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A REVIEW OF MACKEREL MANAGEMENT AREAS IN THE NORTHWEST ATLANTIC

by

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ABSTRACT

The history of the stock unit presently used for management of Northwest Atlantic mackerel is reviewed. Although two spawning populations were known to exist, the management area was defined on the basis of mixing of the two populations on overwintering grounds where most of the fishery was then occurring. The biological basis for the definition of the management unit is reviewed and shows that tagging data were the main factor in defining the management area. Recent genetic analyses do not suggest modifying the currently used management area.

RÉSUMÉ

L'historique du choix de l'unité de gestion présentement utilisée pour le maquereau de l'Atlantique du nord-ouest est présenté. Malgré que l'existence de deux populations reproductrices soit connue, l'unité de gestion a été définie pour tenir compte du mélange des deux populations sur les lieux d'hivernage où la plus grande partie des captures étaient alors effectuées. Les résultats d'expérience de marquage ont été déterminants dans le choix de l'unité de gestion. De récents travaux génétiques n'indiquent pas qu'il serait pertinent de modifier l'unité de gestion présentement utilisée.

INTRODUCTION

In February 1986, CAFSAC organised a special meeting to discuss stock structure of species within the Gulf of Maine area. This document presents the information on mackerel in the format requested for the meeting.

A. HISTORY OF MANAGEMENT AREA DEFINITION

A.1. Current management area

The mackerel stock complex is currently managed as a single stock over its whole area of distribution, i.e. NAFO Subareas 3 to 6 (minor catches are occasionnally made in 2J) although two different main spawning groups are known to exist. Managing the two groups as a single stock was felt to be the only approach to take into account the important catches that were made on mixed overwintering concentrations in SA 5 and 6 in the late sixties and early seventies.

Mackerel is a transboundary stock which is presently managed independently by Canada and the USA. Each country informally takes into account the anticipated performance of the other in adopting management measures.

A.2. History of the management area

The Atlantic mackerel fishery dates back to the seventeenth century off the northeast coast of North America. Large fluctuations in catches were attributed not only to factors such as market conditions and changes in fishing methods and areas, but also to natural fluctuations in stock abundance (Sette and Needler, 1934). The species has been studied since the late 1800's but stock assessments and investigations of the effects of fishing were not begun until the early 1970's (Anderson and Paciorkowski, 1980).

The first assessment (Anderson, 1973) was reviewed by ICNAF in 1973. It dealt only with SA 5 and 6 as an international fishery had recently developed particularly in those areas. Based primarily on the work of Sette (1943, 1950), it was assumed that a single stock was being exploited.

The report of the 1973 meeting of the ad hoc Mackerel Working Group states that (ANON, 1973 - p. 87):

> "The discussions were based on the assumptions that the Subarea 5 and Stat. Area 6 fisheries exploit a single stock, inhabiting these areas. Information on tag returns (Res. Doc. 73/82) indicated that mackerel from Subarea 3 migrate to the area of the Subarea 5 and Stat. Area 6 fishery. This brings into question the assumption that mackerel in the ICNAF Area are divided into two biologically distinct stocks, the northern and southern. If there is only one stock in the ICNAF Area, the assessment

considered here is affected only slightly, because catches in Subareas 3 and 4 are currently relatively very small. If two stocks are involved, with the northern stock overwintering in the southern area the effect on the assessment will depend on the degree to which "mixing" varies from year to year, and no data is available on this matter. More information relating to stock identification is urgently needed to solve these questions, although there is no reason to suppose, at the present time, that the broad conclusions expressed here would be affected".

Information presented at the January 1974 ICNAF meeting of the ad hoc Mackerel Working Group led to the following statement in the report of the W.G. (ANON, 1974a, p. 31):

"The assumption that the mackerel in the ICNAF Area are divided into two biologically distinct stocks (northern and southern) with some mixing in SA 5 and 6 during the winter was discussed on the basis of new information (Res. Doc. 74/8, 9). It was not possible to estimate the degree of mixing of these spawning stocks, although it was accepted that mixing occurs. A tagging experiment on substantial scale would be required if the problem is to be resolved, and it was recommended that this matter be discussed at the 1974 Annual Meeting."

The subject was discussed again at the May-June meeting and the Assessment Subcommittee report states that (ANON, 1974b, p. 93):

"Data on the distribution of the fishery, on the biological characteristics of the fish, and some additionnal evidence from tagging on the range of migration of mackerel in SA 3 and 4 all indicate that these fish are either a migrating component of mackerel fished in SA 5 and 6, or, if they form a truly separate biological unit, then their distribution and the fisheries on the two stocks overlap in SA 5 and 6 during part of the year. The TAC appropriate to either situation and its allocation to subareas depends on the degree of this mixing. It is possible, for example, that the present TAC level for SA 5 and 6 is adequate for the exploitation of mackerel throughout the ICNAF Area, and it is even possible it may allow over-exploitation of any discrete component which migrated annually to SA 3 and 4. These possibilities cannot be resolved at present, nor is the Subcommittee optimistic that they can be resolved in the near future (See Annex 2 for Report of the ad hoc Mackerel Working Group).

> Under the circumstances it might be most appropriate to include all mackerel within a single assessment, but, having regard for the already existing uncertainties for SA 5 and 6, the Subcommittee concluded that such an assessment was not possible at this meeting and strongly recommends that it be carried out for the 1975 Annual Meeting".

This was done in the following year (Anderson, 1975; ANON, 1975) and the northwest Atlantic mackerel has since been assessed and managed as a single stock.

The determining factor in revising the management unit in 1975 has undoubtedly been the tagging experiments that have shown that the northern population was indeed exploited in the Distant Water Fleet (DWF) winter fishery in SA 5+6. An additionnal reason was the difficulty or impossibility of doing separate assessments for the two populations owing to the impossibility of determining the stock of origin of the catches.

B. REVIEW OF THE BIOLOGICAL BASIS FOR DEFINITION OF UNIT STOCKS

B.1. Literature review

Sette (1943) recognized the existence of two main spawning areas (figure 1). When analysing length compositions of mackerel catches from various locations in the USA and in Nova Scotia, Sette (1950) noted that the length frequencies of summer caught fish off Nova Scotia were different from those caught off New England. He also noted that, during brief periods (end of May-early June and the end of autumn), landings from southern New England appeared to show a mix of these two length frequency groups. The persistence of these differences for several years, the absence of some year-classes in one or the other region, combined with the known existence of two spawning areas (Sette, 1943, 1950) led him to suggest the existence of two distinct groups of mackerel in the northwest Atlantic. He called these groups "contingents" but the term "population" proposed by MacKay (1973) is used here. It should be noted that Sette (1950) never suggested that the two populations were genetically distinct although he said that:

> "... it would appear that the two contingents are well separated from each other when spawning. This separation during reproduction would favor an hypothesis that the two contingents were genetically distinct races. Eventually this may prove to be true. For the present, however, it does not appear to be consistent with other evidence..." (p. 286).

Sette's (1950) observations were that, generally, the southern population comprised smaller sizes that the northern population (figure 2). This was persistent over the years and one could have proposed the

hypothesis that the southern area contained mostly younger ages that would later move to the northern contingent. Sette (1950) dismissed that hypothesis on the following grounds:

> "This (hypothesis) would be consistent with the evidence afforded by the 1928 class of mode C but would be utterly contrary to the behavior of the 1923 class of mode B which continued prominent in the southern contingent for more than 9 years and never was represented strongly enough in the norther be detectable." (p. 287).

Sette (1950) was non committal on the nature of the two contingents or populations, and no further in depth investigation of this subject has been pursued since.

Several authors (Anderson, 1975; Beckett et al., 1974; MacKay, 1973; Moores et al., 1975; Stobo and Hunt, 1974) have reviewed the two populations hypothesis proposed by Sette (1950) and all have accepted his conclusions. However, biochemical and meristic analysis (MacKay, 1967; MacKay and Garside, 1969) as well as parasitological studies (Isakov, 1976) did not show any differences between the two contingents. MacKay and Garside (1969) concluded that there were sufficient exchanges between the two populations to maintain relatively stable characteristics. Tagging studies (Beckett et al., 1974; MacKay, 1967; Parsons and Moores, 1974; Sette, 1950; Stobo, 1976) indeed suggest that the two populations are probably mixed on overwintering grounds.

B.2. Characteristics of the fishery

The Canadian fishery is mostly an inshore summer fishery. Catches generally follow the migration pattern described by Sette (1950) and reproduced here as figure 3 with some annual variations. Mackerel are first caught on the Scotian Shelf in May-June. The progression of catches can be followed from Yarmouth to Cape Breton, then into the Gulf of St. Lawrence in June-July (figure 4). Catches in the northern part of the Gulf of St. Lawrence are usually in August-September. On the east coast of Newfoundland, the first significant catches are made in August and the fishery may extend into November.

The Distant Water Fleet fishery was carried out from Georges Bank southward although water temperature data indicated that suitable temperatures are found from Sable Island southward. It lasted usually from November to March. The present USA joint ventures are presumably conducted in the same areas.

The domestic USA fishery is relatively small (3,000 t) and is mostly a spring-summer fishery. Mackerel is an important species in the charter/party boat sports fishery. Annual catches in that fishery have been estimated to reach 10-20,000 t (Anderson and Paciorkowski, 1980).

B.3. Unpublished genetic data on stock structure

Introduction

The value of genetic markers has been recognized in the identification of population structure of species. Electrophoretic technics provide an important tool for measuring genetic discretness of stocks and has recently attained a primary position among the methods used for stock identification (Ihssen et al., 1981).

Atlantic mackerel stock structure has never been clearly established despite biochemical and meristic analyses of Mackay (1967) and Mackay and Garside (1969). In order to shed light of this important problem, genetic characteristics from 20 enzymes were compared between the northern and the southern contingent of mackerel.

Materials and methods

Sampling

Mackerel sampled during the spawning season off New-Jersey (NJ84) and New-York (NY85) were compared to mackerel fished in the Gulf of St. Lawrence (BC84 and IPE85) (figure 5). The characteristics of the samples are as follows:

Sample	Date	Sample size	Fishing gear
BC 84	16 July 1984	225	pair seine
IPE 85	17 July 1985	180	purse seine
NJ 84	7-8 May 1984	78	jigger
NY 85	4 May 1985	161	jigger

Age determinations were done at the Quebec City laboratory of the Department of Fisheries and Oceans.

Isoelectric focusing

In 1984 intact mackerel were kept at -20°C until tissues were excised and stored at -60°C whereas in 1985, tissues were excised from fresh fish and then frozen on dry ice (-105°C) and stored at - 60°C.

For each fish, one eye and 0.5 g of liver were individually homogenized at 4°C for 5 seconds with a Polytron at medium speed in a solution of 0.75 ml sucrose 250 mM (1984) or in a homogenising buffer (1985) (Tris-HCL 15mM pH 7.5; $MgCl_2$ 1mM; DTT 1mM; glycerol 50% (V/V)). For skeletal muscle, 1.5 ml were used for 0.5 g of muscle. The homogeneous solutions were then

centrifuged at 4°C, 1200 g for 10 minutes and kept at -60°C. The gel used was 0.2 mm thick and had the following composition:

- acrylamide 4.8% W/V
- bisacrylamide 0.2% W/V
- ampholytes 2% W/V
- glycerol 10% V/V
- dithiothreitol (DTT) 0.1 mM
- ammonium persulfate 3.5 mM
- tetramethylethylenediamine (TEMED) 10mM

Various ampholytes were used in varying proportions (table 1). Anions and cations were respectively L-glutamic acid 0.04M and L-histidine 0.2M. The exact conditions for the focusing of the 20 enzymes are given in table 1. The IEF was made at 10°C over 5 cm (10 cm for CAE) during 20 minutes (50 minutes for CAE) at 15W.

The techniques of Harris and Hopkinson (1976) were used to stain the ACON, ADH, CAE, CBR, GDH, GPD, DID, GSR, HAGH, MPI, PGD, SOD enzymes, those of Eicher and Womack (1977) for ALT, Ayala et al. (1974) for AAT, Tracey et al. (1975) for GPI, Ayala et al. (1972) for IDH and MDH-OD, Allen (1961) for LDH, Laylock et al. (1965) for MDH and Chagnon et al. (1981) for PGM. These enzymes were chosen because literature shows they had a good probability of being polymorphic and because of the availability of the staining technics.

Genetic models

The molecular structure of the enzymes examined, the number of loci as well as the number of alleles found at these loci in other species and the specificity of the tissues in which these loci were expressed, were all used to interpret the IEF patterns and to construct the genetic models.

As allelic variations were observed in the samples, the genetic models were adjusted by increasing the number of alleles. Several replica were made, especially when specimens showed variations in the IEF patterns of some of the enzymes.

Statistical analysis

The differences between (inter) and within (intra) samples were tested using a maximum likelihood technique (Smouse and Ward, 1978) applied to the proportions of the different alleles found in the samples. Also, a chi-square goodness of fit test was applied to the distributions of the various phenotypes in order to verify if the polymorphic loci were in Hardy-Weinberg equilibrium and also to confirm the proposed genetic model. In addition, the data were analysed with a multidimensional non-metrical scaling followed by a cluster analysis (UPGMA; Rohlf et al., 1981; Legendre and Legendre, 1979). The multidimensional scaling was required because of the non-metrical nature of genetic distances (Nei, 1972). A principal component analysis was then calculated on the results of the

multidimensional non-metrical scaling so that the major trends of variation in the reduced space are lined up with the coordinate axes (Rohlf et al., 1981).

Results

Length, age and maturity

Length distributions and age distributions of the samples are shown on figure 6 and figure 7, respectively. The U.S. samples showed a wider range of ages and lengths than the Canadian samples. BC84 fish were immature (stages 1 to 3) while IPE85 fish had already spawned (stages 7 and 8). Distribution of maturity stages of NY84 fish was as follows: 60% were ripe (stage 5), 20% were running ripe (stage 6) and 20% were immature (stages 1-3). Maturity stages of the NY85 sample were not determined.

Genetic models

Six enzymes, ACON, CAE, DID, GDH, GPI and SOD showed genetic variations in the IEF patterns for the two years studied. Table 2 shows the number of specimens per phenotype as well as the estimated allelic frequencies. Only alleles having frequencies of 1% or greater are shown.

Results indicated that ACON was coded at one locus, as there was one main band with sometimes one or two secondary bands more anodic. Two anodic alleles (3 and 5) and one cathodic (4) compared with the most common allele (1) could be detected. An anodic band (2), intermediate to bands 1 and 4 was also observed. It was not retained because of the inconsistencies of the results between 1984 and 1985. The enzymatic activity of ACON appeared relatively fragile as a number of individuals showed little or no activity. Therefore they were not included in the analysis for that enzyme.

CAE showed a more complex pattern. Nine to 13 bands, produced at 2 or 3 loci, were detected depending on the individual examined. The locus showing variations showed one main band with 3 secondary cathodic bands. Three anodic alleles (3,5,7) and 4 cathodic (2,4,6,8) to the most common allele (1) are observed.

Only one band coded at one locus was observed for the DID and GDH with occasionally a more anodic secondary band. The one allele that was found to vary (2) for each of the enzyme is cathodic compared with the common allele (1). As for ACON, some of the specimens collected in 1984 could not be retained for analysis due to very low activity.

Three to five bands are observed for GPI with a sixth one being added in the variants. At least two loci and possibly 3 coded this enzyme. The locus showing variations produced one or two bands for the common and variant phenotype respectively. Four alleles could be detected: one anodic (3), two cathodic (2,4) compared with the most frequent allele. One or two secondary anodic bands were occasionnally observed.

Three bands were produced at two loci for SOD, the intermediate band being an association of the other two. A cathodic variant (allele 2) was detected at the most cathodic locus.

According to their tissular activity, the GPD and IDH would each be coded at 2 loci, the LDH at 3 and the MDH at 2 or 3 loci. The 10 enzymes other than those previously mentioned would be coded at one locus. Without variations allowing to verify the genetic model of the MDH and of the other loci of the GPI and CAE, the minimal number of loci possible (2) was postulated for these enzymes. Therefore, 28 loci were studied among the 20 enzymes of the study.

Sample comparison

Of the 20 enzymes studied, six appeared to be polymorphic i.e. had several different alleles, eleven did not show any variation and 3 showed inconsistent variations. Table 2 shows the distribution of the phenotypes and the allelic frequencies of the six polymorphic enzymes for the four samples analyzed. The chi-square test of the Hardy-Weinberg equilibrium showed no significant difference at $\alpha = 0.05$ for the six polymorphic loci for the 1984 and 1985 samples. The chi-square test has also been applied to each locus after regrouping the samples to artificially create a mixed population in case the two groups were distinct. No significant difference was found.

Table 3 shows the results of the maximum likelihood test on the allelic proportions of the samples (table 2). When the variability between regions (inter) was compared with an anova to the variability within regions (intra) at the level of the individual loci or of their sum, no significant differences were found ($p > 0.05$). The within region comparison can also be considered as a between year comparison. However, if the individual values of the statistic lambda (Λ), which have approximately a chi-square distribution, are considered, it appeared that a number of these values are significant between the regions (ACON and GDH) and within the regions (ACON-NORTH; GDH-NORTH; SOD_2-NORTH and SOUTH).

To try to evaluate the source of variability found within the regions, analyses taking into account the ages were carried out. Only the groups having at least 20 individuals of the same age for one or the other of the polymorphic loci have been retained for the analysis.

Table 4 shows the number and proportions of alleles found in the four groups that met the aforementioned condition. These were age 2 BC84, age 3 IPE85, age 3 NY85 and age 4 NY85. The proportion of Acon-3 allele is much larger in the BC84-2 group than in the rest of the samples.

Figure 8 shows the results of the cluster analysis made on the genetic distances found between the age groups (table 5) and figure 9 shows the principal component analysis on the multidimensional non-metrical scaled results. These two figures lead to the same conclusions. BC84-2 and

IPE85-3 appear to be grouped together and NY85-3 and NY85-4 are grouped together (figure 8). These groupings were also suggested in the first principal component (figure 9). The maximum likelihood analysis of the two groups thus formed was not significant when tested with an anova (table 6). However, if the individual lambdas are examined, it was noted that the within region variability (intra) was entirely in the northern region for ACON, GDH and SOD_2. Also a significant variability for ACON and SOD_2 was found between regions.

Discussion

The cluster and principal component analyses suggested some separation of the northern and southern areas although not statistically significant according to the maximum likelihood test. This inconclusive result may stem from particular characteristics of the northern area samples.

It is interesting to note that BC84 and IPE85 were more different from one another, even if it is essentially the same year-class sampled in two consecutive years, than NJ84 and NY85 (table 3) which show a more heterogeneous age and length composition. This could come from an effect of the sexual maturation occurring between age 2 and age 3 on the genetic characteristics of mackerel.

The quality of the biochemical analyses does not appear to be responsible for these inconsistencies, since the same techniques have been used on both samples. It should be noted however that the genetic tags showing the greatest heterogeneity in the northern samples (ACON, GDH, SOD), sometimes had patterns difficult to interpret depending on samples or individuals examined. These results are not conclusive enough to warrant a change in the conclusion reached in ICNAF.

B.4. Conclusions on stock structure in the Gulf of Maine Area

The conclusions on mackerel stock structure in the Gulf of Maine Area are unaltered from those previously reached in ICNAF. In the winter, a mixture of the southern and northern populations is exploited if the fishery is prosecuted in SA 5+6. The extent of actual mixing on the fishing grounds is unknown and the two populations, although occupying the same general area, may be geographically segregated. In the spring, the northern population leaves SA 5+6 to spawn in the Gulf of St. Lawrence. In the summer, the two populations are generally separated and the catches could probably be attributed to either population based on the area of capture.

C. IMPLICATIONS OF CONCLUSIONS ON STOCK STRUCTURE TO DEFINITION OF OPTIMAL BOUNDARIES FOR STATISTICAL AND MANAGERIAL PURPOSES

It is not presently possible to draw a "best line" to define the two mackerel populations. The critical area is not likely to be close to the International Court of Justice (ICJ) line, but rather somewhat southward of the ICJ line.

The ICJ line has no impact on mackerel management. The important factor to consider is the relative contribution of the two populations to a potential fishery on overwintering grounds.

D. RECOMMENDATIONS FOR FUTURE RESEARCH

Future research should focus on the relative sizes of the two populations. This could be achieved by stock size estimates based on egg production calculations. These however tend to be very sensitive to various parameters and assumptions. Investigation of the relative importance of the two populations and mixing on the overwintering grounds could also yield information on this subject. A potentially fruitful area of work is backcalculation of length at age 1. Based on the fact that fish born in the southern population start growing about 60 days before the northern fish, some separation could be found in l_1 lengths. This has been the subject of some investigations (Kulka and Stobo, 1981; Hunt, pers. comm.) but a comprehensive study now appears to be required.

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Table 1. Specific conditions used for the isoelectric focusing of 20 mackerel enzymes. O=eye, F=liver, MS=skeletal muscle. Pharmalytes (Pharmacia) and Ampholytes (gradient 7-9; LKB) were used to create pH gradients. A dash - means that the gradient was not used.

Enzymes	Relative parts of pH intervals used				Applications	
	2.5-5	4.6-5	5-8	7-9	Tissues analyzed	Dilution of* supernatant
Aconitate hydratase** (ACON; 4.2.1.3)	1	4	-	-	F	1/2
Alanine transaminase (ALT; 2.6.1.2)	1	2	1	-	F	1/2
Alcool dehydrogenase (ADH; 1.1.1.1)	-	1	2	-	F	-
Aspartate aminotransferase (AAT; 2.6.1.1)	-	4	1	-	F	1/10
Carboxylesterase (CAE; 3.1.1.1)	1	1	-	-	O	1/2
Cytochrome b_5 reductase (CBR; 1.6.2.2)	1	4	-	-	F	-
Glucose dehydrogenase (GDH; 1.1.1.47)	-	1	-	-	F	-
Glucosephosphate isomerase (GPI; 5.3.1.9)	1.5	-	4	2.5	O	1/10
Glutathione reductase (GSR; 1.6.4.2)	1	1	-	-	F	1/4
Glycerol-3-phosphate dehydrogenase (GPD; 1.1.1.8)	1	-	2	-	MS F	1/6 1/8
Hydroxyacylglutathione hydrolase (HAGH; 3.1.2.6)	1	-	2	-	F	1/2
D-Iditol dehydrogenase (DID; 1.1.1.15)	-	2	1	-	F	-
Isocitrate dehydrogenase ($NADP^+$) (IDH; 1.1.1.42)	-	1	2	-	MS	1/5

Table 1. (cont'd)

Enzymes	Relative parts of pH intervals used				Applications	
	2.5-5	4.6-5	5-8	7-9	Tissues analyzed	Dilution of* supernatant
Lactate dehydrogenase (LDH; 1.1.1.27)	1	-	5	1	0	1/4
Malate dehydrogenase (MDH; 1.1.1.37)	1	-	2	-	F	1/10
Malate dehydrogenase (oxaloacetate-decarboxilant). ($NADP^+$) (MDH-OD; 1.1.1.40)	1	-	1	-	F	1/2
Mannosephosphate isomerase (MPI; 5.3.1.8)	-	1	1	-	F	1/2
Phosphoglucomutase (PGM; 2.7.5.1)	1	-	3	1	F	1/10
Phosphogluconate dehydrogenase (decarboxilant) (PGD; 1.1.1.44)	1	3	-	-	F	1/10
Superoxide dismutase (SOD; 1.15.1.1)	-	3	1	-	F	1/12

* The dilution may change between samples and to a lesser extend between individuals.

** The pH gradient used in 1985 was made of Pharmalytes from a single pH interval 4.5-5.4

Table 2. Phenotypic distribution and allelic frequencies observed at 6 polymorphic loci of Atlantic mackerel sampled in 1984 and 1985 in the Gulf of St.Lawrence (BC84, IPE85) and off the U.S. Coast (NJ84, NY85). Alleles and phenotypes having frequencies smaller than 1% are not included.

Enzymes Loci	Phenotypes	Numbers observed						Allele	Allelic frequencies ± standard error					
		Gulf of St.Lawrence			U.S. Coast				Gulf of St.Lawrence			U.S. Coast		
		BC84	IPE85	Total	NJ84	NY85	Total		BC84	IPE85	Total	NJ84	NJ85	Total
ACON	1	71	126	197	46	127	173	1	0,72±0,03	0,92±0,03	0,82±0,02	0,80±0,04	0,93±0,03	0,89±0,02
	1-3	53	18	71	24	18	42	3	0,27±0,03	0,06±0,01	0,16±0,02	0,18±0,03	0,06±0,01	0,10±0,01
	3	10	0	10	1	0	1	4	0,01±0,01	0,02±0,01	0,02±0,01	0,02±0,01	0,01±0,01	0,01±0,01
	1-4	2	6	8	3	3	6							
	3-4	1	0	1	0	0	0							
		137	150	287	74	148	222							
CAE_2	1	74	58	132	34	51	85	1	0,61±0,03	0,63±0,03	0,62±0,02	0,65±0,04	0,59±0,03	0,61±0,03
	1-2	19	6	25	7	11	18	2	0,07±0,01	0,05±0,01	0,06±0,01	0,06±0,02	0,06±0,01	0,06±0,01
	2	2	0	2	0	1	1	3	0,31±0,02	0,31±0,03	0,31±0,02	0,28±0,04	0,33±0,03	0,31±0,02
	1-3	78	45	124	20	56	76	6	0,01±0,01	0,01±0,01	0,01±0,01	0,01±0,01	0,02±0,01	0,02±0,01
	2-3	4	8	12	2	6	8							
	3	22	14	36	10	18	28							
	1-6	6	1	7	2	5	7							
	3-6	0	2	2	0	1	1							
		205	135	340	75	149	224							
DID	1	132	49	181	71	46	117	1	0,98±0,01	0,99±0,01	0,98±0,007	0,98±0,01	0,96±0,02	0,97±0,01
	1-2	6	1	7	3	4	7	2	0,02±0,01	0,01±0,01	0,02±0,007	0,02±0,01	0,04±0,02	0,03±0,01
		138	50	188	74	50	124							
GDH	1	115	113	228	54	97	151	1	0,94±0,01	0,95±0,01	0,95±0,01	0,99±0,01	0,995±0,005	0,99±0,02
	1-2	15	13	28	1	1	2	2	0,06±0,01	0,05±0,01	0,05±0,01	0,01±0,01	0,005±0,005	0,01±0,02
		130	126	256	55	98	153							
GPI_2	1	118	39	157	59	36	95	1	0,90±0,02	0,87±0,03	0,89±0,02	0,89±0,03	0,88±0,03	0,89±0,02
	1-2	23	8	31	12	10	22	2	0,09±0,02	0,11±0,03	0,10±0,01	0,10±0,02	0,10±0,03	0,10±0,02
	2	1	1	2	1	0	1	3	0,01±0,01	0,02±0,01	0,01±0,01	0,01±0,01	0,02±0,01	0,01±0,01
	1-3	1	1	2	1	2	3							
	2-3	1	1	2	0	0	0							
		144	50	194	73	48	121							
SOD_2	1	124	45	169	65	49	114	1	0,93±0,02	0,99±0,01	0,95±0,01	0,93±0,02	0,99±0,01	0,95±0,01
	1-2	19	1	20	9	1	10	2	0,07±0,02	0,01±0,01	0,05±0,01	0,07±0,02	0,01±0,01	0,05±0,01
	2	0	0	0	1	0	1							
		143	46	189	75	50	125							

Table 3. Maximum likelihood analysis of the 6 polymorphic loci between the Gulf of St.Lawrence (north) and the U.S. coast (south). Lambda (Λ) is the likelihood statistic and df are the degrees of freedom. Only known age individuals were included in the analysis. a: $p < 0.05$; b: $p < 0.01$; c: $p < 0.0005$.

Variation	ACON		CAE_2		DID		GDH		GPI_2		SOD_2		Total	
	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df
Inter-region	8.88^a	2	0.07	3	1.02	1	5.55^a	1	0.35	2	1.08	1	16.95	10
Intra-region	51.59^c	4	3.66	6	1.69	2	5.31	2	2.17	4	13.00^c	2	77.42^c	20
North	47.92^c	2	1.01	3	0.68	1	5.05^a	1	1.34	2	5.40^a	1	61.40^c	10
South	3.67	2	2.65	3	1.01	1	0.26	1	0.83	2	7.60^b	1	16.02	10
Total	60.46^c	6	3.73	9	2.71	3	10.86^a	3	2.52	6	14.08^c	3	94.36^c	30
F	0.66		0.04		1.21		2.09		0.32		0.17		0.44	
df	(3.6)		(3.6)		(1.2)		(1.2)		(2.4)		(1.2)		(10.20)	

Table 4. Observed numbers (N) and proportions (P) of the alleles found at 6 polymorphic loci in the Gulf of St.Lawrence (BC84, IPE85) and U.S. (NY85) samples. Only those groups having at least 40 alleles (20 individuals) were included in the analysis.

Locus	Allele	BC84-2		IPE85-3		NY85-3		NY85-4	
		N	P	N	P	N	P	N	P
ACON	1	185	0.72	211	0.91	37	0.88	66	0.92
	3	70	0.27	16	0.07	5	0.12	6	0.08
	4	3	0.01	5	0.02	0	0.00	0	0.00
		258		232		42		72	
CAE_2	1	240	0.60	130	0.58	27	0.64	46	0.62
	2	26	0.07	10	0.05	1	0.02	6	0.08
	3	122	0.31	76	0.35	12	0.29	22	0.30
	6	6	0.02	4	0.02	2	0.05	0	0.00
		394		220		42		74	
DID	1	258	0.98	95	0.99	13	0.93	34	0.94
	2	6	0.02	1	0.01	1	0.07	2	0.06
		264		96		14		36	
GDH	1	233	0.95	216	0.99	33	0.97	52	1.00
	2	13	0.05	2	0.01	1	0.03	0	0.00
		246		218		34		52	
GPI_2	1	244	0.89	81	0.86	12	0.86	30	0.83
	2	26	0.10	11	0.12	1	0.07	5	0.14
	3	2	0.01	2	0.02	1	0.07	1	0.03
		272		94		14		36	
SOD_2	1	253	0.94	85	0.99	14	1.00	36	1.00
	2	17	0.06	1	0.01	0	0.00	0	0.00
		270		86		14		36	

Table 5. Genetic distances between Gulf of St.Lawrence (BC84, IPE85) and U.S. (NJ84, NY85) samples. Ages are taken into account below the diagonal and are not above the diagonal. Only those groups having at least 20 individuals at one or the other locus were included in the analysis.

	BC84	IPE85	NJ84	NY85	
BC84-2		.0044	.0017	.0042	BC84
IPE85-3	.0040		.0013	.0001	IPE85
NY85-3	.0030	.0011		.0012	NJ84
NY85-4	.0038	.0003	.0009		NY85
	BC84-2	IPE85-3	NY85-3	NY85-4	

Table 6. Maximum likelihood analysis of the 6 polymorphic loci between the Gulf of St.Lawrence (north) and the U.S. coast (south). Lambda (Λ) is the likelihood statistic and df are the degrees of freedom. The groups were formed according to the cluster analyses results (fig. 6). a: $p < 0.05$; b: $p < 0.01$; c: $p < 0.005$.

Variation	ACON		CAE_2		DID		GDH		GPI_2		SOD_2		Total		Λ/df
	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df	Λ	df	
Inter-region	8.33^a	2	0.39	3	2.30	1	1.36	1	2.12	2	4.85^a	1	19.35^a	8	2.42
Intra-region	37.18^c	4	7.54	6	0.68	2	9.84^b	2	2.35	4	4.70^a	1	62.29^c	19	3.28
North	36.80^c	2	1.76	3	0.64	1	7.97^c	1	1.49	2	4.70^a	1	53.36^c	10	
South	0.38	2	5.78	3	0.04	1	1.87	1	0.86	2	0.00	0	8.93	9	
Total	45.51	6	7.93	9	2.98	3	11.20^a	3	4.47	6	9.55^b	2	81.64^c	27	
F	0.48		0.10		6.76		0.28		1.80		0.17		0.74		
df	(3.6)		(3.6)		(1.2)		(1.2)		(2.4)		(1.1)		(9.21)		

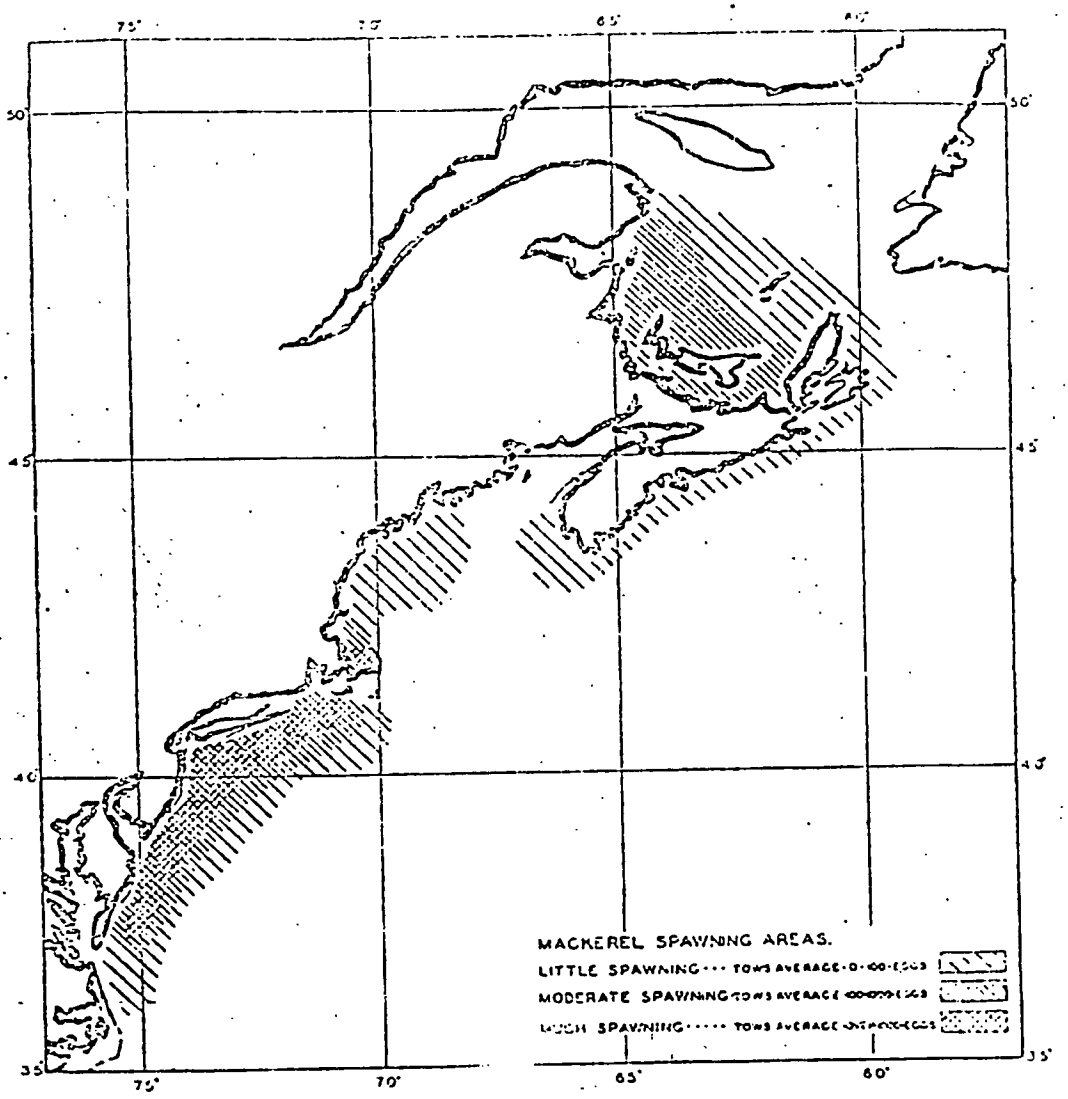

Figure 1. Relative intensity of mackerel spawning in various regions along the Atlantic coast of North America, as indicated by the average number of eggs caught in plankton nets. (From Sette, 1943, p. 163).

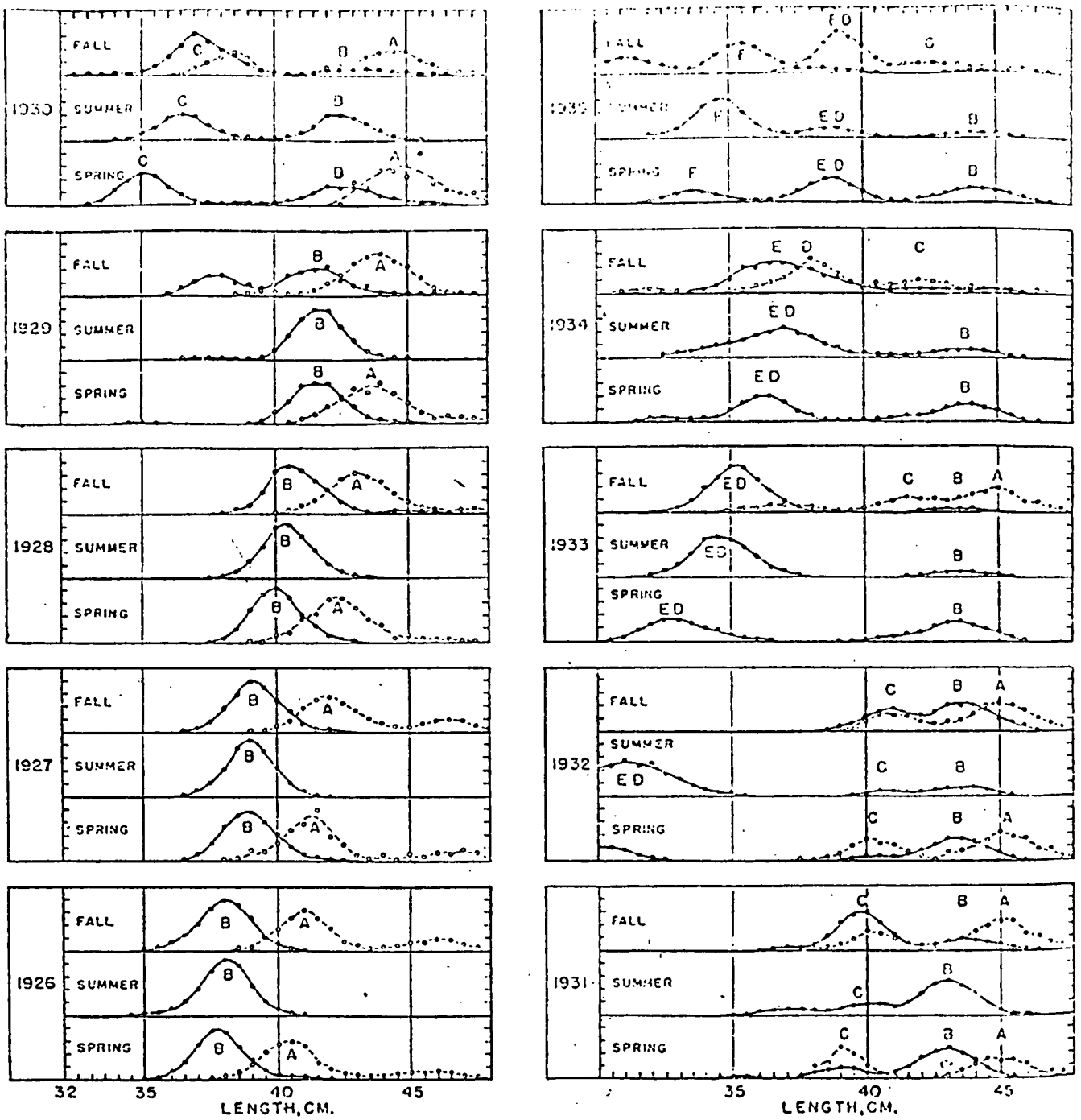

Figure 2. Length-frequency distributions illustrating the size composition of the two types of mackerel population: southern contingent (solid dots and solid lines) and northern contingent (open circles and broken lines), during 10 seasons. The curves are on a percentage basis and the graduation marks on the vertical axis represent 5 percent intervals. Letters identify mode corresponding to different year classes (From Sette, 1950, p. 282).

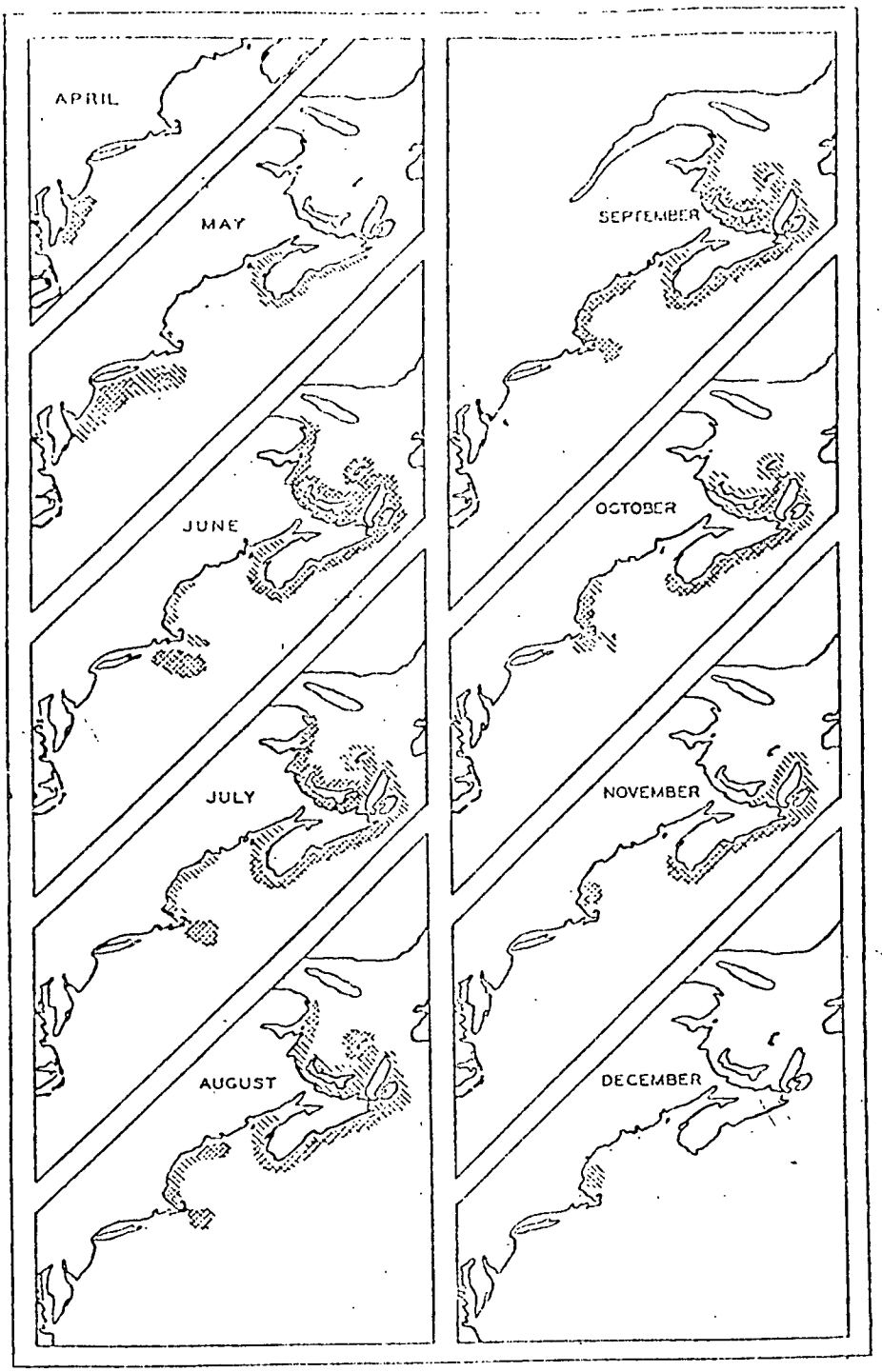

Figure 3. Approximate seasonal distribution of the mackerel as indicated by location of the commercial fishery in the various months of the fishing season. (From Sette, 1950, p. 255).

21.2	Week
7.62	Temperature (°C)
30.72	Salinity (0/00)
/9/	Fishing area

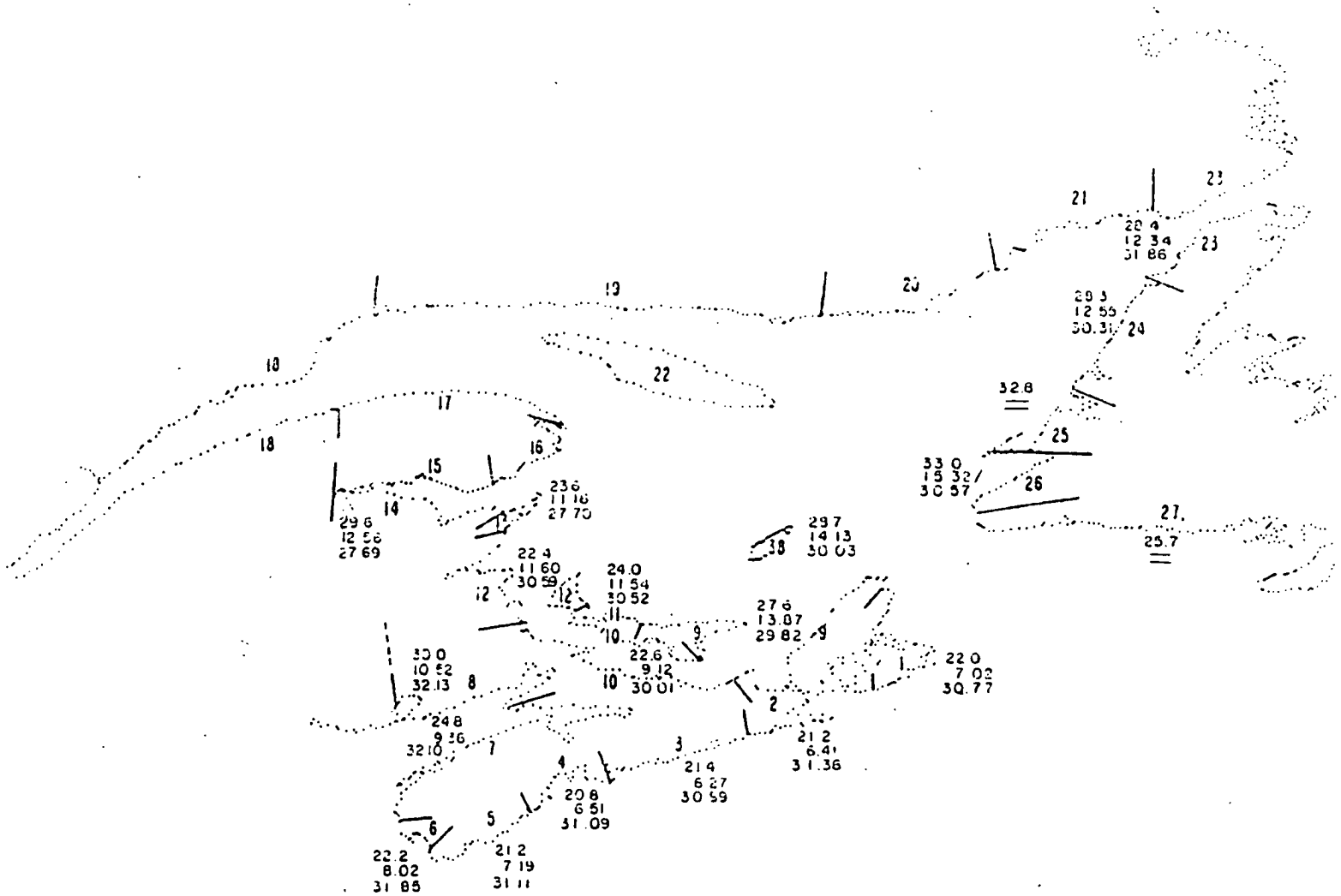

Figure 4. Spatial distribution of average temperature data, salinity and week of arrival of mackerel as determined from the level of 5% of cumulative catch.

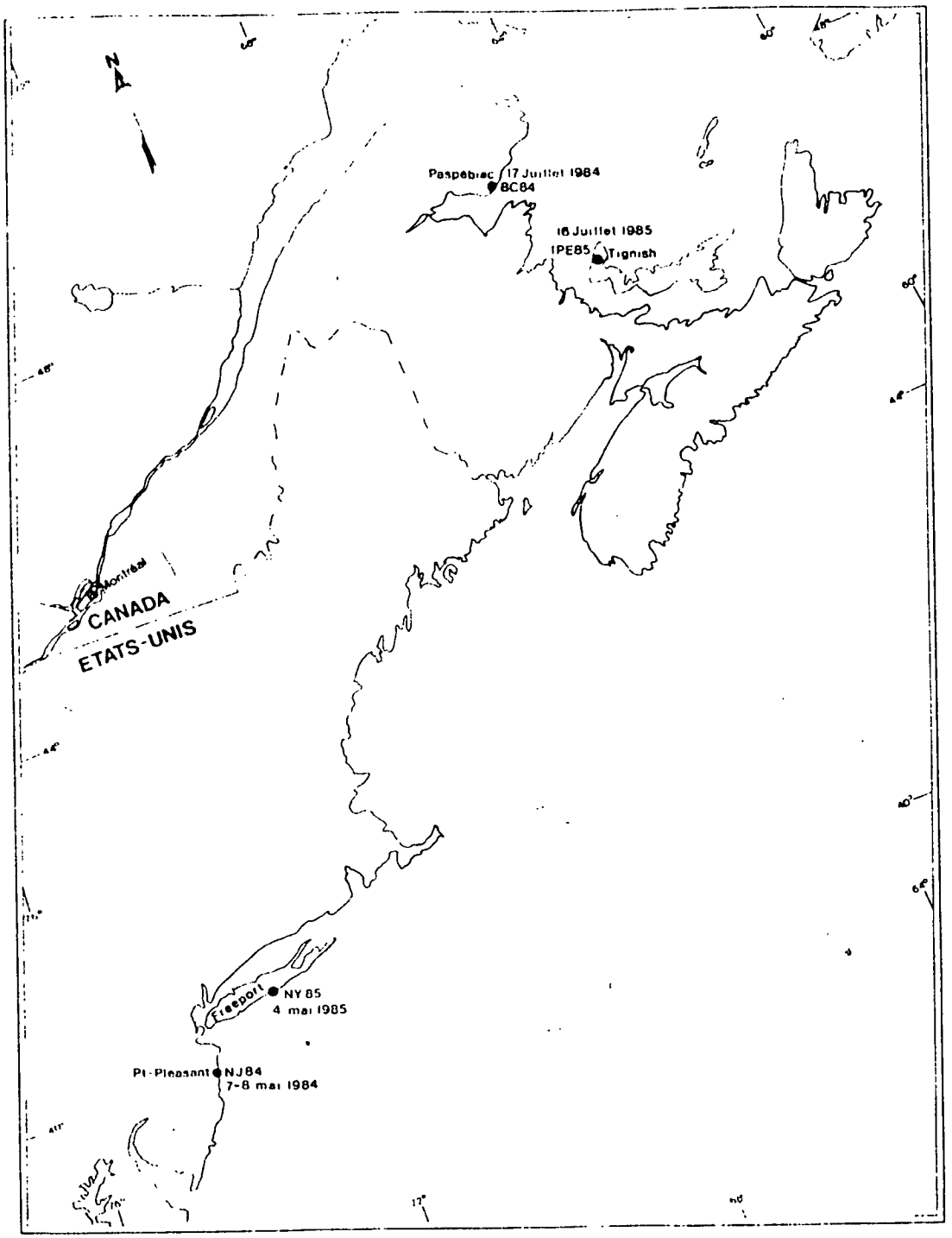

Figure 5. Geographic locations of sampling sites of Paspebiac, Chaleurs Bay (BC84), Tignish, Prince Edward Island (IPE85), Point Pleasant, New Jersey (NJ84) and Freeport, New York (NY85).

Figure 6. Length distributions of BC84 (a), IPE85 (b), NJ84 (c) and NY85 (d).

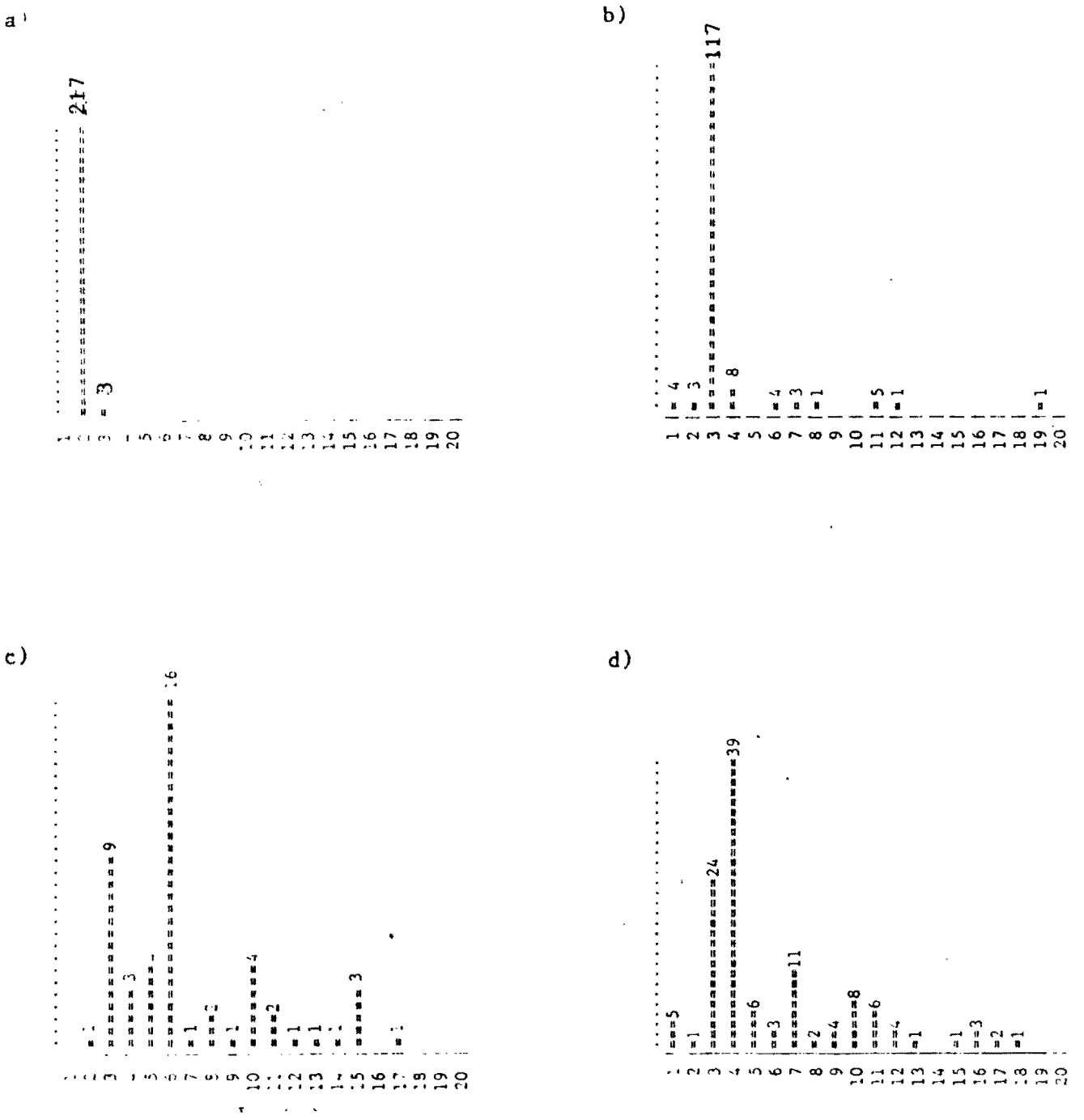

Figure 7. Age distributions of BC84 (a), IPE85 (b), NJ84 (c) and NY85 (d).

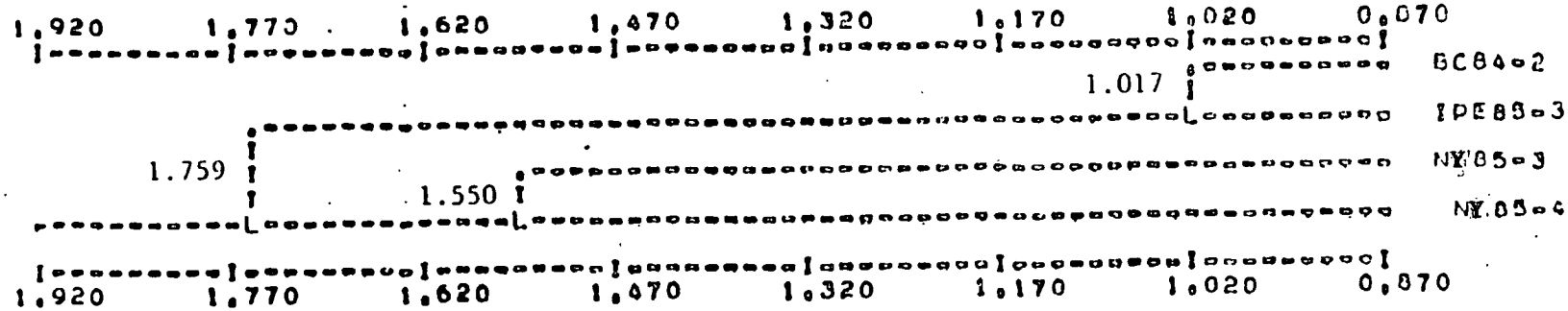

Figure 8. Cluster Analysis of the genetic distances observed between the Gulf of ST. Lawrence mackerel samples (BC84-2, IPE85-3) and those off the U.S. (NY85-3, NY85-4). A vertical bar indicates the level at which two groups are linked. Only the groups having more than 20 individuals for one or the other of the loci studied were used in the analysis. The correlation between the original data and the regrouped data is r=0.836.

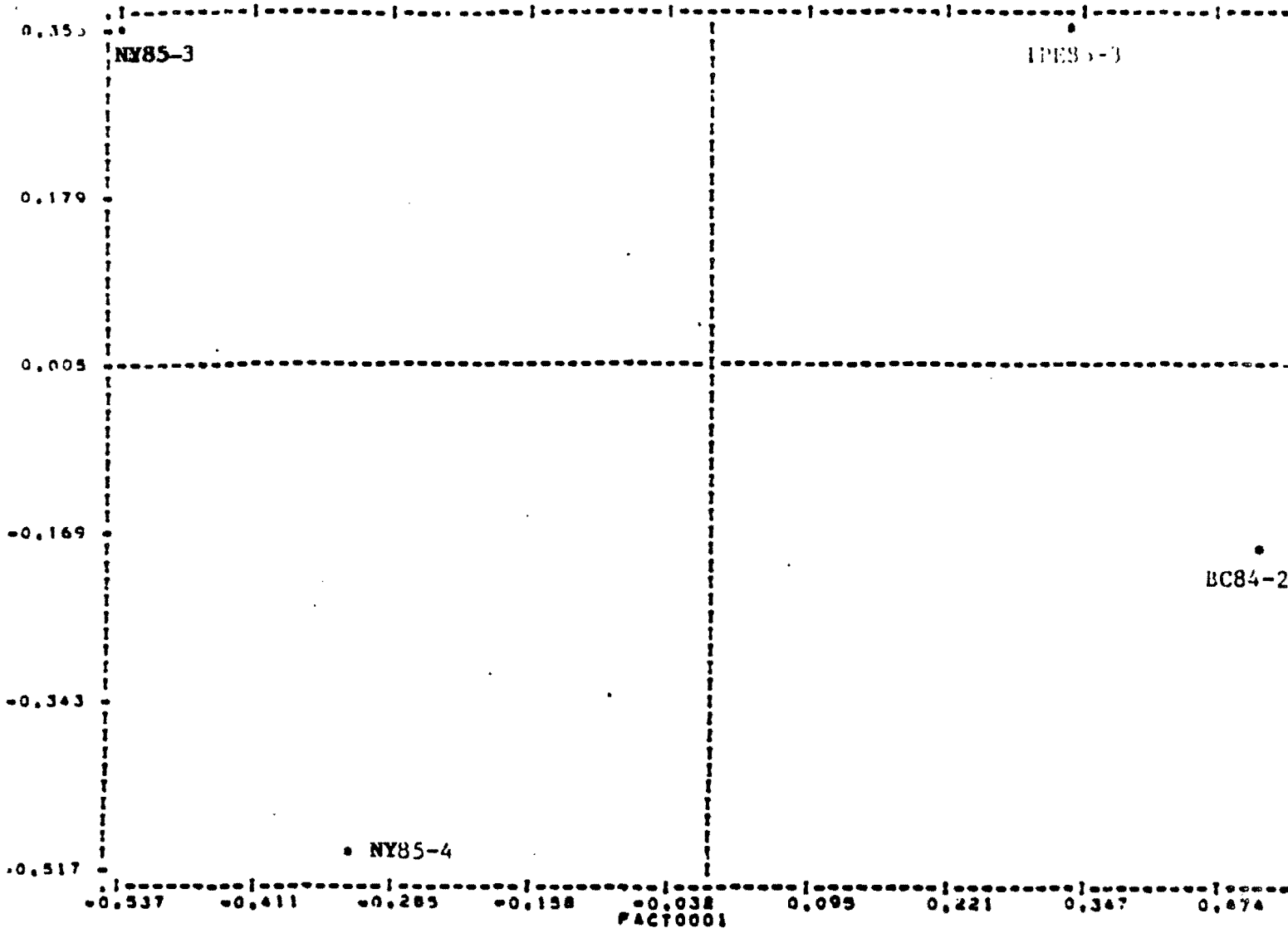

Figure 9. Principal component analysis of the multidimensional scaled results of the genetic distances between Gulf of St.Lawrence mackerel samples (BC84, IPE85) and those from the U.S. (NY85). Only the groups having more than 20 individuals for one or the other of the loci studied were used in the analysis. Factors 1 and 2 represent respectively 58% and 41% or the variability.