer-autumn, so that embryogenesis also takes place in waters having a distinctly different temperature.

The polymorphism of the vertebral mean of populations of the French coast of the bottom of the Bay has been interpreted in a different way. For FURNESTIN (1943) those having a low vertebral formula are probably native; the others - with which they are mixed - belong to the Armorican form, with a slightly higher MV. The mixture of both would give the Aquitaine form. CREAC'H (1951) denies that the Aquitaine form is present in the bottom of the Bay; in his opinion, the fringe between Gijón and the Garonne River, is the meeting point of the North and South Atlantic races, with all the interpenetrations which this meeting implies. On the French coast, the penetrations of southern origin would be weaker, the inverse occurring on the Cantabrian coast with the penetration of sardines of northern origin.

The results discussed in preceding paragraphs on the Galician sardine, also enable us to explain the polymorphism of the vertebral mean of the Bay of Biscay sardine - both have a long spawning period - without adapting the hypothesis of the French scientists, based on the penetration of alloctone sardines which they call northern or southern, depending on whether the vertebral mean of the schools is higher or lower than the sardine considered as native. The different periods of birth of schools in a single well-defined area cause seasonal temperature variations to be felt during embryogenesis, so that the vertebral mean of fishes tends to be higher or lower - within the general trend - depending on whether they come from autumn, winter or spring spawns. Without having recourse to the

hypothesis of grand migrations, which in our opinion should be discarded, at least generally speaking.

The MV, taken alone is very limited in the information it can provide for the characterization of sardine populations. On the other hand, when the number of individuals in the sample is very high, as occurred in the lots of October 19 and 30, 1951 and February 19 of 1952 (Fig. 6.), the fluctuation of the vertebral mean (Fl. of M.) is so low that schools of the same class 0 caught during the same month, and within a few days of each other, would belong to different "races".

b) Variations of the MV of the Atlantic and Mediterranean Sardine

Since data published on the vertebral mean of the Atlantic and Mediterranean sardines were so scattered, it was not easy to get an overall picture of the extent of variation of this character in the different geographical areas where the species is encountered, without first summarizing all this material. In so doing, we were even able to include material which is still unpublished: 41 new vertebral means from Oporto, year 1954, 14 from the Canary Islands, 77 from Castellón and the 39 from the area of Blanes, material which was kindly provided by doctors M. CRUZ, G. LARRANETA, G. CABRERA and BAS respectively and which, combined with the 42 new MV of the Vigo sardine which we have included, gave us an available total of 1,610 vertebral means for the area of distribution of Sardina pilchardus, including counts made on about 234,000 fishes.

We have grouped this material on a purely geographical basis, using the divisions set up by LE GALL (1951) for the French coast. In many cases, the works consulted do not indicate the number of fishes studied, or else the vertebral means were expressed by months and included various lots.

Table VI, of the frequency distribution of vertebral means, has been prepared setting up a class of MV for each five hundredths of a vertebra, covering MV's ranging from 50.41 to 52.55. The mean of the groups will therefore be 50.43, 50.48, 50.53, etc. The data on the different geographical areas have been taken from the following authors:

- English Channel and North Sea: HEINCKE (1898), LE GALL (1928, 1930, 1937, 1939), FURNESTIN (1939), HODGSON (1950), MATTA (1964); MV - 52.12 (n: 3833, grouped in 9 lots).
- Brittany, from the Bay of Saint Michel to the mouth of the Loire River: FAGE (1920), LE GALL & PRIOL (1933), LE GALL (1937, 1938, 1939, 1950), PRIOL (1937), FOREST (1949), LETACONNOUX (1950 b, 1952), KURC (1963); MV - 52.10 (n: 5672, grouped in 62 lots).
- Vendée, from the Loire River to the Garonne: FAGE (1920), BELLOC (1932), LETACONNOUX (1948, 1950 a, 1950 b, 1952, 1953, 1954, 1956, 1958, 1961), LE GALL (1950), KURC (1963); MV - 52.13 (n: 7547, grouped in 79 lots).

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- Bay of Biscay, from the Garonne River to Biarritz:
PAGE (1920), FURNESTIN (1943, 1950), LETACONNOUX
(1948 a, 1950 b, 1952, 1953), CREAC'H (1950),
TOURRASSE (1957); MV - 52.15 (n: 18, 240, divided
into 70 groups).

- Spanish Basque Coast: NAVARRO & NAVAZ (1946),
NAVAZ & NAVARRO (1950, 1952), NAVAZ (1954); MV - 51.99
(n: 2427, grouped in 24 lots).

- Santander: PAGE (1920), DE BUEN [1934, 1937 (corrected
by NAVARRO, 1944)]⁷, NAVARRO (1944, 1948), FERNANDEZ
& NAVARRO (1950, 1952), NAVAZ & NAVARRO (1951),
NAVARRO, FERNANDEZ & CUESTA (1956); MV - 52.01
(n: 7677, divided into 80 lots). We have not taken
into account the data published by E. SANCHEZ (1933).

- Vigo: DE BUEN (1934), NAVARRO (1944, 1948), LOZANO CABO
(1946), OLIVER (1950), OLIVER & NAVARRO (1952),
ANDREU (original data of Table IV); NV - 51.33
(n: 22,042, divided into 144 lots).

- Oporto, from the Minho River to the Aveiro estuary:
RAMALHO & BOTO (1932), NAVARRO (1944), RAMALHO & COL (1950),
M. CRUZ (1954 and unpublished data); MV - 51.32
(n: 27,788, divided into 142 lots).

- Lisbon, from Nazaré to Sines: RAMALHO & BOTO (1932),
RAMALHO & COL (1950), PINTO & BARRACA (1958);
MV - 51.17 (n: 38,859, divided into 319 lots).

- South of Portugal, Portimao, Olhao, Villa Real de San
Antonio: FAGE (1920, corrected by NAVARRO, 1944),
RAMALHO & BOTO (1932), RAMALHO & COL (1950), RAMALHO,
PINTO & COL (1956); MV - 51.10 (n: 3220, divided into
23 lots).

- Morocco: FURNESTIN (1949, 1950 a, 1950 c);
MV - 50.54 (n: 4360, divided into 11 groups).

- Cabo Blanco: CADENAT & MOAL (1955); MV - 50.63
(n: 207, divided into 3 lots).

- Azores Islands: RAMALHO (1929), LETACONNOUX (1954);
MV - 51.63 (n: 255, divided into two lots; excluding
the contribution of FAGE, 1920).

- Madeira Island: RAMALHO (1929); MV - 51.83 (n: 47,
in a single lot).

- Canary Islands, Tenerife: DE BUEN (1934), G. CABRERA
(personal com.); MV - 51.28 (n: 1119, divided into
15 lots).

- Yugoslavia: MUZINIC (1954); MV - 51.66 (n: 36,035,
in 195 lots).

- Languedoc, Gulf of Lion: LEE (1961); MV - 51.65
(n: 8167, in 19 groups).
- Blanes and neighboring coasts: BAS (personal com.);
MV - 51.58 (n: 1846, in 38 lots).
- Castellon and adjacent coasts, including the
Columbretes: NAVARRO (1944), ANDREU & RODRIGUEZ-RODA
(1952), GOMEZ LARRANETA (personal com.); MV - 51.53
(n: 14,782, divided into 143 lots).
- Balearic Islands: NAVARRO (1944, 1948), MASSUTI &
OLIVER (1948), MASSUTTI, VALLS & NAVARRO (1950),
OLIVER & NAVARRO (1952), OLIVER (1959); MV - 51.57
(n: 5809, in 52 lots).
- Málaga: NAVARRO (1947, 1948), BARDAN & NAVARRO (1949);
MV - 51.29 (n: 12,777, in 141 lots).
- Castiglione, Algeria: FAGE (1920), MURAT (1935),
DIEUZEIDE & ROLAND (1957); MV - 51.46 (n: 7982,
divided into 13 groups).
- Turkey and the Dardanelles: LASKARIDIS (1948), DEMIR
(1961, 1963); MV - 51.28 (n: 2982, divided into 15
groups).
- Israel: BEN-TUVIA (1959); MV - 50.95 (n: 664, in
10 lots).

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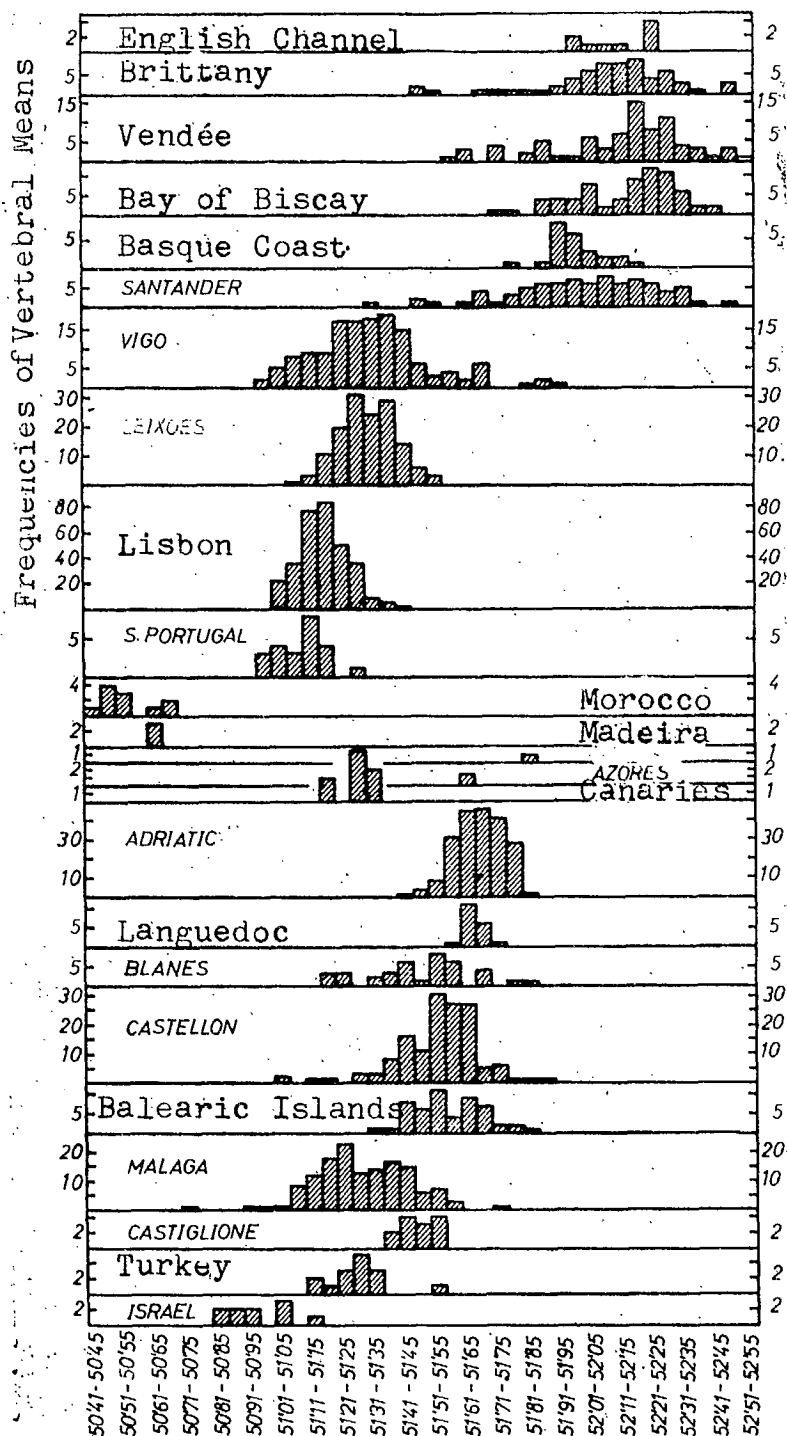


Fig. 7. Frequency distribution of vertebral means in the material studied by different authors on *Sardina pilchardus* (Walb).

The histograms in Figure 7 show the distribution of vertebral means, by regions, within the area of distribution of

Sardina pilchardus. We lack sufficiently representative samples from some geographical areas, for example Cabo Blanco, Azores and Madeira, this last being represented by a vertebral mean obtained from only 47 sardines. The aforesaid Figure 7 demonstrates the existence of two very distinct geographical clines: the first, which begins with the sardine of the English Channel and ends at Morocco and Cabo Blanco, and the second - in the Mediterranean - which extends from the Adriatic to Israel. It is worthwhile mentioning the wide range of variation in the vertebral means of the northern sardine, from the English Channel to Santander, and very especially in this latter locality, of which the boundaries include that of other more northerly zones.

Vigo and Leixoes must be separated from this group, though the sardines of both localities have some vertebral means in common with the Bay of Biscay. The vertebral means of the Vigo sardine show a much wider variation range than those of the North of Portugal and these in turn, a wider one than those of Lisbon. Morocco and Cabo Blanco are completely separated from the rest and from the sardines of the Canary, Azores and Madeira Islands; these latter occupy an intermediate position between the sardine populations of the Atlantic and those of the Mediterranean.

In the Mediterranean, the extreme irregularity in the distribution of vertebral means is worthy of note, especially in

the sardines of Castellón, Málaga and Blanes, as opposed to the uniformity of those of the Adriatic and the Gulf of Lion.

Discarding from the series some very rare, extreme values, which are superposed, we may conclude - with ample criteria - that the vertebral means obtained up to now make possible the separation of the following populations:

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- North Atlantic sardine: MV higher than 51.70, from Santander to the English Channel.
- Western Spanish sardine: MV between 50.95 and 51.70, from the western coasts of Galicia to the Strait of Gibraltar.
- South Atlantic or Moroccan sardine: MV below 50.70.

In the Mediterranean, things are more complicated still: the vertebral means of the sardines from the Adriatic to the Gulf of Lion show a normal distribution and could represent the northern population. Those of Turkey and Israel - of irregular distribution - the southern one. However, there remain those of the Eastern Spanish coasts which, depending on their vertebral means, tend towards one of the two aforementioned groups.

Lastly, the sardines of Madeira, the Azores and Canary Islands, are between the two clines mentioned above; though we are not lacking in criteria on which to base broader commentaries, their Atlantic affinity is obvious - in spite of the low latitude. However, notwithstanding all we have said, going by the vertebral mean, it is possible to confuse the sardines of the

Canaries with those of Oporto and Vigo on the one hand and those of Málaga and Turkey on the other. This fact, in itself, already tells us much concerning the deficiencies of the MV for the characterization of sardine populations.

2. LATERAL LENGTH OF HEAD (LC)

With very few exceptions, the authors who have studied the head length in Sardina pilchardus, give their findings in percentage form, in relation to total body length. In Chapter II, page 431, we already mentioned the disadvantages inherent in indices thus calculated and the severe criticism to which they have been subject. NAVARRO (1955) attempted to compile and compare the findings of the literature, however he mentions that he encounters difficulty since, not only are the criteria of head measurements and body length of fishes not uniform, but in addition - he adds - the personal factor greatly affects the results. He observes that there is negative allometry in adult sardines; that the sardines of Azores and Madeira have a shorter head than those of Casablanca and Portugal; that in the Alboran Sea, Algeria and the Balearic Islands, the index is almost the same as that of Portuguese sardines and that the sardines of the Eastern Mediterranean have a shorter head than those of the Bay of Biscay. /459

In the works consulted, we found very few data concerning the absolute length of the head (LC, Fig. 4.). RODRIGUEZ-RODA (1958) observed that the sardines of Barbate, for equal sized fishes, have a smaller head than those of Larache (Morocco),

this difference becoming reduced as the fishes grow. This author encountered a significant difference between the two populations. BAS (1964) mentions that in Vigo, the head of sardines grows much faster than in the Northern Mediterranean, tending to increase as the animal grows, contrary to what occurs in Blanes. The size of the head of the Vigo sardines, according to said author, exceeds that of the sardines of Isla-Cristina. CREAC'H (1951) suggests that the characters large head and low MV are related in Sardina pilchardus: in individuals of the same length, the length of the head tends to decrease as the number of vertebrae increases.

Tables VII and XXI show the frequencies of lateral head lengths in relation to the length of the material from the 15 different geographical areas studied. With this material, we have calculated the corresponding regressions by means of the classical allometric formula

$$L_c = a \cdot L_t^b$$

in which L_c = lateral length of head, in mm., L_t - total length of the fish expressed in mm. It is very possible that better results could have been obtained with the simple linear regression formula, however we preferred to follow the tendency of modern authors, in order to facilitate further comparisons. The values found for a and b are indicated on the following page.

In Figure 8, we have graphically represented the regressions calculated and the head length mean values for each size group. As we can see, with the exception of the Casablanca (Morocco) sardine,

the lines of regression double and in many cases, cross each other. It is therefore seen that the head length is not a suitable character for the characterization of sardine populations. In addition, the errors in measurement, resulting from the more or less closed position of the lower jaw, are also difficult to overcome. In the Vigo material (Table IX) which is the best represented, we see that the variation of LC fluctuates between 27 and 35 mm. in sardines having a total length of 160 mm. The variation was 7 mm. in those having a total length of from 145 to 190 mm. Variations of 4 and 5 mm. are evident in the size groups of all the localities studied.

Locality	a	b	No. of Fishes	Total Length LT mm.
Maumusson	0,44	0,8402	145	85-200
Santander y Santoña	0,34	0,8882	325	115-225
Vigo	0,28	0,9671	1105	80-235
Oporto	0,62	0,7808	83	128-205
Lisbon	0,26	0,9485	279	89-205
Sanlúcar	0,36	0,8833	257	105-175
Casablanca	0,16	1,0611	20	100-190
Madeira	0,42	0,8504	125	100-205
Azores	3,20	0,6628	136	115-195
Canaries	0,24	0,9602	220	70-220
Yugoslavia	0,57	0,7745	64	105-165
Castellón	0,53	0,7947	234	92,5-162,5
Alicante	0,28	0,9301	52	130-195
Castiglione	0,44	0,8452	42	100-175
Tunisia	0,80	0,7161	72	120-170

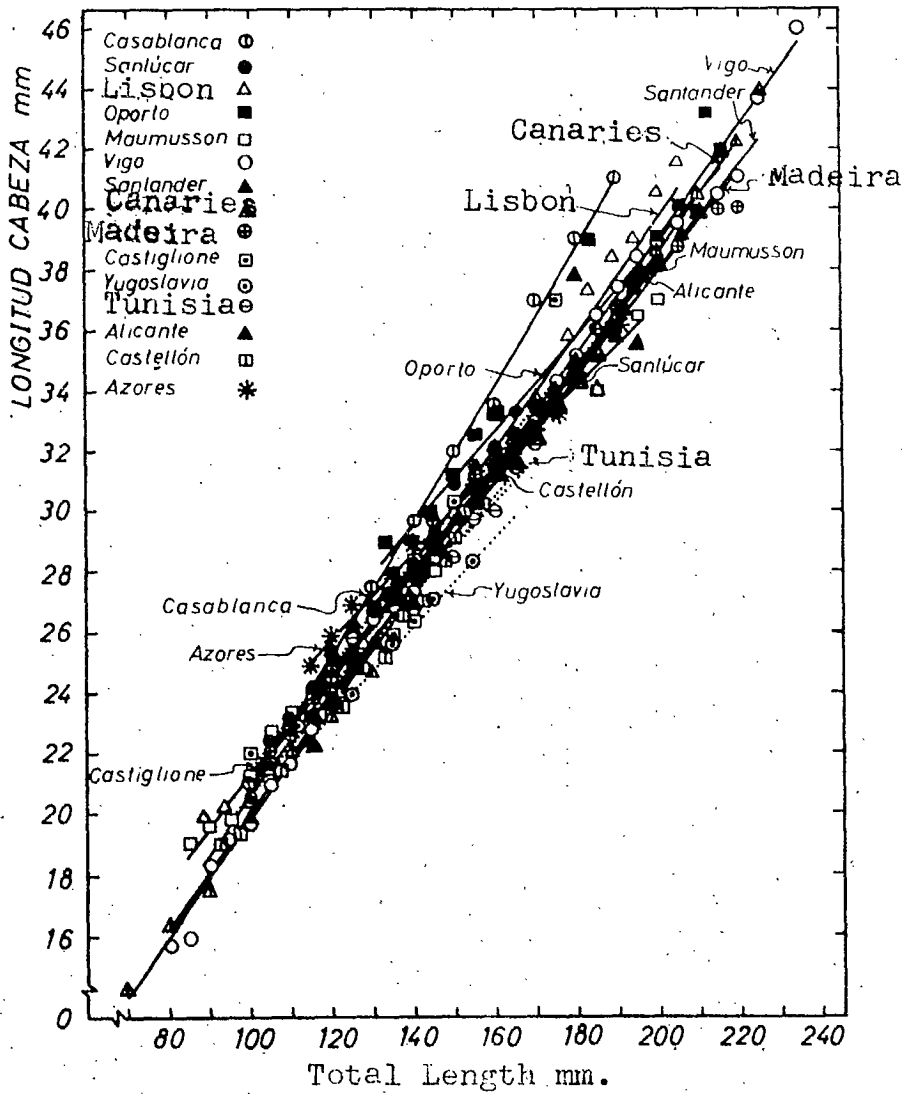


Fig. 8. Regression curves of the lateral head length (LC) in relation to the total length (LT).

Based on the increase rate of the head length of the sardines of each of the areas considered, we may establish the following groups:

- Azores: exponent less than 0.7
- Tunisia, Yugoslavia, Oporto and Castellon: exponents between 0.7 and 0.8

- Maumusson, Castiglione, Madeira, Sanlucar de Barrameda and Santander (including Santona): exponents between 0.8 and 0.9
- Alicante, Lisbon, Canaries and Vigo: exponents between 0.9 and 1.0
- Casablanca: exponent greater than 1.0

It is surprising to encounter Oporto sardines in the Mediterranean group and those of Castiglione and Alicante among Atlantic groups. The regressions corresponding to these three localities should be re-examined using more abundant material. With these exceptions and that of the Azores sardine, which though being Atlantic, has the lowest increase rate encountered, we could mention that the increase rate of the head in the Atlantic sardine, in general, is greater than that of the Mediterranean. It is only when the constants a_1 and b_1 calculated for the sardines of a region₁ are both greater than the constants a_2 and b_2 of those of a second zone₂, that the regression curves remain separated along their entire length, as occurs with the sardines of Oporto and Yugoslavia. However, generally speaking, this does not occur, but rather one of the constants of the sardines of a given zone is lower (or higher) than those of the other region and the other constant is higher (or lower) than those of the first; in these cases, the regression curves intercross. Therefore, it would be senseless, in the majority of cases, to speak of a large or small head. /462

Ratio Increase Rate of Head Length (LC) to Vertebral Mean (MV)

The distribution of points in Figure 9 does not enable us to establish any relationship between the increase rate of LC

and MV, but rather shows a random distribution. The points corresponding to the Atlantic sardines of Casablanca, Lisbon, Canaries, Vigo, Madeira, Santander and Maumusson - considered separately - seem to show an inverse ratio between the two characters. However, this is invalidated by the position of that of Oporto and by the group of points of the Mediterranean sardine and that of the Azores sardine. Therefore, we cannot speak of a relationship between the increase rate of the head length and the vertebral mean.

3. THE GILL RAKERS

We have known for some time that there exists a series of elementary organs of which the number does not remain constant, but rather increases throughout the life of each individual. SCHILDER (1950) demonstrated by means of numerous examples, that the increase rate of the number of elements is not in proportion to the size of the body - as was believed - but rather becomes gradually lessened, so that the ratio between the number of organs and the length of the body cannot be represented by a straight line, but only by a potential curve which passes through the axis of the co-ordinates, of which the exponent, ordinarily, is less than 1. LOPEZ-VELEZ (1956) was able to demonstrate in the ophiuroid Ophiactus amphipholoides Alvarado, that the number of segments of the arms increases with the length according to the power 0.7188 and that the number of said segments increases more slowly than the length of the arm. KINNE & PAFFENHOFER (1965) have observed that the

number of tentacles per hydranth in Clava multicornis tends to have a positive relationship with the length of the body of the hydranth and that this number decreases as the temperature rises. These authors suppose that the structural modifications of the hydranths affect the rate and efficiency of the interchanges between the organism and the environment and that they may be a means of metabolical adjustment.

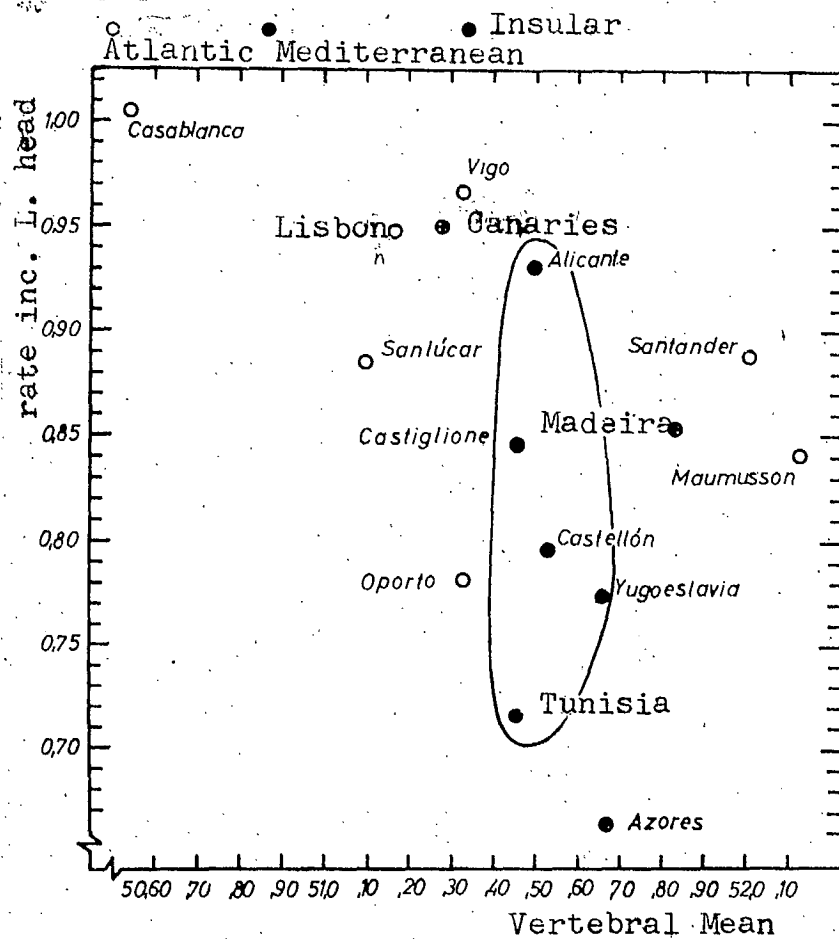


Fig. 9. Ratio between the increase rate of the lateral head length (LC) and the vertebral mean (MV) of the sardines of the different areas studied in this work.

The gill rakers of the sardine and some clupeids possess this neotenic character to an extraordinarily marked degree, while other species lose it at any early age. Below are some of the authors who have dealt directly or indirectly with this type of study in different species of fishes:

Clupeidae: Sardina pilchardus: REGAN (1961), THOMSON (1926); CHABANAUD & MONOD (1926); BARDAN, NAVARRO & RODRIGUEZ (1946); MAUL (1948); FURNESTIN (1950 b); ANDREU (1953); LETACONNOUX (1954 b); CADENAT & MOAL (1955); CABRERA & NAVARRO (1955); ANDREU (1960); LEE (1961, 1965 b); MATTA (1964); ANDREU (1967); Sardinops caerulea: THOMSON (1926); SCOFIELD (1934); PHILLIPS (1942); Sardinops melamosticta: SAKO (1938). Sardinella: MONTEIRO (1954, 1960); ROSIGNOL (1959). Clupea harengus: KREFFT (1954, 1958). Clupea pallasii: McHUGH (1954). Opisthonema: BERRY & BARRET (1963). Alosa: LOZANO REY (1950); FURNESTIN & VINCENT (1958); COTTIGLIA (1963).

Engraulidae: Engraulis encrasicolus: ANDREU (1959). Engraulis anchoita: FUSTER DE PLAZA & BOSCHI (1958). Engraulis mordax mordax: HILDEBRAND (1943); McHUGH (1951). Anchoa starksi: PETERSON (1956). Anchoa marini: FUSTER DE PLAZA & BOSCHI (1961 a). Anchovia macrolepidota: PETERSON (1956). Lycengraulis olidus: FUSTER DE PLAZA & BOSCHI (1961 b). Lycengraulis simulatur: FUSTER DE PLAZA (1962). Cetengraulis mysticetus: HOWARD (1954).

Carangidae: Trachurus trachurus: DA FRANCA (1959); ALONCLE (1964).

Thunnus: Thunnus alalunga: LETACONNOUX (1951); Thunnus thynnus: RODRIGUEZ-RODA (1964).

Coregonidae: SVARDSON (1952).

a) Gill Arches and Lingual Skeleton

In fishes, there are specific differences in the number of gill arches, as there are differences in the number and characteristics of the gill rakers. GRAY (1954) was further able to demonstrate similar differences in the number and size of the respiratory units (gills), relating the gill area to the habitat and the behavior of the fishes.

In Figure 10, we have sketched a diagram of a portion of the hyobranchial skeleton of a Vigo sardine 220 mm. in length, in which we see the tongue, the beginning of the basihyals and the five pairs of gill arches, the last of which has been modified giving way to the lower pharynges. A very similar arrangement has been described by PHILLIPS (1942) in Sardinops caerulea. In the figure mentioned, only the epibranchial bones of the first arches have been sketched. The front edge of the five pairs of arches serves as a support for the same number of series of gill rakers, of which the last four extend over the corresponding basihyals, while those of the first arch extend over the edges of the tongue, so that the network formed by the gill rakers leaves no opening through which food can escape.

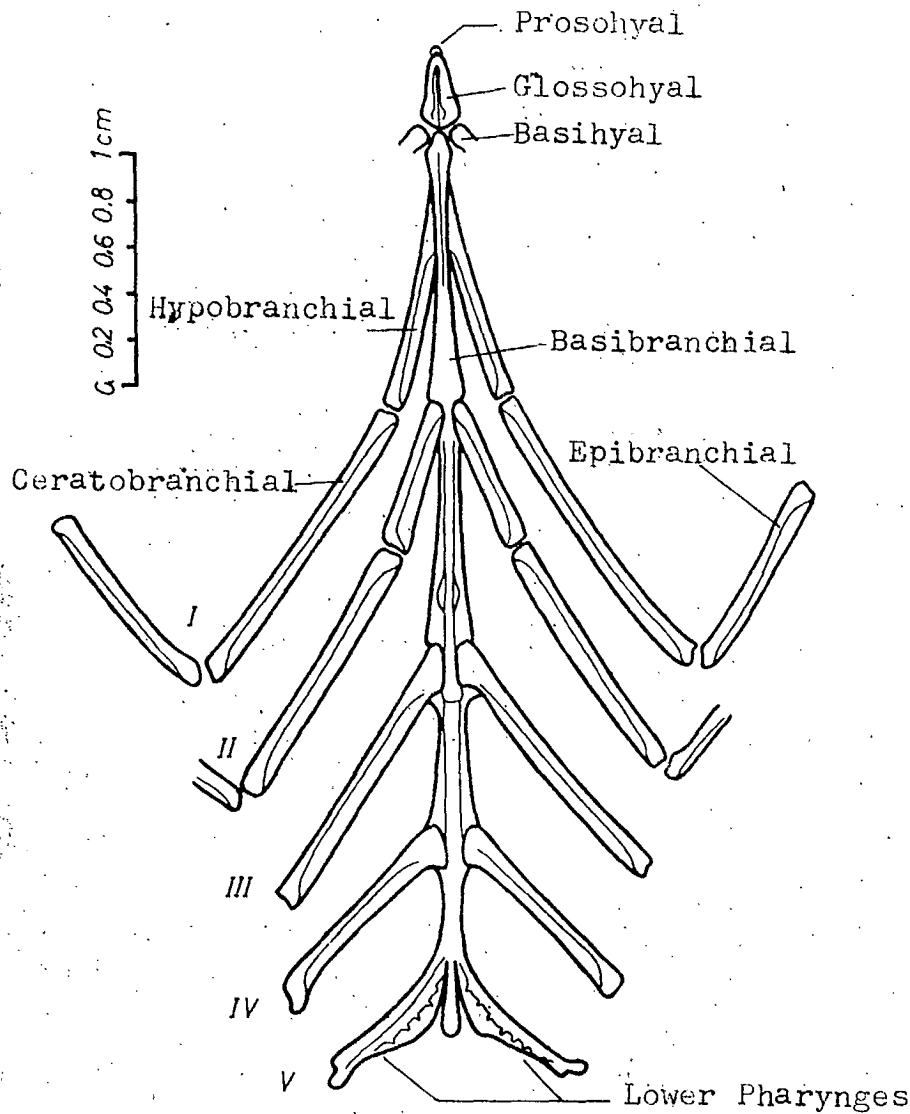


Fig. 10. Arrangement and shape of the gill arches and of the tongue, in the hyobranchial skeleton of a Vigo sardine 200 mm. long (LT) (Diagrammatic).

On the inner surface of each of the opercula, there is a fold without a skeleton and without gill rakers, which however has functional gill laminae on its rear portion, though these are much fewer in number than the following arches, except those of the last pair, which as we have said, is modified and has no gills. Therefore, in Sardina pilchardus, there is a pair of

pseudo arches and 5 pairs of gill arches: the pseudo arches and the first four gill arches have a respiratory function, while the trophic function is reserved for the five pairs of gill arches. The last pair, in addition to having gill rakers on the front edge, is modified and has teeth in the upper rear portion. In Figure 11, we see the arrangement of the gill rakers and the gills on the first left gill arch of a Vigo sardine 200 mm. long and in Figure 12, the three bones (epibranchial, ceratobranchial and hypobranchial) of the first gill arch of a sardine 154 mm. long and also from Vigo.

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b) Morphology of the Gill Rakers

F. DE BUEN (1919) mentioned that there are certain differences between the gill rakers of Vigo sardines and those of San Feliu de Guixols (Garonne), claiming that the narrowing of the teeth was more pronounced in the first and that the teeth appear to be considerably shorter in the San Feliu specimens, their apex failing to touch the edge of the small lamina which serves as a support for them. The observations of NAVARRO (1926), on sardines of the Balearic Islands, refer to teeth similar to those described by DE BUEN, where the narrowing of the teeth is barely noticeable.

In our observations, we were able to demonstrate that the teeth vary greatly in shape, in both Atlantic and Mediterranean sardines. In a previous work (ANDREU, 1953) we described the extreme shapes of teeth observed in the sardine of the Vigo estuary: some very long and slender, with the narrowing barely

noticeable, protruding from the median lamina, while in other, much shorter ones, with a very marked narrowing and an oviform apex, its projection did not extend to the lamina of the gill rakers.

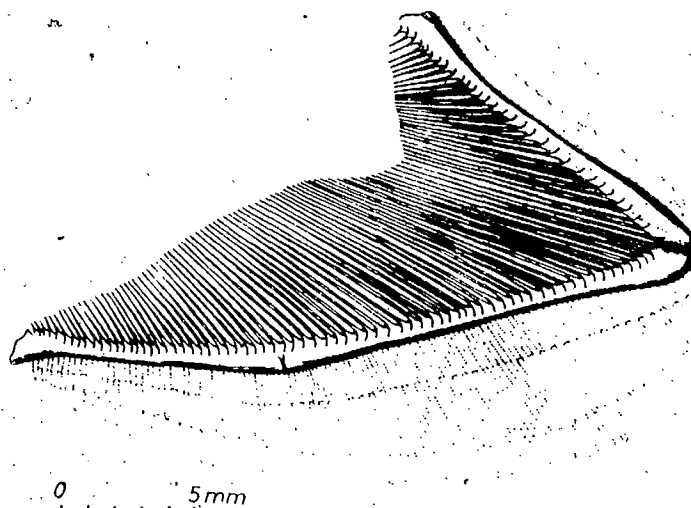


Fig. 11. First left gill arch of a sardine 200 mm. in total length, showing the arrangement of the gill rakers and the gills (diagrammatic).

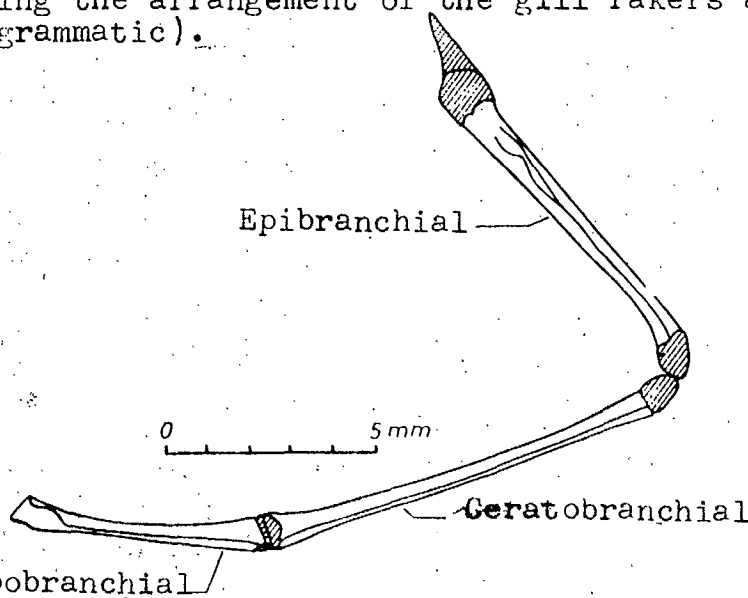


Fig. 12. Skeleton of the first left gill arch of a sardine 145 mm. in total length (diagrammatic).

The teeth are inserted at their base into the corneal lamina of the gill raker, forming an angle of some 45 degrees, so that the apices are completely separated from it. The projection of the teeth on each side of the lamina, and above it, produce the optical effect described by DE BUEN. Figures 17 and 19 illustrate what we have just said.

Not all the basal apophyses of the gill rakers are the same: those of the upper limb of the arch (epibranchial), as well as the majority of those of the lower limb (ceratobranchial and hypobranchial) recall the shape of a dagger handle. The first ceratobranchials, beginning at the tail, are different: the latero-external apophysis is hypertrophied and the main one shorter, recalling the shape of a Y when viewed from the side. The one nearest the articulation of the ceratobranchial and the epibranchial is so constructed that it does not hinder the articulation of the two limbs of the arch as they close over each other: the main apophysis is finer than the following ones.

The apophyses of the gill rakers are not directly inserted into the bones of the arch, but rather over the soft tissues, which solidly hold the apophysis between it and the arch, so that in dissection, the totality of the gill rakers is easily separated, with their ligaments and muscular cords, from the bones which serve as a support (Fig. 13.).

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New gill rakers are formed in the extremities of each of the limbs of the arches, so that the longitudinal growth of the ceratobranchial bone causes the hypobranchial gill rakers to be displaced and come to rest on the ceratobranchial bone. In this way, the separation between the gill rakers spines in the three segments of the arch remains the same, which would not occur without this displacement of the gill rakers which accompanies the longitudinal growth of the intermediate segment

of the arch (ceratobranchial). In their studies on the thread herring (*Opisthonema*) BERRY & BARRET (1963) were able to demonstrate that the number of gill rakers in each of the three segments of the gill arch have the same interspecies relationship as regards the length of the fishes, as well as the total number of gill rakers.

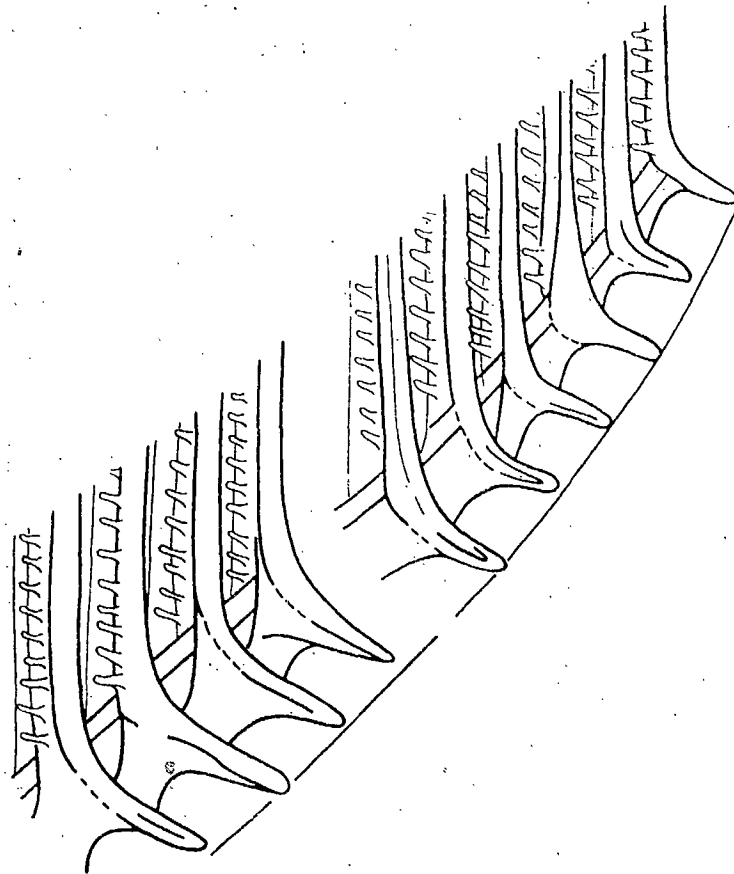


Fig. 13. Set of gill rakers separated from the gill arch with the soft tissues which hold the basal apophysis together. Sardine of Eastern Spain, 115 mm. total length (diagrammatic).

c) Ontogeny of the Gill Rakers

Initial Manifestations:

The fact that the very young sardines of California had a different diet than the adults, led SCOFIELD (1934) to study the development of the gill rakers in Sardinops caerulea. Said author observed that the gill rakers appear in the form of short protuberances, above the gill arch, when the young larvae measure about 20 mm. in length. At 30 mm., they still do not have teeth; these first appear when the young sardines measure 50 mm. in length. At about 70 mm. the spiny nodules begin appearing at the end of the teeth. When the fishes reach this length - says SCOFIELD - it would seem that the sardines are able to filter diatoms from the water, however the protuberances are not completely developed until the sardines measure 100 mm. or more. HUBBS (1929) has already called attention to the importance of these spiny nodules in the filtration of the phytoplankton contained in sea water. /470

The appearance and subsequent development of the gill rakers in young forms of Sardina pilchardus, both of the Atlantic and of the Mediterranean, show a close parallelism with those of California, although the European species shows greater precocity in the structuration of the filtering system; in addition, in the more developed forms (adults) of our sardine, the end nodules of the protuberances seem to form part of the teeth and do not have such a marked spiny appearance as that described by SCOFIELD for the Pacific species.

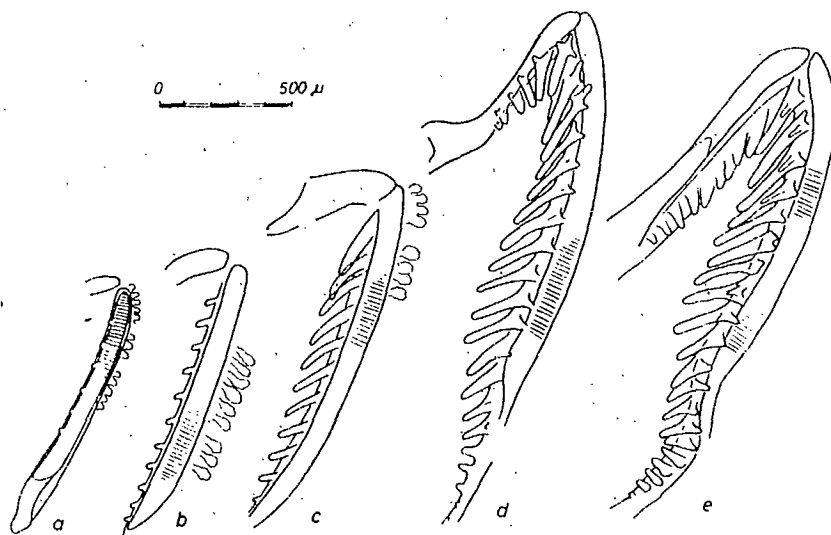


Fig. 14. First gill arches of young forms of sardines showing the appearance of the spines (a) and their development (b, c, d, e). "a", of a sardine larva 15 mm. long of Banyuls-sur-mer; b, c, d, e, belong, respectively, to larvae of the sardine of Castellón, of 19, 23 and 33 mm. LT (diagrammatic).

Generally speaking, in the European sardine, the process takes place as follows (ANDREU, 1960): The first signs of the gill raker spines are observed on the gill arch when the sardine larvae measure about 15 mm.; they increase in length, remaining digitiform, until the postlarvae measure 40 to 45 mm., at which time they begin to take on a laminar form in their proximal half (Figure 14 and 15); it is then that the first rough outlines of the conical protuberances appear. Therefore, we cannot see how KREFFT (1954) was able to encounter numerous long, thin gill rakers in Mediterranean sardine larvae measuring only 15 millimeters in length.

When the young sardines measure about 50 mm., the spines already have a laminar shape, serving as a support for

thinner teeth (Fig. 16.). They take on a club-like shape, with fine denticulations in the terminal portion, when the young, completely pigmented sardines measure 60 mm. or more (Fig. 17.).

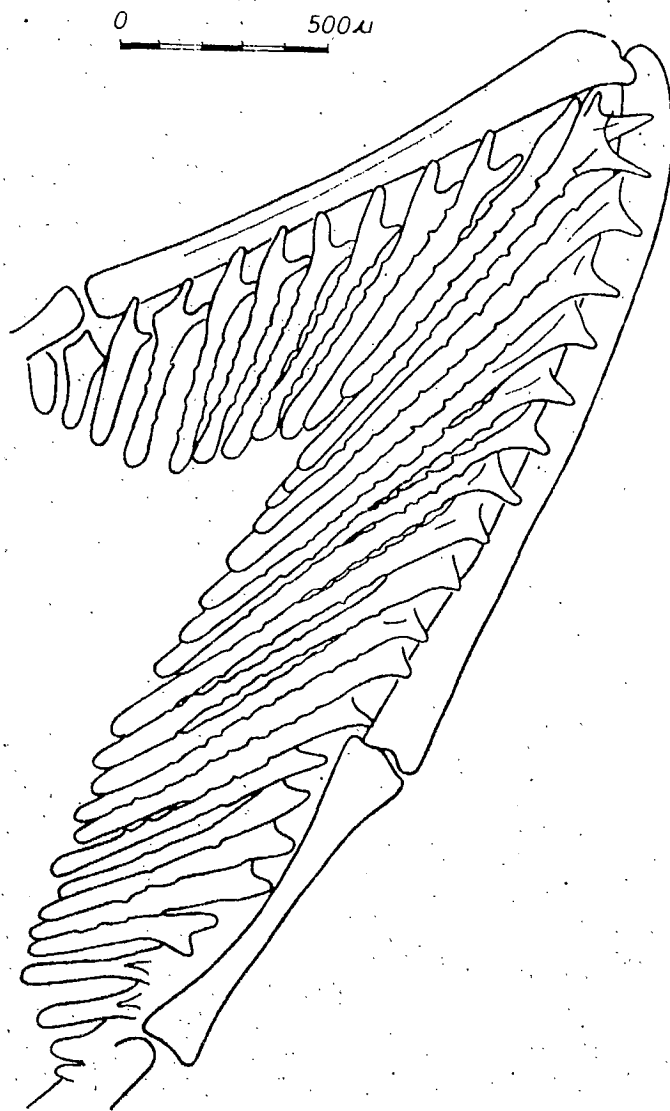


Fig. 15. First gill arch of a juvenile form of the Castellón sardine, having an LT of 41 mm., showing the initial formation of teeth over the spines (diagrammatic).

Increase in Length:

In young forms the length of the gill rakers increases in proportion to the total length following a more or less linear function (Fig. 18.). It is worthwhile mentioning that in the more developed young forms, the gill rakers appear to be more robust in the Castellón material than in that of Atlantic origin and that the teeth are formed somewhat earlier. The same may be said of the California sardine as compared with the European one, though to a greater extent.

Separation Between Gill Rakers:

Though up until now it has not been given proper attention in the literature, this factor greatly affects the diet of filter fish. In a previous work (ANDREU, 1960), we were able to demonstrate that the distance between the gill rakers (measured between the median portion of two adjacent spines, with the gill arch distended) increases with the total length of the fishes following a potential function. In the young forms, as the separation between spines becomes greater, the teeth become longer: as the length of the 40 mm. sardines is doubled, the length of the teeth is tripled. The same occurs with those 50 mm. long. The increased separation between the gill rakers in young forms is therefore more than compensated by the simultaneous increase in the length of the teeth.

The teeth are separated from one another by almost equal distances; those near the base of the spines are longer and closer together, however the others leave a free space, at

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the level of the end nodules, a space which generally varies between 70 and 80 μ . The other dimension, graduated after a fashion by the fishes, will depend on the degree of approximation between the spines in each instance. Since the teeth are not perpendicular to the spines, but rather form an angle of about 45 degrees (Fig. 19.), when two adjacent spines are very close together, they cross, forming a net of which the meshes will measure about 40 μ sideways. This explains how the sardines are able to retain perinidians as small as Prorocentrum, of which the length varies between 50 and 60 μ and even pine pollen, /474 which has been encountered by OLIVER (1951) and OLIVER & NAVARRO (1952 b) in considerable quantities in the stomachs of Vigo sardines examined in early spring. The aforementioned observations refer to Vigo sardines, and are not yet as extensive as those made in other areas of the Atlantic and Mediterranean. What we have studied in adult sardines of both waters, including those of the islands of the Azores, Madeira and the Canaries, is the separation between spines and how this increases with the length of the fishes: we shall give the results in a later chapter.

Rate of Increase in the Number of Gill Rakers (Total Length): /475

In Figure 14 a, which represents the first gill arch of a sardine larva 15 mm. long, the gill rakers appear as small protuberances; we may count up to 6 outlines of future gill rakers. These protuberances always appear in the terminal portion of the arch, where the genesis of the gill rakers will remain uninterrupted during the life of the sardines.

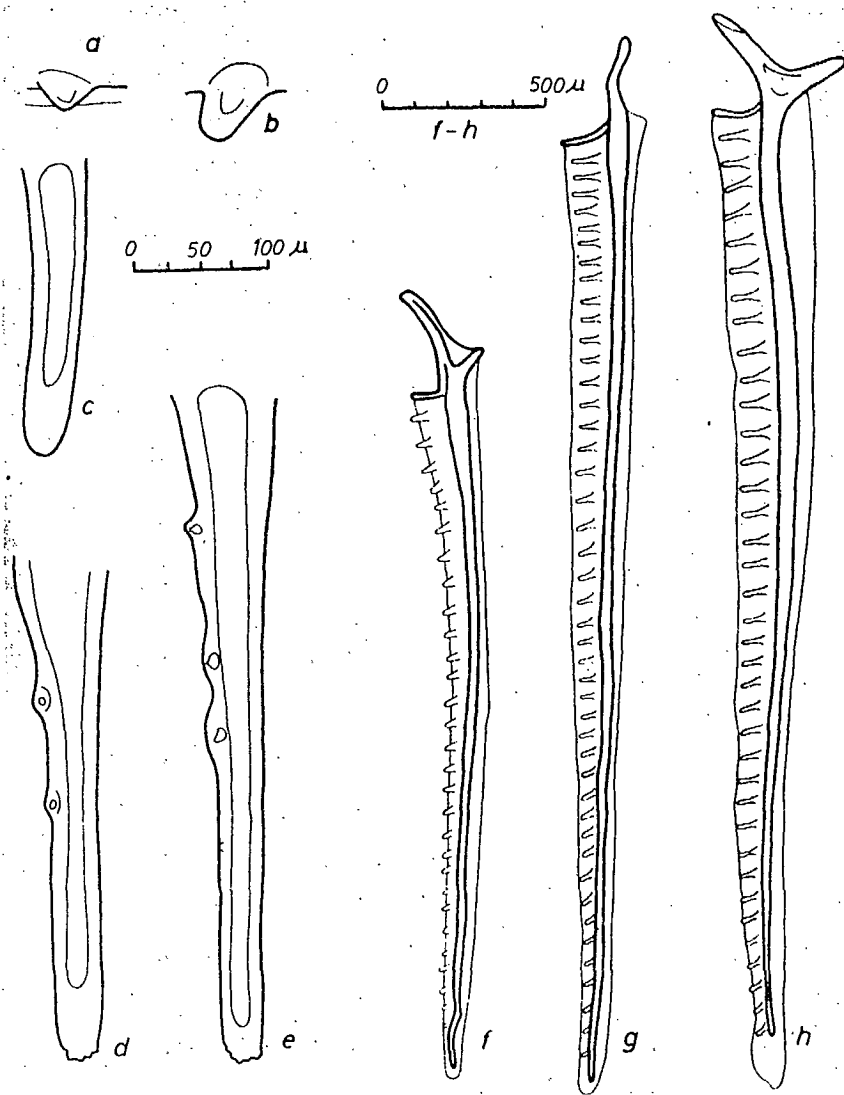


Fig. 16. Appearance and development of the gill rakers in larvae and young forms of sardines of the coast of Castellón and Vigo; a, of a larva 15 mm. long; b, 19 mm.; c, 23 mm., and e, 38 mm. LT; f, of a young form 50 mm. long; g, 60 mm.; h, 70 mm. (a-e of Castellón; f-h of Vigo) (diagrammatic).

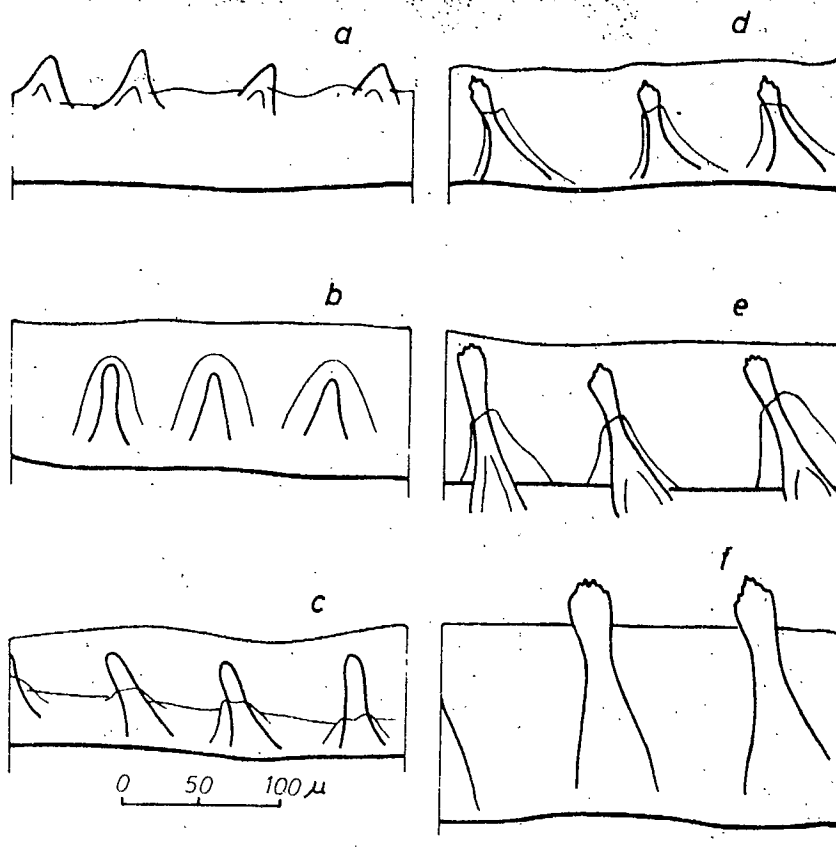


Fig. 17. Evolution of the teeth of the gill rakers in young sardine forms of the Vigo estuary.(diagrammatic).

- | | |
|------------|----------------|
| (a) 42 mm. | (d) 75 mm. |
| (b) 52 mm. | (e) 80 mm. |
| (c) 61 mm. | (f) 111 mm. LT |

We have studied series of larvae and young forms from Vigo, Castellón, Banyuls-sur-mer and Portimao, of which the two former, being much more complete, enabled us to ascertain that the formation of new spines is particularly active up until the time the young forms reach a total length of 55 mm., increasing in number to the 0.9793 and 1.3828 powers of the length of the body, in Vigo and Castellón respectively. Beginning with the length mentioned above, the increase rate is reduced. In

young forms of Vigo, the number of gill rakers increased from 30 to 60, in the size interval between 40 mm. and 105 mm. In Castellón, from 11 to 51 in larvae and young forms measuring from 20 to 105 mm.

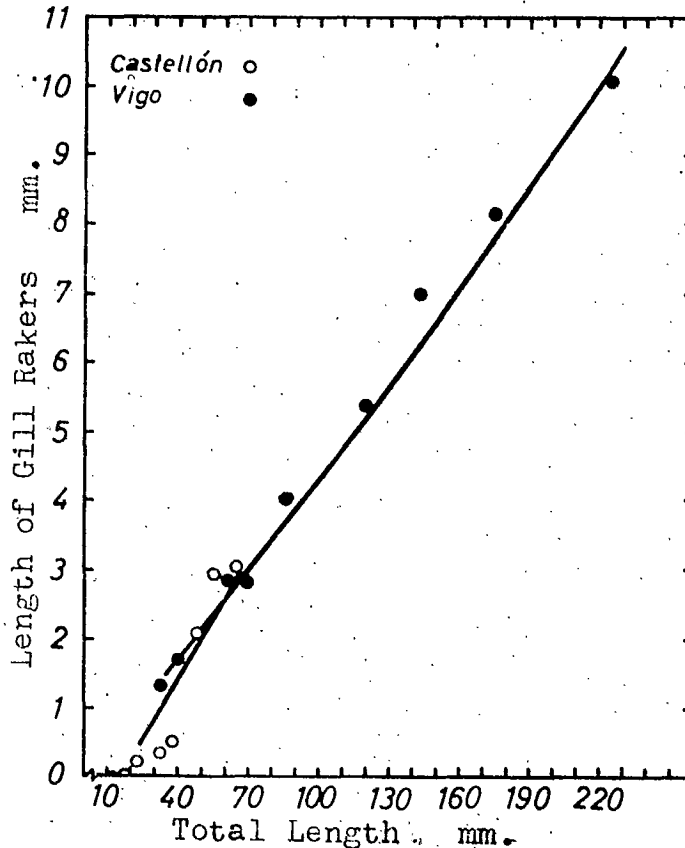


Fig. 18. Growth of the gill raker spines with the length of the fishes. Material from Castellon and Vigo.

Evolution of the Filtering Apparatus and Trophic Changes:

In the digestive tract of the postlarval stages of sardines 12-17 mm. in length (and probably up to the end of metamorphosis), coming from the English coasts, LEBOUR (1921) encountered only copepods, larvae and eggs, while the same author, in the young, metamorphosed forms, up to at least 82 mm. in length, generally

encountered unicellular organisms, mainly Prorocentrum micans; occasionally, copepods and larvae of mollusks. ERCEGOVIC (1940), in the Mediterranean, studied the diet of sardines 30 to 50 mm. in length (postlarval and metamorphosed forms) finding that most of the food in the digestive tract consisted of larvae and postlarvae of crustaceans and other organisms, as well as adult individuals. He also encountered dinoflagellates. Both this author (in Sardina pilchardus) and SOLEIM (1942), ARTHUR (1956) and BERNER (1959), who have studied larvae and young forms of Clupea harengus, Sardinops caerulea and Engraulis mordax respectively, agree in saying that food is not taken in through filtration, but rather the larvae and young forms feed in a selective "hunting" fashion, until metamorphosis has been completed. The digestive tract of larvae of E. mordax which still had unpigmented eyes, did not contain food. Visual acuity greatly influences diet at these stages of development, which lends support to the theory that the ingestion of food ceases almost completely at night.

These results are closely related to the development of the gill rakers. As we have seen, at the end of metamorphosis, when young sardines measure from 45 to 50 mm., the filtering apparatus is not yet able to retain small forms of plankton; beyond 60 mm., the teeth are already able to function effectively, as is demonstrated by the fact that sardines of 60 or more mm. examined by LEBOUR had a large quantity of Prorocentrum in their digestive tract.

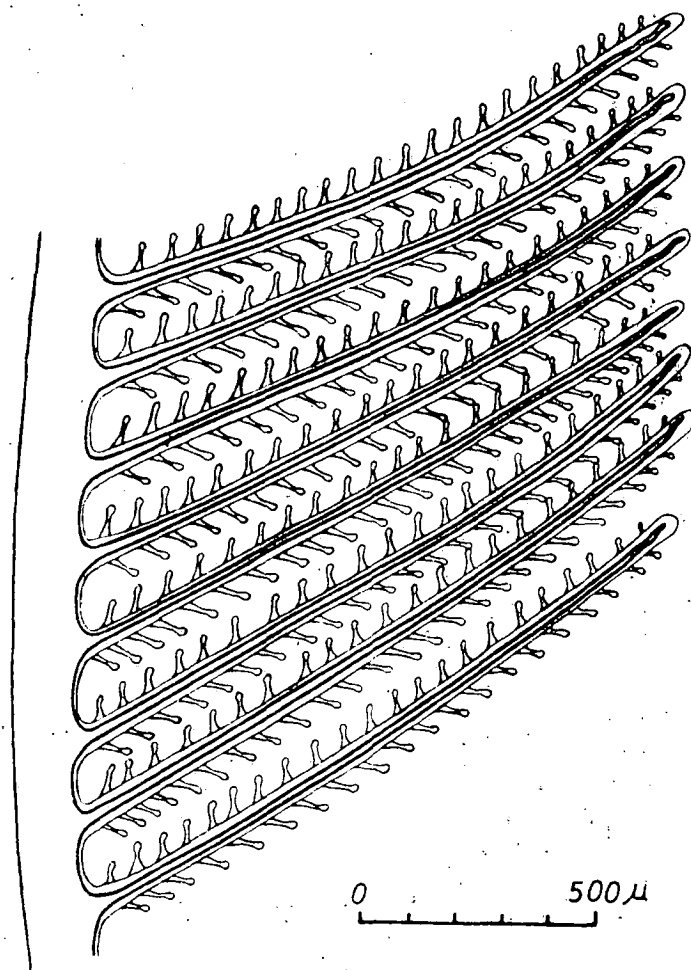


Fig. 19. Arrangement of the gill rakers in a Vigo sardine, 95 mm. LT, showing the net formed by the teeth (diagrammatic).

d) The Gill Rakers in the Adult Sardine

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Studies of sardine gill rakers have generally been limited to the simple counting of the number of spines present on the lower limb of the first arch to calculate extreme and average values or, at most, to search for the direct linear ratio between the number of gill rakers and the length of the fishes. Thus REGAN (1916) studied the gill rakers of sardines of Cornwall, Santander and La Coruña, Madeira, Constantinople

and the Adriatic, indicating only the extreme values: 69-88 gill rakers in that of Cornwall (fishes from 180 to 220 mm. in length); 63-82 in that of Santander and La Coruña (lengths between 110 and 180 mm.); 54-57 in that of Madeira (lengths 175 to 180); 55-60 in Constantinople (lengths 140 to 150 mm.) and 50 to 60 in the Adriatic (lengths between 110 and 180 mm.). As we already stated these results led REGAN to separate the subspecies Sardina pilchardus sardina from Sardina pilchardus, since, in the specimens coming from the Mediterranean, he had encountered less than 60 gill rakers in the lower limb of the first gill arch. CHABANAUD & MONOD (1926) counted 58 and 68 gill rakers in two sardines measuring 75 and 109 mm. and coming from the Lévrier Bay. THOMSON (1926) studied a limited number of sardines from Saint Jean de Luz, Douarnenez and Cornwall (15, 5 and 30 respectively) comparing the results with the standard length (excluding the tail fin). In St-Jean de Luz, the number of gill rakers varied between 65 and 79 (lengths of 140-155 mm.) and in Cornwall between 66 and 83 (lengths 180 to 220 mm.). MAUL (1948) found an average of 53 gill rakers (50-57) in 31 sardine specimens of Madeira measuring from 119 to 185 mm. LT. BARDAN, NAVARRO & RODRIGUEZ (1949), who studied much more abundant material from the Alboran Sea, relating the counts to the total length of the fishes, mention the great individual variability of this character in individuals of the same length. FURNESTIN (1950), in Mediterranean sardines of the Strait of Gibraltar, encountered an average value of 58.4 gill rakers (52 to 63) and in the Atlantic ones

of Morocco 80.0 (65 to 89). We, in a previous work (ANDREU, 1953) demonstrated the close relationship between the number of gill rakers and the length of Sardina pilchardus, both in the Atlantic and in the Mediterranean: in the Vigo sardine, the index of correlation calculated was 0.839 ($P > 0.001$) and in that of Eastern Spain - 0.395 ($P > 0.001$); the linear regressions encountered were, in those of Vigo $N_b = 0.21, L_t + 34.77$ (lengths 125-135 LT mm.) and $N_b = 0.39, L_t + 16.65$ (lengths 85-125 LT mm.). In those of Eastern Spain, $N_b = 0.14, L_t + 42.1$ (lengths 100-160 LT mm.), N_b being the number of gill rakers, and L_t the total length in mm. LETACONNOUX (1954) finds the following averages: La Rochelle, 64.9 gill rakers (60 to 69); Leixoes, 73.2 (62 to 84) and Azores, 52.0 (46 to 56). In the Canary Islands sardine, NAVARRO (1955, personal com.) studied the observations made by CABRERA on groups having a total length of between 140 and 230 mm., finding that the averages varied between 49 and 63 gill rakers; in the most represented size, the variation was only 5 gill rakers. CADENAT & MOAL (1955), in observations carried out on Cabo Blanco sardines measuring 36 to 94 mm. LT, say everything seems to indicate that the number of gill rakers varies in proportion to the total length, remaining constant for the same fraction of a gill arch; these authors found between 25 and 68 gill rakers. LEE (1961) studies the gill rakers of sardines of the Gulf of Lion divided into three groups: from 30 to 45 mm. caught in the Sète Canal; from 50 to 125 mm. from the canal and the open sea, and from 130 to 180 mm. caught in the open sea. In the first group, the

increase in the number of gill rakers in proportion to total length is very rapid; in the second group, the increase is still rapid though less so than in the first one; in the group of adult sardines measuring 130-180 mm. LT, the rate is much slower, and the following regression has been calculated for it: $N_b = 0.66, L_t + 49.81.$ (L_t in millimeters). Comparing the regressions obtained in adult sardines of Rosellon, Sète and Marseilles, there is reason to believe that those of the first locality have a slighty lower number of gill rakers than those of the other two. MATTA (1964) has studied the number of gill rakers in 231 sardines from the English Channel, south of Boulogne-sur-mer, measuring 190 to 240 mm. up to the fork; the linear regression calculated by this author is $N_b = 0.26, L_f + 25.04$ (L_f in mm.), very similar to those which we calculated from the observations of THOMSON (1926) on 30 sardines measuring 180 to 220 mm. in standard length and which we mentioned in the previous work cited (ANDREU, 1953); $N_b = 0.26, L_s + 21.7$ (standard length in mm.).

In the literature consulted on sardines we were unable to find any author having studied the separation of the gill rakers in relation to the total length, or the variation in the length of the gill arch.

In the chapters which follow, we shall give the variations encountered in material from different regions of the area of distribution of the species, from which we were able to obtain material. However, we shall first discuss the relationship existing between the number of gill rakers of the upper and

lower limbs of the first gill arch, and the growth rate of the gill arch in relation to the total length of the fishes.

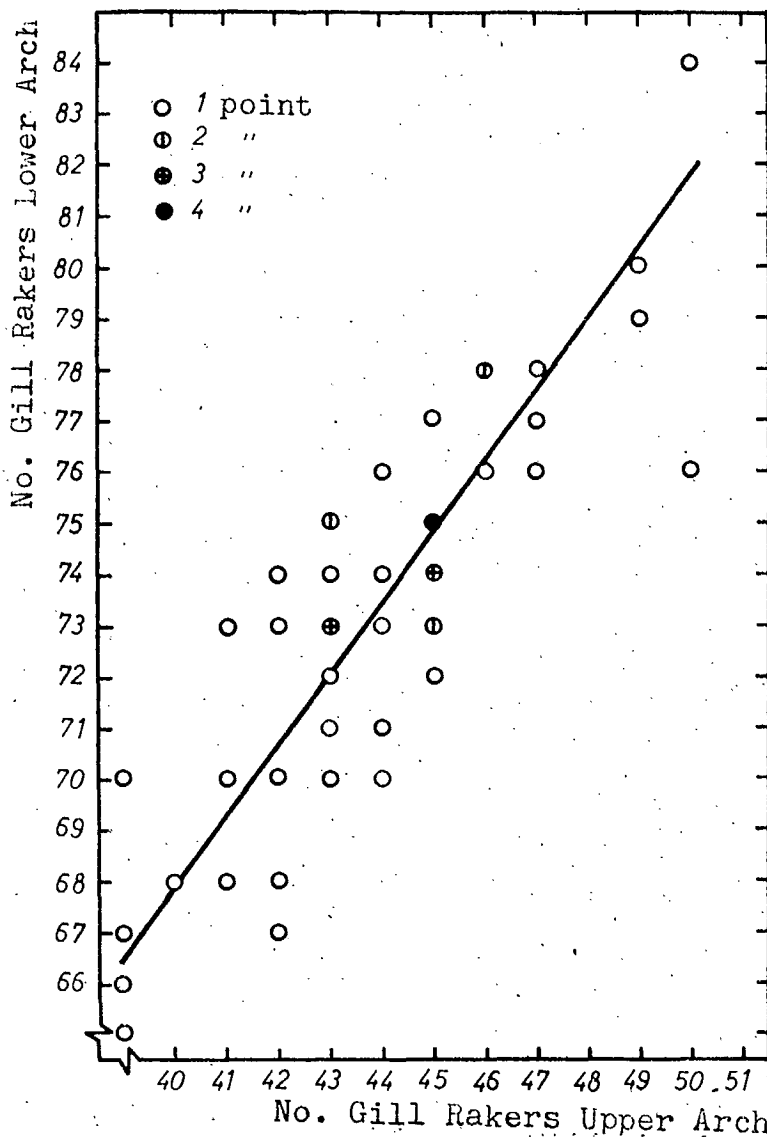


Fig. 20. Ratio between the number of gill rakers of the upper and lower limbs of the first left gill arch, studied in a lot of 50 sardines of the Vigo estuary.

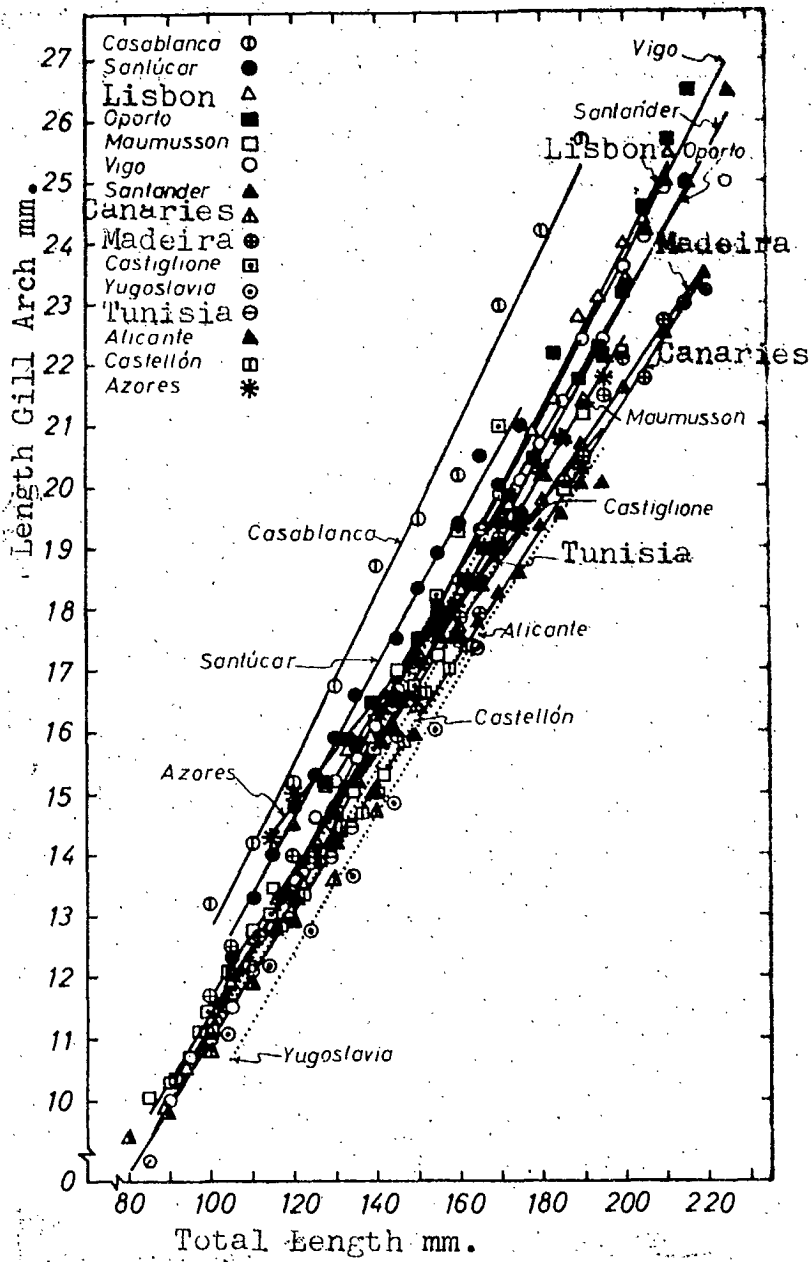


Fig. 21. Increase rate of the length of the lower limb of the first left gill arch in relation to size (LT mm.) in sardines of the different regions studied.

Ratio Between the Number of Epibranchial Gill Rakers (N_{bs}) and Those of the Low Limb (N_{bi}):

Though the counts were always made on the gill rakers of the lower limb of the first left gill arch, we felt it useful to have a term of reference regarding the lower limb. /479

For this purpose, we studied a lot of sardines from the Vigo estuary, consisting of 50 fishes, with total lengths of between 145 and 175 mm. LT. Although this size range is not as wide as one might hope, it nevertheless serves our purposes. /481

Firstly, let us mention that the epibranchial gill raker counts of the left and right arches of each fish show slight variations: in 40% of the cases, the number of gill rakers coincided; in 28% there was an extra gill raker on the left arch and 22% had an extra one on the right arch. In 2% of the cases, two extra gill rakers were counted on the left side and, in 2%, three more on the right side. These differences are compensated, since the average of the 50 fishes showed only one extra gill raker on the left upper limb. The averages of the number of gill rakers (upper limb - lower limb) by sizes varied between 113 and 123. Those of the arches of each side corresponded completely since the differences were at most 0.5, a fraction which can almost be discounted when we consider the extreme variability of this character.

The ratio between the number of gill rakers of the upper and lower limbs of the first left gill arch is shown in Figure 20. The linear regression calculated is as follows:

$$N_{bs} = 1.39 N_{bi} + 12.22$$

The average number of gill rakers in the upper arch is about 60% of the number present on the lower limb. The correlation index calculated between both variables is 0.7223 (P 0.001).

Growth Rate of the Lower Limb (l_i) of the First Gill Arch/Total Length (LT)

We felt it worthwhile to study the growth rate of the lower limb of the first gill arch (l_i) in relation to the total length of the fishes (LT), since said limb is the support on which the gill rakers rest. Measurements were taken of this character in 3,345 sardines, from the 15 geographical areas studied. In Figure 21, we have indicated the average values corresponding to the different size groups and traced the regressions calculated for the sardine of each one of the zones. On the following page, we are giving the allometric constants a and b encountered for the equation.

$$l_i = a \cdot L_t^b$$

Locality	a	b	Number of Fishes	Range of Lengths mm.
Maumussón	0,13	0,9754	83	85-200
Santander & Santoña	0,8	1,0683	283	115-225
Vigo	0,07	1,0885	1047	85-225
Oporto	0,14	0,9594	369	128-216
Lisbon	0,07	1,0887	370	89-211
Sanlúcar	0,12	1,0040	248	105-175
Casablanca	0,10	1,0547	21	100-190
Madeira	0,19	0,8898	145	100-220
Azores	0,48	0,7155	134	115-195
Canaries	0,12	0,9698	205	70-220
Yugoslavia	0,06	1,1087	64	105-165
Castellón	0,15	0,9282	214	92,5-162,5
Alicante	0,16	0,9233	51	130-195
Castiglione	0,08	1,0614	42	100-175
Tunisia	0,08	1,0580	69	120-170

As we can see, with the exception of the sardines of the Azores and Madeira, which have considerably lower exponents than the others, the growth of the lower limb of the gill arch is practically isometric in relation to the length of the sardines. The constant "a" varies little, except in that of the Azores (0.48) which degresses considerably from the remaining ones.

In Tables XXXVI bis, we have combined the original data contained in Tables XXII to XXXVI, of all the material studied. On the basis of the general frequency distribution, we calculated the average values for each size group (LT mm.) and with these averages we obtained the following formula of allometric increase:

$$l_i = 0.11 l_t^{1.0121} \quad (n: 3012)$$

which serves to confirm what we said previously.

It is particularly interesting that the growth of the arch is almost proportionate to the length of the fishes, since the different increase rates of the number of gill rakers encountered in the different zones studied cannot be attributed to variations in the growth of the arch. The same must be said of the separation between gill rakers, character of extraordinary adaptative value, because of its effects on the feeding habits of the fishes.

Tables XXII to XXXVI give the frequencies of arch lengths in millimeters, in relation to the size groups (LT) of the sardines of the different zones considered. The arch length

variation in the most representative size groups is between 1.5 and 4 mm.; usually it is 2 mm., which supposes about 13% of the retained length.

Increase Rate of the Number of Gill Rakers in the Sprat, Anchovy and Horse Mackerel of Galicia:

As we stated previously, the number of gill rakers increases with the size in Sardina pilchardus. The same occurs in Sardinops melanosticta (SAKO, 1938), Opisthonema (thread herring, /483 BERRY & BARRET, 1963), Alosa (FURNESTIN & VINCENT, 1958; COTTIGLIA, 1963), Sardinella (MONTEIRO, 1954, 1960). In the young herring of Northern Europe, (Clupea harengus) there is a positive correlation of some importance between the two variables, however it is insignificant in adult herring (KREFFT, 1954, 1958); the variation in fishes measuring 170-180 mm. was from 41 to 48 gill rakers and from 41 to 51 in those measuring 260 mm. In the Pacific species (Clupea pallasii Val), according to MCHUGH (1954), the number of gill rakers is complete when the fishes attain 100 mm. LS (tail fin excluded). In Engraulis mordax mordax, contrary to what occurs in other anchovies, the number of gill rakers does not increase with the length (HILDEBRAND, 1943; MCHUGH, 1951). This is also the case in Lycengraulis olidus (FUSTER DE PLAZA & BOSCHI, 1961 a). It does not either vary by size of specimen in Trachurus trachurus trachurus and Trachurus trachurus trecae (DA FRANCA, 1959). In Thunnus alalunga Gmelin, though the number may vary between 26 and 31, it shows the same modal value in Atlantic and in Pacific fishes. (LETACONNOUX, 1951). In Thunnus thynnus (L)

RODRIGUEZ-RODA (1964) has observed that in the lower limb, the number varies between 23 and 28 (mode 25), and there is no relation between it and the size of the tuna.

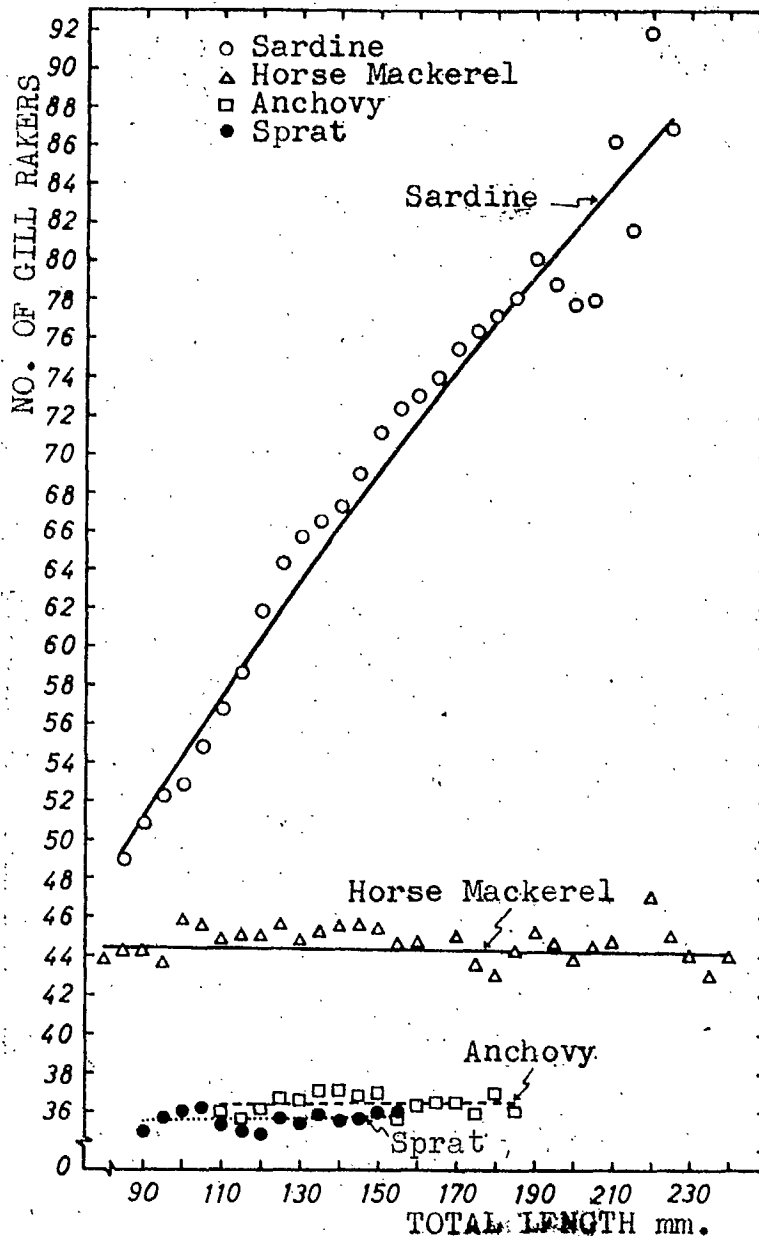


Fig. 22. Ratio between the number of gill rakers and the size (LT mm.) in different pelagic fishes of the Galician coasts. Number of fishes studied: sardine, 1,184; sprat, 95; anchovy, 475; horse mackerel, 236.

In the Vigo estuary, we were able to study the number of gill rakers of the sardine, and also that of other pelagic species accidentally or temporarily displaced, such as the sprat (Sprattus sprattus), the anchovy (Engraulis encrasicolus) and the horse mackerel (Trachurus trachurus), in fishes having a size range of between 90-155 mm., 110-185 mm. and 60-225 mm. LT respectively. Tables XLII, XXXVII, XXXVIII and XXXIX show the frequency distributions of the number of gill rakers of each of the species mentioned. The mean values are shown in Figure 22. As we can see, the number of gill rakers becomes established at an early age in the sprat, the anchovy and the horse mackerel, while in the sardine, the formation of new gill rakers continues throughout the life span of the fishes. In a previous work (ANDREU, 1955), we studied the variation in the number of gill rakers in relation to length in the Galician coast anchovy, and we mentioned that said number increased with the length of the fishes, within an interval of 75-175 mm. LT. However, in the new material now included (lengths 110-185 mm. LT), there is no such increase; in any case, it must only occur up until the time the anchovies reach a total length of 95 mm. Something similar occurs in the horse mackerel where we observed that in young fishes measuring up to 75 mm. LT, the number of gill rakers increases noticeably. Said number is very variable, fluctuating between 9 to 10 units in individual counts in the sprat, the anchovy and the horse mackerel. In the case of the sardine, as we shall see shortly, the variation may be up to 24 gill rakers in fishes of the same size class.

In the sprat, the number of gill rakers, within the size range mentioned previously, fluctuates between 32 and 40 (mode 35). In Angola waters, the two subspecies of Trachurus studied by DA FRANCA (1959) have from 52 to 62 gill rakers (mode 58), Trachurus trachurus trecae (Cadenat) and from 65 to 76 (mode 68) Trachurus trachurus trachurus (L), values which are strikingly different from those encountered by us in the horse mackerel of the Galician coasts. In the horse mackerel of the Moroccan coasts, ALONCLE (1964) encountered values very similar to those given by us for that of the Galician coasts: 41 to 50 (mode 45), while in those of the English Channel and Bay of Biscay, he encounters from 37 to 47 (40) and from 41 to 48 (44) respectively.

Rate of Increase in the Number of Gill Rakers in the Sardina pilchardus of Different regions:

Tables XL and LIV give the frequencies of the number of lower limb gill rakers (c ratobranchial - hypobranchial) by size groups (LT mm.) of all the material studied. The allometric constants "a" and "b" calculated using the formula

$$N_{bi} = a \cdot L_t^b$$

are as follows:

Locality	a	b	Number of Fishes	Range of Sizes LT mm
Maumussón	3,96	0,5715	145	85-200
Santander & Santoña	2,54	0,6460	284	115-225
Vigo	3,66	0,5841	1184	85-225
Oporto	5,22	0,5204	378	128-216
Lisbon	3,26	0,6151	434	89-211
Sanlúcar	6,77	0,4766	251	105-175
Casablanca	4,26	0,589	21	100-190
Madeira	18,25	0,2094	146	100-220
Azores	30,26	0,130	131	115-195
Canaries	9,97	0,3323	205	70-220
Yugoslavia	12,70	0,2915	64	105-165
Castellón	13,6	0,2801	214	92,5-162,5
Alicante	9,83	0,3529	49	130-195
Castiglione	19,17	0,2227	42	100-175
Tunisia	15,36	0,2614	70	120-170

In addition, we have calculated the allometric constants of the observations published by LEE (1961) for the sardine of Sète (Gulf of Lion), with the following results:

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$$a = 19.87 \quad b = 0.2690$$

size range between 90-180 mm. LT; number of fishes 2,729.

Combining the sardines of the different aforementioned regions, taking into account the increase rate of the number of gill rakers, as expressed by the exponents of the different allometric formulae, we obtain the following groups:

Increase Rates:

0.101-0.200: Azores (0.130)

0.201-0.300: Madeira (0.209), Castiglione (0.223), Tunisia (0.261), Sète (0.269), Castellon (0.280), Yugoslavia (0.291)

0.301-0.400: Canaries (0.332), Alicante (0.353)

0.401-0.500: Sanlúcar (0.477)

0.501-0.600: Oporto (0.520), Maususson (0.571), Vigo (0.584), Casablanca (0.589)

0.601-0.700: Lisbon (0.615), Santander (0.646)

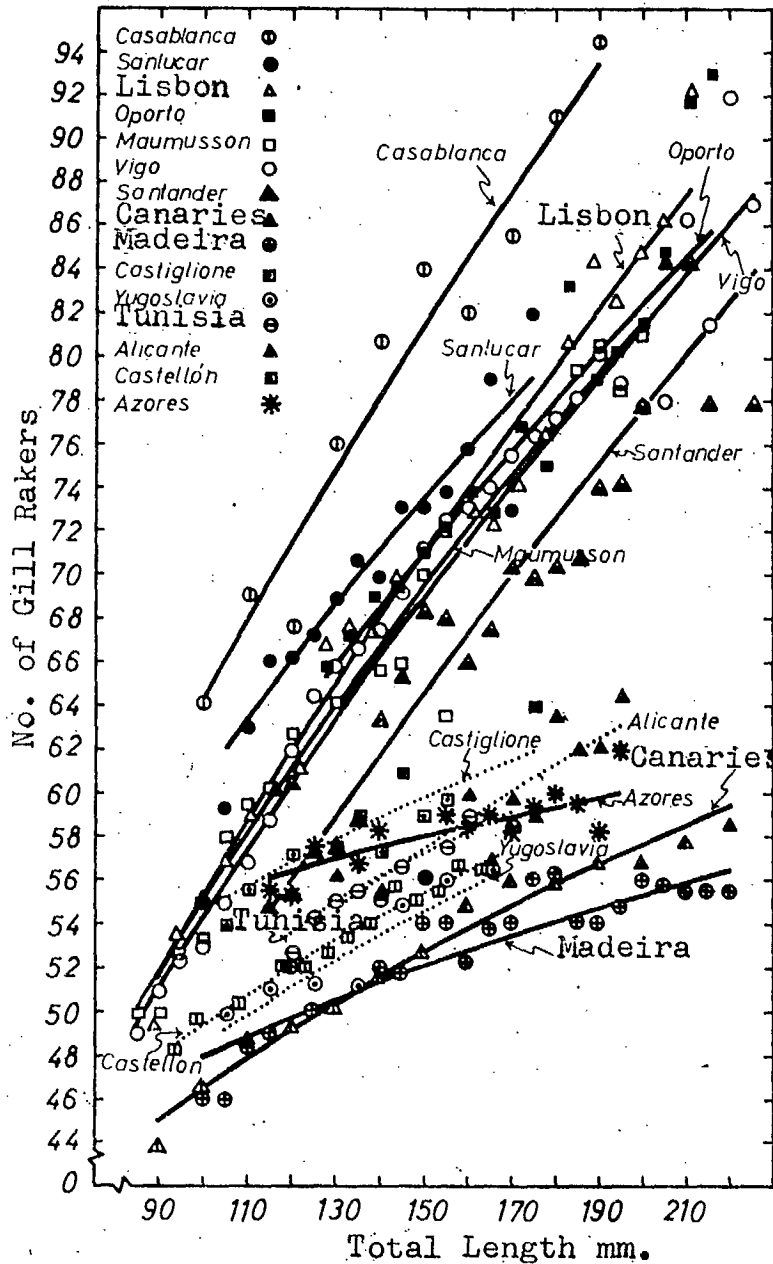


Fig. 23. Ratio between the number of gill rakers and the size in the Sardina pilchardus of the 15 geographical regions studied in this work.

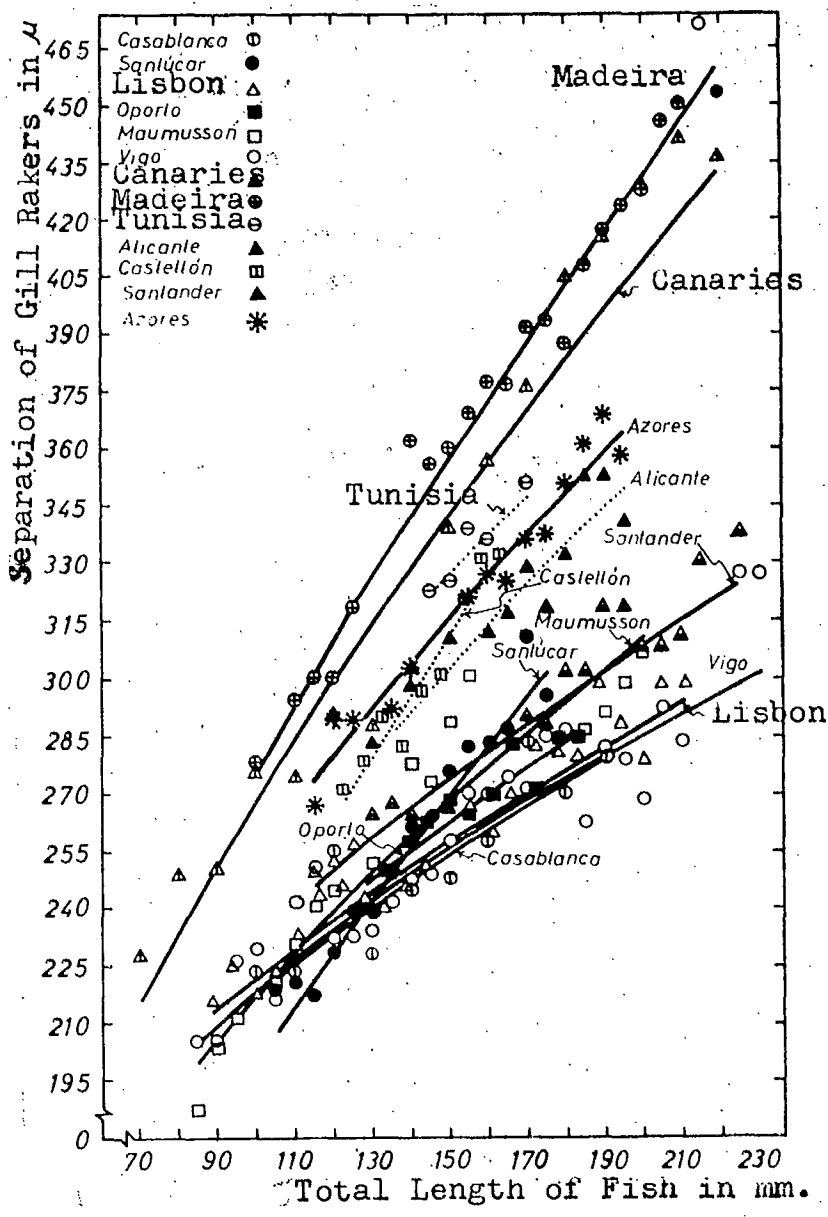


Fig. 24. Variation in the separation between gill rakers in relation to the size (LT mm.) in the sardines of the areas studied.

Firstly, we may separate on the one hand, the Mediterranean and insular sardines (Azores, Madeira and Canarias), with an exponent of less than 0.4 and, on the other, those of the entire Atlantic continental shelf, which have exponents exceeding 0.4.

Secondly, we see that the two latitudinal clines indicated by the vertebral mean (Figure 7.) disappear, in each of these waters, bringing out frequent notable discontinuities in the increase rate of the number of gill rakers, which authorizes us to assume that this is an adaptative character little affected by abiotic habits. However, this aspect of the problem will be discussed later.

In this instance, contrary to what occurs with the increase rate of the length of the gill arch, the constant "a", which indicates the relative position of the curves, is very different in some regions from those of the remaining ones, which explains, for example, why in the sardine of the Azores (Figure 23.), in spite of the low increase rate of the number of gill rakers in the size range considered, the high value of "a" (30.26) brings the curve above those of Madeira, Canaries, Yugoslavia and Castellón, those of the remainder cutting through its extention towards decreasing sizes. The "a" has also shown particularly high values in the sardines of Castiglione (19.17), Madeira (18.25), Tunisia (15.36), Castellón (13.6), and Yugoslavia (12.70); intermediate, Canaries (9.97), Alicante (9.83) and Sanlúcar (6.77). In the remaining localities, the most northerly, to $\ll 5$.

Figure 23 shows the mean values of the number of gill rakers by size groups, in sardines of the 15 geographical regions studied in this work and the calculated potential curves. It is worthwhile mentioning that the extreme curves are that of Casablanca, with the largest number of gill rakers in the size

range considered here, and those of Madeira and the Canaries, with the smallest, in spite of the geographical proximity between the first and last localities mentioned. They are followed - in order by number of gill rakers - by Sanlúcar de Barrameda, the set of curves of Lisbon, Oporto, Maumusson and Vigo and, separated from it, Santander. Between the curve of Santander and that of Madeira are those of the Mediterranean sardines, intersected by the Azores curve, which is the one having the lowest exponent and the largest value of "a" of all those calculated. There is no doubt that the Mediterranean sardine shows greater affinity with those of the Azores, the Canaries and Madeira than with those of the Atlantic continental shelf. Those geographically nearest the Mediterranean (Sanlúcar de Barrameda and Casablanca) are at the opposite end of the aforementioned figure.

The great variability in the number of gill rakers in fishes of equal size and coming from the same locality, definitely limits the range of application of this character for the characterization of populations, unless it is supplemented in part by a wide range of size groups with an adequate number of fishes in each of them. The variation is not equally pronounced in all regions. In Vigo sardines, the maximum variation encountered was 24 gill rakers, in fishes measuring 165 mm. It was 21, 20, 19 and 18 in Santander, Leixoes, Ayamonte and Lisbon respectively (size groups of 140, 155, 145 and 139 mm. LT). Next come Castiglione with 15, Alicante and Castellón with 13, Yugoslavia with 12, the Azores and the Canaries with 11,

Tunisia with 9 and Casablanca and Madeira with 8. This wide range of variation in the number of gill rakers in fishes of equal length is maintained when the counts are compared with the head length or that of the gill arch, which means that they cannot be attributed to individual size variations. Another factor comes into play, the age of the fishes, which we have not taken into account in this work and which must have some effect because of the individual growth differences in the fishes of each of the yearly classes.

The extreme values encountered in individual counts of sardines of the different zones are as follows; the sizes (LT mm.) to which they correspond are indicated in brackets: Maumusson, 49 to 85 gill rakers (85-100 mm.); Santander and Santoña, 50 to 92 (120-125 mm.); Vigo, 47-93 (90-225 mm.); Oporto, 61 to 96 (139-211 mm.); Lisbon, 45-95 (89-211 mm.); Sanlúcar de Barrameda, 57 to 84 (105-160 mm.); Casablanca, 61 to 96 (100-190 mm.); Madeira, 45 to 60 (100-205 mm.); Azores, 49 to 64 (115-195); Canaries, 37 to 61 (70-200 mm.); Yugoslavia, 46 to 62 (105-1,965 mm.); Castellón, 48 to 63 (92.5-147.5 mm.); Alicante, 54 to 72 (130-180 mm.); Castiglione, 49 to 77 (100-160 mm.); Tunisia, 51 to 61 (120-170 mm.).

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We see that the range of variation in the number of gill rakers in fishes belonging to the same size group, and the increase rate of the number of spines in relation to the total length of the sardines, are closely connected, with greater to lesser plasticity in the sardines of the Atlantic continental shelf, those of the Mediterranean and the insular ones (Azores,

Madeira and the Canaries), in that order, as if said variability became progressively lower as latitude diminishes.

Separation Between Gill Rakers in the *Sardina pilchardus* of Different Regions

In previous chapters (pages 469-474) when we study the appearance and development of the gill rakers in young forms of sardines coming from Banyuls-sur-mer, Castellón and Vigo, we note the close relationship between the development of the filtering apparatus and the diet. We shall now consider up to what point the separation between gill raker spines in the adult sardines of the different areas studied may be related to the diet.

In Tables LV and LXVII, we noted the frequencies of distances between adjacent spines, referring to size groups (L_t mm.); the distances were measured with an ocular micrometer, four times in each fish, so as to obtain more representative data. The tables mentioned show all measurements taken and their equivalents in μ .

The allometric constants "a" and "b" have been calculated using the formula

$$S_b = aL_t^b$$

in which S_b = separation between spines in micrometric divisions (1 division = 15 μ) and L_t = total length in mm. The results are shown on the following page.

Figure 24 shows graphically the results of our observations on sardines in which the size ranges between 70 and 235 mm.

The size range examined varied according to the geographical areas from which the material was taken; in part, it remains a comparative value of the regressions obtained, as is the case with the other characters examined, but nevertheless the sets of curves are sufficiently indicative for our purposes. Some experimental mean values digress considerably from the calculated line of regression; this is due - generally speaking - to the fact that these points are represented by one or very few fishes.

Locality	a	b	Number of Fishes	Range of Sizes LF mm.
Maumussón	1,40	0,5095	51	85-200
Santander & Santoña	2,30	0,4141	74	115-225
Vigo	4,23	0,3245	211	85-235
Oporto	2,16	0,4184	91	128-183
Lisbon	2,57	0,3805	104	89-211
Sanlúcar	0,47	0,7298	87	105-175
Casablanca	2,55	0,3783	18	100-190
Madeira	0,91	0,6520	74	100-220
Azores	1,38	0,5429	61	115-195
Canaries	1,08	0,6099	67	70-220
Castellón	0,53	0,7238	36	122,5-162,5
Alicante	1,34	0,5442	40	130-195
Tunisia	2,10	0,4686	19	145-170

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Following the arrangement of the different curves shown in Figure 24, we may distinguish the following affinities:

1. Sardines of Madeira and the Canaries: in which the spines separate rapidly as the size of the fishes increases.
2. Atlantic sardines of the continental shelf: on the one hand, we have the curves of the sardines of Oporto, Vigo, Lisbon and Casablanca, which form a very narrow ray, especially the three last, where separations between spines are almost

similar. On the other, Maumusson and Santander (Bay of Biscay) with slightly larger separations, though maintaining the tendency of the previous ones.

3. Mediterranean sardines: Tunisia, Castellón and Alicante occupy an intermediate position between the first two groups mentioned, though showing more affinity with the first.

Last come the sardines of Sanlúcar de Barrameda where, because of their high separation rate, the curve cuts widely into the second group, and those of the Azores, situated among the Mediterranean sardines.

Going by the increase rates of the separations (exponents of the allometric formulae), we obtain the following groups:

Exponents

- 0.301-0.400: Vigo (0.324), Casablanca (0.378), Lisbon (0.380)
0.401-0.500: Santander (0.414), Oporto (0.418), Tunisia (0.469)
The curve of this last was calculated with only 5 points.
0.501-0.600: Maumusson (0.509), Azores (0.543), Alicante (0.544)
0.601-0.700: Canaries (0.610), Madeira (0.652)
0.701-0.800: Castellón (0.724), Sanlúcar (0.730)

Sanlúcar and Castellón have the lowest values of "a" (0.47 and 0.53), which further accentuates the slope of these two curves.

As we can see, the groups with high exponents - indicating rapid separation between gill raker spines as the size of the fishes increases - correspond to more southerly sardine populations

(Mediterranean and the islands of the Azores, Madeira and the Canaries), with the exception of the Morocco sardines which, in this regard, are exactly similar to those of Vigo and Lisbon, which have low exponents like the rest of the North Atlantic sardines.

Below are indicated the average separations between spines (in μ) in the sardines of the size groups of 100, 150 and 200 mm. LT of each one of the regions studied. In those cases where one of the aforementioned size groups is missing, the mean values have been calculated on the basis of the corresponding regression formula, however the values thus obtained are indicated in brackets.

Locality	Average Separation in μ			Maximum & Minimum Separations Encountered,	Size Ranges Studied
	Size Group			in μ	LT mm.
	100	150	200		
Maumussón	221	288	306	180-315	85-200
Santander & Santoña	(232)	265	307	240-345	115-225
Vigo	230	258	269	135-345	85-235
Oporto	(223)	268	(298)	210-330	128-183
Lisbon	217	258	279	180-345	89-211
Sanlúcar de B.	219	276	(334)	165-330	105-175
Casablanca	223	247	282	195-300	100-190
Madeira	277	360	427	270-495	100-220
Azores	(253)	320	369	255-405	115-195
Canaries	276	339	429	210-465	70-220
Castellón	(232)	311	(385)	255-375	122,5-162,5
Alicante	(244)	310	352	270-405	130-195
Tunisia	(271)	370	(376)	300-360	145-170

It is assumed, from the above data, that the filtering capacity of the gill rakers of the large sardines (200 mm. LT) of Vigo, Lisbon, Casablanca and Oporto, is equivalent - generally speaking - to that of young sardines (100 mm. LT) of Madeira and the Canaries.

Diet of *Sardina pilchardus*

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We have sufficient bibliographical information concerning the stomach contents of the European sardine, to be able to conclude that the diet of the Mediterranean sardine is substantially different from that of the Atlantic sardine. The works listed below give clear evidence of this.

Atlantic Ocean:

On the English coast of Cornwall, HICKLING (1945) was able to demonstrate that the food of the large-size sardine includes such forms as Prorocentrum micans, sometimes found in their stomachs in large quantities. Though, in general, the copepoda were the most important organisms in the diet, the diatoms were clearly predominant in this diet in spring and autumn, lending a greenish colour to the stomach contents: some stomachs contained exclusively diatoms. The peridinians were important in summer. In sardines of the French coast of Concarneau, DESBROSSES (1933) found a predominance of diatoms, a phenomena which is repeated in the Bay of Biscay (FURNESTIN, 1943); during the winter - according to this last author - the stomach contents consist almost exclusively of a green purée of vegetable origin, combined with the odd copepod and fish spawn. In sardines of

the Galician coasts, MASSUTI (1946) encountered Prorocentrum in relatively large quantities; the diatoms and peridinians were the most important organisms in the diet during a few months and even pine pollen made up an important part of this diet, in addition to copepods and other zooplankton groups (OLIVER, 1951; OLIVER & NAVARRO, 1952 b). On the coast of Portugal, the most important groups encountered in the digestive tract of sardines consisted of copepods and larvae of crustaceans and worms (SILVA, 1954), however in the months of January and May, the diatoms constituted up to 75% of the organisms listed; something similar occurred with the peridinians in June, July and November; PINTO (1951) had already mentioned the importance of phytoplankton in the diet of the Portuguese sardine, his attention having been caught by the lack of consistency between the stomach contents and the composition of the plankton: the diatoms Chaetoceros and Rhizosolenia were missing from the diet, and these are extremely abundant in Portuguese waters .

Mediterranean Sea:

MASSUTI (1946), who studied simultaneously the diet of Atlantic sardines (Vigo) and those of the Mediterranean (Malaga), found that Prorocentrum and almost all the other peridinians and diatoms were lacking in the stomachs of these latter, encountering few differences as regards the copepods. In the stomach contents of the sardines of the Balearic Islands (Mahon), MASSUTI & OLIVER (1948), in addition to the copepods, included among the main components: cladocerans, tintinnids,

and peridinians. This opinion is largely shared by LEE (1961), /494
as he refers to the young sardines of the Gulf of Lion which, according to this author, feed mainly on phytoplankton, while the adults feed on zooplankton. Particularly interesting are the contributions of VUCETIC (1955, 1963, 1964) on the Adriatic sardine. According to this woman author, the stomach contents of the Yugoslavian sardines studied by her consisted exclusively of zooplankton. Only in a single sample, composed of sardines of less than 120 mm. LT, did she encounter a certain quantity of phytoplankton. VUCETIC (1955) states that the sardine eats practically nothing during the night; in her 1964 work, she says that the maximum trophic activity occurs at 17:00 hours.

We have not been able to obtain information on the diet of the sardines of Morocco, the Azores and the Canary Islands.

The Gill Rakers in Relation to the Diet of *Sardina pilchardus*

From the foregoing, we may conclude that the sardine is essentially a filter feeder though, as MARGALEF (1960 a) mentions, in environments which have not sufficient elements to maintain its growth, it may complete its diet by means of increasing quantities of small animals chosen selectively. During the winter, on the coasts of Vinaroz, we studied sardines caught at sea bottom with dragging nets, which often had their stomachs full of sediments. PINTO (1951) has encountered small fishes measuring 40 mm. in length in the digestive tract. On the other hand, it has been demonstrated that schools shun waters which are rich in diatoms with aciculate appendices or

other types of undesirable food. MUZINIC (1960) has demonstrated experimentally that sardines throw off a certain type of food after it has been caught.

Therefore, we may assume that the diet of the sardine is, in many cases, selective. The fact that these fishes do not feed during the night except in the presence of artificial light indicates that passive feeding is much less important than was believed up to now. Sight must play a primordial role in the locating and capturing of food, though we still do not know how the sardines of the Atlantic react in this regard in areas which are richest in microplankton, either during the day or in the dark. It is very significant that the industrial canners of Ayamonte, in the South Atlantic region, have a preference for sardines coming from late night or early morning catches, because they have their stomachs empty, as opposed to those of catches made in the early hours of the evening, when stomachs are full.

What we can say is that sardine larvae and the young forms, up to completion of metamorphosis, feed essentially on zooplankton, choosing selectively, and it is only when the gill rakers have completed their development with the appearance of the teeth, that sardines are able to retain phytoplankton.

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We have seen that as the fishes increase in size, the separation of the gill raker spines also becomes greater, since the gill arch grows isometrically, while the increase rate of the number of gill rakers has negative allometry, following rates of separation which are markedly different depending on geographical areas.

The fact that phytoplankton abounds in the stomach contents of sardines of the coasts of England, Brittany, Bay of Biscay, Galician and Portugal could be explained by the low degree of separation between their gill rakers, while the populations of the Mediterranean, of which the spines are more widely separated, would be incapable of retaining anything so small - except for young fishes, where the spines are still very close together - reason for which the food of adult individuals is composed almost exclusively of zooplankton organisms.

Taking into account the filtering capacity of the gill rakers, on the basis of separation between spines, adult sardine populations could be classified as follows, according to diet:

- Microplankton eaters: Atlantic sardines living in the waters of the continental shelf
- Zooplankton eaters: Mediterranean sardines and those of the Azores Islands
- Predominantly selective feeding: sardines of Madeira and the Canary Islands

Of the three groups, those of the first are best able to make use of primary production, and therefore belong to the lowest trophic level. Those of the other two groups have more evolved, more mature ecosystems, especially those of the last.

4. INTERSPECIES COMPETITION

In some geographical areas or during certain times of the year, sardine populations may cohabit and be caught with other pelagic species. Thus in the Galician coasts the sprat (Sprattus sprattus) generally forms mixed banks with the sardine (OLIVER, 1950; ARTE, 1956) and with the anchovy (ARTE, 1956).

According to ANADON (1960), this latter may be encountered with the horse mackerel (Trachurus trachurus) in the months of August to March, however this is not the case from April to July.

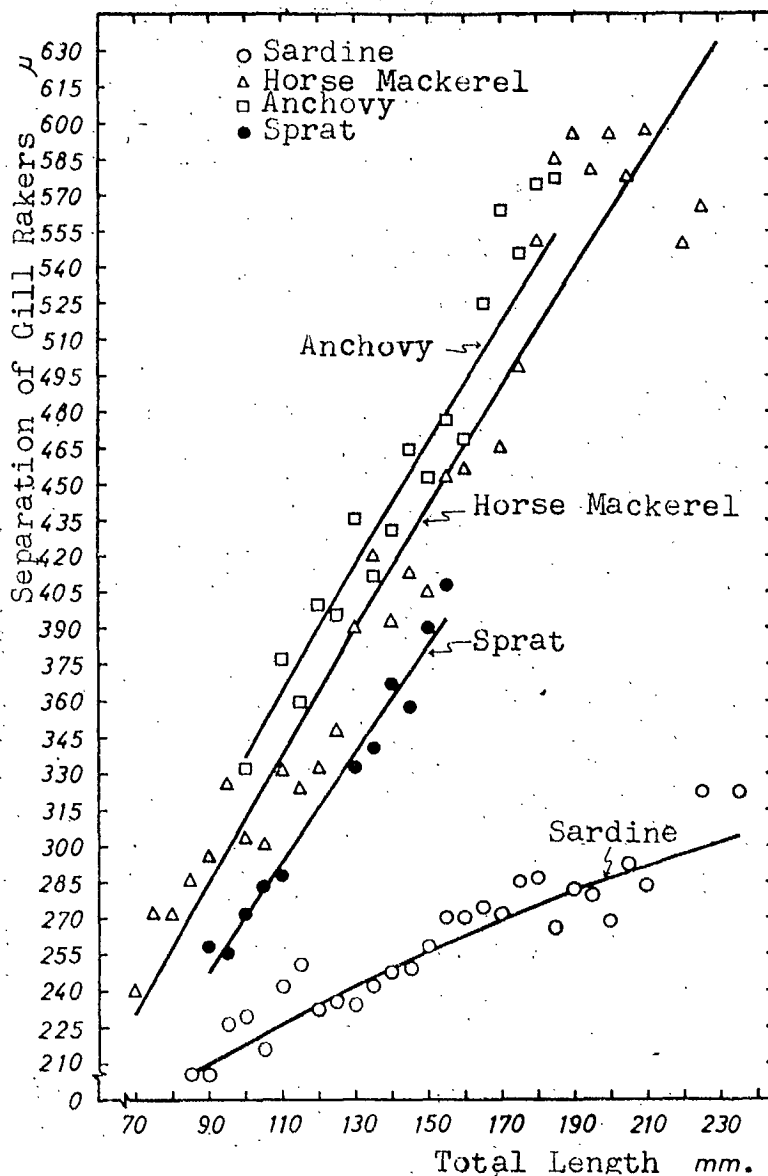


Fig. 25. Variation of the distance between spines; in relation to size (LT mm.) in various pelagic species of the Galician coasts: sardine, sprat, anchovy and horse mackerel.

DE BUEN (1927 a, 1929 b, 1932) was the first to give attention to the phenomenon of alternative substitution in fishing of the pelagic species mentioned, along the Galician /496 coasts, comparing the variations throughout the years as regarded the ratio between the quantities of each of them caught. Subsequently NAVAZ (1946) and ANADON (1950) studied this problem in the same region. LOGVINOVICH (1951) has observed similar alternations in the Azov Sea. Lastly, MUZINIC (1958) compares the catches of Sardina pilchardus, Engraulis encrasicolus, Scomber scombrus and Scomber japonicus colias in the Eastern Adriatic.

ANADON (1950) compared periods of from 27 to 35 years; he discusses the results of his predecessors and mentions that during the most favorable years for the sardine (1929-1938), the sprat gradually decreased, in parallel fashion, until it disappeared in 1938. In the case of the sardine-horse mackerel, the interaction does not appear very evident; though he finds a certain negative correlation between the catches of both species, he mentions that one cannot speak of competition. He finds no relationship between the sardine and the anchovy. MUZINIC (1958), during the period studied by her (1931-1940) in Adriatic waters, encounters opposite fluctuations between the anchovy and the mackerel, however most of all between the mackerel (Scomber scombrus L) and the Pacific mackerel (Scomber japonicus colias Gm), mentioning a strong negative correlation between the catches of sardines and Pacific mackerel. This author says that it is not possible to interpret the mechanisms

which come into play, however that she has encountered negative correlations only in those species having different spawning periods, while the positive correlation has not been proven except in species having almost the same spawning periods. DEMIR (1965), in his synopsis of Engraulis encrasicolus, mentions as competitors of the anchovy Sardina pilchardus, Sardinella aurita, Sprattus sprattus, Trachurus trachurus and Scomber scombrus. In the opinion of MARGALEF (1960 a), the only serious competitors of sardines and related species are filter feeders such as the pelagic Tunicata (goldline), which are capable of massive multiplication. On referring to the alternation of fluctuations, he mentions that these reflect rather a change in living conditions, since there is a certain ecological separation: the sprat prefers waters of lower salinity, so that in the Baltic, the periods of abundance coincide with abundant fluvial contributions; Engraulis and Trachurus thrive in more stable oceanic conditions, so that serious competition is only possible with older sardines. Lastly, he says that these fishes, rather than being true competitors, play the role of indicator organisms.

Considering the problem from the point of view of food competition, taking as a basis the capacity for retention of prey through the filtering action of the gill rakers we see, in Figure 25, that on the Galician coasts the adult sardine has a clear advantage over the other species considered. In Tables LVII, LXVIII, LXIX and LXX, we note the frequencies of separations in 4 corresponding to the size classes studied. However, the

anchovy and the young horse mackerel may become competitors, and the latter may compete with the sprat, in spite of the fact that the sprat has a smaller separation between spines than the horse mackerel and the anchovy. The data given below indicate the average separation between gill rakers (in μ) in size groups of 100, 150 and 200 mm. LT, and more clearly illustrate what we have just said. The figures in brackets were calculated by extrapolation.

Species	Size Class LT in mm.			Max. and Min. Separations		Size Ranges Studied LT mm.
	Aver. Separ.			Encountered in μ		
	100	150	200			
<i>Sardina pilchardus</i>	230	258	269	135-345	85-235	
<i>Sprattus sprattus</i>	271	390	(181)	245-420	90-155	
<i>Engraulis encrasicolus</i>	333	453	(589)	285-630	100-185	
<i>Trachurus trachurus</i>	303	405	595	225-690	70-225	

The average maximum separation between spines in large-size sardines (200 mm. LT) is lower than the average separation between the spines of the young sprat (100 mm. LT), which on the Galician coasts is, of the pelagic species studied, that which follows the sardine in filtering capacity.

A rapid review of some of the works published on the contents of the digestive tract of the pelagic species which may enter into food competition, will permit us to better ascertain the role played by the gill rakers in the diet. On pages 493-494, we already referred to this factor in Sardina pilchardus, the behavior of which varies noticeably from one geographical region

to another. The sprat of the Baltic (Sprattus sprattus) feeds particularly on copepods and cladocerans; in summer it eats at night and in autumn in the daytime (MANKOUWSKI, 1947). That of the Mediterranean coasts, according to VIVES & SUAUE (1956), CAUTIS (1958) and DIMOV (1961) feeds mainly on copepods, which constitute up to 95% of the diet; like the sardine and the anchovy, the Mediterranean sprat feeds mainly during early morning and at sundown (DIMOV, 1961). The herring (Clupea harengus) feed essentially on copepods and their larvae on teleosts: Ammodytes, gadids and clupeids (RICE, 1963). The anchovy (Engraulis encrasicolus), when found in subsurface waters, feeds preferably on copepods, mysids and larvae of crustaceans (PAGE, 1911). NIKOLSKI (1957) mentions that the diet of the anchovy of the Azov sea generally comprises 60% copepods, 20% polychetes and 20% cirripeds and, in the Black Sea, /499 35%-55% copepods, 18%-35% larvae of decapods and thirdly, larvae of mollusks. OKUL (1940) has encountered up to 11% phytoplankton in the stomachs, and this was also mentioned by PAGE (1911) in regard to the anchovies which live near sea bottom and MIRANDA (1931) in regard to those of the Málaga coasts, in the stomachs of which - he says - he encountered copepods all year round, diatoms from January to March, and larvae of decapods.

In the stomachs of the horse mackerel (Trachurus trachurus) MIRANDA (1930, 1931) in August encountered young anchovy forms from 20-30 mm. long and in October, large quantities of larvae of the same species, which were smaller in size; in July sardine

larvae, in addition to schizopods, larvae of decapods, amphipods and larvae of fishes. ANADON (1960) mentions that the horse mackerel seems to feed only in the daytime, since the specimens fished at dawn had empty stomachs and full intestines, while those caught in the early hours of the evening had full stomachs. According to LOZANO (1952), young horse mackerel are exclusively planktivorous, while the adults also feed on fishes, above all on pelagic species: Engraulis, Scomberesox, Ammodytes and Argentina.

Lastly, the horse mackerel of the English coasts studied by STEVEN (1949) give indications of having a very different diet depending on whether the schools come from catches made near sea bottom or those made in subsurface waters, and also depending on the time of year. According to said author, the small quantities of phytoplankton present in stomachs could only have been introduced by filtration, while larger prey are caught in a selective manner: Maurolicus and young fish forms, especially of Clupea, Ammodytes and Onos, together with large larvae of decapod crustaceans such as Corystes and Porcellana, constitute the main food of this species. In the area of Blanes, BAS (1960) has encountered in their stomachs Ammodytes, Engraulis, young fishes (possibly Sardina), Aristeus, tube worms, amphipods, etc. and in the stomachs of the horse mackerel of the coasts of Castellón, ANDREU & RODRIGUEZ-RODA (1953) mention the presence of remains of Sardina and Engraulis and larvae of Sardina.

MUZINIC (1960) was able to demonstrate experimentally that sardines, in the presence of anchovies, seem to keep to a more peripheral position, though this fact did not alter the feeding habits of the former, in spite of the fact that the anchovies are more voracious; they seem to form larger circles in the presence of horse mackerel.

From the works reviewed, we may conclude: 1. that the sprat, herring, anchovy and young horse mackerel are essentially zooplankton eaters; 2. that the adult horse mackerel and mackerel are still occasionally filter eaters, the latter being able to retain small preys such as those constituted by phytoplankton, a 500 vegetable species which are also found occasionally in the stomachs of the anchovy. It is difficult to see how fishes having their gill raker spines so widely separated can filter such small organisms, unless their teeth are very long and are especially equipped for this, aspects which have not been studied.

VIVES & FRAGA (1961) and VIVES (1962) have encountered a very good balance between solar energy and sardine fishing in the areas of Galicia and Portugal, which serves to demonstrate that as primary filter eaters, they are not affected by food competition in high production areas. Greater importance could be attributed to the predator-prey relations of the mackerel, the horse mackerel and the anchovy with the sardine, as well as the mackerel and the horse mackerel with the anchovy, and herring-sprat in those areas where these species form part of the same ecosystem.

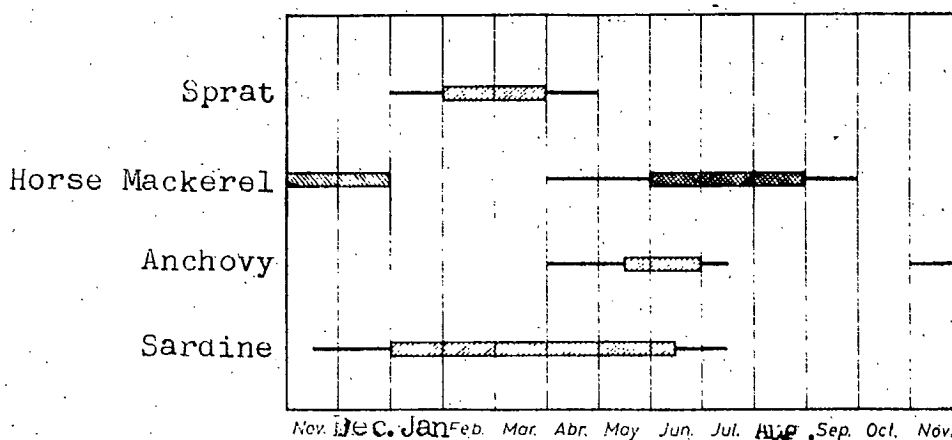


Fig. 26. Spawning period of four pelagic species of the Galician coasts, according to different authors; Sprattus sprattus (ARTE, 1956); Trachurus trachurus (LOZANO, 1952; ANADON, 1960); Engraulis encrasicolus (ANDREU, unpublished data) and Sardina pilchardus (ANDREU, 1955 b).

Horse mackerel: simple bar, large-size pelagic fishes (ANADON); crossed bar, pelagic fishes (ANADON) and fishes caught near sea bottom (LOZANO).

As regards the spawning period of the different pelagic species of the Galician coasts, Figure 26 demonstrates that the sardine has an advantage over the others, while the sprat - according to MUZINIC (1958) - would seem to be in a weaker position in the face of possible competition from the others.

Actually, the size of catches - as has already been pointed out by some of the authors cited - is a weak basis for establishing correlations and discovering possible alternations, since frequently there is interference caused by falsification of statistics by market demands or simply because of the greater or lesser accessibility of the schools.

5. GILL RAKERS AND SPECIATION

We have demonstrated in previous chapters that the increase rate of the number of gill rakers (and consequently, the separation between spines) is a strongly adaptative neotenic character in populations of Sardina pilchardus of the different geographical areas studied. And that the plasticity of this character becomes lessened as the increase rate of the number of spines decreases. It is practically constant in adult individuals of closely related species such as Sprattus sprattus, Clupea harengus, Engraulis encrasicolus and other pelagic fishes (horse mackerel, albacore, tuna, etc.) as more complex trophic levels are reached.

Some authors have attributed the variation in the number of gill rakers to the simple action of temperature. Thus MCHUGH (1951) says that in the Engraulis mordax mordax of the California coasts, the average number of gill rakers, in fishes of equivalent size, decreases regularly from north to south, and concludes that the average yearly temperature must be taken into account if we are to explain this variation. LETACONNOUX (1954) mentions that, in Sardina pilchardus, the number of gill rakers increases and the number of vertebrae diminishes as water temperature rises. LEE (1965 b), also in relation to Sardina pilchardus, says that in the Atlantic, the number of gill rakers diminishes very noticeably from south to north (he compares the sardines of Cape Juby, Vigo and Cornwall), the increase being very rapid in relation to size, while in the Mediterranean - he claims - this increase is less rapid than in

the Atlantic. ALONCLE (1964), in Trachurus, found that a higher temperature corresponded to a larger number of gill rakers. ROSSIGNOL (1959), who has studied the Sardinella aurita of the Mediterranean and French Equatorial Africa, was able to ascertain that the Mediterranean variety has a larger number of gill rakers than the Atlantic variety in spite of the fact that the water temperature is the same, or even lower than, that of the Atlantic area studied by him; he concludes that the variation in the number of gill rakers is not a result of environmental conditions acting directly on this character, but rather depends on the living conditions of the organisms which frequent this environment. BERRY & BARRES (1963) were able to demonstrate that the species of the genus Opisthonema which live in colder waters tend to have a smaller number of gill rakers than those which live in temperate waters. In view of the results noted by the authors cited, with the exception of the first, concerning Engraulis, in all cases a higher water temperature would appear to correspond to a larger number of gill rakers.

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In Sardina pilchardus, in spite of the partial results of LETACONNOUX (1954) and LEE (1965 b), this does not occur, as may be concluded from the simple observation of Figure 23. In this figure, we see a graphic representation of the mean values of the number of gill rakers in relation to size, as well as the curves calculated for each one of the 15 geographical areas studied. Limiting ourselves to the sole Atlantic region, we

can see that there is no relation to latitude: the sardines of Madeira and the Canary Islands, which represent the lowest latitudes studied, correspond to the curves showing the lowest number of gill rakers. However, the curve of the sardines of Casablanca, at a latitude not much higher than that of Madeira, occupies the other end of the figure, with the largest number of gill rakers encountered. The Azores curve seems to digress greatly from those of Sanlúcar de Barrameda and Lisbon, in spite of the fact that the three localities have the same latitude. Lisbon, Oporto, Vigo and Maumusson, with quite different latitudes, show very similar curves, while the curve of Santander is separated from and below the preceding ones.

The area between Madeira, Cape San Vicente and the Moroccan coast, beginning at Cape Juby, and the Canary Islands, is known as a region of permanent negative thermal anomalies (ERIMESCO, 1966, Bull. Inst. Pêch. Mar. Maroc, 14: 8-28), however it is on the Moroccan coasts that the particular hydrographic conditions can sustain species of the temperate zone, boreal and subboreal, such as for example Ostrea edulis and Homarus vulgaris (FURNESTIN, 1948), while the Sardinella aurita, tropical and subtropical species, abounds on the coasts of the Canary Islands, though it occurs only irregularly along that of Morocco. These northerly hydrographic conditions are supposedly what led the Sardina pilchardus to acquire the strongly neotenic character of its gill rakers from the protosardine or primitive sardine, while its vertebral mean is the lowest of the Atlantic cline, that is to say, the most southerly. Another interesting

case is that of the Santander sardine, of which the curve, as we have seen, is below the set of curves representing Lisbon, Oporto, Maumusson and Vigo. In this regard, we might mention the meridionalization of the bottom of the Bay of Biscay as regards the Galician coasts, noted by FISCHER-PIETTE (1957, P. Inst. Biol. Apl., 26: 35-40). However, these two cases - above all the first - and perhaps some others which might be encountered, cannot permit us to generalize as to the effects of temperature on the increase rate of the number of gill rakers. We believe we must consider other, much more complex, ecological factors, in particular those connected with adaptative phenomena and especially with the optimum utilization of available food.

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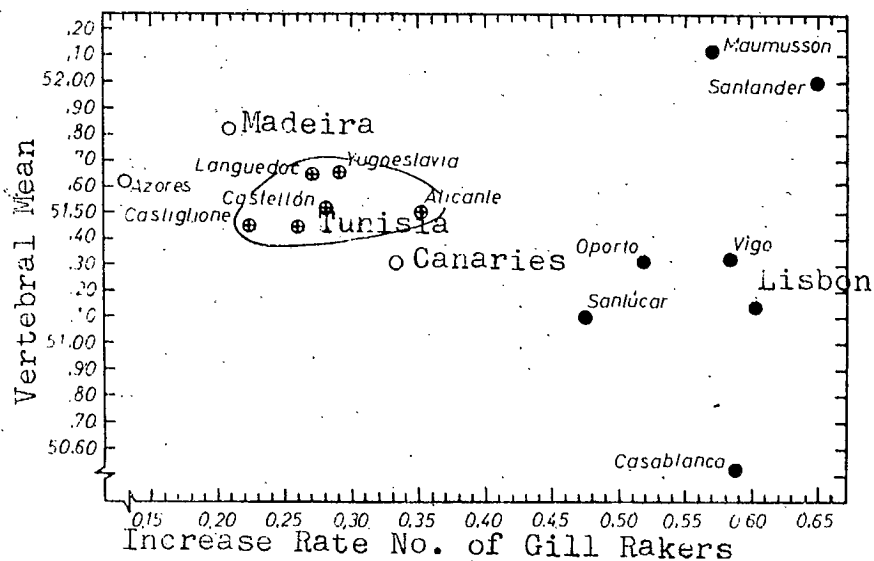


Fig. 27. Ratio between the increase rate of the number of gill rakers and the vertebral mean in sardine populations of different geographical areas.

An argument which further supports what we have just said is provided by Figure 27. In Figure 7, we saw that the vertebral mean showed two very distinct latitudinal clines, one in the Atlantic and another in the Mediterranean. In Figure 27, though at first sight it seems possible to note a certain negative correlation between the increase rate of the number of gill rakers and the vertebral mean, if we separate on the one hand the points corresponding to the Mediterranean sardine and on the other, those of the Atlantic sardine of the continental shelf, we see that this correlation is not to be found in either one of them. In the first case, the points more or less follow a line parallel to the axis of abscissa and in the second, another practically parallel to the axis of ordinates. We thus see that, though in the case of the vertebral mean, the number of vertebrae increases as the temperature decreases, we cannot generalize and say that the opposite occurs with the gill rakers.

SVARDSON (1952) has studied the gill rakers of 94 natural populations of fresh-water coregonids of Sweden. In crosses with progenitors having a known number of gill rakers, in 12 cases this number remained fixed or the offspring differed from the parents by only two units. According to said author, the number of gill rakers is regulated by polygenes and it is the only character used up until now in the coregonids, of which the variation has a proven hereditary basis. The nongenetic variations - he adds - are either very slight or nonexistent. In the case of the clupeids, the comparative study conducted by COTTIGLIA on the shad of Cerdana is really significant. This

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author has studied the free migratory form of Alosa of the Tirso River and that which, for 40 years, remained isolated in the artificial lake of Omodeo. While some somatic characters of the isolated shad have changed considerably, the number of gill rakers has remained practically constant, in spite of the fact that lake fishes are considerably smaller in size than river fishes and in spite of the marked contrast between the abiotic factors of the lake and those which the free form encounters in open sea. The average number of gill rakers of the first gill arch encountered by COTTIGLIA in the isolated form was 47.9 (mode 50, maximum variation 40 to 54) and in the migratory form, it was M - 46.7 gill rakers (mode 46, maximum variation 42-50). The difference in the means is only one whole number, which indicates slightly more than 2%, practically discountable in a character of this nature, which increases with the size of the fishes.

We already mentioned in the preceding chapter that DA FRANCA (1959) had used the gill rakers to separate two subspecies of Trachurus. This character has served as a basis for the separation of species of the genus Alosa, since the other differential characters are not very distinct. Something similar occurs with the thread herring (Opisthonema) where, according to BLAIRY & BARRET (1963) there are only minor morphological differences between the five species investigated, so that the practical differentiation of the species (one from

the Atlantic and four from the Pacific) is based on the geographical area in which they are found, together with the graphic form of variation (profiles) of the number of gill rakers, in relation to size.

Applying a criterion similar to that which has been used for the separation of species of the genera Alosa and Opisthenema, we, too, in view of our findings, could propose the creation of new species, at least for the sardine of Morocco, the Azores, Madeira and the Canaries, respecting the one proposed - and accepted by some authors - for the Mediterranean sardine (Sardina sardina) and keeping the name of Sardina pilchardus for the European sardine which occupies the Atlantic continental shelf. In this way, the genus Sardina would be extended to include five species, as is the case of the other two genera of the family Clupeidae previously commented upon. However, we feel that in Sardina pilchardus the polymorphism encountered in the variation of the number of gill rakers, in relation to size, is due to differences accumulated as a result of natural selection, differences which were introduced as the primitive form of the sardine kept widening its geographical distribution and colonizing new areas which were very different from that in which the original form had lived. Thus, new physiological races have been appearing, though it is not possible at present to account for speciation through morphological and numerical changes. It is a well-known fact that frequently differentiation through isolation radically affects physiological characters.

6. GILL RAKERS AND EVOLUTION

In his work on Ecology, Biogeography and Evolution, MARGALEF (1960 b) mentions - as a general remark - that the geographical distribution of the present species is closely related to the past and present distribution of types of ecosystems and that dispersion routes and possibilities of evolution resulting from the different ecological niches in space and in time have been more important, in the present mode of the distribution of organisms, than the potential dispersion capacities of these organisms and conditions of evolution resulting from the frequency of mutations and the size of populations. And he mentions elsewhere that a frequent manifestation of polymorphism is the presence of forms having different genetic values, in which case, a mechanism is already introduced which may be used for isolation.

Returning to the sardine, it is noted that populations having a high increase rate in the number of gill rakers occupy geographical regions where there are great contrasts in the aquatic environment due to the presence of intensive climatic cycles (sardines of the Bay of Biscay and the Galician and Portuguese coasts) or because of prolonged periodic outcrops (sardines of the Moroccan coasts). In the former, in addition to the rapid increase in the number of gill rakers in relation to size, we noted a wide variation among fishes of equal size, especially in the sardine of the Galician coasts. This variation is accentuated by the cohabitation, in the same geographical area, of two or more annual generations of sardines, born in

completely different environments (abiotic and biotic), preserving their own characteristics free of hybridization because of the different spawning period. In the area of Galicia - and in the entire Bay of Biscay - evolution achieves in time what Mediterranean sardines achieve in space; the Galician coast sardines born in colder waters (with high vertebral mean) have evolved through selection in a different manner (different ecological conditions) than those born a few months later in waters having a higher temperature (lower vertebral mean). By studying the ratio between the number of gill rakers and the size of sardines coming from schools made up exclusively of fishes of Class 0 - before they have become mixed with individuals belonging to other age classes - of sardines coming from winter catches (low MV) and sardines caught in summer (high MV), and calculating separately the increase rates of the number of gill rakers, we obtain the results shown in Figure 28. The allometric constants (exponent "b") are 0.825 and 0.579 respectively; the constants "a", 1.169 and 3.75. This indicates that, in the same fishing area, there are sardines with characteristics showing greater or lesser ecological maturity, relatively speaking. It is very probable that the comparison of the two regressions would not be statistically significant and that the totality of points corresponds to a single regression. However, we should not be surprised if we encounter a different increase rate in the number of gill rakers, depending on whether one or another generation predominates in the adult sardine population, which would be explained by what we have just been saying. In

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the zone of Eastern Spain, MARGALEF (1963) studied the pelagic ecosystem of a small coastal strip between the Ebro delta and the city of Sagunto. He was able to demonstrate that in the northern portion (from San Carlos to Oropesa) the entire ecosystem shows less mature characteristics, with greater production flow per biomass unit and greater fluctuations, than in the southern portion (from Oropesa to Sagunto). In the area where the ecosystem is less mature - he adds - opportunities for breeding are better and spawning and development of the sardine take on greater importance; the spawning period coincides with the time of year in which the entire ecosystem shows characters of low maturity (November to February). As we can see, sardine populations are very sensitive and have a very great capacity for adaptation to the different ecosystems of which they form part, even during the initial months of life, as occurs in Vigo.

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The sardines of the Bay of Biscay and those of the Galician and Portuguese coasts have gill rakers which are very close together, which permits them to utilize phytoplankton to a greater extent; therefore, they may be classed as optional primary filter eaters. Therefore, comparatively speaking, they occupy the lowest trophic level which, combined with a greater production flow per biomass unit, brings about pronounced periodic interannual fluctuations, fluctuations which are often very strongly felt along the Galician coasts (ANADON, 1954). On the Moroccan coasts, and even on the nearby Portuguese coasts, although the sardines belong to as low a trophic level as those

of Vigo, they do not show such marked fluctuations. The greater increase rate of the head length and the low vertebral mean of Moroccan sardines, are other characters which lead us to suppose that these sardines do not adapt to the general evolution pattern which we have attempted to trace.

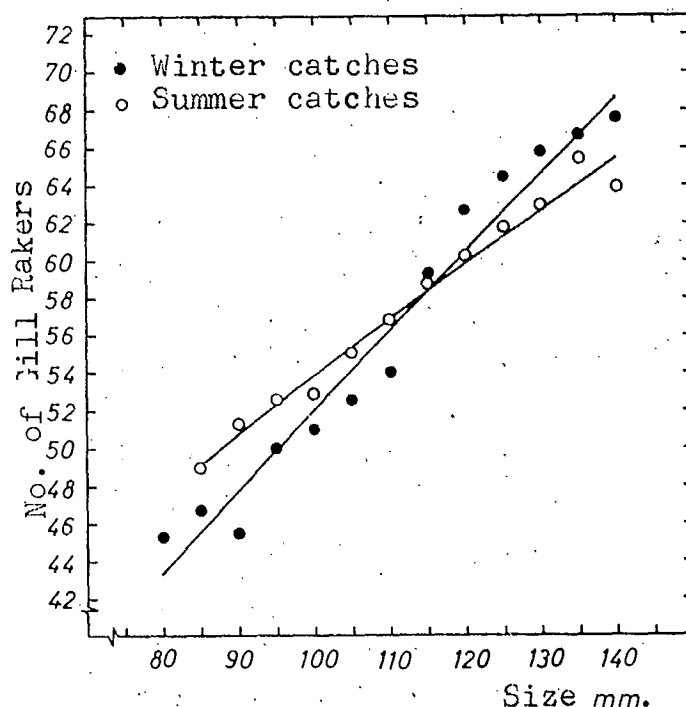


Fig. 23. Ratio of the number of gill rakers to the size in sardines of Class 0 caught in the Vigo estuary, in winter and in spring-summer. Explanation in text.

Sardine populations showing a low increase rate in the number of gill rakers (with greater separation between spines), like those of Madeira and the Canaries, unlike the preceding ones, occupy areas where environmental conditions are much more uniform, forming part of more mature ecosystems; their feeding must be predominantly selective, of the hunting variety.

The sardine of the Azores differs from those of Madeira and the Canaries: the increase in the number of gill rakers in relation to size shows a lower rate than that of the other regions studied, however on the other hand, the growth of the arch on which the spines rest shows strong negative allometry, for which reason the separation between them is much lower than what might be expected going by the low number of gill rakers. For this reason, in Figure 24, the regression curve is situated between those of Tunisia and Castellón, instead of appearing above those of Madeira and the Canaries.

Mediterranean sardine populations, though to differing degrees, occupy an intermediate position between the two large groups mentioned in previous paragraphs, however its diet - in adult individuals - consists exclusively of zooplankton. In these sardines and very especially in those of the Azores, Madeira and Canary Islands, the increase rate of the number of gill rakers in relation to the size, and even the variation in the number of spines in fishes of equal length, is greatly diminished, indicating a marked tendency towards stabilization of this character, with partial loss of the pronounced neotenia which we noted in the southern sardine group.

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More stabilized sardine populations must logically have developed from those having more primitive characteristics; the initial variability has become gradually lessened as they invaded more southerly areas or regions with more intensive seasonal cycles.

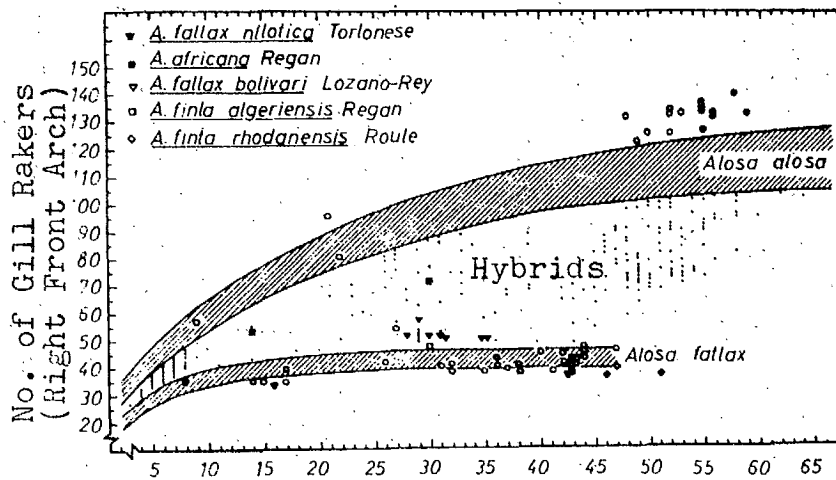


Fig. 29. Variation in the number of gill rakers of the first right gill arch of the Alosae, in relation to size. Taken by FURNESTIN & VINCENT (1958). We have inverted the values of the axis of ordinates so that the figure is more easily comparable with Figure 23, referring to the sardine. The "white circles" correspond to shad of the Bay of Biscay (Garogne) and the Mediterranean (Rodano) and the "points", to Moroccan shad.

On this basis and applying a modern criterion, we might imagine that the initial form of Sardina pilchardus was somewhat similar to that of the more primitive of the two generations found along the Galician coasts, since the other physiological races are a typical consequence of selection resulting from mutations, in harmony with the new ecological conditions of the successive areas colonized by the protosardines and forms derived from them.

If this reasoning is correct, it could also be applied to other clupeids going through periods of evolution similar to those of Sardina pilchardus: FURNESTIN & VINCENT (1958) deny the validity of the species and subspecies of Alosae described up to now for the European and North African coasts, recognizing

only Alosa fallax and Alosa alosa. The others, according to these authors, should be considered as "hybrid" forms (Fig. 29.). In our opinion, the most logical thing would be to assume that there is only one species of shad (Alosa alosa), that having the largest number of gill rakers, and that the remaining species and subspecies described are just so many adapted forms deriving from it. In any case, the others would almost have attained the category of physiological races, of which Alosa fallax would be the most stable form, with an almost constant average number of gill rakers beginning at a length of 25 cm. The same could be said of Opisthonema, except that, in both cases, there were other clear morphological differences which could justify breaking them down into different species.

7. SUMMARY AND CONCLUSIONS

Sardina pilchardus has mainly coastal habits. Its area of distribution covers about 4,000 km. from north to south and 6,000 km. from east to west. This, together with the variety of environmental conditions, and particular coastal and insular geography, cause the isolation and diversification of populations. The main area of abundance of the species lies off the west coasts of the Iberian Peninsula, between the estuaries of La Coruña and Aveiro (Northern Portugal): there are other important areas off the Moroccan coasts and the Spanish South Atlantic region (Fig. 2.). Of the total catches, 80% were fished in the Atlantic Ocean and 20% in the Mediterranean Sea.

The characterization of sardine races and clupeids in general, is one of the problems which has been receiving special attention from scientists of the five continents. The new serological and biochemical methods introduced have not yet enabled us to make significant progress in this field.

In Sardina pilchardus, the somatic characters most frequently used by authors in the characterization of populations are the vertebral mean and the cephalic index. The vertebral mean shows two characteristic latitudinal clines, one Atlantic and the other Mediterranean (Fig. 7.). However, on the one hand, this character, because of the great plasticity of the genotype, has the serious disadvantage of masking authentic hereditary differences which may exist. On the other hand, it is possible to separate statistically - with a high probability level ($P > 0.001$) - in a well-defined area (Vigo estuary), the vertebral means of Class 0 sardines caught in winter from those caught in spring or summer. This phenomenon also occurs in the sardines of the entire Bay of Biscay. The ratio between the lateral head length in sardine populations of the different geographical areas studied and the total body length (Fig. 8.) - with the exception of those of Morocco - shows negative allometry, the regression curves calculated forming a narrow ray, which hinders or prevents its use in the characterization of populations. No relation has been found between the increase rate of the lateral head length and the vertebral mean in the sardines from the 15 geographical areas studied by the author.

Because of the difficulties inherent in these two racial characters - difficulties which are widely discussed in this work - we have tried using the gill rakers, proceeding to study material taken from 15 different geographical areas which cover almost the entire area of distribution of the species (Fig. 3.).

The gill rakers have been studied beginning at the time of their appearance in larvae 15 mm. long, and their subsequent development has been followed, relating the feeding habits of the larvae and young forms to the progressive development of the filtering apparatus (Figures 14, 15, 16, 17 and 19).

We have also studied the arrangement and shape of the gill arches and the tongue in the hyobranchial skeleton of the adult sardine (Fig. 10, 11 and 12) of the Galician coasts.

The observation of gill rakers on adult sardines has been carried out on material taken from the following 15 geographical areas: Maumusson, Santander and Santoña, Vigo, Oporto, Lisbon, Sanlúcar de Barrameda, Casablanca (Morocco), Madeira, the Azores, the Canary Islands, Yugoslavia, Castellón, Alicante, Castiglione and Tunisia. We have studied the allometric increase in the lower limb of the first left gill arch, the number of gill rakers, and the distance between spines, all in relation to the size of the fishes (total length mm.). The lower limb of the first gill arch increases isometrically with the sardine length (Fig. 21.) in all the material studied ($li = 0.11 \cdot L_t^{0.0121}$, $n = 3012$), the sardine of the Azores departing noticeably from this general trend, its allometric constant having been 0.7155.

The increase rate of the number of gill rakers in the lower limb of the first gill arch in relation to the size, calculated by the conventional allometric method (Fig. 23.), enabled us to show that this meristic character may be used, advantageously, in the characterization of populations and in addition has strong ecological and evolutive significance.

Since the growth of the lower limb of the first gill arch is practically isometric in relation to length of the fishes, a larger increase rate of the number of gill rakers would coincide with a lesser degree of separation between spines, and vice-versa. The sardine of the Azores digresses slightly from this because of the fact that the growth of the lower limb has strong negative allometry. The filtering capacity of the different sardine populations (Fig. 24.) is related to the different diet of each, leading to the conclusion that the sardines of the Atlantic continental shelf are optionally phytoplankton-eaters; the Mediterranean ones, and those of the Azores, are zooplankton-eaters, with no phytoplankton to be found in the stomach contents. The sardines of Madeira and the Canaries, must feed in a highly selective manner, hunting their food.

We have studied the possible interspecies competition among four pelagic species of the Galician coasts which were temporarily or accidentally displaced. The comparison of the rate of separation between spines (Fig. 25.) shows us that Sardina pilchardus may compete trophically, and to advantage, with the sprat (Sprattus sprattus), anchovy (Engraulis encrasicolus)

and horse mackerel (Trachurus trachurus), also because of its longer spawning period (Fig. 26.). The analyses of stomach contents made by different authors on different pelagic species, show that the mackerel, the horse mackerel and the anchovy may have a predator-prey relationship with the sardine; the mackerel and horse mackerel with the anchovy, and the herring with the sprat, in those areas where these species form part of the same ecosystem.

There are various observations on the strongly adaptive neotenic character of the increase rate of the gill rakers in various sardine populations studied in the present work, mentioning that the variability of this character becomes lessened as the increase rate is lowered. We discuss the possible influence of temperature on the variations encountered, coming to the conclusion that the polymorphism is due to genetic differences accumulated with time through the process of natural selection, differences which gradually appeared as the primitive sardine (protosardine) began widening its geographical distribution and colonizing new environments, which were markedly different from the original ones. This has given rise to different physiological races, but these morphological and numerical changes are not yet able to justify their speciation.

We attempt to diagrammize an evolution pattern in Sardina pilchardus; sardine populations with a high increase rate in the number of gill rakers occupy geographical regions in which strong climatic variations occur (Bay of Biscay, Cantabrian and Galician and Portuguese coasts) or because of prolonged periodic

outcrops (Moroccan coasts). In the former, aside from the high rate of increase of the number of gill rakers, this number varies greatly in fishes of equal size, especially in the sardine of the Galician coasts; their gill rakers are very close together, and they make greater use of phytoplankton, so that they may be classed as optional primary filter eaters. Comparatively speaking, therefore, they occupy the lowest trophic level and, consequently, are particularly sensitive to interannual fluctuations. The sardines of Morocco, because of the high increase rate of the head length, the low vertebral mean, the low variation in the number of gill rakers in fishes of equal length, and the relatively narrow range of fluctuations, digress from the general evolution pattern proposed. In sardine populations which have a low increase rate of the gill rakers (with greater separation between spines), such as those of Madeira and the Canaries (Fig. 23 and 24), unlike the preceding ones, which occupy areas in which environmental conditions are much more uniform, forming part of more mature (older) ecosystems; their feeding is predominantly selective, as they hunt their food. Mediterranean sardine populations, to varying degrees, occupy an intermediate position between the two aforementioned groups. These sardines and particularly those of the Azores, Madeira and the Canaries, show a marked tendency towards stabilization of this character, with partial loss of the marked neotenia typical of northern sardines.

More stabilized sardine populations must logically proceed from others having more primitive characteristics, the initial

variability becoming lessened as they colonized more southerly areas, or areas having more intensive seasonal cycles. Using this basis and applying a modern criterion, it is suggested that the initial form of Sardina pilchardus would somewhat resemble the more primitive of the two generations now present along the Galician coasts, since the other physiological races, logical consequence of natural selection, are caused by mutations, in relation to the new ecological conditions of the areas colonized by the protosardines and forms derived from them. This same evolutive reasoning is applied to ther clupeids belonging to the genus Alosa (Fig. 29.) and Opisthonema, where the established speciation may still lack sufficient taxonomic arguments supporting it.

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TABLE I

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Annual Sardine Catches, by Countries, Expressed in Tons¹

	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965
Algeria	"	"	4 100	6 100	11 100	14 600	"	9 200	10 400	10 600
Belgium	"	100	100	100	100	100	"	100	"	"
Ceuta	600	300	300	400	800	300	"	"	"	"
Spain	78 300	98 200	98 400	105 000	125 700	140 900	109 300	124 000	119 400	113 700
France	51 200	22 400	28 600	30 700	31 000	38 087	35 900	31 000	30 100	23 300
Holland	"	"	1 200	"	"	200	500	800	200	100
Italy	"	"	31 100	33 600	31 900	35 600	24 500	29 900	27 100	29 600
Melilla	2 900	2 000	1 700	2 000	2 300	3 500	"	"	"	"
Morocco	77 200	113 800	123 700	114 000	117 600	126 000	126 300	127 200	139 700	160 100
Portugal	100 000	112 800	131 500	121 400	139 300	130 400	130 500	118 600	163 600	138 000
United Kingdom	6 000	3 000	4 200	3 700	3 000	2 700	2 000	2 000	1 700	1 300
Yugoslavia	4 800	7 100	9 400	6 100	9 400	11 000	7 000	5 000	5 400	5 700
TOTAL	321 000	354 700	434 300	423 100	471 700	512 387	436 000	447 800	497 600	482 400

1. Data taken from the Statistical Annals of Fishing. FAO. Vols.: 7, 8, 9, 11, 12, 14, 15, 16, 18, 20.
2. Data unavailable.
3. Corrected from the "Revue des Travaux," Vol. 26 (1962).

TABLE II

Yearly Sardine Landings in Spain, by Fishing Regions
Expressed in Tons¹

	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965
Balearic Islands	35	376	80	66	123	88	69	64	89	209
Canary Islands	959	805	1 066	1 757	3 097	2 718	2 973	4 410	7 484	8 860
Cantabrian	935	1 054	3 451	1 478	1 797	3 844	1 705	5 014	2 629	1 620
Eastern Spain	4 260	4 984	3 254	2 875	3 215	3 387	2 630	2 920	4 298	2 529
Northwestern Spain	11 140	14 570	26 298	40 527	36 447	47 369	27 186	28 782	33 761	30 122
South Atlantic	26 614	37 170	41 143	36 055	60 713	59 570	46 381	51 979	40 933	47 036
South Mediterranean	15 551	11 663	6 908	7 826	9 557	13 702	12 550	14 979	14 846	13 855
Northern Spain	15 766	22 581	16 164	14 431	10 829	10 232	15 785	15 775	15 342	9 338
TOTAL	75 260	93 205	98 356	105 016	125 778	140 909	109 279	123 923	119 382	113 629

1. Data taken from Fishing Statistics, Directorate General of Marine Fishing, Madrid.

TABLE III

Origin of Material Studied (Gill Rakers and Lateral Length of Head)
with Indication of the Number of Fishes from each Locality.
The Size Range, LT mm. is Shown in Brackets.

Locality	No. Gill Rakers/ Size	Length Gill Arch/ Size	Gill Sep./ Size	Length Head/Size
Maumusson	145 (85-200)	83 (85-200)	51 (85-200)	145 (85-200)
Santander & Santoña	284 (115-225)	283 (115-225)	74 (115-225)	82 (115-225)
Vigo	1184 (85-225)	1047 (85-225)	211 (85-235)	1105 (80-235)
Oporto	378 (128-216)	369 (128-216)	91 (128-183)	83 (128-205)
Lisbon	484 (89-211)	370 (89-211)	104 (89-211)	279 (89-205)
Sanlúcar	251 (105-175)	248 (105-175)	87 (105-175)	257 (105-175)
Casablanca	21 (100-190)	21 (100-190)	18 (100-190)	20 (100-190)
Madeira	146 (100-220)	145 (100-220)	74 (100-220)	125 (100-205)
Azores	181 (115-195)	134 (115-195)	61 (115-195)	136 (115-195)
Cánaries	205 (70-220)	205 (70-220)	67 (70-220)	220 (70-220)
Yugoslavia	64 (105-165)	64 (105-165)		64 (105-165)
Castellón	214 (92.5-162.5)	214 (92.5-162.5)	36 (122.5-162.5)	234 (92.5-162.5)
Alicante	49 (130-195)	51 (130-195)	40 (130-195)	52 (130-195)
Castiglione	42 (100-175)	42 (100-175)		42 (100-175)
Tunisia	70 (120-170)	69 (120-170)	19 (145-170)	72 (120-170)
TOTAL	8618	8345	933	3159

TABLE IV

Vertebral Mean of the Vigo Sardine. Years 1951 to 1955 & 1964.

Date	Frequencies						N	M	σ	ep	Fl. of M	Min.	Size	Max.
	49	50	51	52	53	54							LT mm Mean	
1951														
9 October		17	90	76	6		189	51,38	0,69	0,03	0,17	100	(111,92)	200
19 »	1	70	485	311	27		894	51,32	0,68	0,01	0,07	95	(106,67)	150
30 »	5	191	1855	1339	9	2	3401	51,38	0,64	0,007	0,036	90	(113,25)	170
1952														
19 February 1		283	1865	951	45	2	3147	51,25	0,63	0,005	0,021	85	(110,31)	155
13 March		7	68	50	3		128	51,32	0,63	0,04	0,18	110	(124,58)	135
24 »		5	60	45	8		118	51,47	0,69	0,04	0,21	135	(142,23)	160
27 June		9	52	33	1		95	51,27	0,64	0,04	0,22	165	(179,06)	225
11 July		4	48	57	3		112	51,53	0,60	0,04	0,19	105	(119,26)	140
8 October		5	53	29	3		90	51,33	0,64	0,04	0,22	125	(140,48)	155
1953														
5 March			28	34	5		67	51,66	0,616	0,05	0,25	140	(162,76)	190
18 May		2	50	43	1		96	51,45	0,56	0,04	0,20	160	(173,85)	200
27 July		1	25	53	18		92	51,85	0,48	0,33	0,17	110	(123,79)	140
5 August		3	33	55	5		96	51,64	0,63	0,04	0,20	90	(111,27)	130
13 »		1	25	60	13		99	51,86	0,71	0,05	0,24	105	(126,15)	145
25 »			12	24	7		43	51,88	0,66	0,07	0,33	115	(126,77)	140
8 September		5	26	54	7		92	51,68	0,69	0,05	0,24	125	(136,61)	155
30 October 1		8	40	43	9		101	51,50	0,81	0,05	0,25	125	(138,49)	160
4 December		1	32	48	6		87	51,68	0,62	0,04	0,20	95	(128,87)	145
19 »		4	38	50	5		97	51,53	0,66	0,04	0,20	120	(132,50)	160
30 »		8	25	43	5		76	51,66	0,66	0,05	0,25	120	(131,41)	145
1954														
19 January		1	47	36	3		87	51,47	0,59	0,04	0,20	120	(131,67)	150
8 February		3	35	36	2		76	51,49	0,62	0,05	0,25	130	(140,26)	180
2 March		5	44	34	3		86	51,40	0,66	0,05	0,25	115	(137,31)	150
11.12 March		9	71	66	6		152	51,45	0,67	0,04	0,20	120	(137,69)	225
7 April		3	41	41	2	1	88	51,51	0,66	0,05	0,25	145	(157,10)	190
14 »		5	50	40	1		96	51,38	0,60	0,04	0,20	145	(153,85)	165
22 June		10	146	137	3		296	51,45	0,58	0,02	0,10	80	(101,55)	115
24 »		8	69	63			140	51,39	0,60	0,03	0,15	85	(101,54)	120
26 July		1	40	34			75	51,44	0,82	0,06	0,30	115	(126,18)	140
6 August		3	37	44			92	51,62	0,69	0,05	0,25	90	(107,66)	125
3 December		6	94	74	3		177	51,42	0,59	0,03	0,15	140	(146,04)	150
1955														
3 February		2	38	43	5		88	51,60	0,64	0,05	0,25	115	(128,69)	155
22 March		1	40	53	3		97	51,60	0,57	0,04	0,20	130	(144,90)	170
31 »		4	38	47	1		90	51,50	0,66	0,05	0,25	140	(149,05)	170
14 April		6	46	39	3		94	51,41	0,66	0,05	0,25	165	(183,19)	210
29 »		4	46	34	4		88	51,43	0,66	0,05	0,25	155	(164,94)	180
25 May		4	57	34	1		96	51,33	0,57	0,04	0,20	170	(190,36)	225
15 June		7	57	13	2		79	51,13	0,58	0,04	0,20	90	(109,05)	140
1964														
8 December		5	62	40	1		108	51,34	0,58	0,04	0,18	190	(207,5)	225
12 »		9	38	29			76	51,26	0,66	0,05	0,25	115	(140)	165
20 »			30	11			41	51,26	0,44	0,04	0,23	145	(160)	175

TABLE V

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Vigo Sardine
Vertebral Mean by Year

Year	% of Frequencies						N	MV	σ	ep.	Fl. of M
	49	50	51	52	53	54					
1951	0,13	6,10	54,19	38,49	0,03	0,04	4484	51,34	0,61	0,006	0,03
1952	0,02	8,48	98,15	31,57	1,70	0,05	3620	51,26	0,63	0,006	0,03
1953	0,00	2,82	35,60	53,56	7,90	.	1025	51,66	0,66	0,013	0,06
1954	.	3,95	49,37	44,82	2,27	0,07	1365	51,28	0,61	0,01	0,05
1955	.	4,43	50,94	41,61	3,00	.	632	51,43	0,68	0,01	0,09
1964	6,22	57,78	35,55	0,44	.	.	225	51,30	0,58	0,026	0,132
Total	0,07	6,27	53,12	38,42	2,08	0,04	11351	51,36	0,64	0,004	0,02

TABLE VI

Distribution of Frequencies of Vertebral Means Obtained by Different Authors
on Populations of *Sardina pilchardus* (Walb)

	English Channel	Brittany	Vendée	Bay of Biscay	Spanish Basque Coast	Santander	Vigo	Leixoes	Lisbon	S. Portugal	MOROCCO	C. Blanco	Azores	Madeira	Canaries	Adriatic	Languedoc	Blanes	Castellón	Balearic Islands	Málaga	Castiglione	Turkey	Israel
50.43											1													
50.48											4													
50.53											3													
50.58											1	3												
50.63											2													
50.68											1													
50.73											2													
50.78																								
50.83																								
50.88																								
50.88																								
50.98									1															
50.98							2		1															
51.03							2		1	3														
51.08							2	1	22	4										2				
51.13							2	1	35	3														
51.18							9	3	77	3														
51.23							17	20	83	8														
51.28							17	31	50	4					3									
51.33							17	31	36	1					7									
51.38							18	24	8						4			3	8					
51.43							19	29	5						4			3	3	1				
51.48		2					15	14	1						1			2	8	1				
51.48							6	6										3	8	8				
51.53		1					3	3										3	11	6				
51.58			1				4	4										6	30	11				
51.63			3				2	2										6	27	4				
51.68		1					4	6					2					8	27	9				
51.73		1	4				6											8	46	6				
51.78		1		1														6	41	1				
51.83		1	2		1													4	18	1				
51.88		1	5		1									1					2					
51.93		2	1		4															2				
51.98	2	4	1		6													1		1				
51.98		4	1		4													1						
52.03	1	6	6		3																			
52.08	1	8	3		2																			
52.13	1	8	7		4																			
52.18		9	15		9																			
52.23	4	4	8		12																			
52.28		6	11		11																			
52.33		3	4		6																			
52.38		1	3		2																			
52.43		1	3		2																			
52.48		3	3																					
52.53			1																					
N (MV)	9	62	79	70	24	80	144	142	319	23	11	3	2	1	15	195	19	88	148	52	141	13	15	10
M	52.12	52.10	52.13	52.15	51.99	52.01	51.33	51.32	51.17	51.10	50.54	50.63	51.63	51.83	51.28	51.86	51.65	51.58	51.53	51.57	51.29	51.46	51.28	50.95

TABLE VII

Sardines of Maumusson and Les Sables d'Olonne
Variation in the Length of the Head in Relation to the Size
(Total Length) of the Fishes

Length Head	Size Groups, LT in mm.																	
	mm 85	90	95	100	105	110	115	120	130	140	145	150	155	185	190	195	200	
19	1	1	4	
20	.	3	11	2	
21	.	.	1	3	
22	.	.	.	1	1	
23	.	.	.	2	2	6	5	1	
24	4	10	6	
25	8	9	
26	2	8	1	
27	1	
28	7	
29	5	1	
30	1	
31	2	1	
32	2	
33	1	.	.	.	
35	1	.	.	
36	1	1	
37	1	1	2
N	1	4	16	8	3	10	20	24	30	18	1	5	2	2	2	2	2	
M	19,0	10,7	10,8	21,4	22,7	23,4	24,1	25,0	26,8	28,3	28,0	30,6	30,5	34,0	36,5	36,5	37,0	

TABLE VIII

Sardines of Santander and SantoñaVariation in the Length of the Head in Relation to Size (Total Length) of the Fishes

Length Head mm	Size Groups, LT in mm.																					
	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	225
22	2
23	1	6
24	.	6	8	2
25	.	1	16	10	1
26	.	1	5	15	5	1
27	.	.	1	5	18	10	1
28	9	18	11	2
29	1	5	22	7	2
30	1	3	12	1	2
31	3	3	6	2	1
32	1	2	8	3	1
33	5	7	2	1
34	5	5	1
35	2	1	8
36	2	4	6	1
37	1	3	2	.	1	1	.	.
38	3	2	6	2	1	1	.
39	3	2	2	3	2	.
40	3	1	4	.
41	1	4	.
42	1
44	1
N	8	14	90	32	34	35	37	24	7	8	5	9	15	10	15	12	8	8	9	8	1	1
M	22,8	23,8	25,0	25,7	27,1	27,9	28,7	29,7	30,4	31,3	31,6	32,4	33,5	34,3	35,2	36,8	37,9	38,3	39,1	39,9	42,0	44,0

TABLE IX

Vigo Sardines

Variation of Length of Head in Relation to Size (Total Length) of Fishes

Length Head mm	Size Groups, LT in mm.																																		
	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220	225	235				
15	1																																		
16	3	1																																	
17		4	1	2																															
18		4	4	8																															
19		1	1	8	8																														
20			1	8	11	8																													
21					1	18	10	2																											
22						3	10	9	1																										
23						1	1	15	7	5																									
24								4	6	10	2																								
25									2	10	27	9	15	6	1																				
26										12	29	29	24	13																					
27										10	36	33	36	35	5		2																		
28											5	19	31	38	6		1																		
29												10	14	49	12	9		2																	
30													5	32	12	8	5	2	3																
31														6	16	23	10	2	6																
32															5	12	9	7	4	2	1														
33																2		3	9	5	6	5		1											
34																		3	4	3	1	2													
35																	1	1	1	10	14	2	4												
36																				4	9	11	6	1	2										
37																					3	7	6	5	1	2	1								
38																						1	5	9	6	4	3					1			
39																							9	5	9	5	3	3							
40																							1	2	2	3	8	8							
41																								2	2	2	4	4				1	1		
42																									1	2	1								
43																																2	1		1
44																																	1		
46																																			1
47																																			1
N	4	10	7	16	20	25	21	32	24	64	81	106	116	174	58	52	90	27	29	25	34	28	37	21	22	22	20	1	1	3		1			
M	15.7	15.9	18.3	19.1	19.6	20.9	21.6	22.8	24.0	25.2	26.4	26.8	27.3	28.4	29.9	30.7	31.2	32.1	32.2	34.3	35.1	36.5	37.4	38.4	38.9	39.5	40.5	40.5	41.0	43.7		48.0			

TABLE X

Sardines of Leixoes

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length	Size Groups, LT in mm.											
	mm 128	139	144	150	155	172	178	183	189	194	200	205
29	1	1										
30		2	1									
31		1	2		1							
32			2	8								
33				3	1							
34				1	2							
35				1	1		6	2				
36							3	2				
37							5	4	1			
38							1	3	3	1		
39						1		3	5			
40								1	5	2		
41									1	1		
42										1		1
43											2	
44											1	
N	1	4	5	13	5	1	15	15	15	5	3	1
M	29,0	30,0	31,2	32,6	33,4	39,0	36,1	37,4	39,1	40,2	43,3	42,0

TABLE XI

7539

Sardines of Lisbon

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.															
	89	94	100	105	111	116	122	128	133	139	178	183	189	194	200	205
19	1	2	2
20	4	18	15	2
21	.	5	9	7	1
22	.	.	.	13	4	1
23	.	.	.	2	17	19	4
24	3	5	17	3
25	1	5	13	.	1
26	8	2	3
27	4	17	9
28	2	4	9
29	1
34	1
35	7
36	5	1
37	6	6	1	.	.	.
38	5	3	1	.	.
39	3	.	.	.
40	1	1	.
41	1	1
42	1
N	5	25	26	24	25	26	26	30	24	22	19	12	4	2	2	2
M	19,8	20,1	20,8	21,6	22,9	23,2	24,0	25,6	27,2	27,2	35,8	37,8	38,4	39,0	40,5	41,5

TABLE XII

540

Sardines of Ayamonte and Sanlúcar de Barrameda
Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.														
	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175
22	2
23	1	8	2	3
24	.	2	8	8	2
25	.	.	5	21	7	1
26	.	.	.	14	14	7
27	.	.	.	3	15	20	8	1
28	3	4	15	11	3
29	5	5	7	1	1
30	5	3
31	2	8	2	2	.	.	.
32	3	8	5	.	.	.
33	3	4	1	.
34	2	1	1
N	3	10	15	49	41	32	28	17	17	15	11	10	6	2	1
M	22,3	23,2	24,2	25,1	26,2	26,8	27,9	28,2	29,3	30,9	31,5	32,1	33,3	33,5	34,0

TABLE XIII

/541

Sardines of Casablanca

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

head Length mm.	Size Groups, LT in mm.									
	100	110	120	130	140	150	160	170	180	190
20	1									
22	1									
23		2								
24			1							
25			1							
27				1						
28				1						
29					1					
30					2					
32						2	1			
35							1			
37								2		
38									1	
40									1	
41										2
N	2	2	2	2	3	2	2	2	2	2
M	21.0	23.0	24.5	27.5	29.7	32.0	33.5	37.0	39.0	41.0

TABLE XIV

Sardines of Madeira

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head length mm	Size Groups, LT in mm.																						
	100	105	110	115	120	125	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220
20	1																						
21	1																						
22		1	2																				
23			3	5																			
24				1	1	1																	
25						1																	
26						1																	
29							2	2															
31								1	1	5													
32									1	3	3	1											
33											3	5	2										
34												1	1	1									
35															2	2							
36																3	1	2					
37																2	4	11	5	1			
38																		5	9	6			
39																		3	5	11	5	7	1
40																			1	2	11	7	1
41																					4	4	1
42																							1
N	2	1	5	6	1	8	2	8	1	6	8	6	7	3	3	7	5	21	20	20	20	19	2
M	20,5	22,0	22,6	23,2	24,0	25,0	29,0	29,7	31,0	31,2	32,0	32,5	33,0	33,3	34,7	36,0	36,8	37,4	38,1	38,7	39,9	39,9	40,0

TABLE XV

543

Sardines of the Azores

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.													
	115	120	125	135	140	155	160	165	170	175	180	185	190	195
25	2
26	.	6
27	.	.	11
28	.	.	.	11
29	6
31	2	6	2
32	7	15	5	4
33	5	18	9
34	1	1	5	4	.	.	.
35	1	3	2	.	.
36	1	1	.	3	.
37	1	1	.
38	1	.	2
N	2	6	11	11	6	2	13	23	24	20	8	4	4	2
M	25,0	26,0	27,0	28,0	29,0	31,0	31,5	32,2	32,8	33,3	34,6	36,3	36,3	38,0

TABLE XVI

1544

Sardines of the Canaries

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.															
	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	220
13	1															
14	5															
15	4															
16		9														
17		6	9													
18			4	1												
19			2													
20				8												
21				1	2											
22					10	1										
23					3	10										
24						4										
25							5									
26							10	1								
27								6								
28								9								
29								6	4							
30									8							
31									2	2						
32									1	4						
33										5						
34											1	5	1			
35												7	4			
36												3	6	1		
37													3	3		
38													2	7	1	
39															6	
40															2	5
41															8	4
42																3
43																4
44																2
																1
																1
N	10	15	15	10	15	15	15	22	15	12	15	16	11	12	16	6
M	14.5	16.4	17.5	19.9	22.1	23.2	24.7	25.9	29.0	31.4	33.0	35.1	36.5	38.6	40.4	42.2

TABLE XVII

1545

Sardines of Yugoslavia

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.						
	105	115	125	135	145	155	165
21	6						
22	4	6					
23		4	1				
24			9				
25				4			
26				6			
27					9	2	
28					1	3	
29						5	
31							2
32							2
N	10	10	10	10	10	10	4
M	21.4	22.1	23.9	25.6	27.1	28.3	31.5

TABLE XVIII

1546

Sardines of Castellón

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.												
	92,5	97,5	107,5	117,5	122,5	127,5	132,5	137,5	142,5	147,5	152,5	157,5	162,5
19	3	2
20	.	1	1
21	.	.	1
22	.	.	4	1
23	.	.	.	2	9
24	.	.	.	3	16	8	5
25	16	13
26	3	7	13	5
27	1	11	19	4	.	.	.
28	1	3	16	.	.	.
29	1	8	8	2	.
30	2	10	14	.
31	5	7	3
32	5
33	1	.	.
N	3	3	6	6	25	27	26	25	28	30	24	23	8
M	19,0	19,3	21,5	23,3	23,6	24,8	25,1	26,5	27,0	28,3	30,0	30,2	31,6

TABLE XIX

547

Sardines of Torrevieja (Alicante)

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.											
	130	140	150	160	165	170	175	180	185	190	195	
25	9											
26	4											
28		1	1									
29			4									
30			3									
31			1	2								
32				4	1	3						
33				2	1	2		1	1			
34				1		1	1	4				
35									1	4	1	
36										1	1	
37								1		2		
N	7	1	9	9	2	6	1	6	2	7	2	
M	25,6	28,0	29,4	32,2	32,5	32,7	34,0	37,7	34,0	35,7	35,5	

TABLE XX

1548

Sardines of Castiglione

Variation in the Length of the Head in Relation
to Size (Total Length) of the Fishes

Head Length mm.	Size Groups, LT in mm.														
	100	105	110	115	120	180	195	140	145	150	155	160	170	175	
21	1														
22	4		1												
23	1	1	3												
24			1	1	2		1								
25					2										
26					1			1							
27							2								
28							2		2	3					
29									1	1	1				
30										1		1			
31											2	1			
33													2		
34													1		
37														1	1
N	6	1	5	1	5		5	1	3	5	3	2	3	1	1
M	22,0	23,0	23,0	24,0	24,8		26,8	26,0	26,8	28,6	30,3	30,5	33,3	37,0	37,0

TABLE XXI

7549

Sardines of Tunisia

Variation in the Length of the Head in Relation
in Size (Total Length) of the Fishes

Head Length mm	Size Groups, LT in mm.									
	120	125	130	135	140	145	150	155	160	170
24	4
25	.	8
26	.	9	4	1	6
27	.	1	6	6	1	1
28	.	.	.	8	8	4	3	.	.	.
29	3	2	3	1	.
30	1	.	2	.	.
31	1	.	1	1	.
32	1
33	1
N	4	13	10	10	10	10	5	6	2	2
M	24,0	25,8	26,6	27,2	26,7	28,7	28,4	29,7	30,0	32,5

TABLE XXII

/550

Sardines of Maumusson and Les Sables d'Olonne

Variation in the Length of the Lower Limb of the Gill Arch

(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.															
	85	90	95	100	105	110	115	120	130	140	145	155	185	190	195	200
10,0	1	2	1													
10,5			6	1												
11,0		1	9	5												
11,5				2	1											
12,0					1	2										
12,5					1	2	1									
13,0						4	7	2								
13,5						2	7	2								
14,0							3	1	1							
14,5							1		1							
15,0							1		3	1						
17,0											1	1				
17,5												1				
20,5													1			
21,0														1		
21,5													1	1	1	
22,0																1
22,5																1
23,0															1	
N	1	8	16	8	8	10	20	5	5	1	1	2	2	2	2	2
M	10,0	10,3	10,7	11,1	12,0	12,8	13,5	13,4	14,7	15,0	17,0	17,2	20,0	21,2	22,2	22,2

TABLE XXIII

Sardines of Santander and Santona

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.																						
	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	225	
12.0	.	1	.	1
12.5	2	3
13.0	1	2	3	2
13.5	.	4	4	3
14.0	.	2	5	9	5
14.5	.	2	5	3	1
15.0	.	.	8	6	8	9	3
15.5	6	3	1
16.0	.	.	.	1	7	8	9	2
16.5	2	6	4
17.0	5	9	6	3	3
17.5	3	1
18.0	7	1	3	2
18.5	1	.	1	.	1	.	1	2
19.0	1	.	4	3	1	.	1
19.5	2	3	1	.	.	1
20.0	3	4	2	4	1
20.5	1	1	1	5
21.0	1	2	4	3	2
21.5	1	.	3	3
22.0	3	1	.	3
23.0	1	.	3	2	1	1
23.5	2	.	1	1
24.0	2	1	2	2	.	.	.
24.5	1	1
25.0	2	3	3	1	.	.	.
25.5	2
26.0	1
26.5	1
N	3	14	25	25	27	27	32	20	5	6	4	10	13	11	16	12	7	8	8	8	1	1	
M	12.7	13.3	14.2	14.2	15.2	15.8	16.5	17.2	17.5	17.5	18.4	19.5	19.6	20.2	20.8	21.4	22.1	23.4	24.2	25.0	25.0	26.5	

TABLE XXIV

Sardines of Vigo

Variation in the Length of the Lower Limb of the Gill Arch (Ceratobranchial + Hypobranchial)
in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.																												
	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220	225
9,0	1																												
9,5		2																											
10,0		11	4	1																									
10,5		8	5	1	1																								
11,0			9	18	6	2																							
11,5			1	1	6	1																							
12,0			1	8	7	11	6																						
12,5						2	2																						
13,0					1	8	11	18	5																				
13,5							1	5	4	1																			
14,0							3	7	23	4	2	1																	
14,5								1	7	14	5																		
15,0								2	15	34	39	12	4	1															
15,5									5	10	23	11	5																
16,0							1	10	20	41	60	35	4																
16,5								1	8	12	11	24	7																
17,0											7	20	62	28															
17,5												2	10	21	4		2												
18,0													18	25	6	8	1												
18,5															17	7	1	1	1										
19,0															5	4	2	1											
19,5															10	4	13	5	3	1									
20,0															1	2	2	1	1										
20,5														1		2	10	8	12	6	2								
21,0																	2	5	2		2								
21,5																	3	4	2	10	4	3	1						
22,0																			1	2									
22,5																			2	2	2	2	1	1					
23,0																					3								
23,5																					1	6	2	1	1				
24,0																													
24,5																						1	1	3	1	2			
25,0																								1		2			
—																									2	3	2		1
26,0																													
26,5																													1
—																													1
27,5																													8
N	1	16	20	19	21	19	23	30	70	86	129	125	166	101	45	22	30	25	23	22	14	12	6	6	5	9	2	8	1
M	9,0	10,0	10,7	11,0	11,5	12,1	12,8	13,6	14,6	15,2	15,6	16,1	16,7	17,0	18,1	18,5	19,3	19,9	20,1	20,7	21,4	22,4	22,4	23,6	24,1	24,9	25,0	27,5	25,0

TABLE XXV

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Sardines of Oporto and Leixoes

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.																
	128	133	139	144	150	155	161	166	172	178	183	189	194	200	205	211	216
14.5	1
15.0	9	4	2
15.5	2	1
16.0	2	8	5	5	1	1
16.5	.	3	2	7	2	1
17.0	.	1	8	30	21	9	4	1
17.5	.	.	.	2	16	7	4
18.0	.	.	.	4	18	27	16
18.5	3	9	5	4
19.0	2	17	19	5	1
19.5	1	6	1	2
20.0	1	2	4	4
20.5	1	.	1	1
21.0	1	.	1	4	3
21.5	3	1
22.0	1	3	2	2	1	.	.
22.5	3	5	2	.	.	.
23.0	1	2	3	.	.	.
23.5	1	.	.	4	.	.	.
24.0	2	1	.	.	.
24.5	1	.	.	.
25.0	1	3	2	.
26.0	1	.	.
26.5	1
27.0	1	.
N	14	17	17	48	68	78	57	15	9	1	3	14	15	14	5	8	1
M	15.2	15.9	16.4	16.9	17.5	18.1	18.5	19.0	19.9	20.5	22.2	21.8	22.3	23.2	24.6	25.7	26.5

TABLE XXVI

Sardines of Lisbon

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.																						
	89	94	100	105	111	116	122	129	138	139	144	155	161	166	172	178	183	189	194	200	205	211	
9,0	1
10,0	3	8	1
10,5	1	6	2
11,0	.	8	11	4
11,5	.	1	5	8
12,0	.	.	3	9	6	.	1
12,5	.	.	.	2	5	2
13,0	.	.	.	2	9	12	5
13,5	2	6	8
14,0	2	12	3	1	1
14,5	5
15,0	1	.	24	13	4
15,5	4	10	6	1
16,0	10	10	14	4
16,5	1	4	8	.	1
17,0	6	2	8	1	2
17,5	1	3
18,0	1
18,5
19,0	2	1	3	1	8	.	.	1
19,5	1
20,0	3	4	4	1
20,5	1	1
21,0	1	8	1
21,5	1	1	1
22,0	1	5	1	1
22,5	1
23,0	1	.	.	1	1	6	5	1	.	.	.
24,0	1	2	2	6	.	.
24,5	1	.	.
25,0	1	5	3
27,0	1
N	5	28	22	20	22	28	21	46	41	33	19	.	11	10	5	10	8	14	9	8	4	12	4
M	9,9	10,5	11,1	11,9	12,6	13,3	13,5	15,1	15,7	15,9	16,7	.	18,0	18,3	19,4	19,7	20,9	21,4	22,8	23,1	24,0	24,4	25,5

TABLE XXVII

1556

Sardines of Ayamonte and Sanlúcar de Barrameda

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.														
	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175
12,0	2														
12,5		2	1												
13,0	1	2													
13,5		4			2										
14,0			4	4	1										
14,5		1	4	12											
15,0			8	24	20	3									
15,5			1	4	6	7	2								
16,0					10	19	4	8							
16,5					1	2	12	4	1						
17,0						2	13	4	5		1				
17,5								1	2	1					
18,0									6	8					
18,5									1	4	1				
19,0										2	6	6		1	
19,5										1			1		
20,0											2	3	1		
20,5												1			
21,0													1	1	1
21,5													1		
N	8	9	13	44	40	33	31	17	15	16	10	10	4	2	1
M	12,3	13,8	14,4	14,8	15,3	15,9	16,6	16,4	17,5	18,3	18,9	19,4	20,5	20,0	21,0

TABLE XXVIII

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Sardines of Casablanca

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm.	Size Groups, LT in mm.									
	100	110	120	130	140	150	160	170	180	190
12,5	1
—
14,0	1	1
14,5	.	1
15,0	.	.	1
15,5	.	.	1
—
16,5	.	.	.	1
17,0	.	.	.	1
—
18,0	2
18,5	1	.	.	.
—
19,5	2
20,0	1
—
—
22,0	1	.	.	.
22,5	1	.	.
—
23,5	1	.	.
24,0	1	.
24,5	1	.
—
25,5	1
26,0	1
N	2	2	2	2	3	2	2	2	2	2
M	18,2	14,2	15,2	16,7	18,7	19,5	20,2	23,0	24,2	25,7

Sardines of Madeira

Variation in the Length of the Lower Limb of the Gill Arch (Ceratobranchial + Hypobranchial)
in Relation to Size of the Fishes

Limb Length mm.	Size Groups, LT in mm.																						
	100	105	110	115	120	125	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220
11,5	1																						
12,0	1																						
12,5		1	4																				
13,0			1	5																			
13,5				1																			
14,0					1	3																	
—																							
15,5							1																
16,0								1															
16,5									1														
17,0							1	1		1													
17,5										1	1												
18,0									5	2	5	1											
—																							
19,0												3	1		1								
19,5												1	1	1	1								
20,0												1	1	2	2	2							
20,5																1			1				
21,0																2	2	7	2	2			
21,5																		1	1				
22,0																		5	7	7	2		
22,5																			1	3	5	2	
23,0																		1	3	2	14	5	1
23,5																		4			1	1	1
24,0																			1		1	8	
N	2	1	5	6	1	3	2	2	1	6	9	6	6	3	3	7	4	13	14	14	28	13	2
M	11,7	12,5	12,6	13,1	14,0	14,0	16,2	16,5	16,5	17,8	17,8	17,9	19,1	19,5	19,9	20,1	20,5	21,5	22,1	21,8	22,7	23,0	23,2

TABLE XXX

Sardines of the Azores

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.															
	115	120	125	135	140	155	160	165	170	175	180	185	190	195		
14,0	1	1	1		
14,5	1		
15,0	.	4	6	.	8		
15,5	.	.	1	.	1		
16,0	.	1	2	.	6	3		
16,5	.	.	1	.	.	1		
17,0	1	2	.	.	1		
17,5	1	5	2	1		
18,0	1	4	5	3		
18,5	4	8	6	3	.	.	.		
19,0	6	10	9	.	.	.		
19,5	4	3	.	1	.		
20,0	3	5	.	2		
20,5		
20,5	2	1	.	2	.		
21,0	2	1	.	.		
21,5	1		
22,0	1	.	1		
N	2	6	11	.	11	6	.	9	18	22	24	20	8	8	4	2
M	14,8	15,0	15,3	.	15,6	16,4	.	17,8	18,0	18,4	18,8	19,3	20,3	20,8	20,9	21,8

TABLE XXXI

Sardines of the Canaries

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.																
	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	220	
7,0	1
7,5	3
8,0	4
9,0	1	6	2
9,5	.	2	2
10,0	.	3	7	1
10,5	.	.	1	3
11,0	.	.	.	5	1
11,5	.	.	.	1	4
12,0	6
12,5	3	3
13,0	12
13,5	4	1	1
14,0	8	5	8
14,5	4	8
15,0	8	8
15,5	3	3
16,0	5	5
16,5	2	2	3
17,0	4	4	3
17,5	2	2
18,0	1	2	2	2
18,5	2	3	3
19,0	3	2
19,5	4	3	1
20,0	2	10	3	1
20,5	1	8
21,0	6	4
21,5	2	4	1	.	.
22,0	1	5	6	.	.
22,5	1	1	.	.
23,0	5	3	.
23,5	2	1	.
25,0	1	.
N.	9	11	12	10	14	15	13	21	15	12	14	16	11	12	15	5	
M	7,8	9,4	9,8	10,8	11,9	12,9	13,6	14,7	16,4	17,4	19,0	19,8	20,7	21,6	22,5	23,5	

TABLE XXXII

Sardines of Yugoslavia

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.						
	105	115	125	135	145	155	165
10,5	3
11,0	4
11,5	2	1
12,0	1	7	2
12,5	.	1	2
13,0	.	1	6	2	.	.	.
13,5	.	.	.	4	.	.	.
14,0	.	.	.	4	3	.	.
14,5	1	.	.
15,0	4	.	.
15,5	1	2	.
16,0	1	6	1
16,5	2	.
—
17,5	1
18,0	2
N	10	10	10	10	10	10	4
M	11,0	12,1	12,7	13,6	14,8	16,0	17,3

TABLE XXXIII

7563

Sardines of Castellón

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.												
	92,5	97,5	107,5	117,5	122,5	127,5	132,5	137,5	142,5	147,5	152,5	157,5	162,5
10,0	2
10,5	1
11,0	.	8
—
12,0	.	.	6	.	1
12,5	.	.	.	2	3	1
13,0	.	.	.	4	6	2
13,5	6	2	1
14,0	5	13	8	10	1
14,5	6	6	4	4
15,0	1	6	13	11	6	.	.	.
15,5	1	2	3	1	.	.
16,0	7	15	7	1	.
16,5	2	4	5	2	.
17,0	1	2	13	3
17,5	2	2	2
18,0	3	1	.
18,5	1
N	3	3	6	6	21	25	21	28	27	29	20	19	6
M	10,2	11,0	12,0	12,8	13,3	14,0	14,4	14,6	15,3	15,8	16,6	17,0	17,4

TABLE XXXIV

1564

Sardines of Torrevieja (Alicante)

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.											
	180	140	150	160	165	170	175	180	185	190	195	
14,0	5											
14,5	1											
15,0	1	1	3									
15,5			1									
16,0			2									
16,5			1									
17,0			2	4		1						
17,5				2	1	1						
18,0				2	1	2		1				
18,5				1			1	1				
19,0						1				1	1	
19,5								1	1	2		
20,0						1		3		1		
20,5										2		
21,0										1	1	
N	7	1	9	9	2	6	1	6	1	7	2	
M	14,2	15,0	15,9	17,5	17,7	18,2	18,5	19,3	19,5	20,0	20,0	

TABLE XXXV

1565

Sardines of Castiglione

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.													
	100	105	110	115	120	130	135	140	145	150	155	160	170	175
11,0	3
11,5	.	.	1
12,0	2	1	3
13,0	.	.	1	1	2
13,5	2	1
14,0	1	1
15,0	3	1	1
15,5	1
16,0	2	1	1
16,5	1	1
17,0	2	.	1	.	.	.
17,5	1
18,0	1	.	.	.
18,5	1	.	.
19,0	1	.	.
19,5	1	.	.	1
20,5	1	.	.
21,0	1	.
N	5	1	5	1	5	5	1	3	5	3	3	3	1	1
M	11,4	12,0	12,1	13,0	13,4	14,5	15,0	15,7	16,4	16,7	18,2	19,3	21,0	19,5

TABLE XXXVI

566

Sardines of Tunisia

Variation in the Length of the Lower Limb of the Gill Arch
(Ceratobranchial + Hypobranchial) in Relation to Size of the Fishes

Limb Length mm	Size Groups, LT in mm.									
	120	125	130	135	140	145	150	155	160	170
12,0	1
13,0	3	2	1
13,5	1	1	2
14,0	.	6	5	4
14,5	.	.	1	3	3	1
15,0	.	1	1	2	6	2
15,5	1	2
16,0	2	1	.	.	.
17,0	2	3	2	.	.
17,5	1	1	.
18,0	1	1	3	1	.
18,5	1
19,5	1
N	5	10	10	9	10	10	5	6	2	2
M	12,9	13,8	13,9	14,4	14,9	15,9	17,0	17,6	17,7	19,0

TABLE XXXVII

7569

Sprat of Vigo

Variation in the Number of Gill Rakers in Relation to Size (Total Length) of the Fishes

No. Gill Rakers	Size Groups, LT in mm.													
	90	95	100	105	110	115	120	125	130	135	140	145	150	155
82	1
83	1	2	1	.	.	1
84	5	1	4	.	1	.	8	2	.	.
85	1	2	1	2	1	1	5	8	2	4	.	7	1	.
86	.	1	8	1	1	1	8	2	1	1	4	8	.	1
87	.	1	.	1	4	.	.	1	1	1	.	.	1	.
88	.	.	2	1	1	.	8	.	.
89	1	1	.	.	.
40	1
N	1	4	6	5	14	6	13	6	5	9	8	15	2	1
M	95,0	95,7	96,5	96,2	95,8	95,0	94,8	95,7	95,4	95,9	95,6	95,7	96,0	96,0

TABLE XXXVIII

Anchovy of Vigo

Variation in the Number of Gill Rakers in Relation to Size (Total Length) of the Fishes

No. Gill Rakers	Size Groups, LT in mm.																
	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	
82	.	1	.	.	1	.	.	1	1	
83	1	2	.	.	1	.	.	1	1	.	.	
84	7	.	5	1	2	2	1	1	1	.	.	
85	.	1	5	1	7	7	4	9	4	4	4	2	3	4	.	.	
86	2	2	7	5	21	12	16	8	8	3	1	9	10	3	.	1	
87	.	8	2	11	16	16	30	8	17	1	6	5	9	3	2	.	
88	.	.	8	4	11	28	10	13	12	2	4	4	4	.	.	.	
89	8	10	15	11	5	.	.	.	2	.	.	.	
40	1	6	3	1	.	.	1	1	1	.	.	.	
41	1	1	1	.	.	
N	2	7	17	21	60	87	81	57	48	12	19	22	31	18	2	1	
M	86,0	85,7	86,2	86,8	86,7	87,2	87,2	86,9	87,1	85,7	86,4	86,6	86,6	85,9	87,0	86,0	

TABLE XXXIX

Horse Mackerel of VigoVariation of the Number of Gill Rakers in Relation to the Size (Total Length) of Fishes

Size Groups, LT. in mm.																															
70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	170	175	180	185	190	195	200	205	210	220	225		
1											1		1																		
	1	1		3	2	1							1		1		1	1						2	2	1	1				
	1	2	4	1	2		3	4		2	2		3		1	2	1	1		1	1	1	1			1					
		1	2	1	4	1	1	1	1	4	1	2	1	4	5	2	2	3		1		1	1	3	2	1	2				
		1	2	2	2	1	2	2	6			6	1	8	1	1	3	1		1			2	1	3	1		1	1		
						5	4	1	2	1	2	3	4	5	3	1	3						1	1	1	3	1				
							5	3		2	5		8	8	3	4								2			1	1			
						1				1	1		1		4								1								
						1												1													
1	2	6	10	10	10	10	15	11	9	10	12	12	14	15	18	11	10	6		1	2	1	4	5	11	6	6	6	1	1	
40.0	42.5	43.8	44.2	44.1	43.6	45.8	45.5	44.8	45.1	45.0	45.5	44.8	45.1	45.5	45.6	45.4	44.6	44.7		45.0	43.5	43.0	44.2	45.2	44.6	43.8	44.5	44.7		47.0	45.0

TABLE XL

1572

Sardines of Maumusson and Les Sables d'Olonne
Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																
	85	90	95	100	105	110	115	120	130	140	145	150	155	185	190	195	200
49		1	1														
50	1	1	2	1													
51		1	4														
52			2	1													
53			1	3													
54			1	1													
55			4			1	1										
56			1			1											
57				1	1		1										
58					1	1	3										
59				1	1	2	1	2	1		1						
60							6	2	1		1						
61						2	5	4	3		1						
62						3	1	2	3								
63								9	4		2		1				
64							1		6		2		1				
65								3	4		1						
66								1	4		1	1					
67									1								
68							1		1		3		2				
69									2								
70								1	1		1						
72											1		2				
76															1		
77														1			
78																1	
79																1	1
82																	1
83														1			
85															1		
N	1	3	16	8	8	10	20	24	31	14	1	4	2	2	2	2	2
M	50.0	50.0	52.5	53.4	58.0	59.5	60.2	62.7	64.2	65.7	66.0	70.0	69.7	79.5	89.5	78.5	81.0

Variation in the Number of Gill Rakers in Relation to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																						
	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	225	
50		1			1																		
51					1																		
52		2	1	2																			
53			1	1																			
54	2	4	2	3																			
55		1	3	3	2	2																	
56	1	2	3	1	5	1	1																
57			4	3	1	2																	
58		1	4	2	1		1																
59			3	3	4	3	1	2															
60		2	2	2	2	3	1																
61		1	1	1	3		4	1															
62				2	3	2	3							2									
63					3	3	2	2	1	1													
64				2			1	1		1	1			1	1								
65						1	1		2				1		1								
66			1			2	2			1			2			1	1						
67							5	3		2	1				1	1	1						
68						3	2	1			1	2	2	2	1	2							
69							3	1	1	1	1	1	2	1	3								
70					1	2		1			1	4	1	1	3								
71							2	1					2			2	1	1					
72							1	2				1	1		1			2					
73						2		1				2	1	2				1			1		
74							2	1							1	1					1		
75						1		1							1								
76															1	1		1					
77								1							1		1						
78								1	1						1		1				1		1
79																							
80													1			1	1						
81																	1		1				
82														1		1			1				
83																2			1				
84														1				2	1				
85																			3	1			
86																							
87																						2	
88																						1	
89																							
90																							
91																		1			2		
92																						1	

N	8	14	25	25	27	27	82	20	5	6	5	10	18	11	16	12	7	8	8	8	1	1
M	54.7	55.5	57.2	57.5	58.9	63.4	65.3	68.4	68.0	66.0	67.6	70.3	69.8	70.4	70.8	74.1	74.3	77.9	84.6	84.5	78.0	78.0

Sardines of Vigo

Variation in the Number of Gill Rakers in Relation to Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																													
	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220	225	
47	.	1
48	.	2	1
49	1	1	1
50	.	2	4	2
51	.	1	1	.	1
52	.	3	4	8	3
53	.	2	3	2	2	3
54	.	2	1	4	5	2	2
55	.	.	3	1	3	2	1
56	.	.	1	2	4	2	2	1	1	.	.	1
57	.	.	1	.	3	2	3	1	1
58	3	3	2	2	1
59	2	2	1	1	2	8	1
60	2	2	3	7	1	3	2	3	3	.	.	.	1
61	8	4	4	4	4	7	3	4	3	2
62	1	3	3	10	6	9	4	4
63	2	2	2	9	12	16	7	5
64	3	3	5	9	20	9	10	2	1
65	2	2	14	15	12	12	8	5	1	.	.	1	1
66	2	2	13	16	18	11	10	4	.	.	1	1
67	12	10	18	22	11	5	1
68	3	9	17	17	16	9	.	3	1	1	8	.	.	.	1
69	3	13	8	12	12	5	3	2	2	1	1	1
70	10	13	14	9	9	3	4	4	1	1
71	1	.	.	.	4	8	7	17	6	6	2	2	4	1	.	.	2	.	.	1
72	4	4	9	8	9	10	2	.	3	1	.	1	.	.	.	1
73	4	4	9	8	9	10	2	.	3	3	.	1	.	.	.	1
74	1	1	.	5	5	6	12	7	3	2	2	3	1	.	1	.	2
75	1	3	13	3	1	4	4	1	1	.	1	.	2
76	2	2	5	8	3	2	6	3	2	.	1
77	1	4	6	6	1	6	3	3	4	.	3	.	1
78	2	2	4	4	1	1	1	1	5	.	1	.	1
79	2	1	1	.	.	1	1	1	.	1	.	3	.	1
80	1	.	.	3	1	3	.	1	.	4
81	2	3	.	1	.	1
82	2	.	1	.	3	.	2
83	1	.	2	.	1	.	1
84	1	.	1	.	1	.	1
85	1	.	1	.	1	.	1
86	1	.	2	.	1
87	1
88
89
90
91
92
93
N	1	14	20	19	23	19	23	28	81	129	151	148	157	101	45	24	39	31	29	26	16	19	10	11	9	10	3	1	3	
M	49.0	50.9	52.3	52.9	54.9	56.8	58.7	61.9	64.4	65.8	66.6	67.4	69.1	71.2	72.5	73.1	74.0	75.5	76.4	77.2	78.1	80.2	78.9	77.8	78.0	86.3	81.7	92.0	87.0	

TABLE XLIII

Sardines of Leixoes (North of Portugal)

Variation in the Number of Gill Rakers in Relation to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																
	128	133	139	144	150	155	161	166	172	178	183	189	194	200	205	211	216
61			2														
62	2			2		1											
63	1	1		1			1										
64		3		1													
65	2	2		3		3											
66	4	2	2		4	3	1	1									
67	1	2	6	2	4	2	1										
68	3	1	1	6	3	4											
69	1	2	2	5	8	4	6	4									
70		1	1	12	8	5	2	1							1		
71		2	2	1	11	9	5						1				
72			1	9	7	7	6						1				
73		1	1	4	10	8	8	1									
74				2	7	6	4	2	1			1	1				
75				1	3	7	4	1	4	1				1			
76			1			9	3	3									
77					1	3	3		1			3		1			
78					1	1	4	1				2		1			
79							4	1	2				2	2	1		
80				1		1	2					2	2	1			
81						1	2				1	1	1	2			
82							1					2	1	1			
83									1		1	1	2	1			
84														2			
85													3	1			
86											1		1	1	1		
87																1	
88														1			
90															1		
92																1	
93																	1
94															1		
96																1	
N	14	17	17	52	67	74	57	15	9	1	3	14	15	14	5	3	1
M	65,8	67,2	69,0	69,4	71,0	72,1	73,8	72,9	76,9	75,0	83,3	79,1	80,3	81,6	84,8	91,7	93,0

TABLE XLIV

Sardines of Lisbon

Variation in the Number of Gill Rakers in Relation to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																								
	89	94	100	105	111	116	122	128	133	139	144	150	155	161	166	172	178	183	189	194	200	205	211		
45	1																								
46	2																								
50		2																							
51	2	4	1																						
52		2																							
53		5	3	2																					
54		2	5	2																					
55		3	5	4	1																				
56		2	3	2	2	1	1																		
57		2	2	2	2	1				1															
58		1	2	2	3	2	2																		
59				2	5	4	5																		
60			1	3	6	7	1			1															
61					2	5	3	1																	
62				1		3	4	4																	
63					1	1		4	3	1															
64							2	7	9	2	1														
65						1	2	1	5	4	1														
66								5	6	4	2														
67							1	4	5	2	2		1		1										
68								7	2	14		1	1		1										
69								6	5	4	2			2			1								
70								8	5	3	2		1		1	1	1								
71								8	5	1	4		1						1						
72									2	1			1	1		1	1								
73								1			3		2		1	1	1								
74										2	2		2			1	1								
75													2	2	1	1	3	4							
76							1						2		1	2	1	2	2						
77														2		1		2	1						
78																	3	1	1	1					
79																1	2								
80														1			1	2	2		1				
81																	3	5	1	2		1			
82																	3	4	5	1	1	1			
83																		3	2	3					
84																		3	1	2		2			
85																		1	1	3	1				
86																		2	5	2		1	2		
87																				1		1	3		
88																					1	1	2		
89																						1			
90																				1		1	1		
91																					1		1	2	
92																								1	
95																									1
N	5	28	22	20	22	23	21	47	41	40	19		11	10	5	10	27	81	21	12	6	14	4		
M	49,5	53,5	55,1	56,8	58,9	60,1	61,1	66,7	67,5	67,4	69,7		72,0	72,8	72,2	74,0	78,8	80,5	82,3	83,6	85,5	85,7	92,2		

TABLE XLV

Sardines of Ayamonte and Sanlúcar de Barrameda
Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.														
	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175
57	1
58	1
59	1	.	.	.	1
60	.	1	.	.	1
61	.	1	2	2
62	1	2	1	3	3	2
63	.	3	.	4	2	.	.	.	1
64	.	.	1	1	2	2	3	1
65	.	.	1	8	2	1	.	1
66	.	1	2	6	1	2	.	1	1	.
67	.	1	.	8	6	5	1	3
68	.	.	4	5	7	3	3	1	3
69	.	.	.	2	4	4	2	2	.	1
70	.	.	1	4	4	2	7	1	.	.	1
71	.	.	1	.	2	4	3	2	2	4	2	1	.	.	.
72	.	.	.	1	2	3	5	1	.	2	1	1	.	.	.
73	.	.	.	1	1	2	1	1	1	2	.	1	.	.	.
74	1	1	1	1	2	3	2	3	.	.	.
75	1	1	4	.	2	1	1
76	1	.	.	1	2	1	1	1	.	.
77	1	1	1	1	1	.	.	.
78	1	1	2	.	1
80	3	1	.
81	6
82	1
83	1	.	.	.
84	1	.	.	.
N	8	9	13	45	41	33	31	17	16	16	10	10	4	2	1
M	59.3	63.0	66.0	66.2	67.2	68.9	70.6	69.9	73.1	73.1	73.8	75.8	79.0	73.0	82.0

TABLE XLVI

Sardines of Casablanca

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.									
	100	110	120	130	140	150	160	170	180	190
61	1
64	.	.	1
67	1	1
71	.	1	1
75	.	.	.	1
78	.	.	.	1
79	1	.	1	.	.	.
81	1	1
84	1	.	.	1	.	.
86	1	.	.	.
87	1
88	1	.	.
90	1	.
92	1	.
93	1
96	1
N	2	2	2	2	3	2	2	2	2	2
M	64,0	69,0	67,5	76,0	80,7	84,0	82,0	85,5	91,0	94,5

TABLE XLVII

Sardines of Madeira

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.																								
	100	105	110	115	120	125	130	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220	
45	1																								
46		1	1	1																					
47	1																								
48			2	1																					
49			1	1		1																			
50				2		1						1					1								
51			1	1		1				2		1		1				1							
52					1				2				1				1		1			1	1		
53										1		1	1	2				2	1	2		1	2	1	1
54										1	2	1	1	2	1	1	1	1	1	4	2	3	5		
55											1		1	3		1			3	2	4	6	3		
56													1		1						5	2	6	5	
57											1									2	4	1	4	2	
58															1		1	1		1	1	4	1	1	
59																	1		1		1				
60																1						1			
N	2	1	5	6	1	3		2	3	1	6	9	6	6	3	3	7	4	18	14	14	23	13	2	
M	46.0	46.0	48.4	49.0	52.0	52.0		52.0	51.7	54.0	54.0	52.3	53.8	54.0	56.0	56.3	54.1	54.0	54.2	56.0	55.3	55.5	55.5	55.5	

TABLE XLVIII

Sardines of the Azores

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.															
	115	120	125	135	140	155	160	165	170	175	180	185	190	195		
49		1														
51					1											
54	1	1							1							
55			3		1				1				1			
56		2	1		1	2		3	3	4			1			
57	1		1		6			2	2	2	3	1				
58		1	1			2		1	3	3	3	2	1			
59		1	3		1	1		2	5	4	5	2	1			
60			2					1	1	2	5	2	2			
61					1				1	5	2	7	1	2		
62									1			2	1	1		
63						1				1						
64								1						1		
N	2	6	11		11	6		2	13	21	23	19	8	3	4	2
M	55.5	55.3	57.5		56.7	58.3		59.0	58.4	59.0	58.3	59.4	60.0	59.7	58.3	62.0

TABLE L

Sardines of Yugoslavia

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.						
	105	115	125	135	145	155	165
46	1
47	2
48	.	1	1	3	.	.	.
49	.	2	2	2	.	.	.
50	2	1	1
51	3	2	1	2	.	1	.
52	1	.	1	2	1	1	.
53	.	1	3	.	1	1	1
54	1	2	1	2	4	1	.
55	.	1
56	2	1	.
—
58	2	3	1
59	1	.
—
61	1
62	1	.
N	10	10	10	10	10	10	4
M	49,9	51,0	51,2	51,2	54,9	56,1	56,5

TABLE LI

Sardines of Castellón

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.												
	92,5	97,5	107,5	117,5	122,5	127,5	132,5	137,5	142,5	147,5	152,5	157,5	162,5
48	2	.	1
49	1	2	2
50	3	1	.	1
51	.	1	.	.	2	3	5	4	4	1	1	2	.
52	.	.	2	.	2	6	5	4	1	4	.	1	.
53	.	.	1	.	1	4	2	5	5	5	1	.	.
54	1	1	2	1	4	6	2	2	2
55	1	3	3	5	5	2	4	2
56	2	2	7	6	7	5	4
57	1	2	3	5	6	2	3
58	1	2	1	.	1	.	3	2
59	2	1	1	.
60	2	1	.	.
61	1
62
63	1	.	.	.
N	3	3	6	6	20	25	21	28	27	20	21	19	6
M	48,3	49,7	50,5	52,2	52,1	52,8	53,5	54,1	55,8	55,2	55,4	56,7	56,5

TABLE LII

Sardines of Torre Vieja (Alicante)

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.										
	130	140	150	160	165	170	175	180	185	190	195
54	8	.	.	1
55	1	.	.	1	.	1
56	1	1	1
57	2	.	.	2	.	1	1
58	.	.	.	2	.	1
59	.	.	.	1	.	.	.	1	1	.	.
60	2	.	1	1	1	.
61	1	.	1	.	2	1
62	.	.	.	1	.	.	.	1	.	.	.
63	2	.	.	1	.
64	1	.	.	1	.	2
65	2	.
66	1
67	1	.	.	.
68	1	1
72	1	.	.	.
N	7	1	8	9	1	6	1	6	2	6	2
M	55.3	56.0	57.5	61.0	57.0	59.8	59.0	63.0	62.0	62.5	64.5

TABLE LIII

Sardines of Castiglione (Algeria)

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.														
	100	105	110	115	120	130	135	140	145	150	155	160	170	175	
49	1	
51	.	.	1	
52	.	.	.	1	
53	1	.	1	
54	.	1	.	.	2	.	1	
55	.	.	1	1	
56	1	.	1	.	1	.	1	
57	1	1	.	1	.	1	1	.	.	
58	1	.	.	1	
59	1	.	1	1	1	.	.	
60	1	1	
61	2	1	.	.	.	
62	1	.	.	
63	.	.	1	.	.	.	1	1	.	.	
64	1	
67	1	
68	1	
69	1	.	.	
70	1	.	
77	1	.	.	
N	5	1	5	1	5	.	5	1	3	5	3	3	3	1	1
M	55.0	54.0	55.6	52.0	57.2	.	57.6	59.0	57.3	61.0	59.0	59.7	69.3	70.0	64.0

TABLE LIV

Sardines of Tunisia

Variation in the Number of Gill Rakers in Relation
to the Size (Total Length) of Fishes

No. of Gill Rakers	Size Groups, LT in mm.										
	120	125	130	135	140	145	150	155	160	165	170
51	2
52	.	3	2	.	1
53	1	2	1	2	1	1
54	1	2	2	1	1	1	1
55	1	2	1	3	4	.	1	1	.	.	.
56	.	1	1	1	1	2	1	1	.	.	1
57	.	.	1	1	.	2	1	2	1	.	.
58	.	.	1	1	1	3
59	.	.	1	1	.	1	1
60	1	.	.	2	.	.	.
61	1	.	1
N	5	10	10	10	10	10	5	6	2	.	2
M	52,8	54,8	55,0	55,5	55,2	56,6	56,2	57,5	59,0	.	58,5

TABLE LV

Sardines of Maumusson and Les Sables d'Olonne
Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro Div. μ	Size Groups, LT in mm.																
	85	90	95	100	105	110	115	120	130	140	145	150	155	185	190	195	200
12 180	2	1															
13 195	2	4	3														
14 210		6	9	10	3	1											
15 225		1	4	11	9	14	10										
16 240				3		8	13	14	3								
17 255						1	9	5	8								
18 270									1	2	3			2	2		
19 285										1	1	3		3	2	2	
20 300												1	4	3	3	5	5
21 315															1	1	3
N	4	12	16	24	12	24	32	10	12	4	4	4	4	8	8	8	8
M div.	12,5	13,6	14,1	14,7	14,7	15,4	16,0	16,3	16,9	18,5	18,2	19,2	20,0	19,1	19,4	19,9	20,4
M μ	188	204	212	221	221	231	240	245	252	273	278	288	300	277	278	279	306
														297	299		

TABLE LVI

Sardines of SantanderVariation in the Separation between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. #	Size Groups, LT in mm.																						
	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	225	
16 240	6	7	5	.	2	2
17 255	5	5	5	9	2	5	8	4
18 270	1	4	6	4	9	7	7	12	4	.	1	2	1	.	1	1
19 285	.	.	.	8	8	2	1	.	.	.	6	8	10	3	8	2	.	1	2	1	.	.	.
20 300	1	5	5	8	6	1	5	8	6	12	.	.	.
21 315	1	.	5	5	4	3	5	6	6	.	.	.
22 330	1	5	7	2	2	4	4	.	2
23 345	3	1	.	.	1	.	.	2
N	12	16	16	16	16	16	16	16	4	.	8	16	16	16	16	16	16	16	16	24	4	.	4
M div.	16,8	16,8	17,1	17,6	17,8	17,6	17,6	17,7	18,0	.	19,0	19,3	19,2	20,1	20,1	21,2	21,2	20,5	20,5	20,7	22,0	.	22,5
M #	249,0	252,0	256,5	264,0	267,0	264,0	264,0	265,5	270,0	.	285,0	289,5	288,0	301,5	301,5	318,0	318,0	307,5	307,5	310,5	330,0	.	337,5

TABLE LVII

Sardines of Vigo

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. #	Size Groups, LT in mm.																													
	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	225	235		
9 135					1																									
10 150		1			1																									
11 165		1			8	1																								
12 180	2	2			1	1					2																			
13 195	1	5			4	1		3	1	1	3																			
14 210	7	5	7	2	4	1		1	8	10	6	5		1											1					
15 225	2	10	5	8	11			5	14	17	11	17	7	4		2		1			1		1	2						
16 240			7	5	5	9	6	1	21	25	16	21	21	7		4	2	6	5		4			4						
17 255			1	1	6	6	9	4	8	10	31	25	15	9	8	6	9	11	1	6	5	5		3						
18 270						4	1	2	4	1	7	10	12	11	14	11	7	9	4	1	4	7	2	4						
19 285						1									2	1	7	5	6	20	6	5	1	2	8	2	4	2	8	
20 300												4		1	1	7	2	10	14	8	3	4	3	3	3	2	1			
21 315																		1	3	4	1	4		2						
22 330																					1				1		4			
23 345																														
N	12	24	20	16	36	24	16	16	58	64	76	84	56	40	28	36	40	44	32	16	20	28	8	24	4	16		4		4
M div.	13,7	13,7	15,1	15,3	14,4	16,1	16,7	15,5	15,7	15,6	16,1	16,5	16,6	17,2	18,0	18,0	18,3	18,1	19,0	19,1	17,7	18,8	18,6	17,9	19,5	18,9		21,5		21,5
M μ	208	206	227	230	216	242	251	233	236	234	242	248	249	258	270	270	275	272	285	287	266	282	279	269	293	284		328		328

TABLE LVIII

Sardines of Oporto

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro.- Div. μ	Size Groups, LT in mm.										
	128	138	139	144	150	155	161	166	172	178	189
14 210	.	.	.	1
15 225	6	8	.	1	1	2	4	.	1	.	.
16 240	6	6	6	10	7	11	7	2	2	.	.
17 255	2	3	6	16	19	15	11	2	7	.	.
18 270	2	2	6	12	19	14	14	6	10	.	1
19 285	.	1	2	8	9	10	8	17	9	4	6
20 300	.	1	.	4	8	7	8	6	2	.	1
21 315	1	1	3	3	1	.	.
22 330	1
N	16	16	20	52	64	60	56	36	32	4	8
M div.	16,0	16,7	17,2	17,5	17,9	17,7	18,0	18,9	18,1	19,0	19,0
M μ	240,0	250,5	258,0	262,5	268,5	265,5	270,0	283,5	271,5	285,0	285,0

TABLE LIX

Sardines of LisbonVariation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. #	Size Groups, LT in mm.																						
	89	94	100	105	111	116	122	128	133	139	144	155	161	166	172	178	183	189	194	200	205	211	
12	180	2
13	195	1	.	1	1	2
14	210	8	4	6	7	3	.	1
15	225	6	8	9	4	5	3	14	8	1	2	.	1	1
16	240	1	4	.	5	5	3	9	16	12	8	6	1	3	1	.	1	2	.	.	1	1	.
17	255	3	8	7	9	10	11	4	4	4	4	3	1	3	1	.	2	.	2
18	270	6	1	6	3	8	6	2	3	7	1	1	6	5	.	2
19	285	2	.	2	1	3	2	6	4	2	4	6	3	3	5	1
20	300	2	6	2	5	3	5	4	5	7	.
21	315	3	1	1	1	1	1	3	1
22	330	4	1	.	1	3	.
23	345	1	.
N	16	16	16	16	16	16	16	48	32	32	16	16	16	16	16	16	16	16	16	16	16	16	16
M div.	14.4	15.0	14.5	14.9	15.5	16.2	16.4	16.2	16.0	16.1	16.7	17.8	17.3	18.0	18.8	18.7	18.6	19.9	19.2	18.6	19.9	19.7	.
M μ	216.0	225.0	217.5	223.5	232.5	243.0	246.0	243.0	240.0	244.0	250.5	267.0	259.5	270.0	282.0	280.5	279.0	298.0	288.0	279.0	298.5	295.5	.

TABLE LX

Sardines of Ayamonte and Sanlúcar de Barrameda
Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.														
	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175
11 165	.	.	1
12 180	.	.	4	1	.	1
13 195	1	1	.	6	1	3
14 210	5	4	2	7	1	2
15 225	4	11	6	6	8	3	2
16 240	2	7	5	12	30	10	8	4	4
17 255	.	1	2	5	8	10	15	14	13	1
18 270	.	.	.	2	.	3	7	11	9	8	4	3	5	.	.
19 285	.	.	.	1	.	.	.	3	5	6	11	11	5	.	1
20 300	1	1	1	2	6	4	3
21 315	2	.
22 330	2	.
N	12	24	20	40	48	32	32	32	32	16	16	16	16	8	4
M div.	14,6	15,1	14,5	15,2	15,9	15,9	16,8	17,4	17,6	18,4	18,8	18,9	19,1	20,7	19,7
M μ	219,0	226,5	217,5	228,0	238,5	238,5	252,0	261,0	264,0	276,0	282,0	283,5	286,5	310,5	295,5

TABLE LXI

Sardines of Casablanca

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div.	μ	Size Groups, LT in mm.									
		100	110	120	130	140	150	160	170	180	190
13	195	.	2
14	210	4	1
15	225	2	1	1	3	3	.	3	.	.	.
16	240	1	4	.	1	3	2
17	255	1	.	2	.	5	2	2	.	3	1
18	270	1	.	1	2	2	2
19	285	.	.	1	.	.	.	1	5	3	3
20	300	1	1	.	2
N		8	8	4	4	12	4	8	8	8	8
M div.		14,9	14,9	17,0	15,2	16,3	16,5	17,0	18,9	18,0	18,8
M μ		228,5	223,5	255,0	228,0	244,5	247,5	255,0	288,5	270,0	282,0

TABLE LXII

Sardines of MadeiraVariation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div.	μ	Size Groups, LT in mm.																						
		100	110	115	120	125	140	145	150	155	160	165	170	175	180	185	190	195	200	205	210	215	220	
18	270	4																						
19	285	4	6	6																				
20	300		10	5	4	1																		
21	315			4		7																		
22	330			1		4				1														
23	345						2	2	2		1													
24	360						3	8	4	7	1	3				1								
25	375						3	1		3	5	5	2	1	3	1			3					
26	390									4	2	7	11	8	8	5		2	1					
27	405											3	3	1	2	2	3	2						
28	420														1	6	8		1	1				
29	435														1	2	3	2	8	6			2	
30	450														1	1	4	5	4	4	4	4	3	
31	465														1			3	1	2	4	4	2	
32	480																		1	3	5	1		
33	495																		1		3			
N	8	16	16	4	12		8	12	4	16	8	16	16	12	12	12	12	20	16	16	16	16	8	
M div.	18,5	19,6	20,0	20,0	21,2		24,1	23,7	24,0	24,6	25,1	25,1	26,1	26,2	25,8	27,2	27,8	28,2	28,5	29,7	30,0	31,4	30,2	
M μ	277,5	294,0	300,0	300,0	318,0		361,5	355,5	360,0	369,0	376,5	376,5	391,5	393,0	387,0	408,0	417,0	423,0	427,5	445,5	450,0	471,0	453,0	

TABLE LXIV

Sardines of the Canaries

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.															
	70	80	90	100	110	120	130	140	150	160	170	180	190	200	210	220
14 210	2															
15 225	8	1	1													
16 240	6	5	7		1											
17 255		9	4	2	2											
18 270		1	4	7	6	2	4	2								
19 285				5	5	8	4	5								
20 300				2	2	4	8	16								
21 315						1		4	1							
22 330						1		4	6	1						
23 345								1	7	1						
24 360									2	4	1					
25 375										2	11	1				
26 390										2	3	4	4			
27 405												5	2	4	1	1
28 420												6	7	5	1	1
29 435													1	2	6	6
30 450													2	4	6	4
31 465														1	2	
N	16	16	16	16	16	16	16	32	16	16	16	16	16	16	16	12
M div.	15,2	16,6	16,7	18,4	18,8	19,4	19,2	20,2	22,6	23,8	25,1	27,0	27,7	22,6	29,4	29,1
M μ	228,0	249,0	250,5	276,0	274,5	291,0	88,0	303,0	339,0	357,0	376,5	405,0	415,5	429,0	441,0	436,5

TABLE LXV

Sardines of Castellón

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.								
	122,5	127,5	132,5	137,5	142,5	147,5	152,5	157,5	162,5
17 255	7	.	1	1
18 270	3	6	2	5	1
19 285	5	10	5	4	5	3	.	.	.
20 300	.	.	5	6	7	9	2	1	.
21 315	1	.	3	.	2	3	7	3	4
22 330	1	1	5	6	7
23 345	2	6	4
24 360
25 375	1
N	16	16	16	16	16	16	16	16	16
M div.	18,1	18,6	19,4	18,9	19,8	20,1	21,4	22,1	22,2
M μ	271,5	279,0	291,0	283,5	297,0	301,5	321,0	331,5	333,0

TABLE LXVI

Sardines of Torrevieja (Alicante)

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.										
	130	140	150	160	165	170	175	180	185	190	195
18 270	4	.	1
19 285	9	5	4	4
20 300	3	7	10	15	2	1
21 315	.	4	8	11	3	6	3	4	.	3	1
22 330	.	.	6	5	3	10	1	5	.	6	2
23 345	.	.	2	5	.	6	.	5	4	4	3
24 360	.	.	1	6	4	4	2
25 375	2	.
26 390	4	.
27 405	1	.
N	16	16	32	40	8	23	4	20	8	24	8
M div.	18,9	19,9	20,7	20,8	21,1	21,9	21,2	22,1	23,5	23,5	22,7
M μ	283,5	298,5	310,5	312,0	316,5	328,5	318,0	331,5	352,5	352,5	340,5

TABLE LXVII

Sardines of Tunisia

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.				
	145	150	155	160	170
20 300	2
21 315	8	9	.	1	.
22 330	8	6	10	3	2
23 345	1	4	8	4	1
24 360	1	.	2	.	5
N	20	19	20	8	8
M div.	21,5	21,7	22,6	22,4	28,4
M μ	322,5	370,5	339,0	336,0	351,0

TABLE LXVIII

Sprat of Vigo

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.										
	90	95	100	105	110	130	135	140	145	150	155
15 225	.	1
16 240	.	6
17 255	3	6	6	2
18 270	1	5	9	3	5
19 285	.	2	2	7	5	.	1
20 300	.	.	3	3	4
21 315	.	.	.	1	2	1	1
22 330	1	3	1	1	.	.
23 345	2	7	3	2	.	.
24 360	4	4	2	.	.
25 375	4	3	1	.
26 390	3	.	2	.
27 405	1	.	1	3
28 420	1
N	4	20	20	16	16	4	16	16	8	4	4
M div.	17,2	17,0	18,1	18,9	19,2	22,2	22,7	24,5	23,9	26,0	27,2
M μ	258,0	255,0	271,5	283,5	288,0	333,0	340,5	367,5	358,5	390,0	408,0

TABLE LXIX

Anchovies of Vigo

Variation in the Separation Between Gill Raker Spines
in Relation to the Size (Total Length) of Fishes

Micro. Div. μ	Size Groups, LT in mm.																	
	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180	185
19 285	.	.	.	1
20 300	.	.	.	3	2
21 315	1	1
22 330	1	2	.	.	4
23 345	2	1	.	.	1
24 360	.	.	2	.	.	1	.	.	2	1
25 375	.	.	3	2	.	.	5	2	2	2	1
26 390	.	.	2	3	1	.	.	2	.	3	1	1
27 405	.	.	1	3	3	.	5	9	.	2	4	1
28 420	7	8	2	1	5	.	3
29 435	2	8	8	3	6	10	4	4	1
30 450	1	11	3	10	7	14	6	4	1
31 465	3	4	3	6	3	7	1
32 480	1	3	.	7	4	7	4	9	1
33 495	2	.	2	4	4	2	6	3
34 510	2	1	1	6	2	4	2	2	.	1	.	.
35 525	1	.	1	.	2	7	1	1	6	4	3	.
36 540	1	2	.	.	.	1	1	2	1	.
37 555	1	4	.	4	.	.
38 570	1	.	.	.	3	1	4	1	2
39 585	1	4	1	1	2
40 600	1	.	.	.	1	2	.	5	.
41 615	1	2	.	.	.
42 630	1	.
N	4	.	8	12	4	8	44	36	44	44	56	32	36	20	16	16	12	4
M div.	22,2	.	25,2	24,0	26,7	26,4	29,1	27,5	28,8	31,0	30,2	31,8	31,3	35,0	37,6	36,4	38,3	38,5
M μ	333	.	378	360	401	396	437	413	432	465	453	477	470	525	564	546	575	578

