

Stock dynamic of the Iberian sardine (*Sardina pilchardus*, W.) and its implication on the fishery off Galicia (NW Spain)*

PABLO CARRERA¹ and CARMELA PORTEIRO²

¹Museo do Mar de Galicia, Avenida Atlántida 160, 36280 Vigo, Spain. E-mail: pablo.carrera@terra.es

²Instituto Español de Oceanografía. Centro Oceanográfico de Vigo. Apdo. 1552. 36280 Vigo, Spain.

SUMMARY: The recent failure of sardine catches off Galicia (NW Spain), an area where landings reached up to 100 thousand tonnes only a few years ago, may be explained by two possible hypotheses. The “depletion” hypothesis states that diminishing sardine catches were due to a decrease in stock biomass resulting from a combination of reduced recruitment and increased fishing mortality. The “change in distribution” hypothesis states that catch failure was due to a change in the distribution of the stock owing to environmental changes. Available information, based on direct observations from acoustic and ichthyoplankton surveys and the fishery, was analysed. When the stock size is high, the spawning area of the sardine extends offshore in the Cantabrian Sea, and spreads along the continental shelf off northern Portugal. Moreover, adult fish undertake feeding migration towards Galician waters. This spawning behaviour results in a recruitment located mainly off Portugal. Low stock size causes a shrinkage in the distribution area throughout coastal waters and in the Cantabrian Sea, reaching the inner part of the Bay of Biscay. This process also affects the migration range and favours a higher retention in coastal waters of the early life stages (from eggs to recruits), which remain primarily in the same area where they were hatched. The lack of sardine in Galicia may be explained by a depletion process which affects both the feeding migration of adult fish and the recruitment occurrence off southern Galicia. This paper also analyses the dynamics of this stock in the context of a metapopulation. Taking this concept into consideration, we also examined the influence of the dynamics of each sub-population and the environmental conditions that might affect the success of the recruitment.

Key words: sardine, stock variability, recruitment, Iberian peninsula, metapopulation.

INTRODUCTION

Sardine, pilchard and anchovy stocks form the basis of commercially important fisheries which are closely related to high-productivity areas. For these fish species, the stock area and distribution are correlated with abundance, and are dependent upon the environmental regime (Lluch-Belda *et al.*, 1989). Favourable regimes are prolonged periods (a decade or longer) of propitious environmental conditions

over large geographic areas (Lluch-Belda *et al.*, 1989, Schwartzlose *et al.*, 1999). During these periods, better recruitment and growth as well as, perhaps, lower natural mortality rates and consequently higher yields are to be expected. In addition, during high abundance periods many stocks may undertake feeding and spawning migrations involving broader areas. Low abundance, reduced geographic distributions and low yields are associated with unfavourable regimes. Regime “shifts” are periods of transition, often abrupt, from one regime type to another. Regime shifts may not be immediately

*Received December 6, 2000. Accepted March 20, 2002.

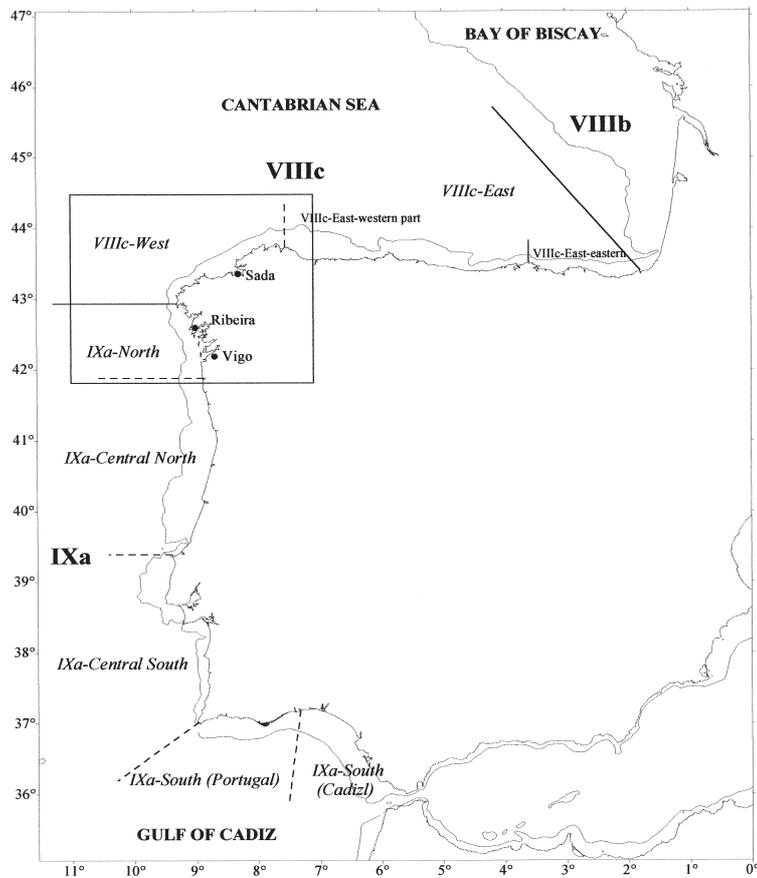


FIG. 1. – Studied area. Surrounded by a box, Galicia and the main location used in this work are shown.

recognisable in fisheries data because of delays in population (abundance) response, noise in data, problems with stock assessment models, or other difficulties. As these fish species are usually short-lived, the success of the recruitment process is crucial to further increase the size of the population. Clupeoid fishes show a high variability in the recruitment process, and hence in population size (Cole and McGlade, 1998). Variability in recruitment is related to the environmental conditions (Lasker, 1975; Cury and Roy, 1989; Bakun, 1996).

The Iberian Peninsula (Fig. 1) is located in the inner part of the Canary system and coastal upwelling occurs from March through October (Wooster *et al.*, 1976; Blanton *et al.*, 1984). In this area, sardine (*Sardina pilchardus*, Walb) have supported one of the oldest fisheries of both Portugal and Spain. The earliest documents of this activity on the Galician coast (northwestern corner of the Iberian Peninsula, see Fig. 1) date from the 14th century (Ferreira, 1998). The development of the sardine fishery was closely related to an increase in the

availability of this species together with a growing sea trade, particularly associated with the salt trade. Moreover, this development would appear to be related to an increase in the water temperature which occurred around 1350-70. Due to the abundance of sardine, the improvement in the salting procedures and trade routes, sardine became one of the most popular foods in this area. The earliest description of the sardine species on Galician coasts was recorded in the 18th century (Cornide, 1788). Ever since the beginning of fishing activity, fluctuations in sardine abundance have been observed, based either on direct reports from the fishery or on the simple examination of salt consumption over the years. Earlier observations of sardine in Galician waters indicate that the presence of this fish species in the area did not depend only on the existence of a resident population but also on an overflow, which mainly occurred in summer. Movements of sardine were known and the species was initially caught using either drift nets or traps, which were placed along the main migratory routes (Ramalho, 1933).

In order to manage the sardine population, extensive studies were started in the early seventies in Atlantic Iberian waters. Since no evidence was found to support the existence of different populations, these sardines were believed to belong to a single stock (Anon, 2000). However, the boundaries of this stock remain uncertain and are still a matter of concern. Spawning occurs in October-May in two main areas: off the coast of Portugal with a peak in winter; and in the Cantabrian Sea with a peak in spring (Re *et al.*, 1990; Solá *et al.*, 1990). The bulk of the recruits at age 0 is found off the northern coast of Portugal during summer and autumn. (Anon, 2000; Porteiro and Pestana, 1997). Although Galician waters are outside these main spawning areas and only the southern part of this region is located in

the vicinity of the main recruitment area, sardine landings in Galicia are substantial, particularly during the middle of the year, which would suggest a feeding movement or migration. According to Fernandez and Navarro (1952) and Porteiro *et al.* (1986), there is an age gradient pattern from the Spanish/Portuguese border, where most of the fish are young, to the Cantabrian Sea where the bulk of the population belongs to older age groups.

Historically, the bulk of the catches were taken in northern Portugal and Galicia (i.e. ICES Sub-Divisions, IXa-North, IXa-Central North and VIIIc-West), as shown in Figure 2. Although in this figure the catches from VIIIc are aggregated, most of them were allocated to VIIIc-West. In spite of the high variability observed in this time series, since 1985

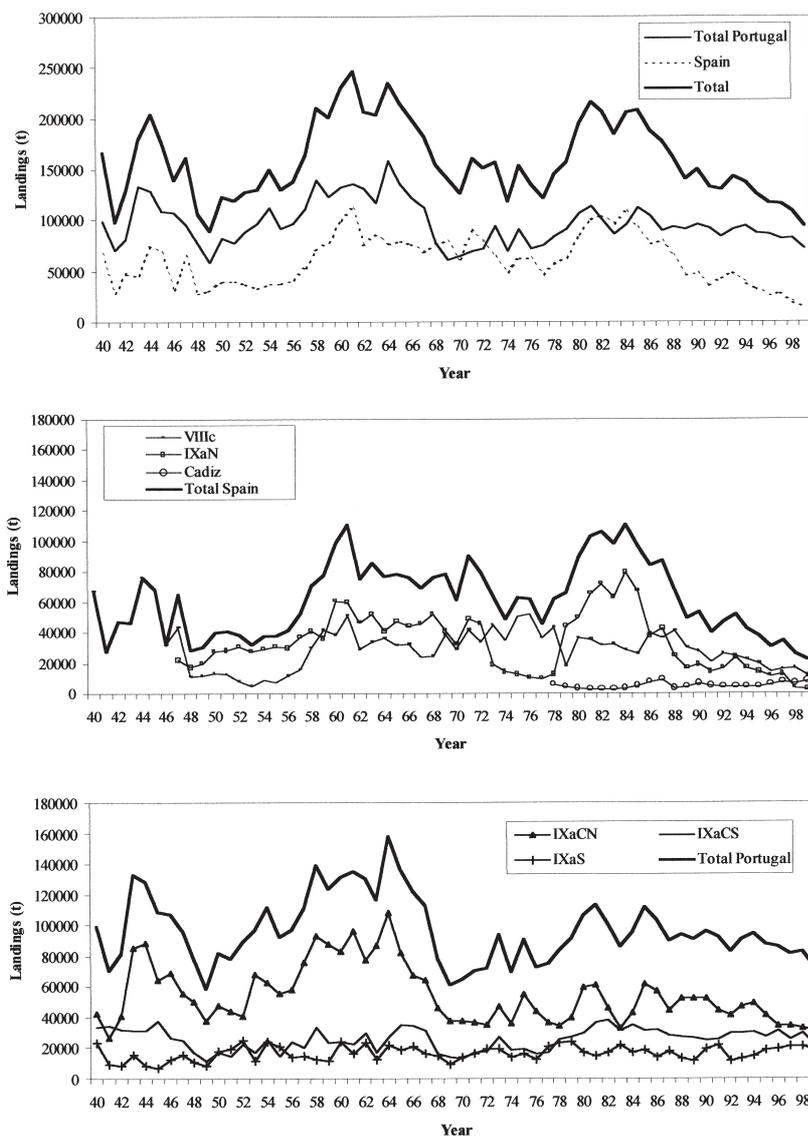


FIG. 2. – Annual landings of Iberian sardine since 1940. Above, landings by country; medium landings in the Spanish ICES Sub-Divisions; and below, landings in the Portuguese ICES Sub-Division

there has been a declining trend in the catches from this area, with the lowest values of the time series in Galicia (IXa-N and VIIIc-West) being reached in recent years. This decline was considerable in IXa-North where the catches in 1998 and 1999 only reached 3.7 and 2.5 thousand tonnes respectively.

In order to explain the disappearance of the sardine from one of its traditional feeding areas, the available information on this stock was re-examined. This paper summarises the available data and discusses possible causes for the decline in catches off NW Spain in recent years.

MATERIAL AND METHODS

Sardine landings off Atlantic Galician waters

Landings from the most important harbours in Galicia, Vigo, Ribeira and Sada (Fig. 1), recorded since 1988, were analysed. The fleet is composed of purse seiners (around 280 boats, with an average GRT of 29 tonnes in the early seventies, increasing to 48 tonnes in the nineties). Sardine is the target fish species of these fleets, especially the larger ones. For the purpose of stabilising prices and decreasing fishing effort, starting in 1990 a number of management measures were introduced. A daily maximum allowable catch of 10,000 kg/fishing day until 1996, which was decreased by 1,000 Kg/fishing day per year until 1999 to reach 7,000 kg per fishing day and a weekly limitation in the number of fishing days (5 days per week) are some of the measures that were implemented. Because catches are landed daily, these fleets have a short displacement range (i.e. no more than 30 nm away from the harbour). Thus, their catches are roughly representative of the local sardine abundance around each location.

Spawning grounds

Stock size is related to the extension of the spawning area (Deriso *et al.*, 1996), which can be estimated in a given zone by the presence/absence of eggs in the surveyed area (Augustin *et al.*, 1996; Borchers *et al.*, 1997). Sardine egg distribution was analysed using direct sardine surveys (whole coverage in 1998, 1997 and 1999, and partial coverage of the Spanish continental shelf in 1990) and other egg surveys targeting different fish species (i.e. mackerel and horse mackerel). Spawning grounds and egg information were thoroughly analysed in Bernal

(1999) and Stratoudakis (1999) and we will refer to the most important findings of these works.

Stock size

Direct estimation of stock size is provided by both acoustic and daily egg production (DEP) surveys. Acoustic surveys are routinely carried out by both countries using the same survey methodology and data analysis (Anon 1997). Spain began to conduct acoustic surveys in the summer of 1983, but only those performed in spring were analysed, these data being available between 1986 and 1999 with no surveys in 1989 and 1994. Since 1997 the surveys have also covered the south of the French continental shelf. Portugal has undertaken surveys in spring, summer and fall. For this study, the fall and spring time survey series were analysed. The fall time series starts in 1984, but shows gaps between 1988 and 1991 and from 1993 to 1996. The Portuguese spring time series starts in 1986 but there are gaps between 1989 and 1994 and in 1987. As of 1995 the area covered was extended southward to the Gulf of Cadiz. Annual landings by the ICES Sub-Division, provided for analytical assessment purposes (Anon., 2001), were used to calculate crude estimates of relative exploitation rates based on catch and survey data without using the stock assessment model as estimated at the ICES. An availability index was formulated as follows:

$$AI = 1 - \left(\frac{\text{Log}(\rho)}{\text{Log}(\psi)} \right)$$

where ψ is the fish abundance (number of fish at age 1+) in a given ICES Sub-Division estimated by the acoustic surveys performed in spring and ρ is the total catch in number obtained in this area. A positive index suggests that the sardine availability in number in spring estimated by the acoustic surveys in a given area is high enough to maintain the fishery during the whole year. In contrast, a negative index in a given area is an indication of an increase in the availability of sardine in this area.

Formulation of hypothesis

The recent failure of sardine fisheries in Galician Atlantic waters is analysed on the basis of two hypotheses: i) The Ibero-Atlantic stock of sardine is immersed in a depletion process; and ii) The Ibero-Atlantic stock of sardine has changed its main distribution area.

The “depletion” hypothesis states that reductions in sardine catch and biomass, especially off Spain, are due to a decrease in stock biomass resulting from a combination of reduced recruitment and increased fishing mortality, particularly of older fish. To formulate this hypothesis, the Iberian sardine stock distribution is assumed to be centred in the south, off Portugal, with another smaller area located in Cantabrian waters. Therefore, if the abundance diminishes in the stock as a whole, the geographic area shrinks towards the south (i.e. Portugal), leading

to an increase in the abundance of older ages in this area. If this is true, the abundance indices based on Portuguese data and catch off Portugal should be relatively constant because the density and area occupied by the sardine have changed very little. Declines in catch and abundance indices based on Portuguese data are not likely to occur unless the sardine stock biomass and area become further diminished.

The “change in distribution” hypothesis states that reductions in catch and biomass off Spain were due to a change in the distribution of the stock relat-

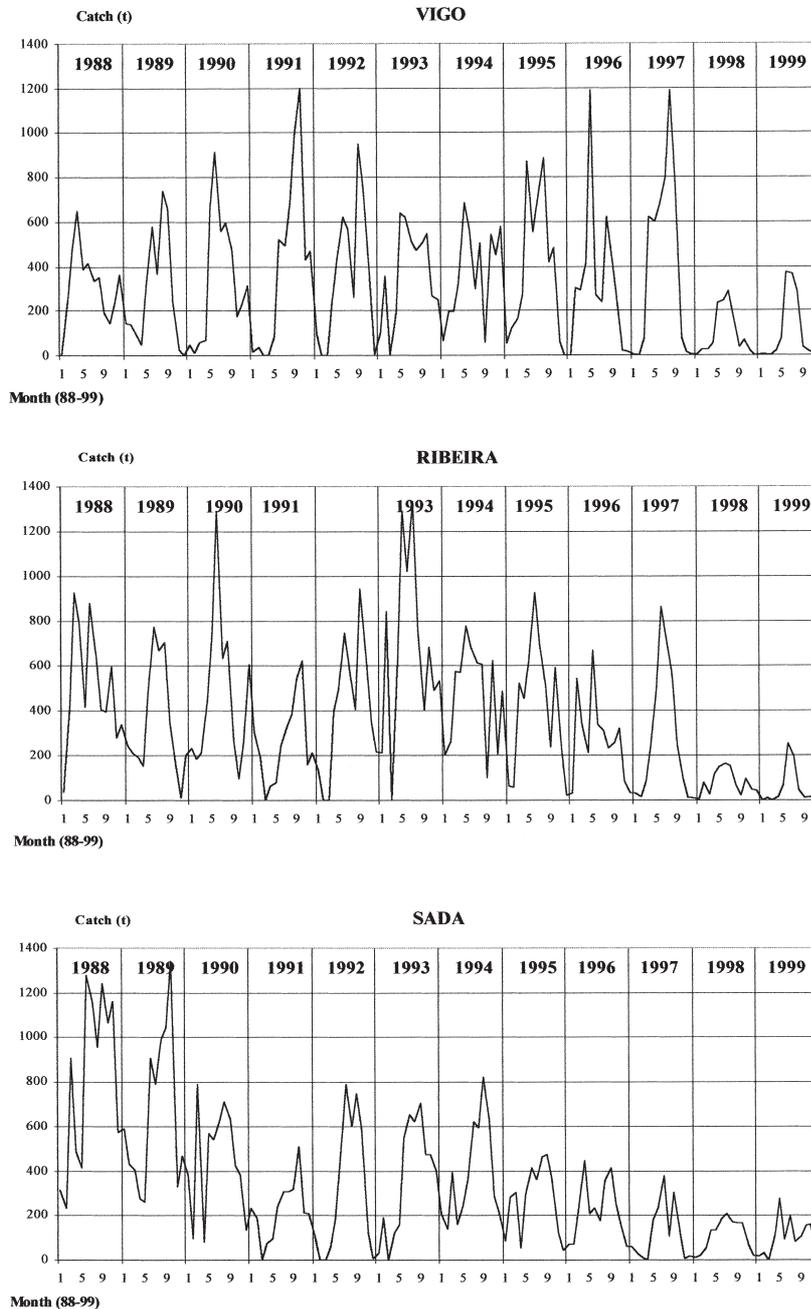


FIG. 2. – Monthly sardine landings in the main Galician harbours.

ed to environmental changes that may not have affected stock productivity. According to this hypothesis, no evidence of changes in stock size will be found and the fluctuations in catches are mainly linked to the availability of fish.

RESULTS

Sardine landings off Atlantic Galician waters

Monthly catches from Vigo, Ribeira and Sada since 1988 are shown in Figure 3. During 1991-93 there was a closure period of 45 days in March-April. In 1998 and 1999 landings in these harbours were almost negligible. In Sada there was a continuous decreasing trend over the time series. On the other hand, in both Vigo and Ribeira sardine landings showed a sharp decrease from 1997 to 1998. An analysis of the landings revealed the existence of an occasional winter fishery, especially in Sada and Ribeira. In Ribeira, this winter fishery took place one year after the occurrence of a good year class. For instance, 1987, 1991 and 1992 had good year classes and winter sardine catches occurred in this harbour in 1988 and during 1992 and 1993. In Sada, the winter fishery appeared to occur two years after a good year class.

As expected, fish availability and catches increased in summer in all harbours.

Spawning grounds

A significant reduction in the spawning area was observed in the Spanish zone (Bernal, 1999). A

drastic reduction occurred off the Galician area, dropping from around 7000 km² estimated in both 1988 and 1990 to only 523 km² estimated in 1997. Moreover, in this region, zero probability of the presence of eggs was predicted for 1997 (Bernal, 1999). In the Cantabrian Sea, there was also a major decline from around 10000 km² in 1988 and 1990 to only 3000 km² in 1997. The inner part of the Bay of Biscay showed a significant decrease from 1988 to 1990 (4600 km² to 2985 km²), while no major changes occurred from 1990 to 1997 (2351 km²). Whereas in the late eighties eggs were distributed throughout the continental shelf and offshore, in the late nineties the spawning area off the Spanish coast was restricted to shallower waters. There was a shrinkage process of the spawning area along the coastal waters of the inner part of the Bay of Biscay. Moreover, an overall reduction in batch fecundity and average weight of females accomplished this process (Pérez *et al.*, 1989; García *et al.*, 1991; Lago de Lanzós *et al.*, 1998). In Portuguese waters, there was a significant reduction of the spawning area (Stratoudakis, 1999). In the late eighties the spawning area was twice the size of the area left in the late nineties. Nevertheless, a drastic reduction only occurred in the northern area, while the southern part remained practically stable at around 4500 km². Unlike the case of Spain, off Portugal, the batch fecundity increased (Cunha *et al.*, 1992 and 1997).

Stock size

Spawning stock biomass and recruitment as estimated by the ICES Working Group on the Assessment of Sardine (ICES 2000) are shown in Figures 4

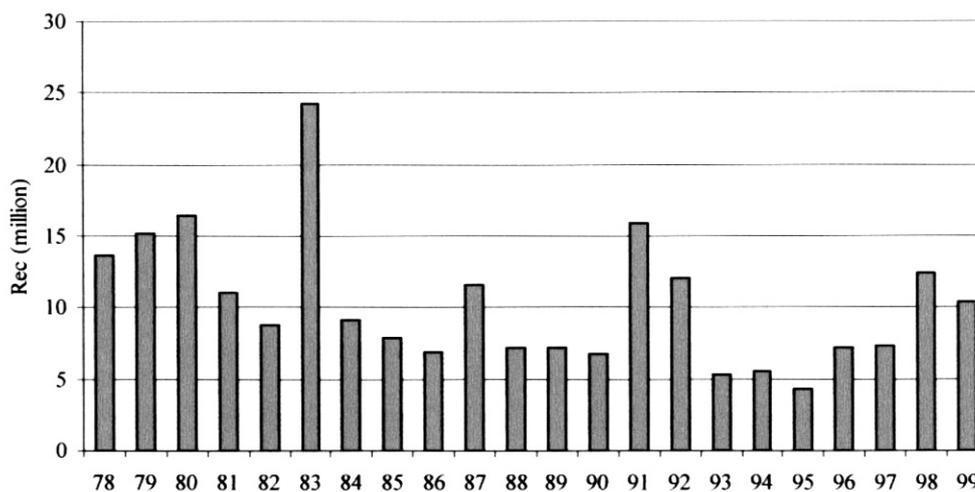


FIG. 4. – Estimated recruitment at age 0 from Anonymous (2001)

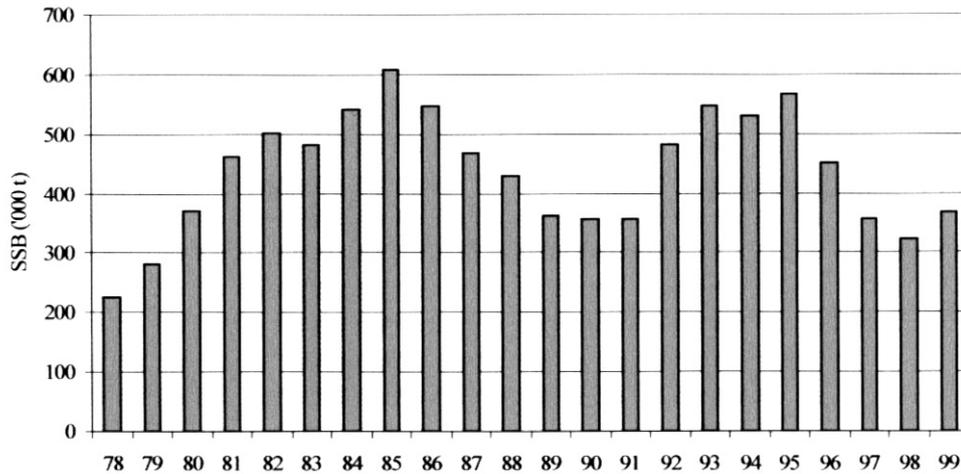


FIG. 5. – Estimated Spawning Stock Biomass from Anonymous (2001)

and 5. Although the absolute values might be biased because of uncertainties in the overall accuracy of the model (see Anon., 2001 for further explanations), trends are quite similar regardless of the input time series used in tuning the model and making assumptions (i.e. separable periods). Spawning Stock Biomass (time series from 1977 to 1999) shows two peaks situated in the mid-eighties and the mid-nineties which were followed by periods of low stock size occurring in the late eighties and late nineties. Recruitment at age 0 in 1978-81, 1983, 1987, 1991-92 and 1998 was above the geometric mean of the time series. The lowest estimated recruitment occurred during the period 1993-95. The exploitation pattern has changed over the time series. In the early eighties most of fish caught belonged to younger age groups (i.e. age groups 0, 1 and 2). Since then, the contribution of younger fish

in the catch-at-age matrix has decreased. According to Azevedo (1999), this change has occurred mainly off the southern region of Portugal.

The availability indices are shown in Table 1 and Figure 6. There was a significant decrease in the number of fish estimated by acoustic surveys off northern Galicia. Low estimates occurred in 1996 and 1998 and are 100 times lower than estimations from the eighties. In Cantabrian waters (ICES Sub-Division VIIIc-East) the number of fish also decreased but since 1996 it has remained fairly stable. In southern Galicia (ICES Sub-Division IXa-N) the number of fish estimated in spring was always lower than in the other regions and reached its lowest value in 1999. Off Portugal there seemed to be an overall decrease from the late eighties to the late nineties. Nevertheless, since 1996 there has been a relatively stable situation, with the only noticeable

TABLE 1. – Number of fish caught in the year (*C*, in million fish), estimated number fish from spring acoustic survey (when available, *S. est.* in million fish), and availability index (*I*, when available) for each year and area.

YEAR	IXa-Ca			IXa-S			IXa-CS			IXa-CN			IXa-N			VIIIc-W			VIIIc-E		
	<i>C</i>	<i>S. est.</i>	<i>I</i>																		
1986	189	na	na	339	2522	0.2562	638	2522	0.1922	1154	3427	0.1337	678	105	-0.4006	312	716	0.1263	388	1490	0.1839
1987	190	na	na	439	na	na	653	na	na	1054	na	na	933	337	-0.1748	384	3315	0.2656	419	1498	0.1741
1988	116	na	na	429	1274	0.1521	586	1274	0.2158	1127	10164	0.2382	373	172	-0.1496	310	1185	0.1892	326	802	0.1345
1989	89	na	na	286	na	na	506	na	na	1051	na	na	296	na	na	288	na	na	259	na	na
1990	151	na	na	434	na	na	473	na	na	1014	na	na	290	134	-0.157	175	496	0.1676	239	490	0.1158
1991	100	na	na	447	na	na	629	na	na	1215	na	na	660	152	-0.2909	166	49	-0.3087	126	1232	0.3195
1992	90	na	na	231	na	na	569	na	na	881	na	na	489	203	-0.1645	282	100	-0.2242	125	300	0.1527
1993	71	na	na	270	na	na	622	na	na	934	na	na	457	380	-0.0309	290	142	-0.1434	101	1667	0.3766
1994	69	na	na	266	na	na	596	na	na	785	na	na	260	na	na	202	na	na	93	na	na
1995	79	na	na	321	na	na	491	na	na	618	na	na	195	na	na	124	na	na	107	na	na
1996	85	3522	0.4553	327	2148	0.2452	634	2148	0.184	757	1036	0.0451	159	209	0.0509	100	15	-0.6884	71	519	0.3166
1997	124	3558	0.41	393	1904	0.2087	484	1904	0.2482	707	4759	0.2251	294	115	-0.198	90	59	-0.1041	138	521	0.2115
1998	224	2279	0.2998	371	1281	0.1729	535	1281	0.2192	781	4750	0.2132	77	247	0.2109	77	14	-0.6272	138	511	0.2093
1999	221	5494	0.3727	298	862	0.157	389	862	0.1126	664	4446	0.2262	48	76	0.1057	55	108	0.1433	99	540	0.2694

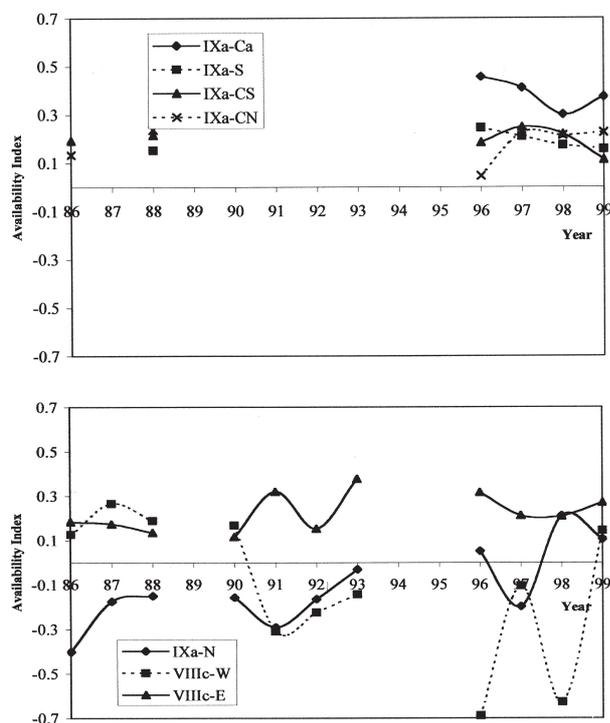


FIG. 6. – Availability index. Above, southern areas; below, northern areas.

occurrence being the decrease in the southern areas of Portugal, which was compensated for by a substantial increase in Cadiz. Temporal changes in this area were analysed by Morais *et al.* (1999), who concluded that changes in fish abundance in each area are significant from winter to spring.

Fish movements are assumed to occur when the availability index in a given area is negative (i.e. the number of fish caught during the year is higher than the number available in the fishery in spring). Accordingly, most of the catches in southern Galicia were taken from migrating fish (negative availability index, Table 1). In northern Galicia, these movements were also detected when the number of fish, as estimated by acoustic surveys, started to decrease in 1991. In recent years the availability of fish in Galicia has been extremely low and the sardine fleet has changed either its target fish species (i.e. horse mackerel) or its fishing grounds by changing harbours. This could explain the change in the availability index which occurred in these areas most recently. In the other areas, no fish movements could be derived from the availability index, as it was consistently positive. Nevertheless, it should be noted that in both IXa-Cádiz and VIIIc-E, sardine is not an important target species, and therefore their catches did not reflect the local abundance.

DISCUSSION

The decline in the Spawning Stock Biomass observed since the mid-nineties is the result of a diminishing spawning area. This shrinkage in the spawning area was located mainly off northern Portugal and in the western part of the Cantabrian Sea. Together with this reduction, a considerable decline in Galician catches occurred in the late nineties, but there was a fairly stable yield off southern Portugal and in the eastern part of the Bay of Biscay.

The regime problem

Schwartzlose *et al.* (1999) analysed the synchrony of the catch trends in several populations of sardines and anchovies. They found a strong positive correlation between sardine catches in the Peru-Chile system, off Japan and California. Food and temperature were identified as the most suitable mechanisms for shifts in regime.

Sea surface temperature (SST) has increased off the Iberian Peninsula in recent years (Lavin *et al.*, 1998; Dias *et al.*, 1992; 1996). Noto and Yasuda (1999) found that the natural mortality from the postlarval stage to age 1 in the Japanese sardine was positively correlated with sea surface temperature. They related the increase in the population size to the low SST period which occurred during 1970-1980, leading to a decrease in the natural mortality of earlier life stages. Unlike the Japanese sardine, the sardines in the Humbolt system have expanded in warm periods (Lluch-Belda *et al.*, 1992), although no relationship between sardine recruitment and temperature was found (Serra *et al.*, 1998). In the Bay of Biscay, both sardine distribution and abundance have increased in the last few years (Massé, pers. com.) as opposed to the trend observed in the Cantabrian Sea. Given the contradictory trajectory of the two neighbouring populations, the effect of the increasing trend in sea surface temperature on stock productivity is still unknown.

Primary production off Galicia is high, reaching values of up to $7.4 \text{ C m}^{-2} \text{ d}^{-1}$ (mean value of $4.3 \text{ C m}^{-2} \text{ d}^{-1}$) during upwelling events (Teira *et al.*, 2000, in press). Even without upwelling events, the primary production is also high and may exceed $1.6 \text{ C m}^{-2} \text{ d}^{-1}$ (Bode and Varela, 1998). For instance, values of $2.6 \text{ C m}^{-2} \text{ d}^{-1}$ were measured in the Canary system (Estrada, 1980). Off northern Galicia microflagellates constituted the bulk of the phytoplankton followed by the diatoms (Casas *et al.*, 1999). It should

TABLE 2. – Summary statistics for the daily upwelling index from 1987 to 1998

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Min	-3682	-3891	-2398	-7564	-8776	-2578	-3767	-4892	-5664	-4397	-3676	-4871
1st Qu.	-593	-468	-259	-570	-332	-201	-485	-456	-385	-482	-472	-428
Mean	-173	-30	31	-177	27	145	-81	-69	4	-138	-172	-65
Median	-53	93	84	41	148	116	12	44	169	16	-80	21
3rd Qu.	371	504	476	376	764	581	430	514	713	352	200	335
Max	2325	3108	1861	2764	3382	2542	2955	1989	2845	2955	2306	3054
Total	181	181	181	181	181	181	181	181	181	181	181	181
NA's	0	0	0	0	0	0	0	0	0	0	0	0
Std Dev.	998	1037	736	1372	1337	890	1079	1046	1302	1072	775	1134

also be noted that the phytoplankton abundance in this area is higher than in the Cantabrian Sea. Sardines appear to be largely omnivorous, their diet ranging from phytoplankton (diatoms and dinoflagellates) to macrozooplankton (essentially copepods) and microzooplankton (nauplius copepods and tintinids) as well as pollen, judging from stomach contents (Oliver and Navarro, 1942; Varela *et al.*, 1985).

Off northern Galicia, the primary production has not changed over the last decade. In addition, values here are higher than those recorded off North Africa. However, from 1989 to 1992, a decrease in the magnitude of diatom blooms as well as an increase in the abundance of microflagellates was observed off northern Galicia. Similarly, changes in dinoflagellate composition were observed in the early nineties in South Galicia (Cariño *et al.*, 2000). As suggested by Corten (1999), changes in abundance and prevalence of zooplankton species might be caused by changes in water inflows which may affect the availability of fish. Nevertheless, given the wide variety of organisms consumed by the sardine and the stability of the primary production in this area, changes in the phytoplankton composition here would appear to be minor (Bode *et al.*, 1994, 1996; Casas *et al.*, 1997; Varela, 1992) and, therefore probably did not affect the availability of sardine in this area.

Relationships between recruitment and environmental conditions have been studied by several authors (Robles *et al.*, 1992; Roy *et al.*, 1994; Cabanas and Porteiro, 1998; Borges *et al.*, 2000). Because of the extensive spawning period and different spawning grounds, the recruitment success of the sardine is the outcome of a long time/space integral. This reproductive strategy allows sardine to increase their chances of coming across a sequence of environmental events favourable to the survival and growth of the early life-history stages (Cole and McGlade, 1998). On the other hand, it makes it dif-

ficult to link the recruitment to a particular oceanographic or climatic event. For instance, Table 2 and Figure 7 show the upwelling indices from 1987 to 1998 for the first half of each year as estimated by Lavín *et al.* (1991). Upwelling is derived from the atmospheric pressure information of a point located off the Galician coast (43°N-11°W). The upwelling regime found in 1995 was similar to that observed in 1991 and 1992. However, the recruitment in 1991 and 1992 was well above the geometric mean of the time series whereas that of 1995 was the lowest (Table 2).

In keeping with our findings, the hypothesis regarding the change in distribution would appear to be unlikely. The losses of both stock area and size in the northern region were not compensated for by an

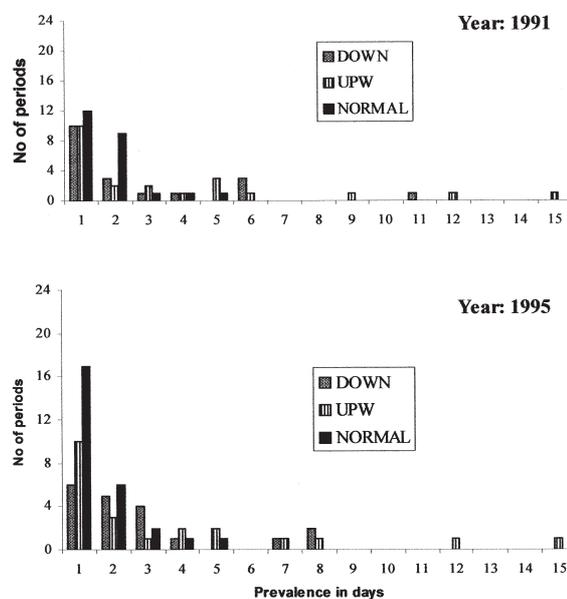


Fig. 7. – Index of prevalence (number of days with similar wind stress and direction) of upwelling events ($-Q_x$ measured in m^3/s km). Down, grouped number of periods of days with $-Q_x$ higher than $200 m^3/s$ km; Upw, those lower than $-200 m^3/s$ km; and Normal, those between 200 and $-200 m^3/s$ km.

increase in the southern region. Moreover, either the increase in sea surface temperature or possible changes in food availability may have affected the overall productivity of the stock. However, since a clear displacement of the stock was not detected, it might be concluded that the lack of sardine off Galicia over the last two years was not caused by a displacement of the bulk of the stock towards southern areas.

Population dynamics and identity

The location of the main area for recruits at age 0 centred off North Portugal was used as the principal basis to support the idea of a single population, although spawning occurs in two different locations (i.e. Cantabrian Sea and off Portugal), peaking in different periods (spring in the Cantabrian Sea and winter off Portugal). As reported by Fernández and Navarro (1952), the abundance of young sardine in the Cantabrian Sea was historically extremely low. This was confirmed in recent investigations on juvenile distribution around the Bay of Biscay (JUVESU, 2nd intermediate report, 2000). A similar pattern was also observed in juvenile mackerel (*Scomber scombrus*). Mackerel spawn in spring throughout the Cantabrian Sea, close to the shelf break and both the number of adults and eggs or larvae off Portugal and South Galicia is low (SEFOS, final report 1995; Lago de Lanzós *et al.*, 1993). In spite of this, the highest catches of juvenile mackerel occurred in South Galicia (JUVESU, 2nd intermediate report, 2000). Although the mechanisms that led to this occurrence have not been studied in depth, this might be explained by wind-driven current responses. During late spring-summer predominant winds are N-NE (Blanton *et al.*, 1984), causing a westward circulation in the Cantabrian Sea and resulting in upwelling off the western coast of the Iberian Peninsula. In the case of a NW wind, coastal circulation in the Cantabrian Sea is eastward, while there is a westward countercurrent close to the slope (Pingree and Le Cann, 1989). According to this general pattern, larvae could reach the western part of the Iberian Peninsula and progress southward depending on the strength of the upwelling event.

However, since the mid-nineties, the reduction of the distribution area, which has occurred mainly in the NW part of the Iberian Peninsula (i.e. in Galician waters), has led to some uncertainties on stock identity. In our opinion, given the available information on recruitment, spawning and catches, the dynamics of the Ibero-Atlantic stock of sardine would seem to

be better understood if the concept of metapopulation, as stated by McQuinn (1997) for the Atlantic herring, is adopted.

According to this concept, the structure of the sardine may be considered as an array of the local populations linked by variable degrees of gene flow (i.e. the Cantabrian sub-population and the Atlantic sub-population). Migration plays an important role in this concept because it is necessary for the survival, endurance and expansion of the metapopulation. In our case, when the two local populations (the Cantabrian and the Atlantic) achieved a large size, as observed during the eighties, older fish were predominant in the Cantabrian Sea and movements between both sub-populations were observed. During the spawning period, the sardine was spread out all over the continental shelf, reaching the Atlantic waters of northern Galicia. Moreover, eggs were even found offshore. Off northern Portugal spawning started earlier and was restricted to the continental shelf (Cunha *et al.*, 1989). In southern Galicia, during the spawning period, only a few schools remained inside the "Rias" which are long, narrow estuaries. From April, with the increased availability of food, schools from northern Portugal moved northward, reaching Galician waters. Similarly, schools from the Cantabrian Sea moved westward, increasing the availability of the sardine off Galicia during the summer, and hence the maximum yield was achieved in this fishery in June-October. In addition, in southern Galicia recruitment at age 0, which occurs mainly in summer, supports an important fishery on juveniles during this period. The high primary production off Galicia may act as a trigger mechanism forcing the sardine to undertake feeding migration to this area. Size- and age-related migrations (Nøttestad *et al.*, 1999) might explain the age distribution pattern observed by Porteiro *et al.* (1986) along the Spanish coast.

Poor recruitment in the mid-nineties as well as an increase in fishing mortality due to a reduction in the overall stock size led to a shrinkage of the Cantabrian sub-population towards coastal waters in the western area (i.e. northwest corner of the Iberian Peninsula) and a fairly stable situation in the inner part of the Bay of Biscay. There was also a decrease in sardine distribution off northern Portugal and a movement of the Atlantic sub-population to the southern part of the Iberian Peninsula. The increase in older fish detected in the southern region of Portugal, both in catches and in acoustic surveys (Azevedo, 1999; Morais *et al.*, 1999), as well as the

TABLE 3. – Estimated mean age (left) and mean length (cm) by area during the Spanish Spring acoustic surveys.

	Mean Age				Mean Legth			
	VIIIc-Ee	VIIIc-Ew	VIIIc-W	IXa-N	VIIIc-Ee	VIIIc-Ew	VIIIc-W	IXa-N
86	4.6	5.0	4.8	3.7	20.9	21.6	21.3	19.5
87	5.6	5.5	4.7	3.1	22.3	22.2	20.6	18.5
88	6.6	6.3	5.8	4.1	22.6	22.0	21.1	19.0
89								
90	5.5	6.5	6.5	3.1	21.6	22.5	22.3	18.7
91	5.6	6.0	5.2	3.5	19.6	21.8	22.6	21.8
92	4.3	5.3	6.0	2.4	20.6	21.8	22.3	18.2
93	7.4	6.9	3.6	2.2	23.1	22.8	20.2	18.4
94								
95								
96	4.7	4.7	4.7	4.3	21.6	21.9	21.7	20.6
97	3.4	3.7	4.8	3.7	20.6	20.8	21.9	19.7
98	3.7	2.2	2.2	1.9	20.4	18.0	18.0	17.0
99	3.2	3.7	2.5	2.8	18.2	21.0	18.5	18.5

increase in batch fecundity in Portugal, agreed with this process. In the Cantabrian Sea, this process appeared to be gradual and hence catches in Sada also underwent a gradual decrease. In Table 3, mean age and mean length by ICES Sub-Division as estimated from the Spanish Spring acoustic survey are shown. Younger and smaller fish were consistently found in southern Galicia (IXa-N), whereas older specimens were located in the Cantabrian Sea (VIIIc-E). The poor recruitment from 1993 to 1995 increased the mean age in IXa-N estimated in 1996, which was quite similar over the surveyed area. When the spawning area in the Cantabrian Sea was restricted to coastal waters and the western part was abandoned (between 1997 and 1998), sardine also failed in southern Galicia. The occurrence of coastal spawning resulted in a retention of both eggs and larvae in shallower waters throughout Cantabrian waters. Fernández *et al.* (1991, 1993) and Varela (1996) explain the mechanism. In winter-spring the Cantabrian Sea is characterised by the presence of a poleward current (Frouin *et al.*, 1990), which plays a crucial role as a barrier to the transport of eggs and larvae. In this context, the decrease in both mean age and length throughout the Cantabrian Sea, estimated during the acoustic surveys undertaken in 1998 and 1999, concurred with the possible retention of larvae and small recruits in coastal waters. Off northern Portugal, the same situation might be suggested. From 1986 to 1999 the estimated spawning area was reduced from 8300 km² to only 3100 km², with the lowest surface area occurring in 1997 (only 1600 km²). Consequently, earlier life stages might have been retained in coastal waters without any northward progression. Furthermore, recent investigations off northern Portugal have indicated that sar-

dine are restricted to coastal waters, and juveniles occurred mixed with adult fish, which creates problems in the normal evolution of the fishery.

The decrease in the stock area and stock size in northern areas has affected the movements of sardine, and at present it would appear that the spawning biomass in the Cantabrian is at a low level and virtually isolated from the northern Portuguese spawners. Moreover, the contribution of the Cantabrian spawners to the recruitment success off the western coast would now be negligible. Low gene exchange between both areas is expected at very low stock sizes. However, neither the northern Portuguese nor the Cantabrian spawning ground was completely abandoned. A recovery of any of these sub-populations will probably occur when a good incoming year class forces an expansion of the sardine distribution area. It should also be noted that the influence of upwelling or other oceanographic events, which take place mainly on the continental shelf, on recruitment success may depend on the size of the spawning area: the more coastal the distribution area the less important the influence of the oceanographic events will be. At low spawning stock sizes, continental conditions, such as river plumes, may play a more important role in recruitment success than the actual oceanic events. The location of the preferential areas of sardine in zones having major river plumes (i.e. the Douro-Aveiro area in Portugal and the Adour and surrounding Basque country rivers in the Cantabrian Sea) agree with this assumption.

From our point of view, the question of the failure of the Galician sardine fishery may be better understood in the context of depletion, especially regarding the northern population. The Atlantic sub-

population also suffered a shrinkage process, but it was less intense than in the Cantabrian sub-population. Under these conditions, the bulk of the distribution remained off the southern area (Portugal), whereas in the northern area only a residual population was observed. The low size of the stock affected the distribution of fish; hence the lack of adult fish in Galician waters. On the other hand, coastal spawning behaviour resulted in the higher retention of earlier life stages (from eggs to recruits), which remain mainly in the same area where they were hatched. The lack of juveniles off southern Galicia may be explained by this mechanism.

Fréon and Misund (1999) reviewed the effect of the metapopulation on fisheries and stock assessment. The depletion of sub-populations is believed to cause long-term diminishing productivity. In the case of the Iberian sardine, sub-populations are mainly distributed in each country and Galician waters make up the area linking the two sub-populations, especially in summer. The interdependence of both sub-populations during periods of high stock sizes together with periods of virtual isolation at low stock sizes bring about major changes in spatial distribution, local abundance and age structure. Because of spatial changes in fish distribution and the shifts in the exploitation pattern owing to stock size, it is difficult to obtain a meaningful comparison between the stock size and the fishing mortality in the mid 1980s and the late 1990s, and to provide robust estimates of the state of the stock using the actual assessment model (Anon., 2000).

The actual knowledge on the Ibero-Atlantic sardine agrees with the concept of metapopulation. Nevertheless, there is still a lack of knowledge in terms of the relationship between the Iberian sardine and populations located in surrounding areas (i.e. the Bay of Biscay, Mediterranean Sea and Moroccan area). It is therefore necessary to carry out a multi-disciplinary study including these areas in order to provide an holistic approach to stock identity. Furthermore, the assessment model should be modified to take into account the special features of stock dynamics (range of migrations, distribution, age structure, etc.) observed in a metapopulation.

ACKNOWLEDGEMENTS

Larry Jacobson helped us in an earlier document presented at the ICES Working Group. His comments, suggestions, and especially the discussions

on the dynamics of pelagic fish, have allowed us to gain a more in-depth knowledge of the dynamics of the Iberian sardine. We are indebted to our colleagues, Manuela Azevedo, Yorgos Stratoudakis and Vitor Marques, who kindly provided the Portuguese data revision which has made this paper possible. We wish to thank the rest of the Scientific Team of Ipimar, Portugal, involved in sardine research projects, for their steadfast dedication to the study of this fish species over the last twenty years. We would also like to express our gratitude to our colleagues at the IEO. Miguel Bernal provided the revision of the egg surveys in the Spanish area. Some results from the SEFOS project (AIR2-CT93-1105) and JUVESU (FAIR CT97-3374) were also used. Finally, we are indebted to the anonymous referees who have greatly contributed to the improvement of the early manuscript.

REFERENCES

- Anonymus. – 1997. Report of the Planning Group for Pelagic Acoustic surveys in ICES Sub-Areas VIII and IX, a Coruña, 30-31 January 1998. *ICES CM 1998/G: 2*.
- Anonymus. – 2000. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. Copenhagen. *ICES CM 2000/ACFM: 05*.
- Anonymus. – 2001. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. Copenhagen. *ICES CM 2001/ACFM: 06*.
- Augustin, N.H., M.A. Muggleston, and S.T. Buckland. – 1996. An autologistic model for the spatial distribution of wildlife. *J. Appl. Ecol.*, 33: 339-347.
- Azevedo, M. – 1999. Exploratory data analysis for Iberian sardine (*Sardina pilchardus*). WD Report of the Working Group on the Assessment of Mackerel, Horse mackerel Sardine and Anchovy. *ICES CM 2000/ACFM: 5*.
- Bakun, A. – 1996. *Patterns in the Ocean: Ocean processes and marine population dynamics*. La Jolla. CA: California Sea Grant 323 pp.
- Bernal, M. – 1999. Preliminary results on a two stage modelling of sardine (*Sardina pilchardus*, Walb) egg presence and abundance off the Spanish coast and its implication for stock assessment. WD. Report of the Working Group on the Assessment of Mackerel, Horse mackerel Sardine and Anchovy, *ICES CM 2000/ACFM: 5*.
- Borges, M.F., M. Santos, N. Crato, H. Mendes and B. Mota. – 2000. Sardine recruitment and climatic changes off Portugal in the last decades. WD Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. Copenhagen. *ICES CM 2001/ACFM: 06*.
- Blanton, J. O., L. P. Atkinson, F. Fernández de Castillejo and A. Lavín Montero. – 1984. Coastal upwelling off the Rias Bajas, Galicia, Northwest Spain I: Hydrographic studies. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 183: 79-90.
- Bode, A. and M. Varela. – 1998. Mesoscale estimations of primary production in shelf waters: a case study in the Golfo Artabo (NW Spain). *J. Exp. Mar. Biol. Ecol.*, VOLUME NUMBER: 111-131
- Borchers, D.L., S.T. Buckland, I.G. Priede and S. Ahmadi. – 1997. Improving the precision of the daily egg production method using generalised additive models. *Can. J. Fish. Aquat. Sci.*, 54: 2727-2742.
- Cabanas, J.M. and C. Porteiro. – 1998. Links between the North Atlantic sardine recruitment and its environment (in press).
- C. Cariño, E. Fernández, J. Mariño, M.J. Campos, Y. Pazos and J.

- Maneiro. – 2000. Long-term variability of dinoflagellate abundance in relation to decadal changes in atmospheric forcing. 31st Annual Symposium of the Estuarine and Coastal Sciences Association. Bilbao, 2000
- Casas, B., M. Varela and A. Bode. – 1999. Seasonal succession of phytoplankton species on the coast of A Coruña (Galicia, northwest Spain). *Bol. Inst. Esp. Oceanogr.* 15(1-4): 413-429.
- Cole, J. and J. McGlade. – 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. *Rev. Fish Biol. Fish.* 8: 445-471.
- Cornide, J. – 1788. *Ensayo de una Historia natural de los Peces y otras Producciones marinas de la costa de Galicia, arreglado al sistema del caballero Carlos Linné. Con un tratado de las diversas pescas y de las redes y aparejos con que se practican.* A Coruña, 91-94.
- Corten, A. – 1999. The reappearance of spawning Atlantic herring (*Clupea harengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. *Can. J. Fish. Aquat. Sci.*, 56: 2051-2061.
- Cunha, M.E., I. Figueiredo, A. Farinha and M. Santos. – 1989. Estimation of sardine spawning biomass off Portugal by the daily egg production method. *ICES CM 1989/H: 41*
- Cunha, M.E., I. Figueiredo, A. Farinha and M. Santos. – 1992. Estimation of sardine spawning biomass off Portugal by the daily egg production method. *Bol. Inst. Espan. Oceanogr.*, 8: 139-153
- Cunha, M.E., V. Marques, E. Soares and A. Farinha. – 1997. Preliminary results from the joint sardine (*Sardina pilchardus*) DEPM and acoustic surveys in ICES Division IXa (Lat. 41°50'N, 36°00'N) ICES CM 1997/Y:5
- Cury, P. and C. Roy. – 1989. Optimal environmental window and pelagic fish recruitment process in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680
- Dias, C., E. Amorín and E.M. Das Dores Vacas. – 1992. Sea-surface temperature: seasonal variation between in the Iberian coast and the Madeira Islands. 1981-1987. *ICES Mar. Sci. Symp.* 195: 177-186
- Dias, C.A., G. Pestana, E. Soares and V. Marques. – 1996. Present state of sardine stock in ICES Divisions VIIIc and IXa. WD ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. Copenhagen, 1996. 45 pp.
- Deriso, R.B., J.T. Barnes, L.D. Jacobson and P.R. Arenas. – 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*), 1983-1995. CalCOFI Rep., 37
- Estrada, M. – 1980. Phytoplankton biomass and production in the upwelling region of NW Africa. Relationships with Hydrographic parameters. *Mar. Biol.*, 60 63-71
- Fernández, R. and F. De P. Navarro. – 1952. La sardina de Santander. *Bol. Inst. Esp. Oceanogr.*, 55.
- Fernández, E., A. Bode, A. Botas and R. Anadón. – 1991. Microplankton assemblages associated with saline fronts during a spring bloom in the Central Cantabrian Sea: differences in trophic structure between water bodies. *J. Plankton Res.*, 13: 1239-1256
- Fernández, E., J.L. Cabal, A. Acuña, A. Bode, J. Botas and C. García-Soto. – 1993 Plankton distribution across a slope current-induced front in the southern Bay of Biscay. *J. Plankton Res.*, 15: 619-641
- Ferreira, E. – 1998. *O Desenvolvimento da actividade pesqueira desde a alta Idade Media ó século XVII* (Development of the fishing activity from the High Middle Age to the XVIIIth Century). In *Historia da Pesca em Galicia*. Chapter II. Coordinated by Carmen Fernández Casanova. Servicio de Publicacións e Intercambio Científico da Universidade de Santiago de Compostela.
- Fréon P. and O.A. Misund. – 1999. *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment*. Fishing News Books. Blackwell Science Ltd.
- Frouin, R., A.F.G. Fiuza, I. Ambar and T. Boyd. – 1990. Observations of a poleward surface current off the coasts of Portugal and Spain during winter. *J. Geophys. Res.*, 95: 679-691
- García, A., N. Pérez, C. Porteiro and P. Carrera. – 1991. Estimates of the sardine spawning stock biomass off the Galician and Cantabrian coast. *ICES CM 1991/H:35*.
- Lago de Lanzós, A., A. Solá, L. Motos and C. Franco. – 1993. Mackerel (*Scomber scombrus*, L) egg distribution and stage I egg production estimates in Division VIIIb,c and IXa-N in 1988, 1990 and 1992. *ICES CM 1993/H:34*
- Lago de Lanzós, A., L. Quintanilla, A. Solá and C. Franco. – 1998. The egg production method applied to the spawning biomass estimation of sardine (*Sardina pilchardus*, Walb) in the north-Atlantic Spanish coast. *ICES CM 1998/BB:17*
- Lasker, R. – 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. US*, 73: 453-462
- Lavín, A., G. Diaz del Rio, J. M. Cabanas and G. Casas. – 1991. Afloramiento en el Noroeste de la Península Iberica. Indices de afloramiento para el punto 43° N 11° W. Periodo 1966-1989. *Inf. Téc. Instit. Esp. Oceanogr.*, 91: 1-40.
- Lavín, A., L. Valdés, J. Gil and M. Moral. – 1998. Seasonal and interannual variability in properties of surface water off Santander (Bay of Biscay) (1991-1995). *Oceanlog. Acta*, 21(2): 179-190
- Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose and P. E. Smith. – 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. *S. Afr. J. mar. Sci.*, 8: 195-205.
- Lluch-Belda, D., D.B. Lluch-Cota, S. Hernández Vázquez and C.A. Salas-Zavala. – 1992. Sardine population expansion in eastern boundary systems of the Pacific Ocean as related to sea surface temperature. In: A. Payne, K. Brink, K. Mann and H. Hilborn (eds), *Benguela Trophic Functioning*. *S. Afr. J. mar. Sci.* 12: 147-155.
- Morais, A., M.F. Borges and V. Marques. – 1999. Changes on Sardine distribution pattern and trends of recruitment spawning stock abundance in the Portuguese area as directly estimated by acoustic surveys from 1984-1999. WD Report of the Working Group on the Assessment of Mackerel, Horse mackerel Sardine and Anchovy, *ICES CM 2000/ACFM:5*
- McQuinn, I.H. – 1997. Metapopulations and the Atlantic herring. *Rev. Fish. Biol. Fish.*, 7: 297-329
- Noto, M. and I. Yasuda. – 1999. Population decline of the Japanese sardine, *Sardinops melanostictus*, in relation to sea surface temperature in the Kuroshio Extension. *Can. J. Aquat. Sci.*, 56: 973-983.
- Nøttestad, L., J. Giske, J.C. Hols and A. Huse. – 1999. A length-based hypothesis for feeding migration in pelagic fish. *Can. J. Aquat. Sci.*, 56(Suppl.1): 26-34.
- Oliver, M and F. De P. Navarro. – 1952. Nuevos datos sobre la sardina de Vigo. *Bol. Inst. Esp. Oceanogr.*, 56.
- Pérez, N., A. García, N. Lo and C. Franco. – 1989. The egg production method applied to the spawning biomass estimation of sardine (*Sardina pilchardus*, Walb) in the north-Atlantic Spanish coasts. *ICES CM 1989/H:23*.
- Pingree, R.D., and B. Le Cann. – 1989. Celtic and Armorican slope and shelf residual currents. *Prog. Oceanog.*, 23: 303-338
- Porteiro, C., F. Alvarez, and J. A. Pereiro. – 1986. Sardine (*Sardina pilchardus*, Walb) stock differential distribution by age class in ICES Divisions VIIIc and IXa. *ICES CM 1986/H:28*.
- Porteiro, C. and G. Pestana. – 1997. Atlantic Iberian sardine (*Sardina pilchardus* Walb.) WD GLOBEC/SPACC W.G. Dartmouth, June 1997
- Ramallo, A. – 1933. Notice sur la pêche et quelques aspects de la biologie de la sardine au Portugal. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*, 84:29-40.
- Ré, P., R. Cabral e Silva, E. Cunha, A. Farinha, I. Meneses and T. Moita. – 1990. Sardine Spawning off Portugal. *Bol. Inst. Nac. Invest. Pescas*, Lisboa 15: 31-44.
- Robles, R., C. Porteiro and J.M. Cabanas. – 1992. The stock of Atlanto-Iberian sardine: possible causes of variability. *ICES mar. Sci. Symp.*, 195: 418-423.
- Roy, C., C. Porteiro and J.M. Cabanas. – 1995. The optimal Environmental Window Hypothesis in the ICES A Area: The example of the Iberian Sardine. *ICES. Coop. Res. Rep. no 206*.
- Schwartzlose, R.A., J. Alheit, A. Bakun, T.R. Baumgartner, R. Cloete, R.J.M. Crawford, W.J. Fletcher, Y. Green-Ruiz, E. Hagen, T. Kawasaki, D. Lluch-Belda, S.E. Lluch-Cota, A.D. MacCall, Y. Matsuura, M.O. Nevárez-Martínez, R.H. Parrish, C. Roy, R. Serra, K.V. Shust, M.N. Ward and J.Z. Zuzunaga. – 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. mar. Sci.* 21: 289-347
- Serra, R., P. Cury and C. Roy. – 1998. The recruitment of the Chilean sardine (*Sardinops sagax*) and the "optimum environmental window". In M.H. Durand, P. Cury, R. Mendelssohn, C. Roy, A. Bakun and D. Pauly (eds), *Global versus Local Changes un Upwelling Systems*, pp. 267-274. ORSTOM, Paris.

- Solá, A., L. Motos, C. Franco and A. Lago. – 1990. Seasonal occurrence of pelagic fish eggs and larvae in the Cantabrian sea (VIIIc) and Galicia (Ixa) from 1987 to 1989. *ICES, C.M. 1990/H:25*.
- Stratoudakis, Y. – 1999. Temporal changes in estimated spawning area and distribution of sardine (*Sardina pilchardus*) eggs off Portugal WD. Report of the Working Group on the Assessment of Mackerel, Horse mackerel Sardine and Anchovy, *ICES CM 2000/ACFM:5*
- Teira, E., P. Serret and E. Fernández. – 2000. Phytoplankton size-structure, particulate and dissolved organic carbon production and oxygen fluxes through microbial communities in the NW Iberian coastal transition zone. *Mar. Ecol. Prog. Ser.*, (in press)
- Varela, M., A. Larrañaga, E. Costas and B. Rodríguez. – 1988. Contenido estomacal de la sardina (*Sardina pilchardus*, Walb) durante la campaña Saracus 871 en las plataformas Cantábrica y de Galicia en febrero de 1987. *Bol. Inst. Esp. Oceanogr.* 5(1): 17-28
- Varela, M. – 1996. Phytoplankton ecology in the Bay of Biscay. *Sci. Mar.*, 60(Supl. 2) 45-53.
- Wooster, W.S., A.S. Bakun and D.R. McLain. – 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 36(2): 131-141.