

Fol. 41 H

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International Council for the
Exploration of the Sea

CM 1984/H:52
Pelagic Fish Committee

THE CESTODE PARASITE GRILLOTIA ANGELI AS A
BIOLOGICAL TAG FOR MACKEREL IN THE EASTERN NORTH ATLANTIC

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ABSTRACT

The trypanorhynch cestode Grillotia angeli Dollfus, 1969, infects mackerel Scomber scombrus L. up to the age of two years and survives thereafter as an encysted plerocercus for as long as the mackerel lives. In the eastern North Atlantic infection can only take place in and to the south of ICES sub-area VII, ie to the south and west of Britain and Ireland. In year classes 1977 and earlier, 13.8% of mackerel which originated from nursery grounds in sub-area VII were infected with G. angeli; in year classes 1978 and later, prevalence decreased to 1.2%.

Data from year classes 1977 and earlier indicate that: (1) mackerel caught off the north coast of Spain (sub-area VIII) and off Portugal (sub-area IX) were of different nursery origin from those caught further north; (2) mackerel caught in the southern North Sea (Division IVc) were predominately of southwestern origin; (3) to the northwest of Scotland (Division VIa north of 58°N) the proportions of mackerel of southwestern origin decreased from approximately 50% in September to 10% in January-February, then increased to >50% in March-April; (4) approximately 30% of all mackerel caught in the Norwegian Sea (Division IIa) and the northern North Sea (Division IVa) were of southwestern origin. Prevalence data from different areas suggest that mackerel of year classes 1978 and later from southwestern nursery grounds have been migrating into northern areas in greater numbers than earlier year classes.

RESUME

Le cestode trypanorhynche Grillotia angeli Dollfus, 1969, infecte le maquereau Scomber scombrus L. jusqu'à l'âge de deux ans et persiste par la suite comme plérocercus enkysté tant que le maquereau vivra. Dans la partie orientale de l'Atlantique Nord l'infection ne peut se produire qu'à l'intérieur et au sud de la zone VII du CIEM, c'est-à-dire au sud et à l'ouest de la Grande-Bretagne et de l'Irlande. Dans la classe 1977 et les précédentes 13.8% des maquereaux provenant de viviers situés dans la zone VII étaient atteints de G. angeli; dans la classe 1978 et les suivantes la fréquence a diminué jusqu'à 0.9%.

Les données relatives à la classe 1977 et aux antérieures indiquent que: (1) les maquereaux capturés devant la côte septentrionale de l'Espagne (zone VIII) et au large du Portugal (zone IX) ne provenaient pas des mêmes viviers que ceux qui ont été pris au nord des zones précitées; (2) la plupart des maquereaux pris dans la partie méridionale de la mer du Nord (zone IVc) provenaient du sud-ouest; (3) au nord-ouest de l'Ecosse (zone VIa, au nord de 58°N) la proportion de maquereaux provenant du sud-ouest, chiffrée à environ 50% en septembre, a diminué à 10% en janvier-février, pour augmenter ensuite à 50% en mars-avril; (4) environ 30% de tous les maquereaux capturés dans la Mer de Norvège (zone IIa) et dans la partie septentrionale de la mer du Nord (zone IVa) provenaient du sud-ouest. Sur la base des fréquences constatées dans plusieurs zones on a lieu de croire que les maquereaux migrateurs faisant partie de la classe 1978 et des suivantes et provenant de viviers situés dans le sud-ouest sont entrés en plus grand nombre dans les zones septentrionales que ceux qui faisaient partie des classes antérieures.

INTRODUCTION

Previous reports (MacKenzie, 1981; MacKenzie and Mehl, 1982) have described the selection and use of the plerocercus larva of the trypanorhynch cestode Grillotia angeli Dollfus, 1969, as a biological tag for mackerel Scomber scombrus L. In this paper, all of the data so far collected in this study are analysed and discussed.

The only known definitive host of G. angeli is the monkfish or angel-shark Squatina squatina (L.). The distribution of this definitive host determines the area within which teleost second intermediate hosts, including mackerel, are exposed to infection. The monkfish occurs commonly throughout and to the south of ICES sub-area VII but is considered to be a rare fish to the north of Ireland and in all parts of the North Sea. The previous reports referred to above presented evidence which suggested that all infection of mackerel with G. angeli occurs in the first two years of life and that the life span of the plerocercus in mackerel is probably equal to that of the infected fish. Infection of mackerel with G. angeli is therefore an indication that infected fish originated from nursery grounds in or to the south of sub-area VII. This is not equivalent to saying that all infected mackerel are of the "western stock", which refers to mackerel which spawn on grounds to the west and southwest of Britain and Ireland. Evidence from the present study and from that of Eltink (1983) shows that some mackerel which originated from southwestern nursery grounds have subsequently spawned in the North Sea and so would be classified as "North Sea stock". To avoid confusion, mackerel identified as having originated from nursery grounds in or to the south of sub-area VII will be referred to in this paper as "southwestern" and those identified as having originated from nursery grounds in the North Sea or to the west of Scotland (Division VIa) will be referred to as "northern".

MATERIALS AND METHODS

Samples of mackerel were taken from research vessel and commercial catches and preserved by deep-freezing, apart from some of the first samples of juvenile mackerel which were preserved in 10% formalin. Figure 1 shows the positions of capture of all samples examined so far. The otoliths of all mackerel examined were removed for age determination and the length and sex of each fish were recorded. The alimentary tract of each mackerel was removed and examined under a dissecting microscope at a magnification of X6 for G. angeli plerocerci encysted in the stomach wall or on the outer surface of the stomach, pyloric caeca or intestine.

Prevalence, expressed as a percentage, is the measure of parasitic infection used in this paper. Prevalence is the number of individuals of a host species infected with the parasite divided by the number of hosts examined. The chi-squared test was used as a test of statistical significance between prevalence values. In any samples taken from the North Sea or from areas VIa or IIa, an estimate of the proportion of mackerel of southwestern origin in the population sampled was obtained by dividing the prevalence in the sample by the mean prevalence in area VII, where it was assumed that all mackerel caught were of southwestern origin. Ninety-five percent confidence limits for the prevalence Pr in a sample of n mackerel were then calculated as

$$Pr \pm \left[(1.96 \sqrt{\frac{Pr(1-Pr)}{n}}) - \frac{1}{2n} \right] \times 100$$

To obtain 95% confidence limits for the proportion of mackerel of southwestern origin in the sample, each prevalence confidence limit was then divided by the mean prevalence in area VII.

RESULTS

A total of 9639 mackerel aged from O-ring to 18 rings were examined for infection with G. angeli.

1 Variations in prevalence between year classes

Mackerel year classes fell into two distinct groups according to the prevalence of G. angeli. In all mackerel examined the mean prevalence in year classes 1977 and earlier was 6.9%, but in year classes 1978 to 1982 it fell abruptly to a new mean level of 0.9% (Fig. 2). Differences in prevalence between the two groups of year classes were apparent in all parts of the study area, but were greater in some parts than in others (Table 1). It is clear that these two groups of year classes must be treated separately.

2 Variations in prevalence between areas

2.1 Year classes 1977 and earlier

The variations between areas shown in Table 1 were highly significant ($P < 0.001$). The highest prevalence was recorded in mackerel caught in sub-area VII and the

lowest in those caught in Divisions IVb and IIIa (central North Sea and Skagerrak). Three areas lie contiguous to sub-area VII: Divisions IVc (southern North Sea), VIa south of 58°N (west of Scotland) and sub-area VIII (Biscay). Only in IVc was prevalence not significantly different ($P>0.05$) to that in sub-area VII. Mackerel caught in four different Divisions of sub-area VII (Table 2) showed no significant ($P>0.10$) variations in prevalence. Most of the mackerel from sub-area VIII were caught in the southern part of the area, near the north coast of Spain.

2.2 Year classes 1978 to 1982

Table 1 shows that prevalence was low throughout the study area. Variations in prevalence between different parts were not statistically significant ($P>0.10$).

Sub-area IX is represented by a single sample taken near the coast of Portugal (see Figure. 1). No mackerel in this sample was infected with *G. angeli*, but four were infected with another trypanorhynch cestode *Nybelinia* sp., which was not found in any other area.

3 Variations in prevalence between age groups

3.1 Year classes 1977 and earlier

Figure 3 shows variations in prevalence of from zero to 14% over the entire range of age groups represented. The highest prevalences were in age groups 16-18, 3 and 2. More than 80% of the mackerel in these three age groups were caught in sub-area VII and Division IVc, where the highest mean prevalences for all age groups were recorded (Table 1). All mackerel of age group 1 were caught in Divisions IVa and IVb (northern and central North Sea) and none was infected. In the remaining 12 consecutive age groups from 4 to 15 the mackerel examined were more evenly distributed throughout all parts of the study area and over this age range there were no statistically significant variations in prevalence ($P>0.10$).

3.2 Year classes 1978 to 1982

There were no statistically significant variations in prevalence ($P>0.10$) between the age groups represented in this group (Fig. 3).

4 Seasonal variations in prevalence

4.1 Year classes 1977 and earlier

Data from each ICES area were analysed as mean monthly prevalences for all years of the study combined. In Divisions IIa, IIIa, and sub-areas VIII and IX, sampling was limited to either a single month or two consecutive months so no seasonal analyses were possible. In none of the remaining six areas from which samples were taken at different seasons (Table 3) were the monthly variations statistically significant ($P>0.10$), but in Division VIa, north of 58°N, there was a clear trend of decreasing prevalence from September to January, followed by an increase from January to April. Assuming the prevalence of 13.8% in sub-area VII to be the true mean value for mackerel of southwestern origin, the estimated proportions of southwestern mackerel in Division VIa north of 58°N were calculated for the different months in which mackerel were caught. Figure 4 shows that the proportions decreased from about 50% in September to less than 10% in January-February, followed by an increase to just over 50% in March-April. Prevalence in

mackerel caught in Divisions IVa and IVb (northern and central North Sea) in May indicate that approximately 30% of these fish were of southwestern origin. The timing suggests that they would have spawned in the North Sea.

4.2 Year classes 1978 to 1982

Prevalence was generally too low to show significant seasonal variations.

DISCUSSION

The value of G. angeli as a biological tag for mackerel has been greatly reduced by the dramatic decrease in prevalence in recent year classes. Possible reasons for this change are discussed by MacKenzie, Smith and Williams (1984). The prevalence of 13.8% which is taken as an approximation to the true mean value for mackerel of southwestern nursery origin applies only to mackerel of year classes 1977 and earlier. Provided that large numbers of mackerel of these year classes are examined, this figure of 13.8% can be used to estimate the size of the component of southwestern origin in mixed populations of mackerel. However, the proportion of mackerel of year classes 1977 and earlier in the general population is decreasing rapidly and catches are now dominated by fish of year classes 1978 and later. Whilst data from these more recent year classes cannot be used to quantify the component of southwestern origin in mixed samples, they can serve as more general indicators of trends in mackerel distribution. If the pattern of distribution indicated by data from year classes 1977 and older had been maintained, mackerel of later year classes infected with G. angeli should have been very scarce indeed in areas north of VII. In fact, Table 1 shows that infected mackerel were spread fairly evenly over all areas. These results suggest that mackerel of year classes 1978 and later may have been migrating from their southwestern nursery grounds into northern areas in greater numbers and possibly at younger ages than before.

The recording in sub-area VII of the highest regional prevalence for year classes 1977 and earlier is not surprising considering that the only known definitive host of G. angeli, the monkfish, is common throughout that area. The monkfish, however, is also common in sub-area VIII, where prevalence was significantly lower than in sub-area VII. The prevalence data suggest that a large proportion of the mackerel caught off the north coast of Spain originated on different nursery grounds from mackerel caught in sub-area VII. Dawson's (1983) analysis of otolith L_1 measurements suggested that mackerel caught near the north coast of Spain may constitute a separate group within the current definition of the western stock. The occurrence of the cestode Nybelinia sp. only in sub-area IX suggests that the mackerel population in this area may also be separate from those in other areas.

Prevalence in Division IVc was not statistically different from that in sub-area VII, which suggests that the mackerel population in the southern North Sea may be entirely of southwestern origin. Eltink (1983) came to the same conclusion on the basis of comparisons of age compositions of southern North Sea mackerel with those of western and North Sea stock mackerel and from conventional tagging data.

Considerable interest has recently centred around the question of the proportions of western and North Sea stock mackerel in the population in Division VIa north of 58°N (Anon., 1984b). The estimates shown in Figure 4 agree well with the migration patterns described by Anon. (1981). They do, however, apply only to year classes 1977 and earlier, which now constitute a minority of the total mackerel population in VIa (Anon., 1984a, b). The results from year classes 1978 to 1982 suggest that the proportions of mackerel of southwestern origin in the population as a whole were probably greater than shown in Figure 4. (All mackerel aged from 1 to 3 caught in this area were considered by Anon. (1984b) to be western stock.) Prevalence in mackerel of year classes 1977 and earlier caught in that part of VIa south of 58°N indicated that just over half of the population in that area were of southwestern origin. It is worth reiterating here that the remaining northern component were not necessarily of North Sea origin; some or all of them may have originated from nurseries in area VIa. Over the entire study period, mean prevalence data indicate that approximately 30% of mackerel of year classes 1977 and earlier in areas IVa and IIa were of southwestern origin. The corresponding figure for areas IVb and IIIa was approximately 12%. Norwegian tagging experiments indicated that in the years 1981 to 1983 up to 90% of mackerel older than age 2 caught in area IIa were of southwestern origin (Anon., 1984b).

Mackerel of year classes 1977 and earlier caught in area VII since about 1979 have continued to give prevalence values of around 13.8% despite the fact that G. angeli has infected only 1.2% of mackerel in later year classes. This means that those mackerel which were infected before 1979 have apparently not lost any parasites, which provides strong supporting evidence of a long life-span for G. angeli in mackerel.

ACKNOWLEDGEMENTS

We wish to thank the following people who collected and preserved samples of mackerel for us: Dr J. L. Cort of the Laboratorio Oceanografico, Santander, Spain; Mr A. Eltink and other sea-going staff of the Netherlands Institute for Fishery Investigations, Ijmuiden, The Netherlands; Dr J. Gueguen of the ISTPM Laboratory, Lorient, France; Mr D. P. Hojgaard of I/F Havsbrun, Fuglafjordur, Faroe Islands; Dr S. J. Lockwood and other sea-going staff of the MAFF Fisheries Laboratory, Lowestoft, England; Prof Dr M. Carvalho Varela of the Escola Superior de Medicina Veterinaria, Lisbon, Portugal. We are grateful to Mr M. Walsh of DAFS Marine Laboratory, Aberdeen and to Ms H. Gill of the Institute of Marine Research, Bergen, Norway, for age determinations of mackerel, and to Miss A. M. Shanks and Mr D. Thomson of the DAFS Marine Laboratory, Aberdeen for help with statistical methods.

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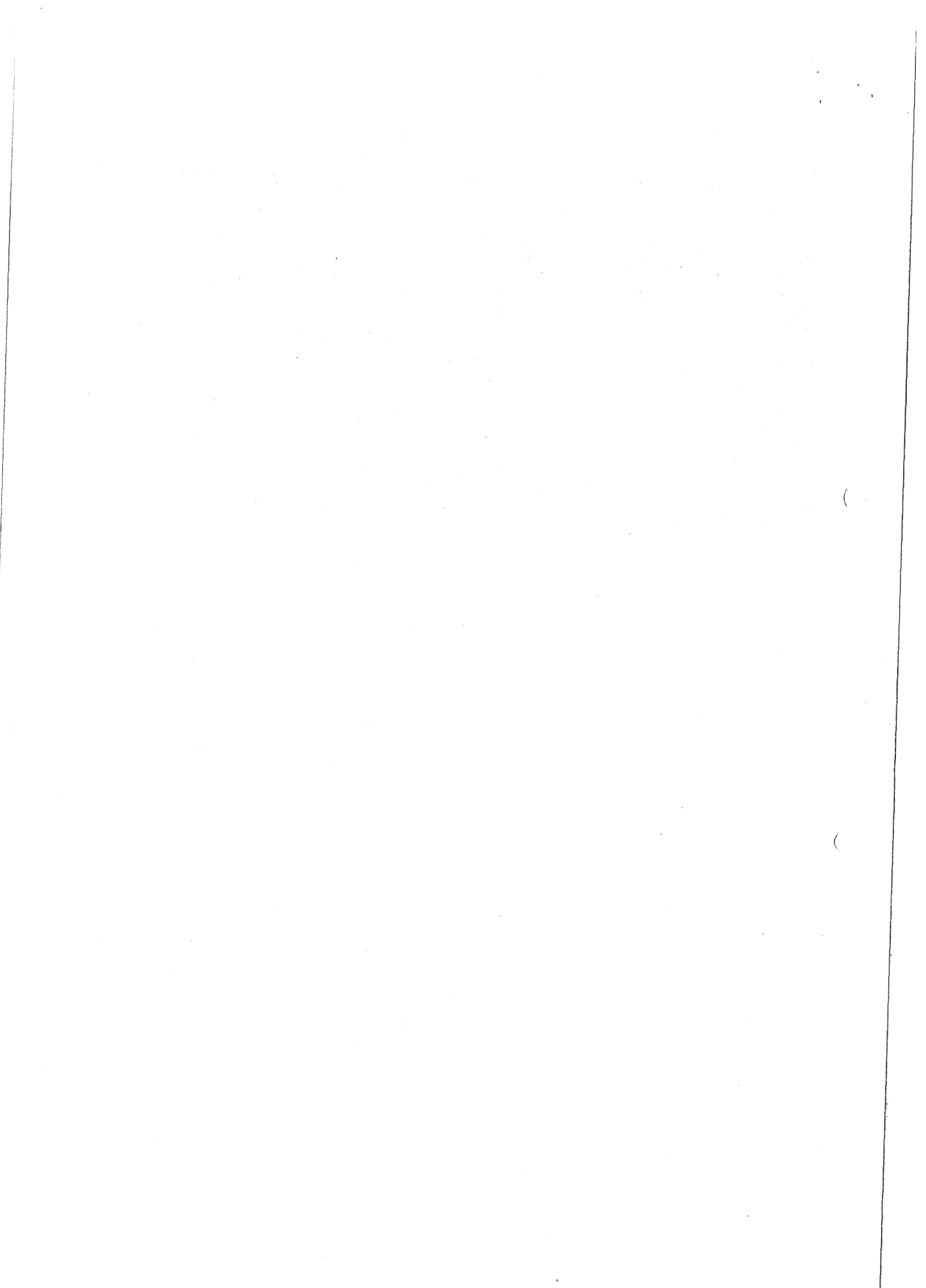


TABLE 1

Prevalence of G. angeli in mackerel caught in different ICES sub areas or divisions.
 N=total number of mackerel examined, n=number infected, Pr=percentage prevalence.

	IIa	IIIa	IVa	IVb	IVc	Via south of 58°N	Via north of 58°N	VII	VIII	IX
Year classes N	210	64	1102	315	228	200	1611	952	201	1
1977 and earlier n	9	1	45	5	25	16	92	131	15	0
Pr	4.3	1.6	4.1	1.6	11.0	8.0	5.7	13.8	7.5	0
Year classes N	69	1	214	376	323	647	1024	1499	513	89
1978 to 1982 n	2	0	0	4	4	7	4	18	5	0
Pr	2.9	0	0	1.1	1.2	1.1	0.4	1.2	1.0	0

TABLE 2

Prevalence of G. angeli in mackerel of year classes 1977 and earlier caught in four different divisions of ICES sub area VII. N=total of mackerel examined, n=number infected, Pr=percentage prevalence.

	Sub area			
	VIIb	VIIc	VII e	VII j
N	78	27	662	185
n	14	2	92	23
Pr	17.9	7.4	13.9	12.4

TABLE 3

Monthly variations in prevalence of *G. angeli* in mackerel of year classes 1977 and earlier caught in different ICES sub areas or divisions. N=total number of mackerel examined, n=number infected, Pr= percentage prevalence.

Area	Month (all years combined)												
		J	F	M	A	M	J	J	A	S	O	N	D
IVa	N		72		24	330		31	35	389	153		
	n		7		1	14		2	1	16	3		
	Pr		9.7		4.2	4.2		6.5	2.9	4.1	2.0		
IVb	N	*3	*152	*2		60		7	3	71	17		
	n	0	0	0		3		1	0	1	0		
	Pr	0	0	0		5.0		14.3	0	1.4	0		
IVc	N					168				37	23		
	n					21				3	1		
	Pr					12.5				8.1	4.3		
VIa north of 58°N	N	53	30	152	41					602	340	242	151
	n	0	1	10	5					41	18	12	5
	Pr	0	3.3	6.6	12.2					6.8	5.3	5.0	3.3
VIa south of 58°N	N		46	20						9		70	55
	n		4	0						0		8	4
	Pr		8.7	0						0		11.4	7.3
VII	N		193		364	129	18	118					130
	n		26		51	20	1	13					21
	Pr		13.5		14.0	15.5	5.6	11.0					16.2

* Juvenile (early 1-ring) mackerel

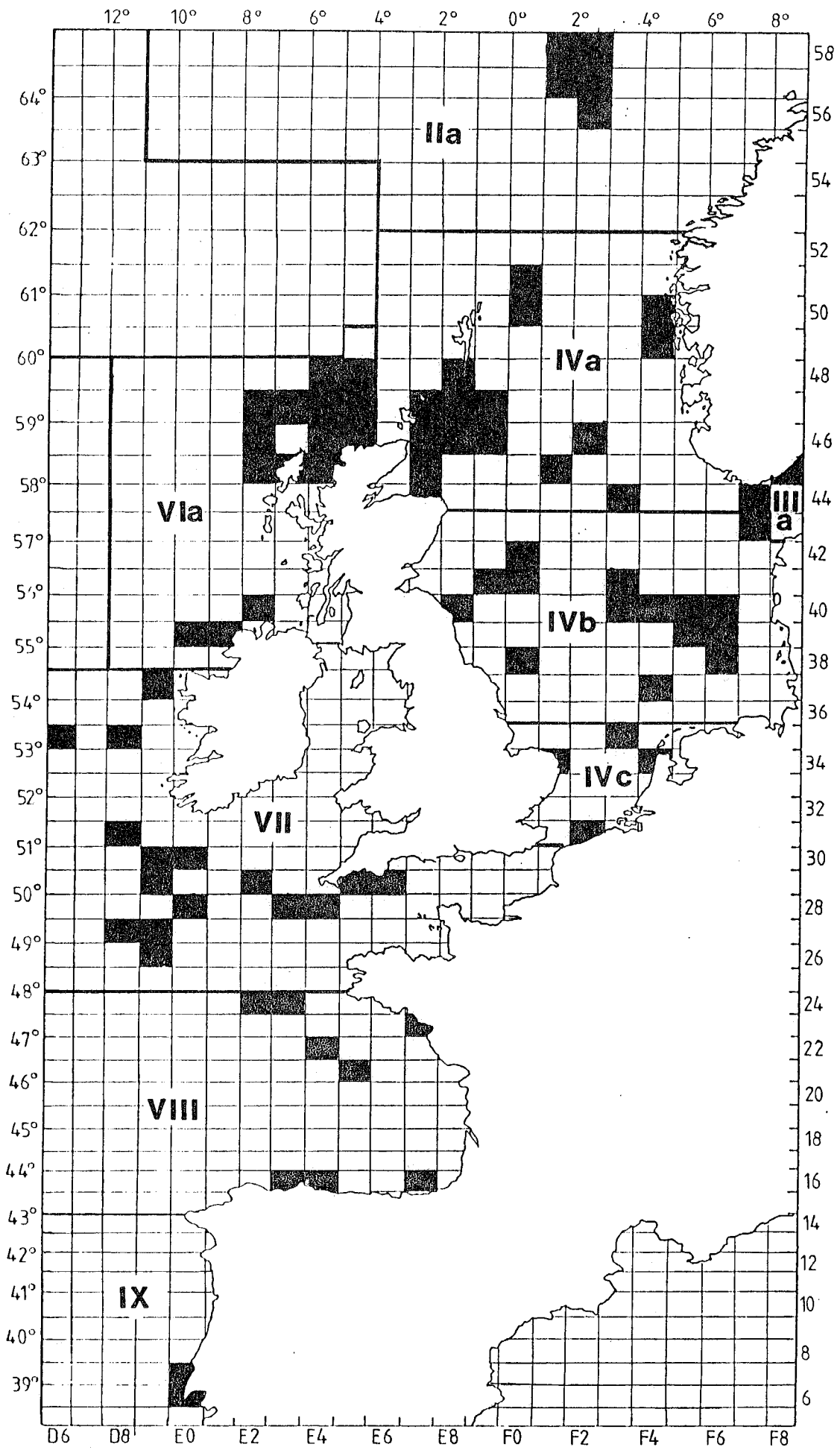


Figure 1 The study area showing statistical rectangles (shaded) from which mackerel samples were taken.

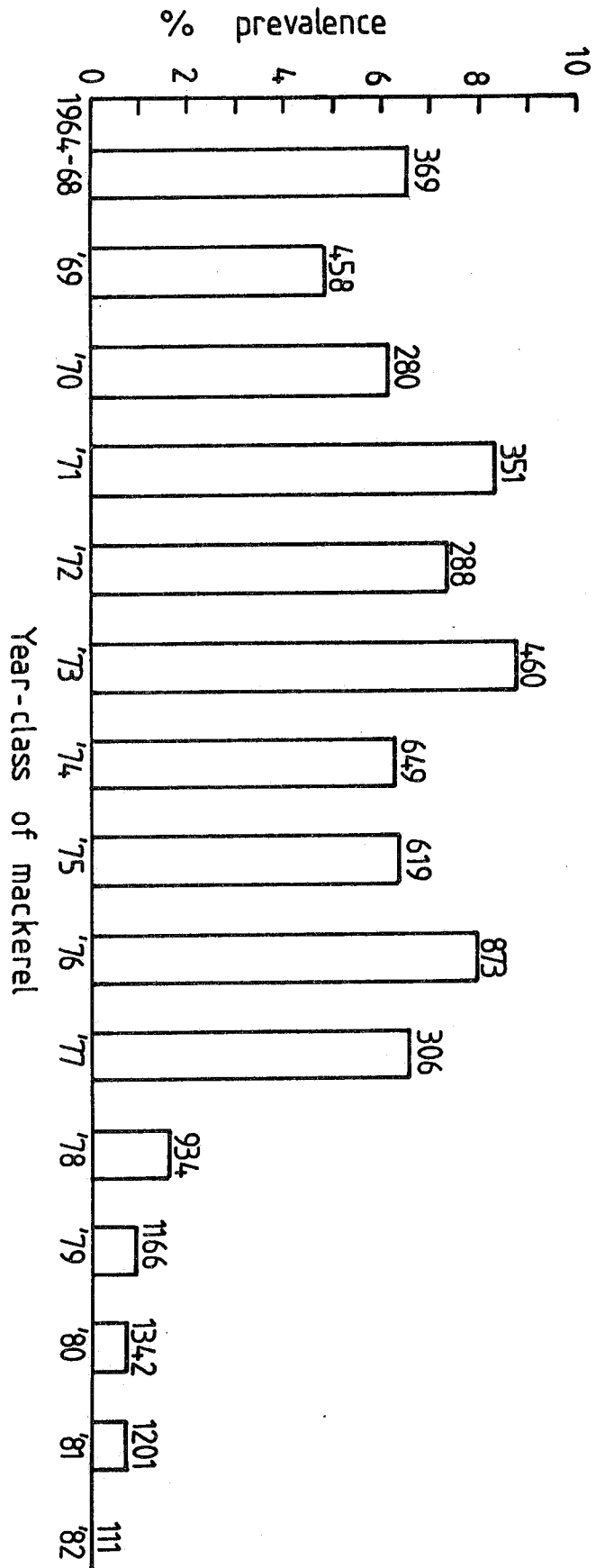


Figure 2 Variations in prevalence between mackerel year classes: all ages and areas.

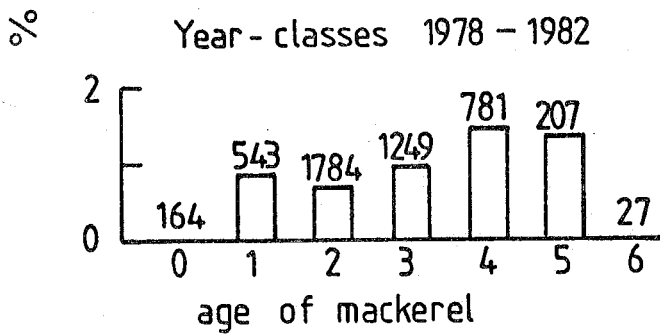
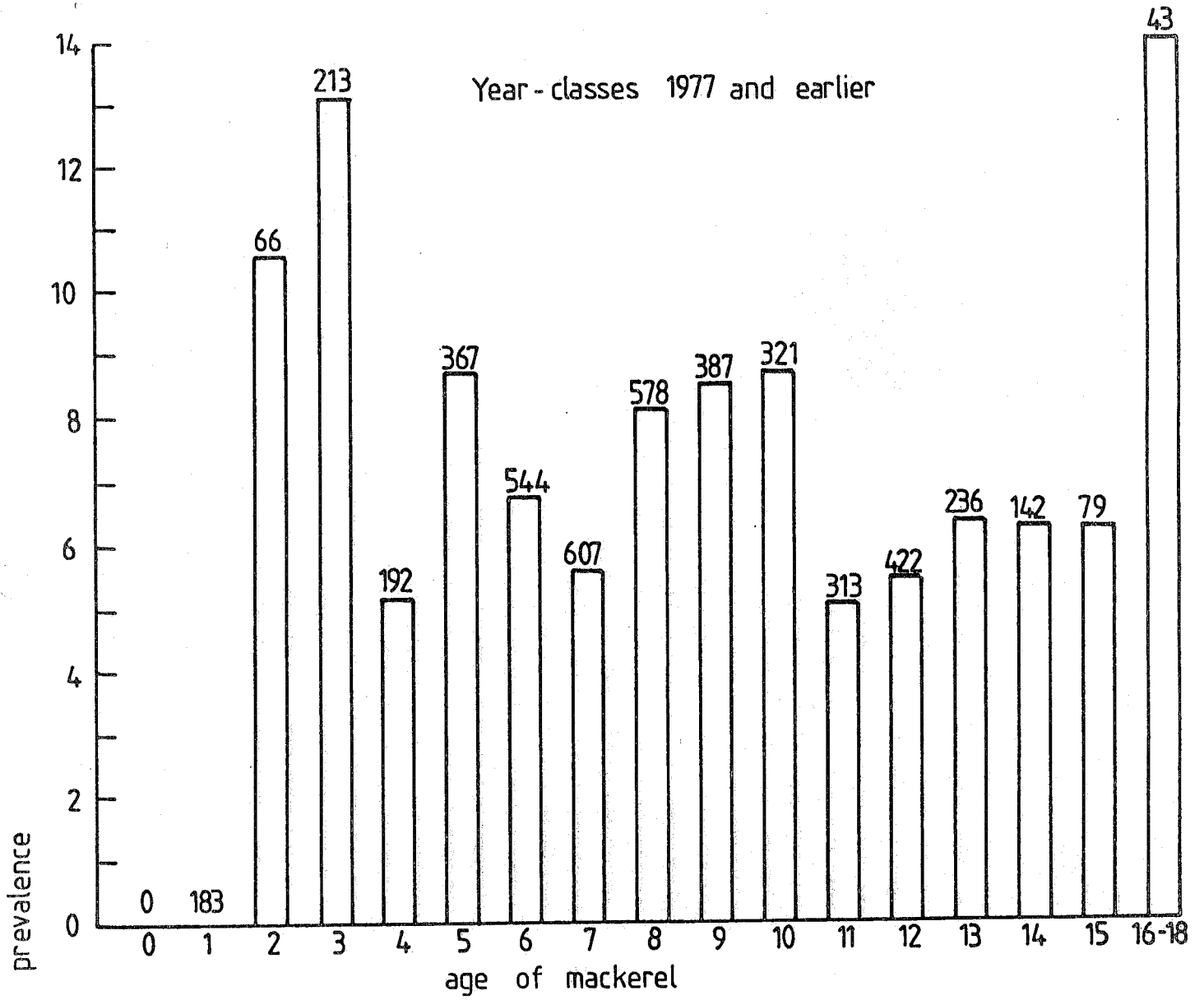


Figure 3 Variations in prevalence between mackerel age groups: all areas.

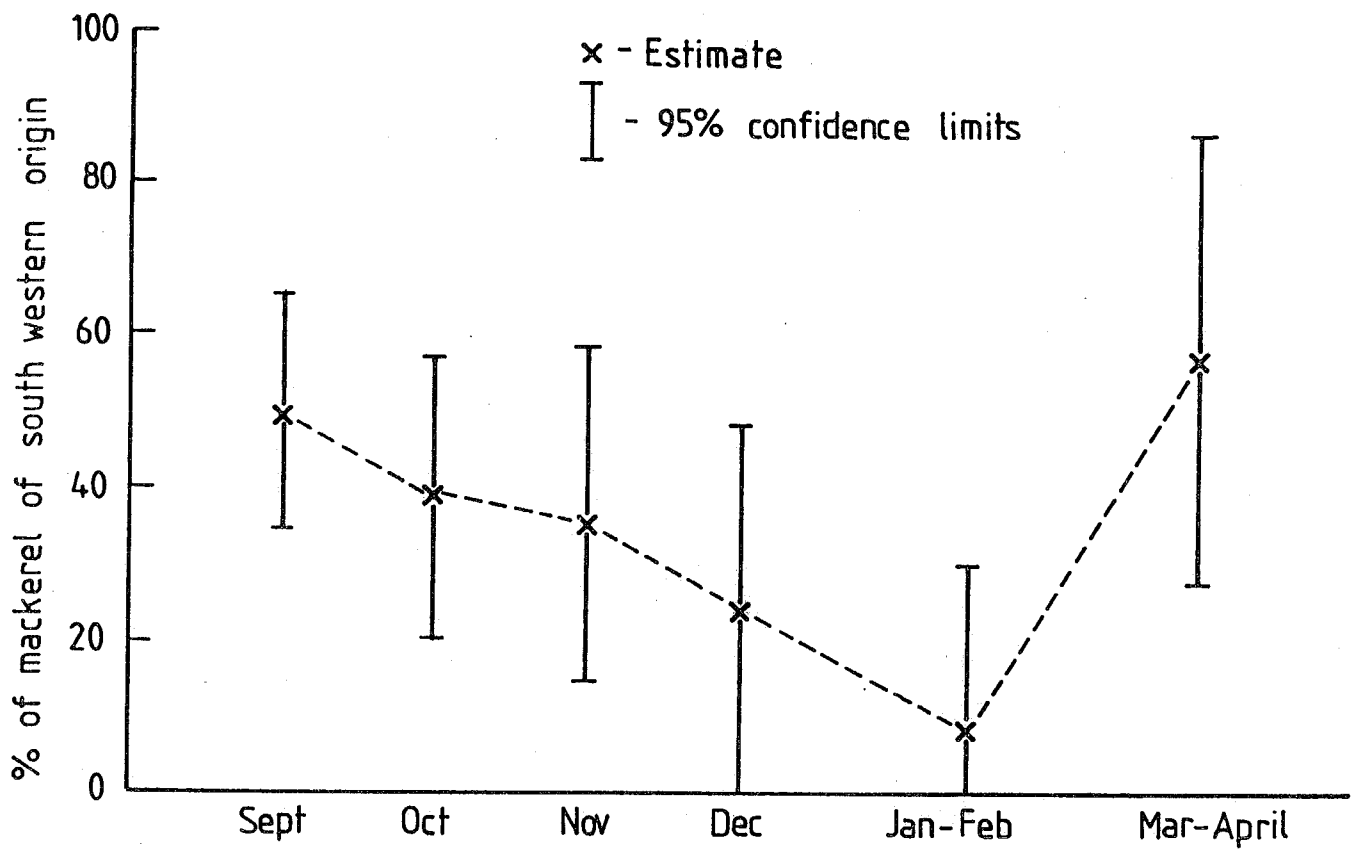


Figure 4 Estimated proportions of mackerel of southwestern origin in samples of year classes 1977 and earlier caught in Division VIa north of 58°N from September 1979 to March 1984.