Distribution and abundance of megrim (*Lepidorhombus boscii* and *Lepidorhombus whiffiagonis*) on the northern Spanish shelf

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The distribution and abundance patterns of the two species of megrim, *Lepidorhombus whiffiagonis* and *L. boscii*, in ICES Divisions VIIIc and IXa, were analysed using the data provided by bottom-trawl surveys and the Spanish fishing fleet in European Atlantic waters. The consistency of year-class strengths estimated over time from these surveys was taken as an indication of the reliability of the survey data to monitor megrim population abundance. Recruitment strength was, to a large extent, the main factor governing abundance found in successive years. This is due to the fact that the greater percentage of accessible biomass comprises 1, 2 and 3-year-old individuals. Four spot megrim (*L. boscii*) is currently the most abundant species in this zone due to the weak recruitment of *L. whiffiagonis* in recent years. As a consequence of these species' sexual differences in growth, there is a predominance of females in the larger-sized individuals of the population. From 4 years onwards, males show a higher mortality rate than females.

No evidence of geographical migrations was found, although a bathymetric expansion occurs with age: juveniles are more stenobathic than adults are. A degree of specialization can be observed in the two species' habitats, probably due to their different feeding systems, with *L. whiffiagonis* occupying shallower waters. Production statistics from the Spanish fishing fleet in the north-east Atlantic show a far wider distribution of *L. boscii* than was indicated by data available previously.

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Key words: megrim, *Lepidorhombus whiffiagonis*, four spot megrim, *Lepidorhombus boscii*, distribution, abundance, mortality, Cantabrian Sea, Galicia, east Atlantic, ICES area.

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Introduction

The genus *Lepidorhombus* is represented in eastern Atlantic waters by two species: *L. boscii* and *L. whiffiagonis*. These two species replace each other within their area of distribution, each giving way to the other as the environmental conditions vary, from the Meditteranean to Iceland (Furnestin, 1935). The area covered by the present study has been considered an overlapping area for the distribution of these two species (Whitehead *et al.*, 1986), and previous research in this area appears to show a degree of interspecific segregation in their habitat (Sánchez, 1993).

In ICES Sub-areas VI, VII, VIII and IX, megrim are caught by various types of bottom-trawling gear in multispecific fisheries where, in most cases, they are the target species. In Divisions VIIIc and IXa they are caught by the Portuguese and Spanish fleets, along with hake, *Nephrops* and monkfish. In Division VIIIc, both species have a particularly important commerical value, despite representing a mere 5% of landings, while in Division IXa, only *L. boscii* shows significant landing levels (Trujillo *et al.*, 1993).

Until a few years ago, data available on the study area were largely from landings at commercial ports, but the abundance by age-class and by zone for both species had not been analysed. The recent increase in information, particularly regarding growth, provided by the series of trawl surveys in the area, enables us to study differences in distribution of these two closely-related species, and changes in distribution with age, and also to estimate mortality
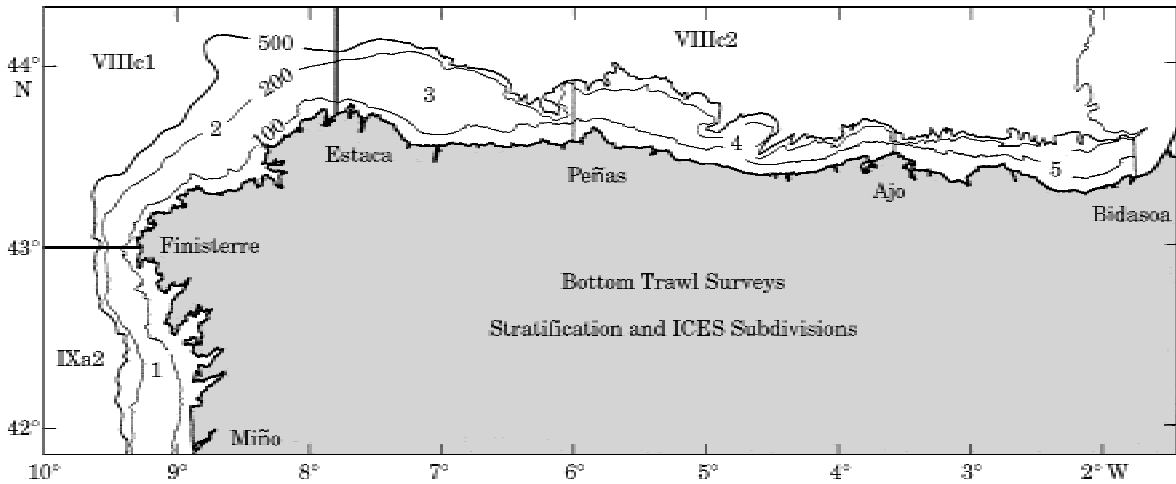
Figure 1. Stratification used in the study area.

rates, sex ratios and patterns within and between the species.

Material and methods

This study is based on bottom-trawl surveys conducted by the Instituto Español de Oceanografía (IEO) on the northern continental shelf of Spain (ICES Subdivisions IXa2, VIIIc1 and VIIIc2). The RV Cornide de Saavedra conducted surveys in autumn (September and October) from 1983 to 1994 (except 1987). The methodology used in these surveys remained unchanged throughout this historic series. Trawling operations were carried out by day, at a speed of 3 knots. Hauls lasted 30 minutes, using a *baka* 44/60-type gear (ICES, 1991; Sánchez *et al.*, 1991; Sánchez and Pereiro, 1992; Sánchez *et al.*, 1994), similar to those used by the Spanish fishing fleet in the region. The mean horizontal opening of the gear estimated with Scanmar equipment, was 22 m with a vertical opening of 1.9 m, resulting in an approximate sweep area of 60 000 m². The distance between otter-boards, depending on the trawl depth and the length of wire let out, varied from 75 to 150 m.

A stratified random sampling design was applied to the entire area, covering depths of between 30 and 500 m (with special hauls as deep as 650 m) from the mouth of the Miño River (Spanish–Portuguese border) to the mouth of the Bidasoa River (Spanish–French border). The criteria for stratification of haul distribution were determined by selecting five biogeographical sectors and 100, 200 and 500 m isobaths, resulting in fifteen strata (Fig. 1). For practical purposes, and to simplify the presentation of some of the results of this investigation, we grouped together the original geographic sectors so that they coincide with the ICES Subdivisions: Miño-Finisterre=IXa2; Finisterre-Estaca=VIIIc1 and

Estaca-Bidasoa=VIIIc2 (Cantabrian Sea). The strategy used involved sampling the stratum in proportion to the surface area, as well as considering the number of ship-days available, which meant a mean of 110 hauls per survey. As an abundance index, the stratified mean catch per 30-min trawl was used, following the same methodology described by Cochran (1971) and Grosslein and Laurec (1982). The stratified mean and variance are, respectively,

$$\bar{Y}_{st} = \frac{1}{A} \Sigma A_h \bar{y}_h$$

and

$$S_{\bar{Y}_{st}}^2 = \frac{1}{A^2} \Sigma \frac{A_h^2 S_h^2}{n_h},$$

where,

A=total surface area
A_h=surface of stratum h
$\bar{y}_h$=mean catch per haul in stratum h
n_h=number of hauls in stratum h
S_h^2=variance in stratum h

For each haul, we obtained catches in weight and in number of all individuals, and length distributions by sex (males, females and indeterminates). Also, in each ICES Subdivisions a fixed number of otoliths was extracted per length-class to determine age, and age-length keys were made for each survey from 1990. Age conversions for the 1983–1989 period were made using a mean age-length key for 1990–1993. Therefore, more importance is given in this study to the results by age-class corresponding to the period subsequent to 1989. Owing to the differential growth between males and females (Landa *et al.*, 1996), independent keys were applied for each sex.

To estimate the association between depth and abundance for each age and for the entire population, we constructed the cumulative empirical frequencies for depth (x_i) and for abundance (y_i) with respect to depth, respectively as follows:

$$f(x_i,t) = \sum_{i=1}^{n} I(x_i)/n,$$

and

$$g(y_i,t) = \sum_{i=1}^{n} y_i I(x_i) / \left(\sum_{i=1}^{n} y_i \right),$$

where,

$$I(x_i) = \begin{cases} 1, \text{ if } x_i \leq t, \\ 0, \text{ otherwise.} \end{cases}$$

The total number of tows independent of strata membership is $n(=\Sigma_h n_h)$ and t ranges from the minimum to the maximum depth. The curves $f(x_i,t)$ and $g(y_i,t)$ were compared using the Kolmogorov-Smirnov test. First we compared depth frequency distributions for each age with the frequency distribution for bottom depth. We used the same test to compare the abundance distributions of two consecutive ages. To compare the abundance distributions of a group of ages (more than two), we used the Kruskal-Wallis test. For these analyses, we used the number of individuals per age-class, caught by haul.

In the bathymetric distribution analysis, new depth ranges were defined based on constant intervals of 50 m. Mean catches per 30-min haul were obtained for each depth range, with the corresponding standard deviation. In order to compare graphically the bathymetric distributions by ages, these means were standardized by depth ranges, subtracting the total mean, and dividing by the standard deviation. This deviation from the mean, measured in standard deviation units, is called standardized residual (Sokal and Rohlf, 1969) and has a mean of 0 and a standard deviation (s.d.) of 1.

$$\text{Standardized residual of mean} = \frac{\bar{y}_h - \bar{Y}}{SD_{\bar{Y}}}.$$

The CPUE of the fleet was calculated using data obtained from shipboard observers working on the "Discards of the Spanish Fleet in ICES Divisions" project (Pérez *et al.*, 1995), financed by the European Communities Commission.

Results

Both species attained their highest values of the biomass indices in the series during 1988 (Fig. 2). From 1989 onwards, the biomass of *L. boscii* remained relatively constant, with high levels relative to its values at the beginning of the series: nearly 2 kg/haul. Biomass values for *L. whiffiagonis* were high from 1988 to 1990, but since then have fallen to levels similar to those of the first years of the series.

Regarding estimates of *L. boscii* biomass per zones, we observed no marked differences among the ICES Subdivisions (Fig. 2). The annual variations found in each zone were basically similar to those observed throughout the area as a whole. The biomass indices indicate that *L. whiffiagonis* (Fig. 2) is found mainly in Subdivision VIIIc2 (Cantabrian Sea), being very scarce to the south of Cape Finisterre (Subdivision IXa2). Likewise, the annual variations found in each zone are nearly the same as those found throughout the area as a whole.

Figures 3 and 4 show the abundance indices by length-class and sex of the two species during the final years of the series, along with the sex ratio. Population size structure varies with the differences in the strength of recruitment (length ranges between 6 and 8 cm, in the case of *L. boscii*, and between 8 and 10 cm for *L. whiffiagonis*). We also found that from 20–25 cm onwards, the percentage of females gradually increases, so that nearly all of the *L. boscii* individuals measuring more than 30 cm, and *L. whiffiagonis* specimens longer than 35 cm, were females.

The numerical abundance indices by age-class are given in Table 1, showing the cohorts with a sufficient number of ages that are remarkable for having extreme values over the last 5 years. The 0-age-class of these species was not totally recruited to the gear during season when the surveys were carried out. This was due to their small size and the morphology particular to the individuals. Therefore, we did not analyse recruitment strength considering the 0-age-class alone, but rather took into account the abundance indices of age-class 1 (Fig. 5). In the case of *L. boscii*, the 1991 year-class is notable, with estimated recruitment for 1990 and 1993 being the lowest in recent years. *L. whiffiagonis* recruitment shows variations in the indices for the first period of the historic series (Table 1). Except for 1991, these statistics show a downward trend from 1987 onward, with estimated recruitment for 1990, 1992 and 1993 being the lowest for the entire series. We may say that, in general terms, recruitment trends are similar for both species (Fig. 5). Figure 6 presents the abundance indices by age-class and the sex ratio since 1991, showing how strong the 1991 annual class was for both species, and the weak 1993 cohort. The largest population contingent in the area that is accessible to trawling comprises 1, 2 and 3-year-old individuals, which make up approximately 80% of the biomass.

Sex ratios vary with the age of the individuals. In the case of *L. boscii*, it is similar up to 4 years, and from then on, there is a higher proportion of females. As regards
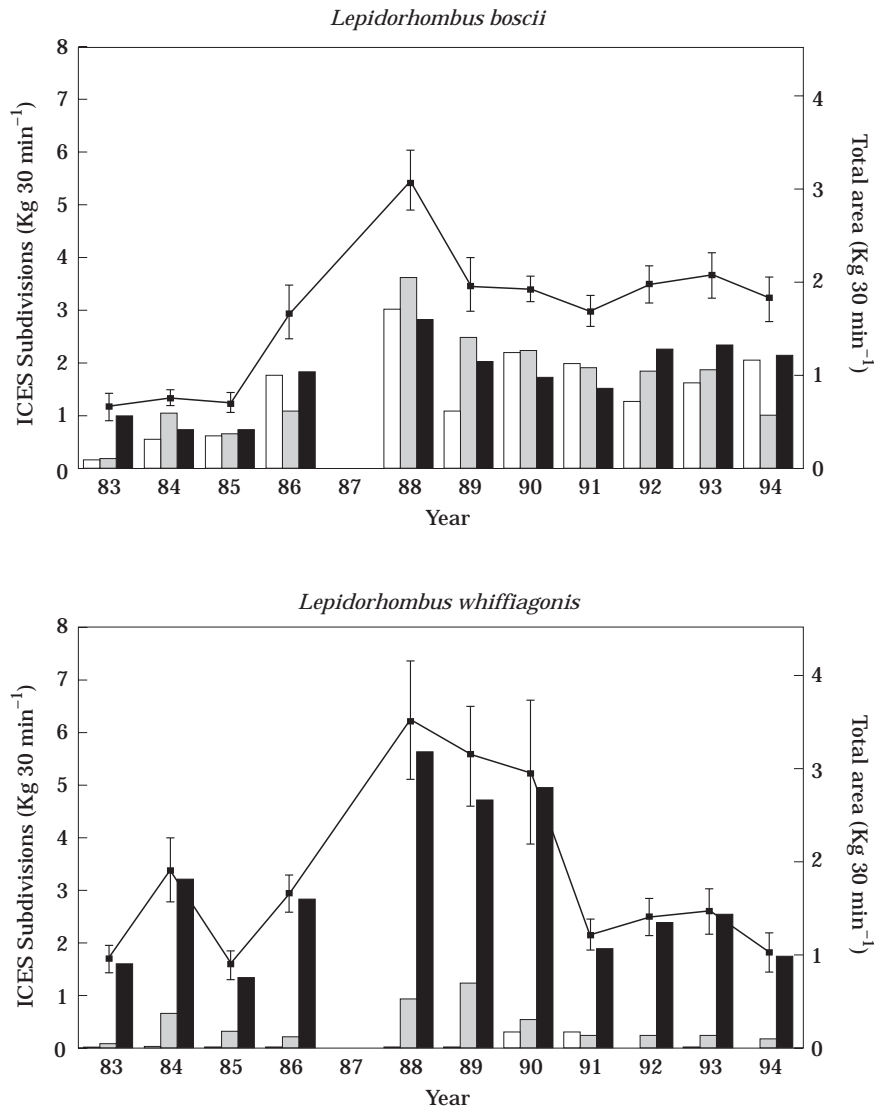
Figure 2. Historic series of biomass indices (kg 30-min^{-1} trawl) and standard error (s.e.) in Subdivisions IXa2 (□); VIIIc1 (▨); and VIIIc2 (■) and for the total area surveyed (— ■ —).

L. whiffiagonis, the results are more variable, although in general, after 4 years, the ratio of males decreases considerably. To analyse the possibility of differential mortality rates by sex based on this age, we used the catch curves obtained from the mean abundance indices for each age-class for 1991 and 1994 (Fig. 7). Following the hypothesis that, at this age, catchability is independent of recruitment strength, and considering the good coverage of these surveys and the type of bottoms frequented by these species, they are unlikely to become inaccessible to this fishing gear, and the results showed a higher mortality in males. The differences are more marked in *L. boscii*, with an estimated Z value for males 0.8 times greater than for females.

In order to estimate whether the distribution patterns of an annual class remain stable throughout the first years of life, with no migrations able to affect their catchability, we examined the situation in the study area of the 1991 and 1992 cohorts for each of these species (Figs 8–11). 0-age-class *L. boscii* appear throughout the study area and beyond the 200 m iso-bath. 0-age-class *L. whiffiagonis* appear mainly in the Cantabrian Sea, near the 200 m isobath. The distribution areas in the first 3 years of a cohort are similar, overlapping being observed in the areas with higher concentrations, with the older individuals occupying the same areas where they were recruited, although with a wider range of depths.
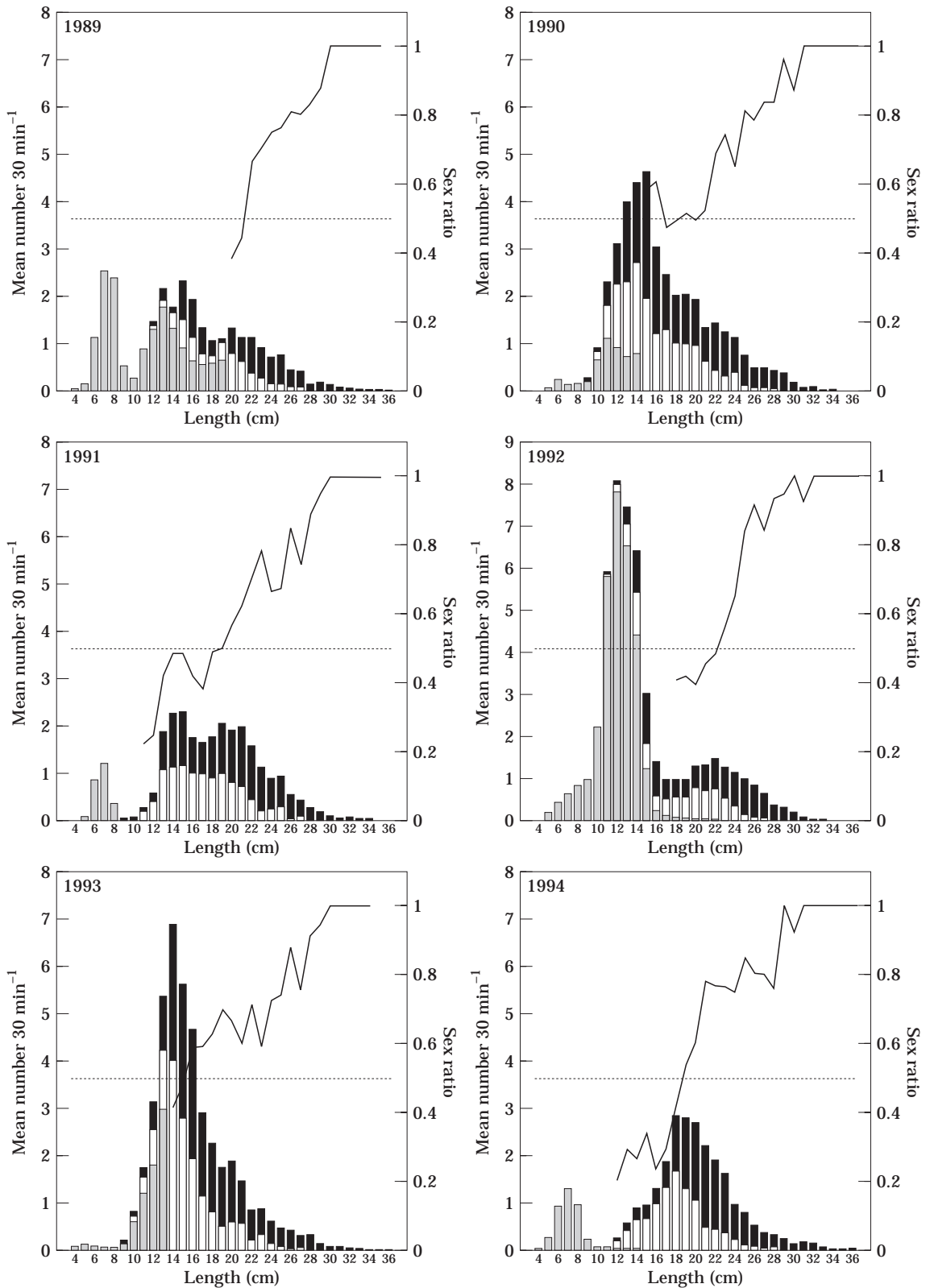
Figure 3. Length distributions (number 30-min^{-1} trawl) and sex ratios for *L. boscii* (1989–1994). Males (□); females (■); indeterminates (▨).
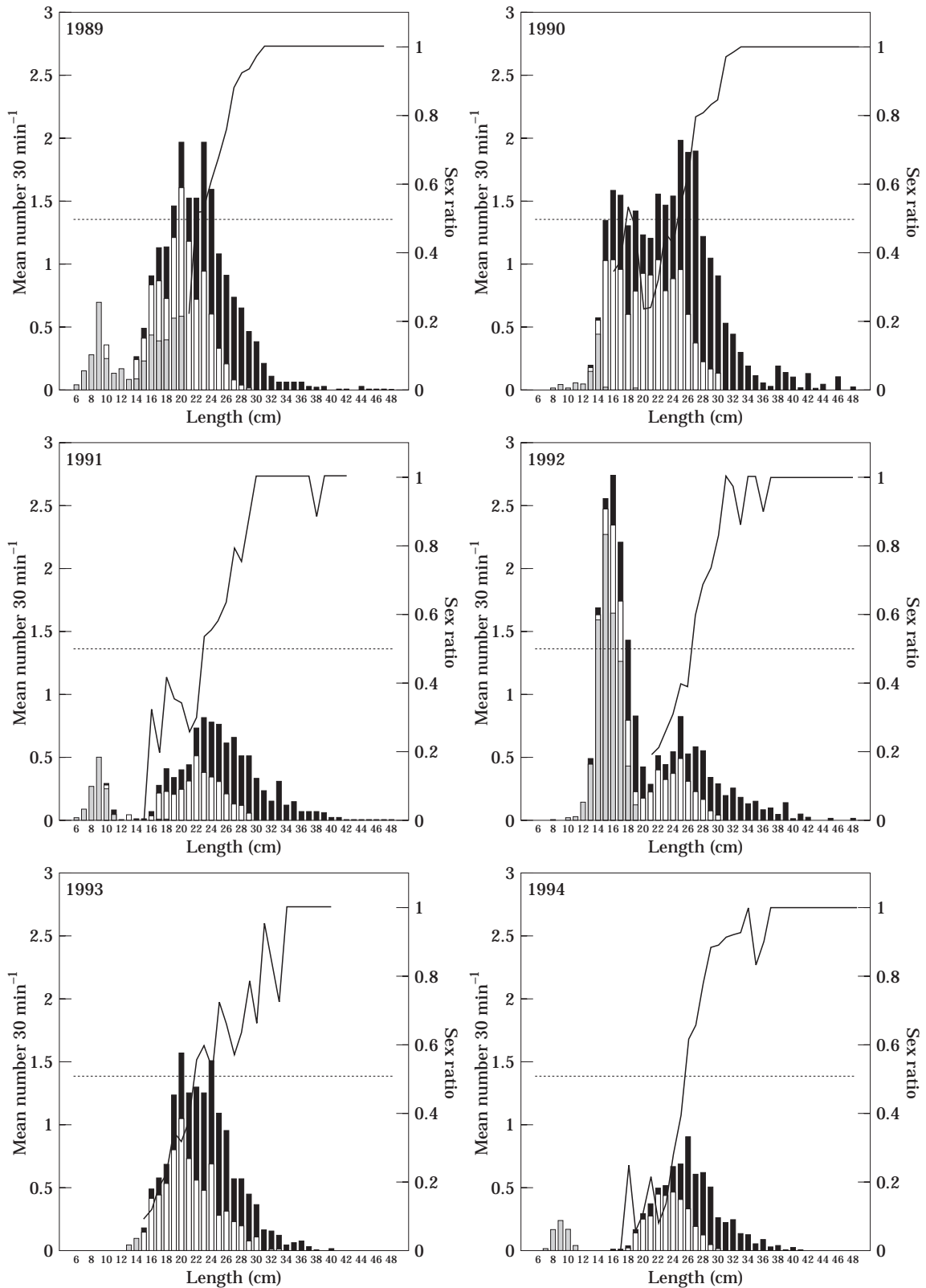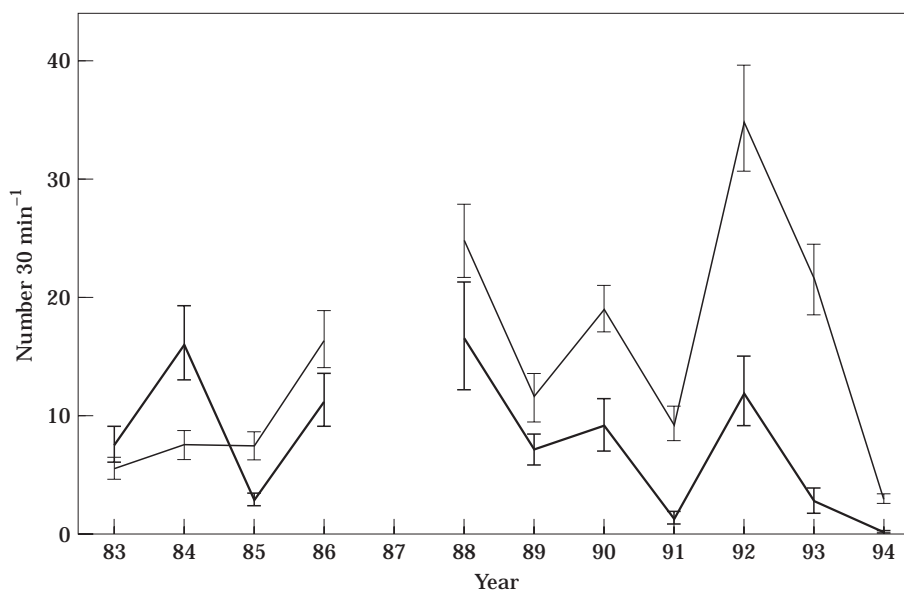
Figure 4. Length distributions (number 30-min^{-1} trawl) and sex ratios for *L. whiffiagonis* (1989–1994). Males (□); females (■); indeterminates (▣).

Table 1. Abundance indices (number × surface 30-min^{-1} trawl) by age-class for the total area (1983–1994).

	Lepidorhombus boscii											
Age	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
0	240	440	37	730		652	2082	**112**	<u>619</u>	604	74	888
1	1414	1922	1825	4009		5491	4086	4677	**2266**	<u>8925</u>	5301	749
2	705	952	859	1686		5177	2049	3183	2280	**1037**	<u>4150</u>	2848
3	342	370	369	790		1761	893	546	896	1057	**563**	<u>1606</u>
4	209	211	197	454		876	513	696	396	537	384	**371**
5	116	113	91	223		383	258	386	254	250	131	184
6	42	41	33	67		117	81	181	51	100	88	115
7+	26	20	28	26		51	23	88	21	11	43	94

	Lepidorhombus whiffiagonis											
Age	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
0	460	79	24	3377		135	710	**26**	<u>310</u>	2	0	154
1	1891	3939	672	2743		4445	3420	2184	**337**	<u>3067</u>	685	12
2	495	1223	570	837		2600	2744	1824	792	**273**	<u>2181</u>	166
3	264	589	312	422		1305	1316	718	356	400	**164**	<u>1082</u>
4	302	644	373	492		1381	1382	854	451	570	419	**332**
5	119	220	124	179		456	360	297	214	290	210	180
6	39	86	61	67		173	118	322	57	53	42	69
7+	30	91	32	49		132	104	364	7	39	2	9

Figure 5. Recruitment (age 1) indices (number 30-min^{-1} trawl) and standard error (s.e.) for the two species *L. boscii* (——); *L. whiffiagonis* (——).

According to the abundance indices obtained to analyse bathymetric distribution (Fig. 12), *L. boscii* has a preferential depth range of between 100 and 450 m (mode in 250 m), and *L. whiffiagonis* of between 50 and 300 m (mode in 200 m). During the first years of the decade studied (1983 and 1984), the predominant species, at depths from 50 to 225 m, was *L. whiffiagonis*, and from 250 m and below, it was clearly *L. boscii*, there being a certain bathymetric segregation between the two species, probably to minimize interspecific competition. In the final years of the study (1992 and 1993), the predominance of
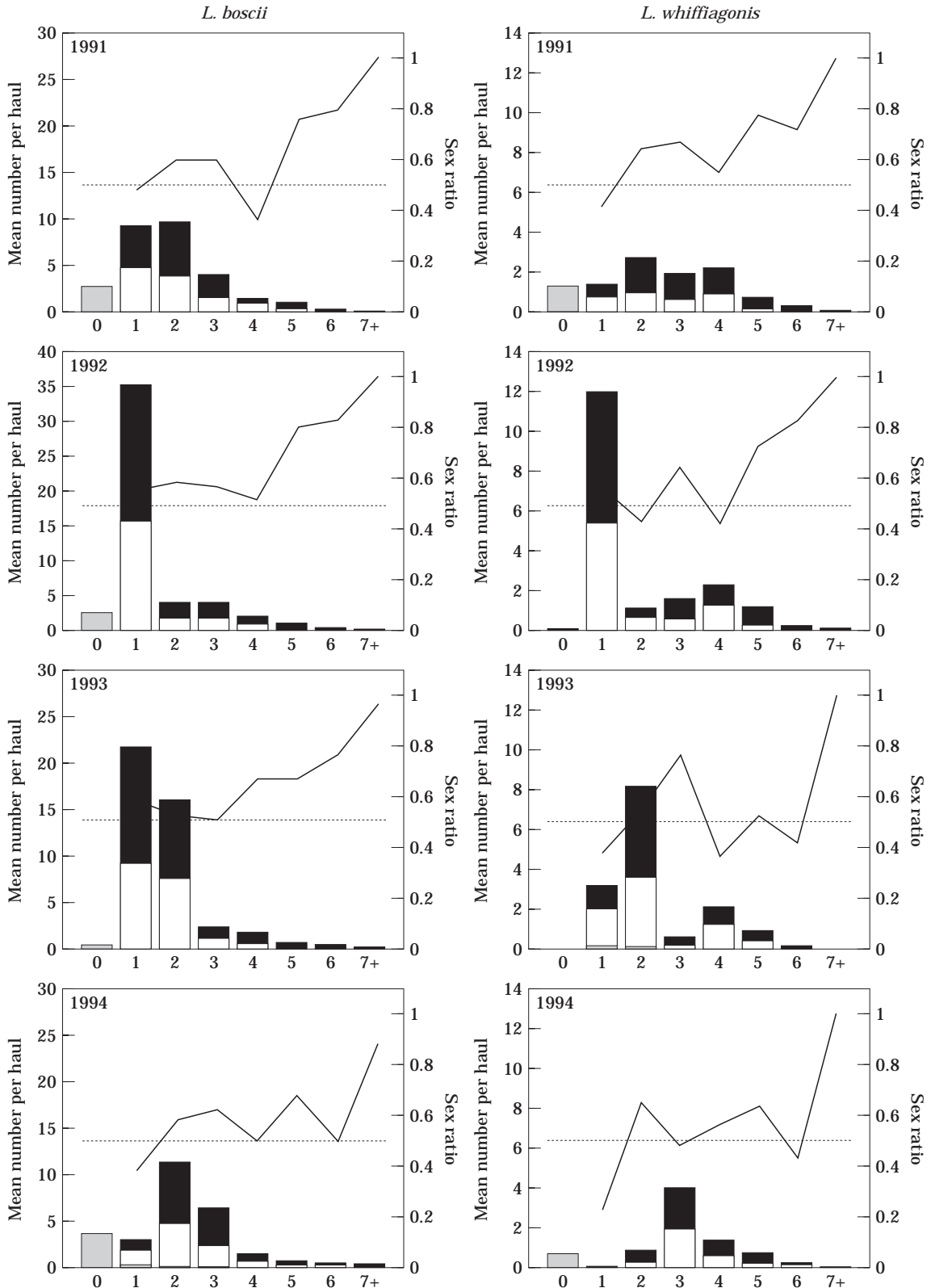
Figure 6. Abundance indices (number 30-min^{-1} trawl) by age class and sex of the two species (1991–1994). Males (□); females (■); indeterminates (▨).
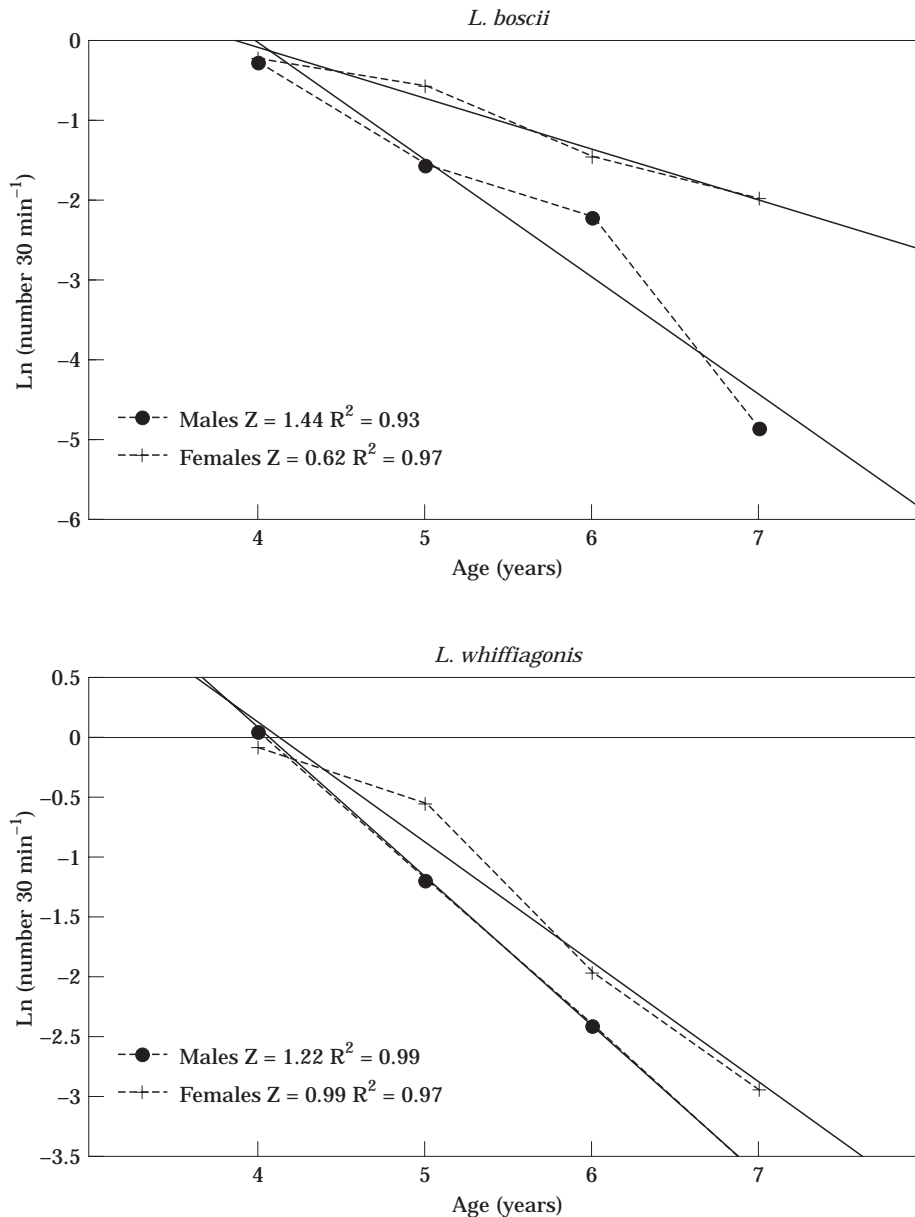
Figure 7. Catch curves (ln number 30-min^{-1} trawl) by sex of the two species, 1991–1994.

L. boscii on all types of bottoms was marked. Nevertheless, both species maintained their distribution modes at the same depths in both periods (200 m for *L. whiffiagonis*, and 250 m for *L. boscii*), the only change being in their relative abundance.

Both species appear to show a gradual expansion in their bathymetric distribution throughout their lifetimes, with the larger individuals tending to occupy shallower waters than the juveniles do; this was more patent in *L. boscii*. The Kolmogorov-Smirnov test shows that the abundance distribution of *L. boscii* is not associated

with depth, except for older specimens (Table 2). Juveniles appear more stenobathic than the rest of the population, almost exclusively inhabiting depths of between 200 and 300 m (Fig. 13). With age, they gradually widen their bathymetric distribution to between 100 and 350 m at 5 years. If we compare the distributions of all ages globally (Table 3), we see that there are significant differences among them. This indicates that the species does not maintain the same bathymetric distribution throughout its lifetime. A comparison between the abundance distribution of two consecutive ages
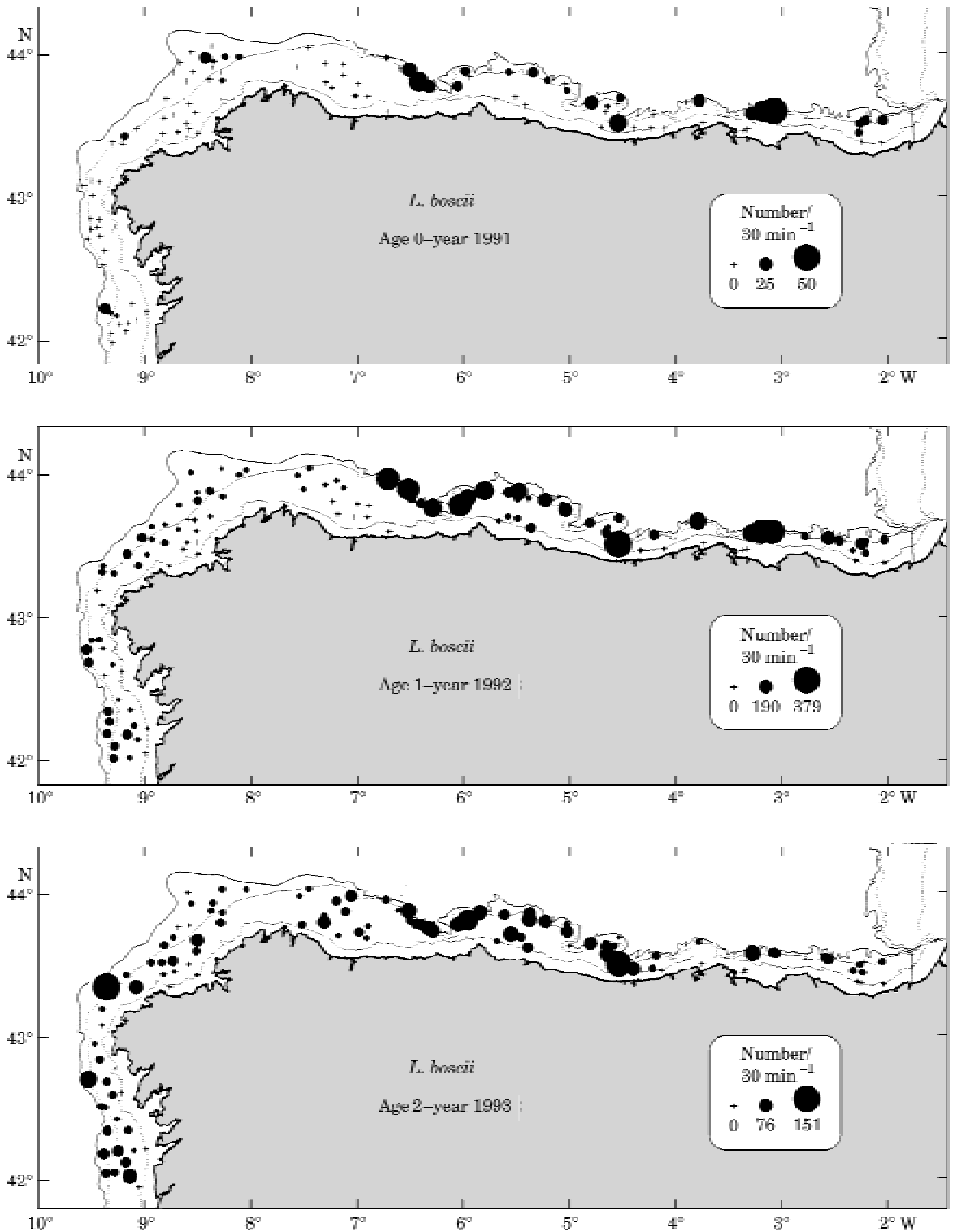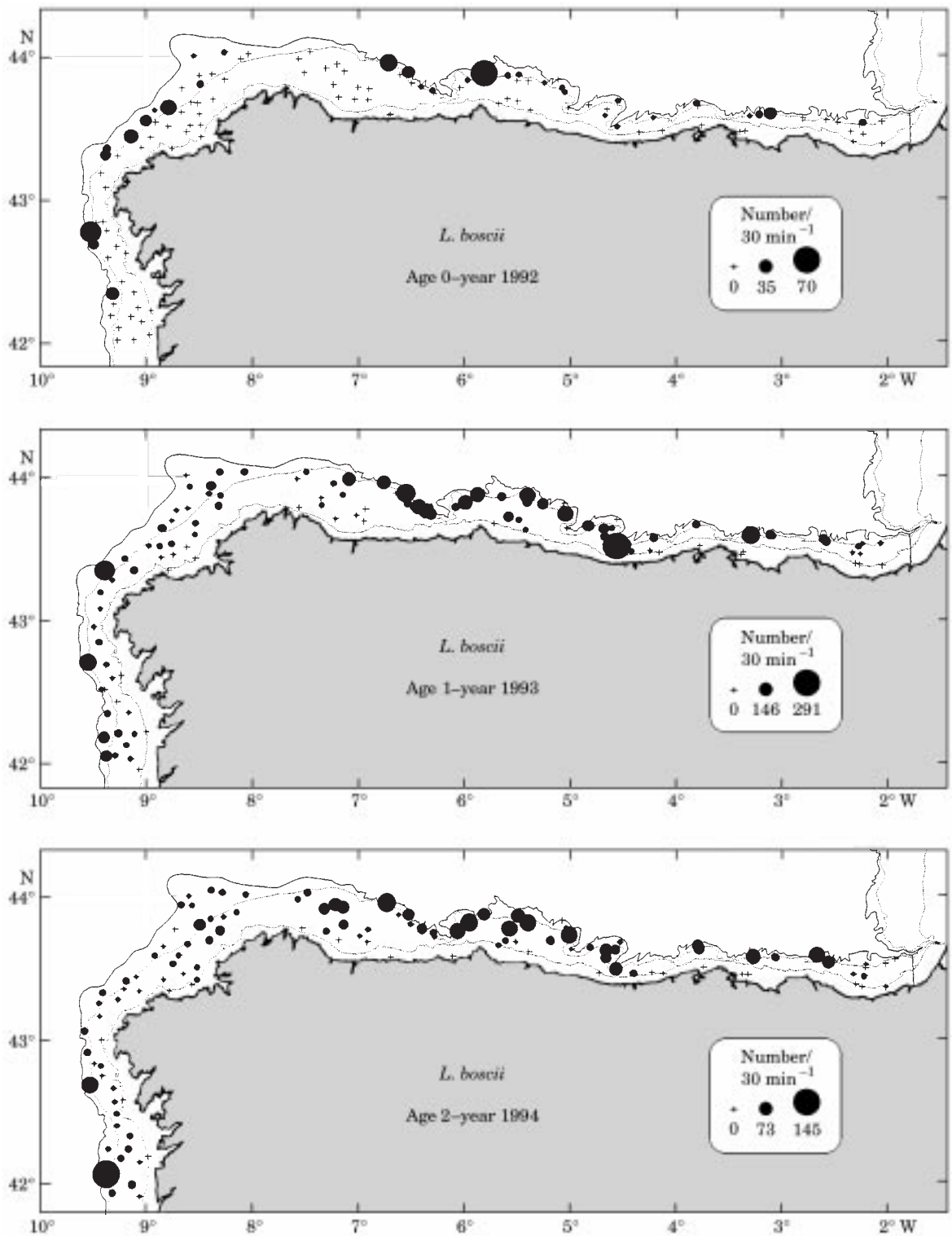
Figure 8. Geographic distribution of the 1991 cohort of *L. boscii.*

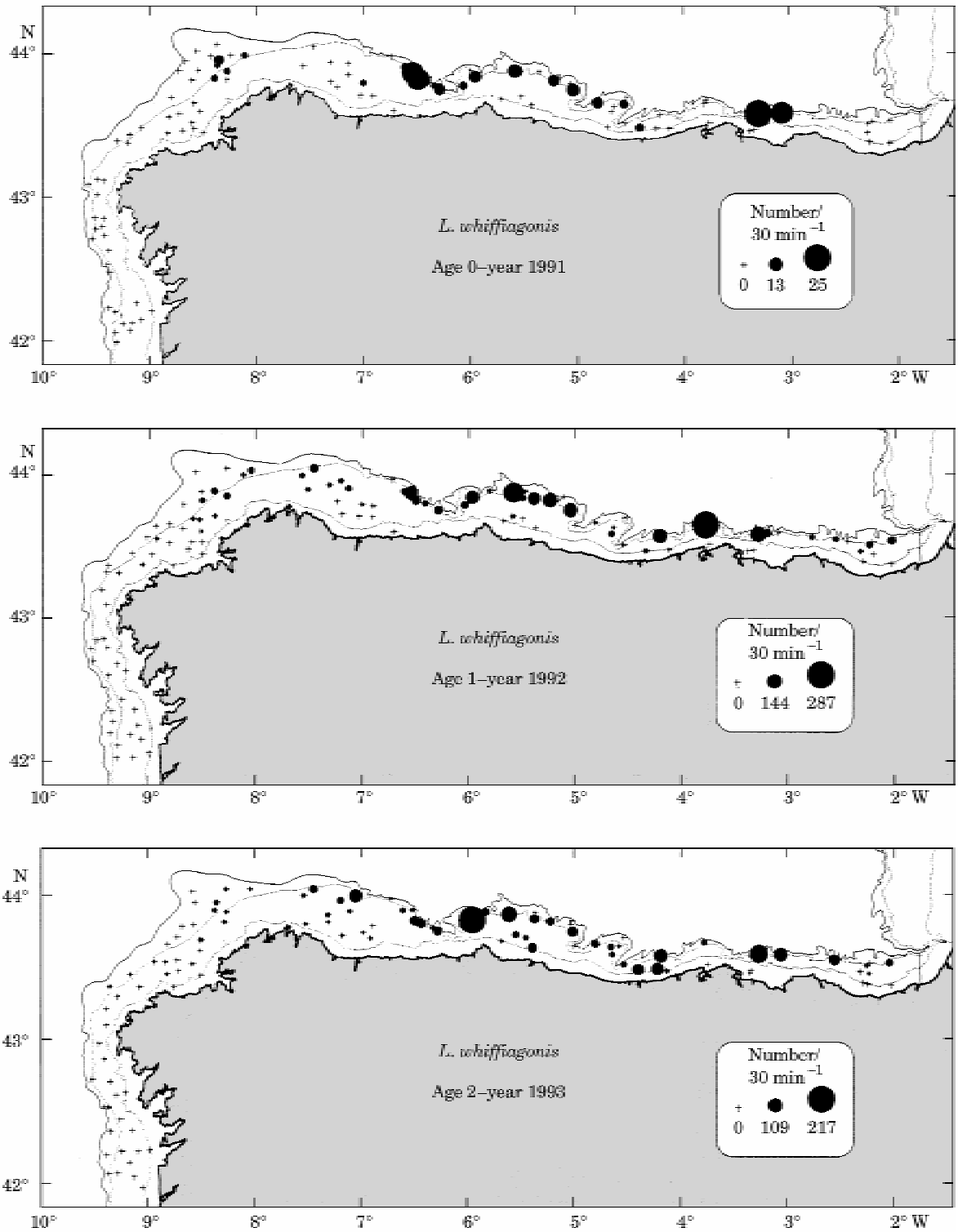Figure 9. Geographic distribution of the 1992 cohort of *L. boscii.*

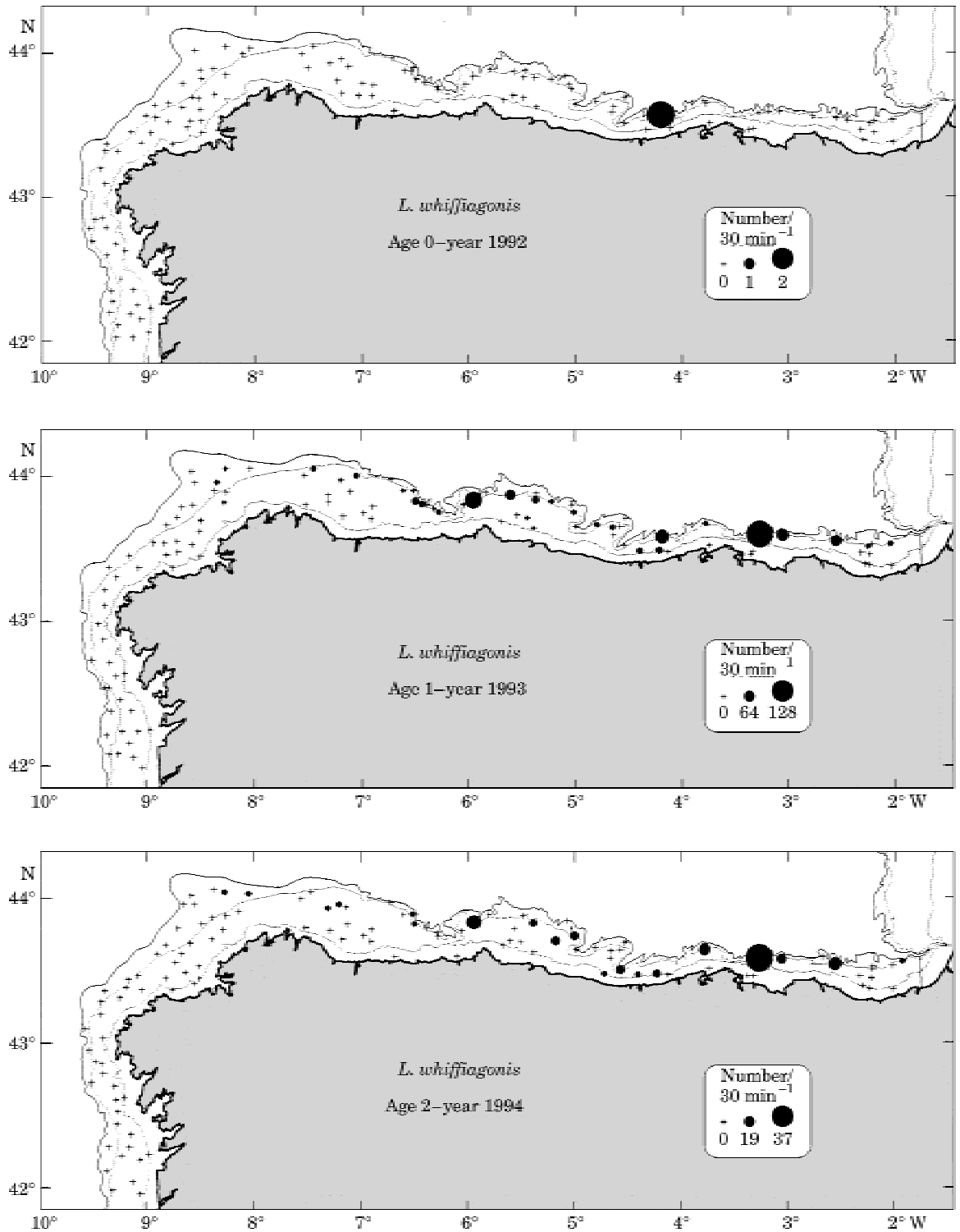Figure 10. Geographic distribution of the 1991 cohort of *L. whiffiagonis*.

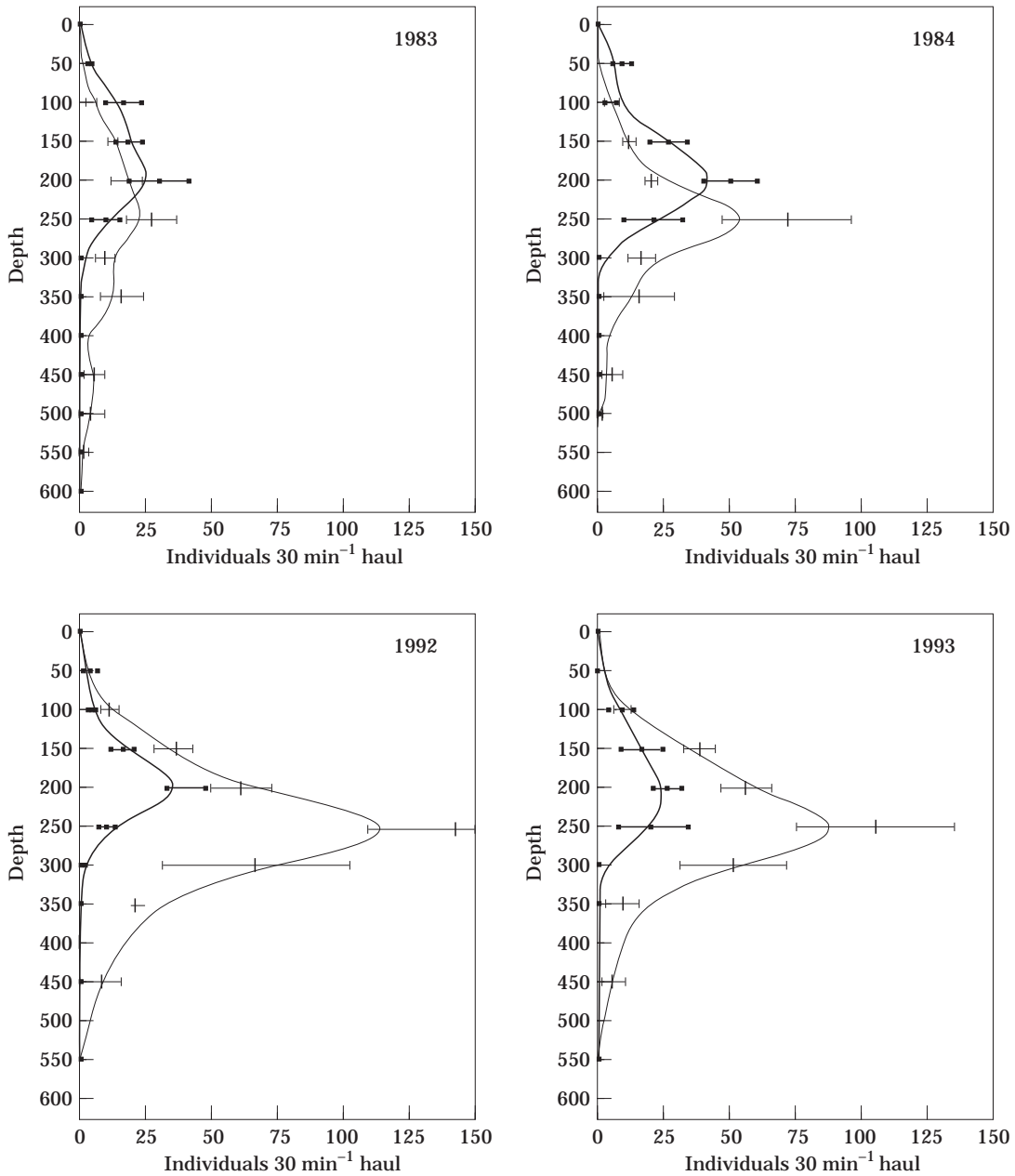Figure 11. Geographic distribution of the 1992 cohort of *L. whiffiagonis.*

Figure 12. Bathymetric distribution and standard deviation of the two species in 1983, 1984, 1992 and 1993. *L. boscii* (———); *L. whiffiagonis* (——).

shows significant differences in bathymetric habitat between the ages of 0 and 3. However, from 3 years on, significant differences are not observable in their distribution, indicating that a significant expansion in its bathymetric habitat occurs up to this age.

L. whiffiagonis mainly inhabits depths of between 150 and 250 m up to 2 years, widening its distribution from that age onwards, mainly to shallower depths. As in the case of *L. boscii*, the Kolmogorov-Smirnov

test shows that the abundance distribution of *L. whiffiagonis* is not associated with depth, except for older specimens (Table 2). While the first age-classes are distributed throughout a smaller range of depths, as the individuals grow, they expand into other bottoms (Fig. 13). A slight tendency to inhabit shallower waters as they grow larger can also be observed. A comparison between the abundance distribution of two consecutive age-classes shows that only ages 1

Table 2. Results of Kolmogorov-Smirnov tests comparing depth frequency distributions of each age with frequency distributions of bottom depth. (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$, (ns) no significant difference.

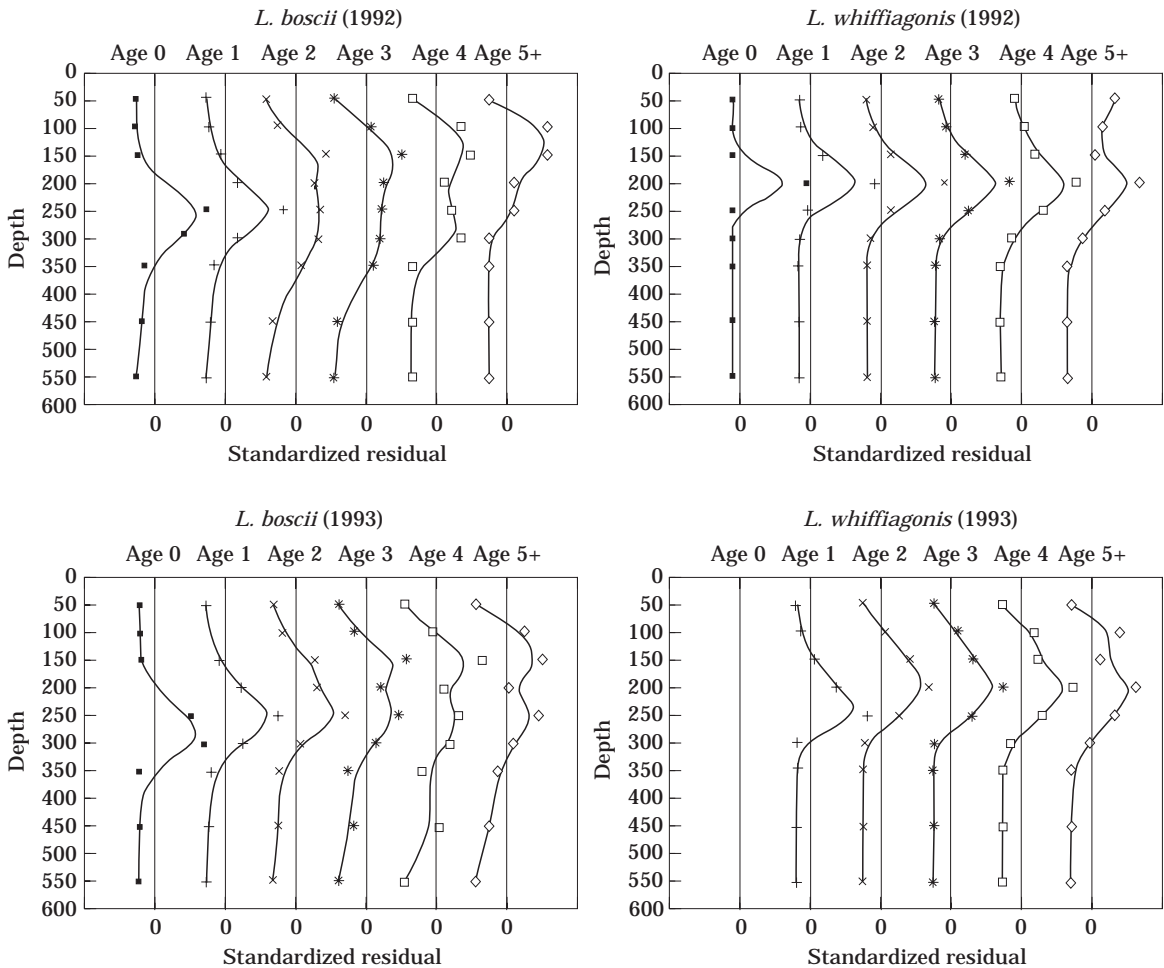|	*L. boscii*				*L. whiffiagonis*		
Variables	Test	1992	1993	Variables	Test	1992	1993
Depth-age 0	K-S	***	***				
Depth-age 1	K-S	***	***	Depth-age 1	K-S	***	***
Depth-age 2	K-S	***	**	Depth-age 2	K-S	**	***
Depth-age 3	K-S	**	ns	Depth-age 3	K-S	*	ns
Depth-age 4	K-S	*	ns	Depth-age 4	K-S	ns	*
Depth-age 5+	K-S	ns	ns	Depth-age 5+	K-S	ns	ns
Depth-all ages	K-S	***	***	Depth-all ages	K-S	***	***

Figure 13. Bathymetric distribution of the two species by age-class in 1992 and 1993 (x-axis: standardized residual of the mean by depth ranges). The mean of 0 has been included in the graphs (vertical line perpendicular to the x-axis) for each age-class to show values above and below the mean. These lines are displayed on the graph in constant intervals for the sake of better visualization.

and 2 have significant differences in their bathymetric habitat (Table 3). Therefore, it appears that the most important bathymetric displacement in this species' lifetime occurs at these ages. A global comparison between the distribution of 2-year-old specimens and older individuals does not show significant

Table 3. Results of Kolmogorov-Smirnov and Kruskal-Wallis tests comparing depth frequency distributions between ages, for both species. (***) $p \leq 0.001$, (**) $p \leq 0.01$, (*) $p \leq 0.05$, (ns) no significant difference.

	L. boscii				*L. whiffiagonis*		
Variables	Test	1992	1993	Variables	Test	1992	1993
Age 0–age 1	K-S	***	***				
Age 1–age 2	K-S	***	***	Age 1–age 2	K-S	***	***
Age 2–age 3	K-S	*	***	Age 2–age 3	K-S	ns	ns
Age 3–age 4	K-S	ns	ns	Age 3–age 4	K-S	ns	ns
Age 4–age 5+	K-S	ns	ns	Age 4–age 5+	K-S	ns	ns
All ages	K-W	***	***	All ages	K-W	ns	***
Age 0 to age 3	K-W	***	***				
Age 3 to age 5+	K-W	ns	ns	Age 2 to age 5+	K-W	ns	ns

differences between them for any of the 2 years analysed, indicating that from this age on, their bathymetric distribution does not vary significantly.

Finally, the yields obtained from the Spanish trawler fleet (Pérez *et al.*, 1995) fishing in the north-east Atlantic (Figs 14 and 15) indicate a wide distribution for these two species, which are caught up to parallel 59°N. A greater presence of *L. whiffiagonis* was observed in ICES Sub-area VII, and yields of *L. boscii* in the north zone were higher, despite its being considered a more southern species.

Discussion

Data from bottom-trawl surveys conducted off the coasts of various countries on the Atlantic continental shelf would seem to indicate that the two species of megrim have different distributions, *L. boscii* occupying more southerly waters, *L. whiffiagonis* inhabiting the northern zone. The cohabitation zone for both species, with similar abundance values, would seem to be the Cantabrian Sea (Sánchez, 1995; Sánchez *et al.*, 1995). By the same token, surveys in the French region of the Bay of Biscay (Quero *et al.*, 1989; Poulard, 1989) and in Sub-area VII (Boon, 1984; ICES, 1994), show very low yields of *L. boscii*, leading to the conclusion that this species is very scarce in these waters. Nevertheless, yields from the Spanish trawler fleet (Pérez *et al.*, 1995) fishing in ICES Sub-areas VI to XI are high, in the case of *L. boscii*, as far north as 58°N. This shows that on certain bottoms, the abundance of this species maintains the same level as *L. whiffiagonis*, despite the latitude, with a wider distribution than that estimated by the surveys in the ICES area. This may indicate either that the gear used in these surveys was not well suited to this species or that the sampling depths were limited and failed to cover their entire distribution area.

The fishing gear used in Spanish surveys presents certain advantages as a sampler of benthic species as opposed to GOV 36/47, considered a standard in the surveys within the ICES area (ICES, 1996). This is due to the design of the ground-rope and the sweeps which work half-buried in the substratum and are more efficient at trapping benthic species. It has been estimated that the *baka* fishing gear is 3.3 times better at catching the two species of megrim than GOV (Sánchez *et al.*, 1994). Therefore, the distribution of these species in the ICES area has been overestimated, as far as their relative abundance in Divisions VIIIc and IXa is concerned, with regard to the rest of the Atlantic continental shelf (ICES, 1994). This is due to the fact that the abundance indices obtained by the two gears are included without modifications, although their efficiency in megrim fishing is very different.

The separation between Divisions VIIIc and IXa (Cape Finisterre) seems to be important as a southern distribution limit for *L. whiffiagonis*. This is corroborated by the low abundance indices estimated in the research surveys conducted in waters on the Portuguese continental shelf (Fernández *et al.*, 1981) and in the Gulf of Cádiz (Sobrino, 1992; Sobrino *et al.*, 1993), with the same vessel and fishing gear used for the present study. However, *L. whiffiagonis* has been recorded as far south as the Mediterranean, and yields from the Portuguese trawler surveys were very low (Cardador, 1983; Silva and Azevedo, 1994). Conversely, north of the Cantabrian Sea, the abundance of *L. whiffiagonis* gradually increases, reaching a maximum in the Celtic Sea (Poulard *et al.*, 1993; ICES, 1994), coinciding with data from the Spanish fishing fleet in this area.

Bearing in mind that the two species have similar characteristics, a certain degree of interspecific competition may be assumed. Segregation has been reported in the Cantabrian Sea (Sánchez, 1993, 1995), on the basis of the bathymetric distribution of these species, with the most abundant of the two (*L. whiffiagonis*) occupying shallower (more productive) waters. The inverse phenomenon, with *L. boscii* occupying shallower waters in
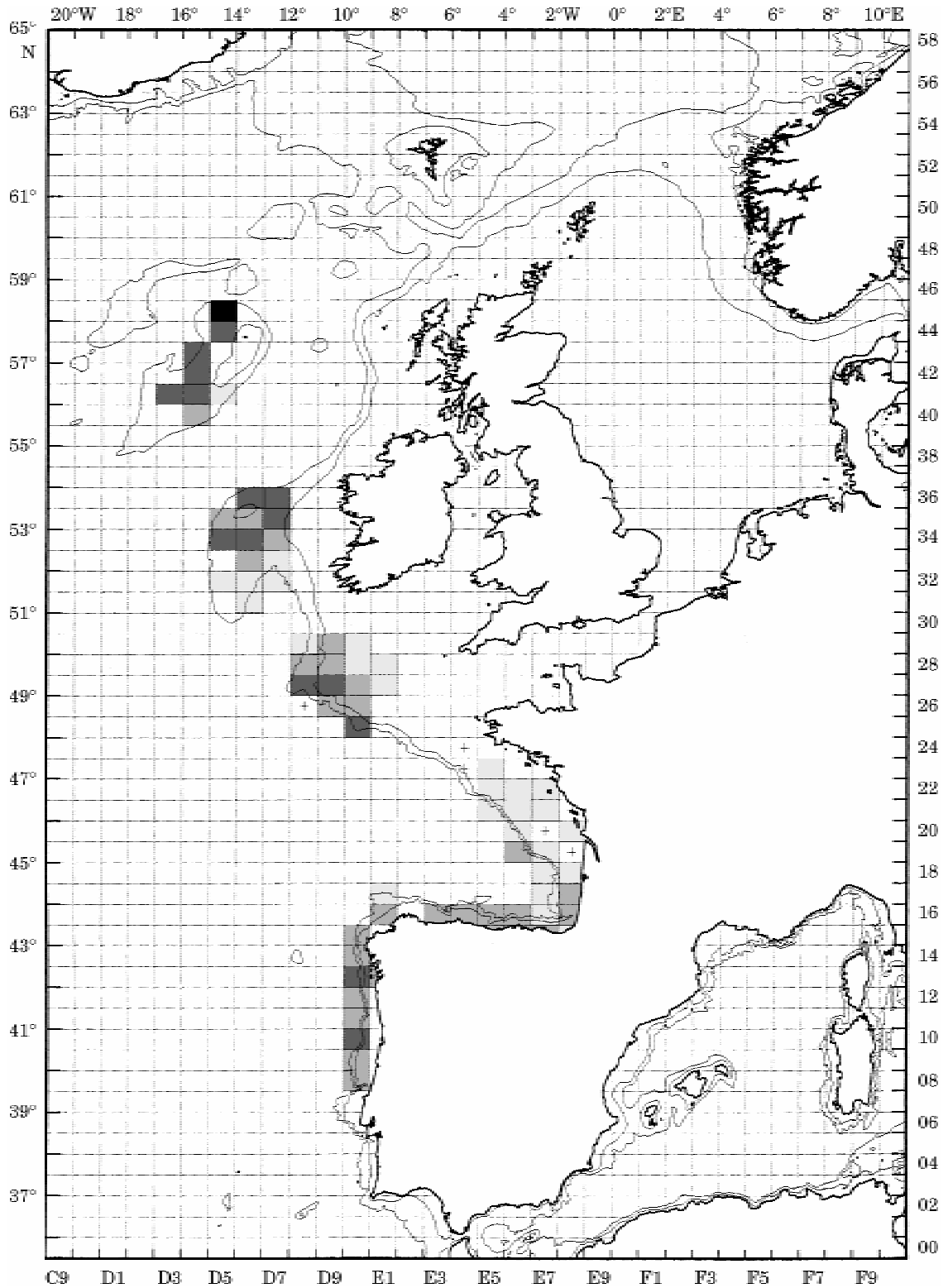
Figure 14. CPUE (kg hour $^{-1}$) of the Spanish fleet in the *L. boscii* ICES area (based on Pérez *et al.*, 1995). 0.0–1.0 (▯); 1.0–5.0 (▨); 5.0–25.0 (▦); 25.0–75.0 (■).
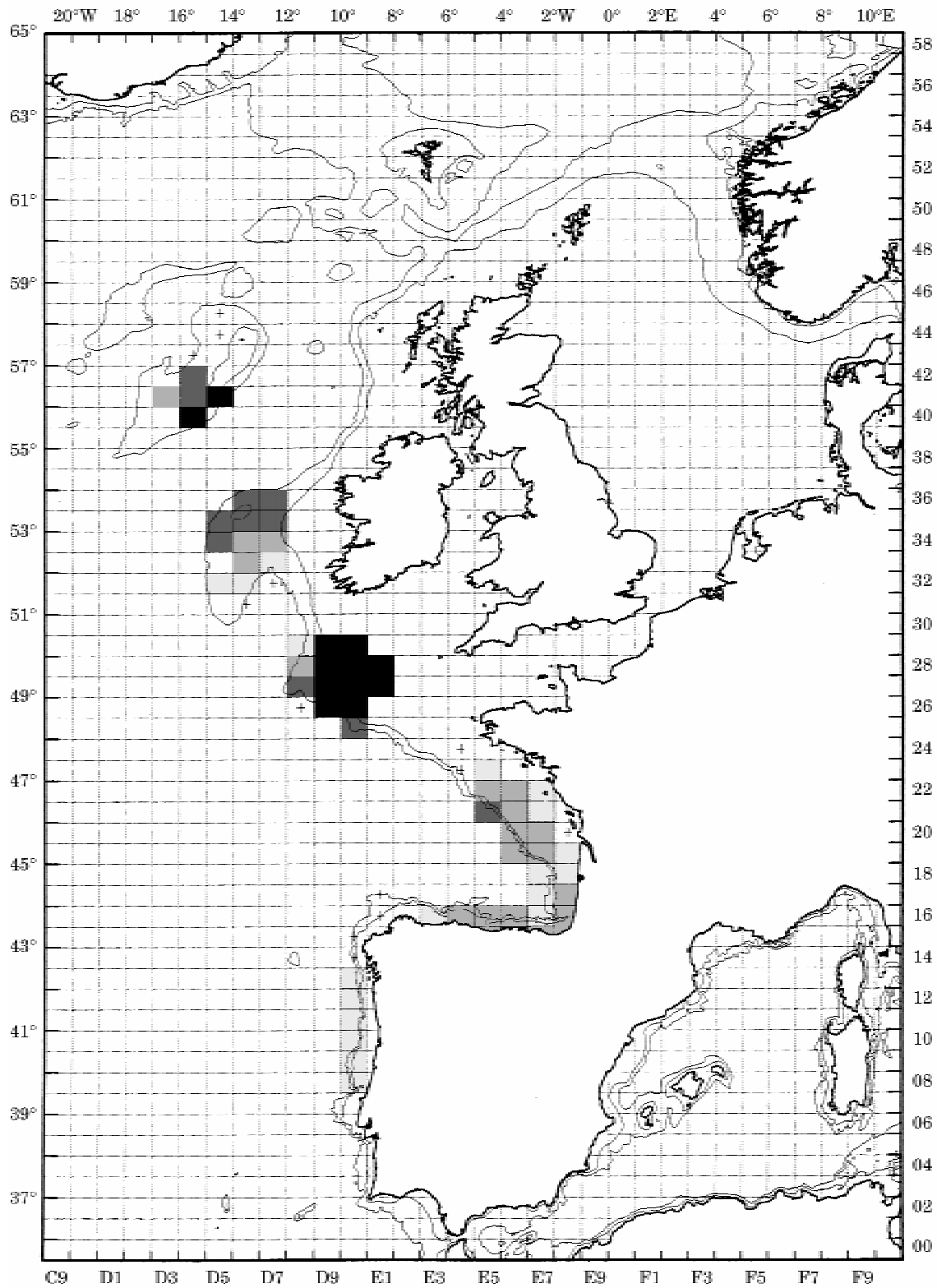
Figure 15. CPUE (kg hour $^{-1}$) of the Spanish fleet in the *L. whiffiagonis* ICES area (based on Pérez *et al.*, 1995). 0.0–1.0 (□); 1.0–5.0 (□); 5.0–25.0 (▦); 25.0–75.0 (■).

the Mediterranean, where it is the predominant species (Dwivedi, 1964), may be due to a difference in diet: *L. boscii* mainly feeds on crustaceans inhabiting muddy bottoms (Rodríguez-Marín and Olaso, 1993), as opposed to the other species of the genus, which is more ichthyophagous. Such bottoms appear in the Cantabrian Sea at a greater depth than in the Mediterranean, since the internal Cantabrian continental shelf has a rocky structure (Rey and Medialdea, 1989). However, more recent data, showing a greater presence of *L. boscii*, seem to indicate that this species is predominant on all the soft bottoms of the continental shelf (Sánchez, 1994; Sánchez *et al.*, 1995). Segregation of and competition between species may be the result of several niche aspects (depth distribution, diet, etc.). In the Mediterranean demersal fish community, Macpherson (1981) observed that the diet dimension is the most important factor contributing to the segregation of fish species, and also to the avoidance of possible competition. We have already noted that a possible cause of the decrease in *L. whiffiagonis*, which was the species with the highest abundance between 1983 and 1990, is its low recruitment strength in recent years. This gradual increase in abundance of *L. boscii* has modified the two species' distribution pattern in the zone. If we consider the first 2 and the last 2 years of the study period, we may see how the abundance and bathymetric distribution of *L. whiffiagonis* indicate that it is the predominant species at depths of less than 200 m during the first years. The progressively greater presence of *L. boscii*, which behaves as a eurybathic species, means that it currently dominates the entire distribution area, excepting shallower waters (less than 100 m), where we find older specimens of *L. whiffiagonis*, usually near hard bottoms.

No independent trends have been observed regarding abundance in the three ICES subdivisions considered in this study. This may indicate a degree of uniformity in the zone for these species. An efficient follow-up of the cohorts, based on indices from the surveys, indicates that they are extremely reliable. Weight yields evolve in a similar manner for both species, with abundance after years of good recruitment, and a drop in the indices after years of poor recruitment. This is due to the fact that the higher percentage of accessible biomass includes 1, 2 and 3-year-old individuals. Therefore, the high abundance rate of *L. boscii* in 1988 is due largely to good recruitment in the previous 2 years, and the drop in the abundance rates in 1991 and 1994 for this species can be attributed to the low recruitment levels of the preceding years. Abundance values for *L. whiffiagonis* remained high from 1988 to 1991. This was due in large part to the good recruitment levels in previous years, as 1 and 2-year class abundance in the following years indicates. The substantial drop in 1991 and the low indices recorded during the following years can be attributed to

the progressive reduction in recruitment from 1988, which has relegated this species to second place after *L. boscii*. It appears that their annual trends coincide; this is probably due to the fact that, in their larval and pre-recruitment stages, they are subjected to the same environmental dependencies.

The differing sex ratios by length class, shown in the sex ratio curve for these two species, are due to the differential growth rate between males and females, as described by Landa *et al.* (1996). The result is an accumulation of more smaller-sized males, and larger-sized females. The differential growth rate between sexes, typical of pleuronectiforms, may be due to the difference in metabolic activity, this being more marked in males, with a higher oxygen consumption (Pauly, 1994a, b) or a difference in feeding (more active in females), as found by Lozán (1992) for another flatfish species (*Limanda limanda*).

The higher number of females from 4 years upwards, as shown by the sex ratio curve by age-class, may be due to the difference between the sexes' mortality rate. Based on the estimated Z values, and assuming that the fishery acts equally on both sexes, it could be deduced that the females' natural mortality rate would be lower than that of males. This phenomenon is more patent in the case of *L. boscii*, where the estimated Z values for the same ages show marked differences between the two sexes. However, Beverton (1964) suggested that males are more accessible than females in the English North Sea plaice fishery, especially at spawning time. Rijnsdorp (1993) showed that fishing mortality is determined also by the increase in males' vulnerability during the spawning period. This leads to the consideration that the differences in mortality may be due not only to natural mortality, as in Scott and Scott (1988) and Cárdenas (1996), but also to male megrim's lesser accessibility to the fishing gear; however, this has yet to be demonstrated. Migration to other regions is unlikely, as may be deduced from the low number of movements of the cohorts.

Juveniles of most demersal species in the study area were concentrated on bottoms located in shallower waters than adults were. This positive size-depth correlation is very common in fishes (Helfman, 1978), and Keast (1978) has suggested that it may serve to minimize intraspecific competition. In the case of megrim, the inverse process occurs, since we find juveniles on deep-lying bottoms. This may be due to the fact that they do not need pelagic organisms from the zooplankton, as do a large proportion of demersal species, which are semipelagic during their initial life stages. Previous studies on megrim show their independence of zones with hydrographic instabilities that foster the vertical interchange of organic matter (Sánchez and Gil, 1995). Juveniles of this species mostly feed on detritivore crustaceans inhabiting deep-lying muddy bottoms (Rodríguez-Marín and

Olaso, 1993; Olaso and Rodríguez-Marín, 1995). This means that they go where these are found, which may partly explain the different age distribution, noted by Poulard *et al.* (1993), in *L. whiffiagonis* between the Celtic Sea and south of parallel 48°N (a region adjacent to the continental shelf in question), in view of the different distribution of mud deposits on these bottoms. For this same reason, megrim do not follow the guidelines of many of the species inhabiting the study zone, juveniles being concentrated on the Galician shelf for feeding reasons, due to their substantial primary productivity, and adults on the Cantabrian shelf (Sánchez and Pereiro, 1992). It appeas, therefore, that more bathymetric migrations occur according to age than geographic migrations, which is what we observed when following up the distribution of each cohort in the zone during the first three years.

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References

Beverton, R. J. H. 1964. Differential catchability of male and female plaice in the North Sea and its effect on estimates of stock abundance. Rapp. P.v. Reun. Cons. Int. Explor. Mer, 155: 103–112.

Boon, M. J. 1984. The UK megrim fishery in ICES sub-area VII: A preliminary analysis. ICES CM 1984/G: 17, 14 pp.

Cardador, F. 1983. Contribuiçao para aumentar a precisao dos índices de abundancia obtidos nas campanhas Portuguesas de investigaçao ''tipo demersal''. Bol. Inst. Nac. Invest. Pescas (9) Jan.-Abr. 1983: 17–67.

Cardenas, E. 1996. The females ratio by length as an indicator of sexual differences in mortality at ages 8+ of Greenland halibut (*Reinhardtius hippoglossoides*). NAFO SCR Doc. Nº 96/35 N2710, 10 pp.

Cochran, W. G. 1971. Muestreo estratificado aleatorio. Muestreo sistematico. *In* ''Técnicas de muestreo''. Ed. by Continental S. A. Mex. 127–297.

Dwivedi, S. N. 1964. Ecologie, morphologie et biologie comparées des deux espèces du genre *Lepidorhombus*: *L. megastoma* (Donovan) et *L. boscii* (Risso) étude de leurs races et populations. Rev. Trav. Inst. Pêches marit. 28(4): 321–399.

Fernández, A., Cascalho, A., Limas-Dias, M., and Pereiro, F. J. 1981. Peces capturados en la campaña ''Cigala-79'' a lo largo de la plataforma atlántica de la península iberica (División IX-a del CIEM). Bol. Inst. Espa. Oceano. Tomo VI, 309: 89–109.

Furnestin, J. 1935. La cardine (*Lepidorhombus megastoma* DONOVAN=*Lepidorhombus whiff* WALBAUN). Résumé des connaissances acquises sur la biologie de ce poisson. Rev. Trav. Inst. Pêches Marit., 8(2): 203–249.

Grosslein, M. D. and Laurec, A. 1982. Bottom trawl surveys design, operation and analysis. CECAF/ECAF Series 81/22 (En).

Helfman, G. S. 1978. Patterns of community structure in fish: summary and overview. Envionmental Biology and Fish, 3: 129–148.

ICES 1991. Report of the study group on the coordination of bottom trawl surveys in Subareas VI, VII and VIII and Division IXa of ICES. ICES CM 1991/G: 13, 33 pp.

ICES 1994. Report of the study group on bottom trawl surveys in Sub-areas VI, VII and VIII and division IXa. ICES CM 1994/G: 6, 31 pp.

ICES 1996. Report of the international bottom trawl survey working group. ICES CM 1996/H: 1.

Keast, A. 1978. Trophic and spatial relationships in the fish species of an Ontario temperature lake. Environmental Biology and Fish, 3: 7–31.

Landa, J., Piñeiro, C., and Pérez, N. 1996. Megrim (*Lepidorhombus whiffiagonis*) growth patterns in the northeast Atlantic. Fish Research, 26: 279–294.

Lozán, J. L. 1992. Sexual differences in food intake, digestive tract size, and growth performance of the dab, *Limanda limanda* L. Netherlands Journal of Sea Research, 29: 223–227.

Olaso, I. and Rodriguez-Marín, E. 1995. Alimentación de veinte especies de peces demersales. Inf. Tec. Inst. Esp. Oceanogr., 157: 56 pp.

Macpherson, E. 1981. Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. Vol., 4: 183–193.

Pauly, D. 1994a. On the sex of fish and the gender of scientists: essays in fisheries science. Fish and Fisheries series. Chapman and Hall, London: 264 pp.

Pauly, D. 1994b. A framework for latitudinal comparisons of flatfish recruitment. Netherlands Journal of Sea Research, 32(2): 107–118.

Pérez, N., Pereda, P., Uriarte, A., Trujillo, V., Olaso, I., and Lens, S. 1995. Discards of the Spanish Fleet in ICES Divisions. PEM/93/005.

Poulard, J. C. 1989. Distribution saisoniere et evaluation des resources halieutiques du Golfe de Gascogne. tome I et II. Ifremer, DRV de Lorient: 246 pp.

Poulard, J. C., Peronnet, I., and Rivoalen, J. J. 1993. Depth and spatial distributions of *Lepidorhombus whiffiagonis* (WALBAUM, 1792) by age group in celtic sea and bay of Biscay. ICES Statutory Meeting G: 43 Poster.

Quero, J. C., Dardignac, J., and Vayne, J. J. 1989. Les poissons du Golfe de Gascogne. IFREMER. Paris: 229 pp.

Rey, J. and Medialdea, T. 1989. Los sedimentos cuaternarios superficiales del margen continental español. Publ. Espec. Inst. Esp. Oceanogr., 3: 29 pp.

Rijnsdorp, A. D. 1993. Selection differentials in male and female North Sea plaice and changes in maturation and fecundity. *In* The exploitation of evolving resources, pp. 19–36. Ed. by T. K. Stokes, J. M. McGlade and R. Law. Springer Verlag, Berlin.

Rodriguez-Marín, E. and Olaso, I. 1993. Food composition of the two species of megrim (*Lepidorhombus whiffiagonis* and *Lepidorhombus boscii*) in the Cantabrian Sea. Actes du IIIème Colloque d'Oceanographie du Golfe de Gascogne. Arcachon 1992: 215–219.

Sánchez, F. 1993. Las comunidades de peces de la plataforma del Cantábrico. Publ. Espec. Inst. Esp. Oceanogr., 13: 137 pp.

Sánchez, F. 1994. Campãna de evaluación de recursos pesqueros Demersales 0991. Inf. Téc. Inst. Esp. Oceanogr., 155: 51 pp.

Sánchez, F. 1995. Distribución espacial de los principales recursos demersales del norte de España. Actes du IVème Colloque d'Oceanographie du Golfe de Gascogne. Santander 1994: 39–47.

Sánchez, F., De la Gándara, F., and Gancedo, R. 1995. Atlas de los peces demersales de Galicia y el Cantábrico.

Otoño 1991–1993. Publ. Esp. Inst. Esp. de Oceanogr., 20: 100 pp.

Sánchez, F. and Gíl, J. 1995. Influencia de anomalías térmicas de mesoscala sobre la distribución de peces demersales. Actes du IVème Colloque d'Oceanographie du Golfe de Gascogne. Santander 1994: 49–54.

Sánchez, F. and Olaso, I. 1987. Results of the bottom-trawl survey ''Cantábrico 86'' made in ICES Division VIIIc. ICES Demersal Fish Committee CM 1987/G: 20, 16 pp.

Sánchez, F. and Pereiro, F. J. 1992. Resultados de la campaña de arrastre demersal ''Carioca 90'' en aguas del Cantábrico y Galicia. Inf. Téc. Inst. Esp. de Oceanogr., 127: 71 pp.

Sánchez, F., Pereiro, F. J., and Rodriguez-Marin, E. 1991. Abundance and distribution of the main commercial fish on the northern coast of Spain (ICES Divisions VIIIc and IXa) from bottom trawl surveys. ICES Demersal Fish Committee CM 1991/G: 53, 30 pp.

Sánchez, F., Poulard, J. Ch., and De la Gándara, F. 1994. Experiencias de calibración entre los artes de arrastre BAKA 44/60 y GOV 36/47 utilizados por los B/O Cornide de Saavedra y Thalassa. Inf. Téc. Inst. Esp. de Oceanogr., 156: 48 pp.

Scott, W. B. and Scott, M. G. 1988. Atlantic fish of Canada. Canadian Bulletin of Fisheries and Aquatic Science, 219: 731 pp.

Silva, A. and Azevedo, M. 1994. Abundance and distribution of megrims, *Lepidorhombus boscii* and *L. whiffiagonis*, in ICES Division IXa (Portuguese waters). ICES CM 1994/G: 21, 12 pp.

Sobrino, I. 1992. Informe Campaña ARSA-1092. Informe Interno IEO (unpubl.).

Sobrino, I., Jimenez, M. P., and Ramos, F. 1993. Informe Campaña ARSA-0393. Informe Interno IEO (unpubl.).

Sokal, R. R. and Rohlf, F. J. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco: 776 pp.

Trujillo, V., Meixide, M., Porteiro, C., Pérez, N., and Pereiro, F. J. 1993. Cambios de malla y esfuerzo en las pesquerías multiespecíficas en aguas atlánticas de la Península Ibérica. Bol. Inst. Esp. Oceanogr., 9(1): 23–40.

Whitehead, P. J., Bauchot, M. L., Hureau, J. C., Nielsen, J., and Tortonesse, E. 1986. Fishes of the North-eastern Atlantic and the Mediterranean. Volume III. UNESCO, Paris.