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THE STOCK IDENTIFICATION OF THE CAPE HORSE MACKEREL, *TRACHURUS*
TRACHURUS CAPENSIS (PISCES: CARANGIDAE).

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Submitted in fulfillment of the requirements for the degree of Master of Science in the Department of Ichthyology and Fisheries Science at Rhodes University.

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ABSTRACT

Three stocks of the Cape horse mackerel, Trachurus trachurus capensis, have been recognised in the ICSEAF convention region off southern Africa (Figure 1) on the basis of catch distribution and biological analyses. They were identified as being off Namibia (ICSEAF Divisions 1.3 and 1.4), off the West Coast of South Africa (Div. 1.6) and off the South Coast (Div. 2.1 and 2.2). Recently, speculation as to the accuracy of the classification of the South African populations has arisen. The aim of this study was to determine the number of stocks in Divisions 1.6, 2.1 and 2.2, using methodology which assessed the spatial and temporal nature and the phenotypic and genotypic characteristics of the species.

The distribution of horse mackerel was evaluated by studying the trends in catch data and length frequency distributions obtained from the demersal industry during 1986 to 1988 and from the demersal biomass cruises in 1987 and 1988. Adult fish, found in Div. 2.1 and 2.2, probably migrated; during the months in which horse mackerel were expected to spawn, CPUE values were higher over the central Agulhas Bank than in the east of the study region. During the quiescent period, catches and numbers were higher in the latter region. Juvenile horse mackerel were found in the nursery areas utilised by pelagic fish and it is likely that they were transported northward from the Agulhas Bank. A decrease in biomass of individuals in Div. 1.5 indicated a separation between a northern and a southern population.

Analyses of the phenotype, or epigenetic characters, of horse mackerel were used as a further test of stock integrity. Monthly samples were drawn from Div. 1.6, 2.1 and 2.2 during May 1988 to June, 1989. Comparisons for the values obtained from growth, length-at-50%-maturity and the season of otolith ring formation from each region showed no significant variation in the phenotype. Morphometric analysis proved inconclusive. Monthly gonadosomatic indices show that fish south of the Orange River share the same spawning season. Reports from the literature show that horse mackerel in the latter region differ from those of northern Namibia in spawning season, age-at-50%-maturity and season of otolith ring formation.

The genetic structure of the populations of horse mackerel was evaluated by means of a restriction enzyme analysis of the Mitochondrial DNA of 37 fish collected from Divisions 1.4, 1.5, 1.6, 2.1 and 2.2. Two composite genotypes of horse mackerel were found; one belonging to fish in Div. 1.4 and one to fish in Div. 1.6, 2.1 and 2.2. The genetic distance between the two genotypes, 0.07, was the expected distance between two populations at a subspecies level. Fish in Div. 1.5 consisted of both genotypes and may be a region of mixing between the two populations. The

interpretation of results was cautioned; previous work has shown that the migration of a small number of individuals between two stocks can be expected to maintain a low variation between the populations.

In concluding, it was recommended that the horse mackerel be managed as two stocks; one in Div. 1.3 and 1.4 and one in Div. 1.6, 2.1 and 2.2.

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This thesis is dedicated to my car, which had a remarkable propensity to break down regularly and without which my study would have been impossible.

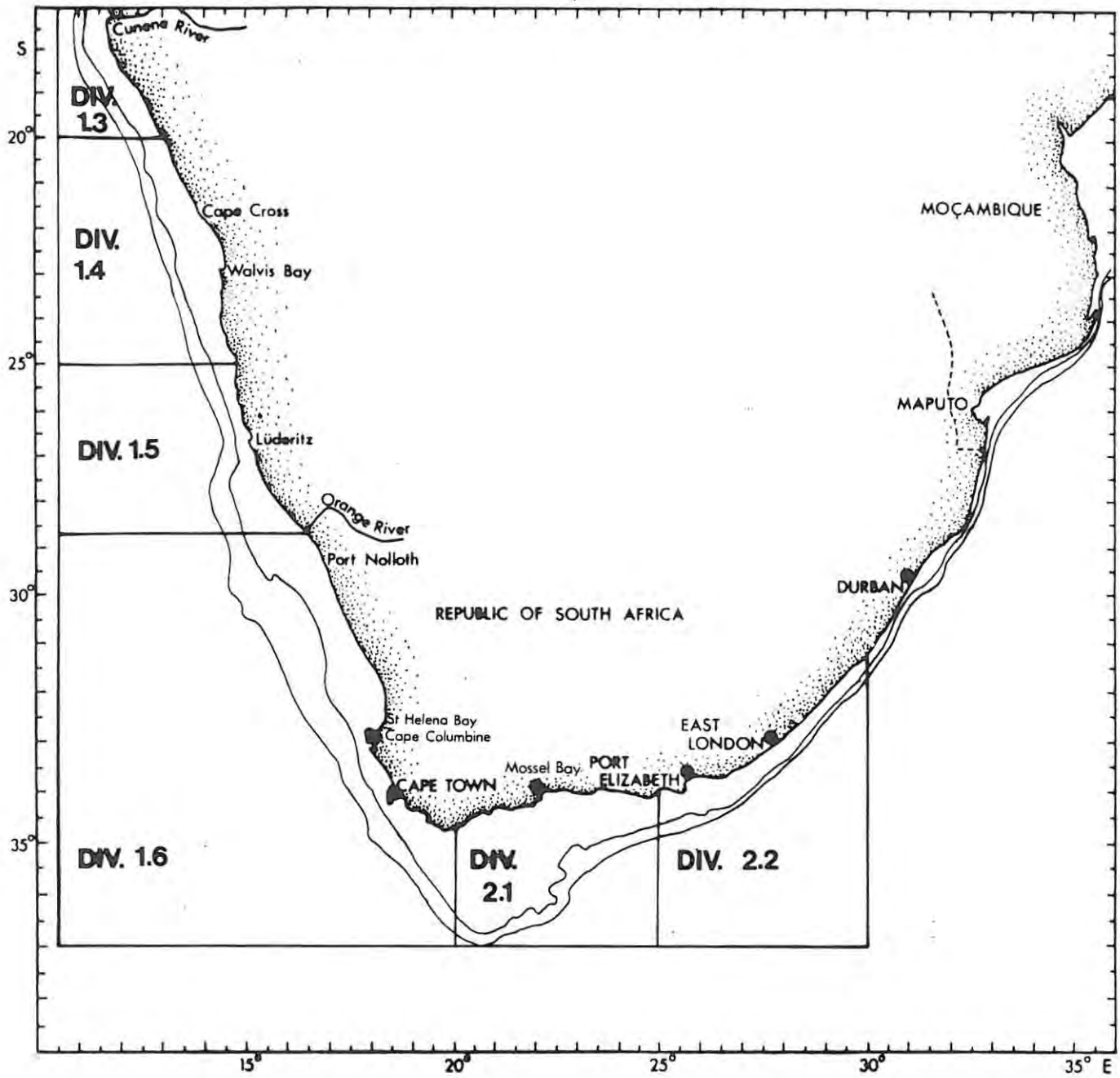


FIGURE 1. Map showing the ICSEAF convention regions and the study area.

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CHAPTER 1 : INTRODUCTION

INTRODUCTION

The Cape horse mackerel, *Trachurus trachurus capensis* Linnaeus 1758 has a distribution range from southern Angola on the west coast of southern Africa to Delagoa Bay on the east coast (Smith-Vaniz, 1986). A further two species of the same genus are found at the extremities of this range ; *Trachurus trecae* in the west and *Trachurus delagoa* in the east. *T.t.capensis* has been deemed one of the most important commercially exploited species in the region controlled by the International Commission for the Southeast Atlantic Fisheries (ICSEAF) (Payne, 1986 ; ICSEAF, 1986 ; Hecht, 1989); the full area is shown in Figure 1.

Historically, juvenile horse mackerel were the first to be exploited. The pelagic fishery exploited horse mackerel on the West Coast (ICSEAF division 1.6) in the 1940s in response to a demand for canned fish during the second world war (Geldenhuys, 1973; Crawford, 1980). During those years the species sometimes accounted for up to half of the catch of pelagic fish. Horse mackerel catches formed a significant part of the pelagic landings until 1958, but thereafter, there was a steady decline. Adult *T.t.capensis* were often caught too by demersal trawlers targeting for Cape hake or Agulhas sole on the South-East Coast and, more recently, midwater trawlers have been employed specifically for the purpose of catching the species directly. Midwater trawlers (the majority belonging to foreign fleets) have operated predominantly off Namibia (ICSEAF Divisions 1.3, 1.4 and 1.5), although just prior to South Africa's declaration of an Exclusive Fishing Zone in November 1977, heavy midwater effort was also deployed off the south coast (Div. 2.1 and 2.2), (Payne, 1986; Payne and Crawford, 1989). A growing internal market for horse

mackerel fished off South Africa has led to increased effort on the resource by the local industry. In 1989, certain companies equipped their trawlers with midwater gear designed to catch horse mackerel. Such increasing effort (and, therefore, increasing catches) necessitates consideration of an appropriate management strategy. Until recently, however, the Cape horse mackerel off South Africa received little research attention and, until 1989, were placed under "precautionary" quotas (Hatanaka, 1985; Payne, 1986; Kinloch *et al.*, 1986). During 1989, researchers at the Sea Fisheries Research Institute co-operated with others at the University of Cape Town in carrying out a more rigorous stock assessment of the species. The aim was to determine a Total Allowable Catch (TAC) so that uncontrolled escalation of catches and effort could be halted. A TAC for the species east of Cape Hangklip was set at 35 000 tons for 1990. However, many questions relevant to stock assessment remain unanswered, particularly whether there is a relationship between the horse mackerel caught by purse-seiners on the West Coast (Div. 1.6) and the adults on the South Coast. The present work will attempt to set about answering some of the questions.

Of primary importance in the development of an appropriate management strategy is the establishment of the number of 'stocks' of a species occurring within its exploitation range. The term 'stock' is vague in terms of a taxonomic status (Saila and Jones, 1983, cited in Brown *et al.*, 1987), but it has been labeled as a sub-unit of a species with properties distinct from those of another sub-unit. Defined as "a relatively homogeneous and self-contained population whose losses by emigration and accessions by immigration, if any, are negligible in relation to the rates of growth and mortality" (ICNAF, 1960), a stock

is deemed to have characteristic rates of growth, reproduction and mortality and is therefore genetically distinct (Ricker, 1972; Larkin, 1981; Booke, 1981; Ferris and Berg, 1987; Brown *et al.*, 1987). Given that, as inferred in the previous paragraph, stock assessments have to utilize such parameters for determining appropriate levels of exploitation, it can be expected that a population with parameters substantially different from those of a second population will be either over- or under-exploited, if the strategy for the latter population is applied to the former.

Three stocks of *T.t.capensis* have been identified in the ICSEAF region. The first, found off the coast of Namibia (ICSEAF Divisions 1.3, 1.4 and 1.5), has been shown to be genetically distinct from individuals found off South Africa (Zenkin and Komarov, 1981). Based on differential catch rates (De Villiers, 1977) and biological analyses (Draganik, 1977), it seemed that two other stocks may exist off the west (Div. 1.6) and east (Div. 2.1 and 2.2) coasts of South Africa. The hypothesis was apparently further substantiated by studies of the catch distribution of horse mackerel by the pelagic industry (Crawford, 1980): few catches were recorded north of latitude 30°S or east of 20°E, (Div.1.6). The purse-seiners were, therefore, thought to be exploiting a different population from that found on the South-East Coast. In studying the demersal fishery of the Agulhas Bank, Payne (1986) suggested that the declining juvenile stocks on the west coast were supported by the adult stocks on the Agulhas Bank, similar to the situation for anchovy, *Engraulis capensis* (Shelton and Hutchings, 1982). This would indicate a single southern stock, but studies by Hecht (1976) had earlier rendered this a moot point. Hecht (1976) proposed that the presence of a substantial population at the eastern extremity of the Agulhas Bank indicated a possible separation

in the ecosystem over the Bank. Recently, however, Hecht (1989) has challenged the former view by means of a biological comparison between the aforementioned stocks. He found that there was no basis for separation between the South African stocks on the grounds of this comparison. All this research was preliminary, however, and it is the purpose of this study to establish firmly the status the stocks of *T.t.capensis*.

Traditionally, the identity of a stock has been determined by means of physical characteristics (e.g. Lux, 1963; Copeman, 1977; Lindholm and Maxwell, 1988), but such characters have been shown to be sensitive to environmental factors (Clayton, 1981; Lindsey, 1981). Tagging experiments, length frequency distributions and analyses of catch distribution have proved successful in some cases (Sette, 1950; Stobo, 1976; Kearney, 1983; Calaprice, 1986), as have biological comparisons (Lux and Nichy, 1969; Ross and Sullivan, 1987). Recently, biochemical analyses have provided a further means of stock identification (Allendorf and Utter, 1979; Ferris and Berg, 1987; Avise, 1987a).

In attempting to establish the stock integrity of the Cape horse mackerel, it has been deemed wise to utilize differing methods, each independent of each other. Should differences or similarities be found, a common underlying factor (for example, an environmental effect) will not be seen as a bias affecting the data. It is for this reason that the stock identity of *T.t.capensis* is determined in this study, utilizing methods which may be placed into three categories. The first methods, grouped under population dynamics, will include studies of spatial and temporal distribution of the species. The second, the study of physical characteristics, will include the

morphology, reproduction, growth and maturity of *T.t.capensis*. Lastly, the third category, the characterization of the genotype, will attempt to determine the number of genetic stocks of the species.

CHAPTER 2 : CATCH AND LENGTH FREQUENCY DISTRIBUTION

INTRODUCTION

The determination of spatial and temporal distributions of populations within the range of a species is an important consideration in stock identification. Population distribution is often the character by which sympatric stocks are initially recognized (Ihssen *et al.*, 1981). Attempts at assessing the dynamics of stock distribution have been in the form of tagging (Lux, 1963; Casselman *et al.*, 1981; Beardsley, 1985), studies of the distribution of eggs and larvae (O'Toole, 1977; Badenhorst and Boyd, 1980; Shelton and Hutchings, 1982), commercial catch distribution (Parrack, 1981; Farrugio, 1981; Schulein, 1986; Payne, 1986) and length frequency distribution (Sette, 1950; Cruickshank, 1989). The last two methods have the advantage in showing regional changes in density and in life history patterns using data collected in routine monitoring processes.

It is the province of this study to examine the catch distribution of *Trachurus trachurus capensis* south of the Orange River in recent years, given that original assessments of the stock integrity of horse mackerel were conducted by the same method (De Villiers, 1977; Draganick, 1977; Crawford, 1980). The present attempt will be supported by studies of length distribution on the basis that life history patterns can be explored with such data. The findings will be compared to those of previous studies, available in the literature. It must be stressed that the results of this study are expected to serve as a preliminary insight into the distribution of the southern horse mackerel stocks, thereby facilitating the precise methods of stock identification to be applied.

METHODS

The aim of the present study was to test the hypothesis forwarded by Draganik (1977) and Crawford (1980). Both authors divided *T.t.capensis* south of the Orange River into two stocks on the basis of differential catch distribution recorded by the fishing activities of the pelagic fleet. The stocks were identified as existing off the west and east coasts of South Africa respectively. With the assumption that the pelagic industry exploited primarily juvenile fish, the catch distribution and biomass of adult fish was assessed here. Further, an attempt was made to explore the age-specific distribution patterns of horse mackerel, rendering the exploration of life-history patterns possible.

1. Catch Data Analyses

Catch distribution and seasonal catch rates of adult horse mackerel south of the Orange River were assessed using catch data collected from the demersal industry and processed at the Sea Fisheries Research Institute (SFRI) in Cape Town. Using a grid system devised by the SFRI which covers all the trawling grounds, data logs were compiled during each sea trip by all commercial trawlers. The following, among other parameters, were recorded at the completion of each net drag; catch locality by grid number, catch composition by mass, fishing effort in drag hours and depth in meters. The data were collated at SFRI and the catch-per-unit-effort (CPUE) per grid per month and per year calculated. Effort was standardized to that of a particular vessel class. The corrected CPUE was therefore used in this study.

For the purpose of this study, the fishing areas were divided into six regions according to bottom topography and fishing grounds (Fig. 2.1),

and the CPUE per grid per month was calculated. As horse mackerel has traditionally been a by-catch of the fisheries for Cape hake and sole, all catches in which horse mackerel was recorded were used for the calculations. As stated in the previous chapter, directed catching of horse mackerel has only commenced in earnest in the late 1980s. The procedure of taking all by-catches of horse mackerel for the analysis, irrespective of size or whether there was some perceived effort towards exploiting the resource, is defensible. Discarding practices have, for this analysis, been taken as being constant. Offshore and inshore catches were treated separately.

2.Length Frequency Distribution

Length frequency distribution was determined from data obtained during the R.S. *Africana* cruises in years 1987 and 1988. Six demersal cruises were conducted during this period; on the west coast during January and July 1987, and in February and August 1988; on the east coast during September 1987 and May 1988. Trawls were conducted at randomly selected stations on the basis of a stratum grid as described by Payne *et al.*, 1989. A 180 ft German bottom trawl net (the cod-end lined with pilchard netting to retain small fish) was trawled for a bottom time of 30 minutes at each station during daylight. Length measurements of the total catch, or a subsample if the catch was large, were used to map distributions of the size classes. Further, total biomass of horse mackerel was estimated by means of the aerial expansion method (Payne *et al.*, 1985) and is described as follows. Given that three values (the net mouth spread, the distance over which the net was dragged and the time of trawling) were known, the biomass per area trawled was determined. Values obtained for all regions trawled were then used to estimate the total biomass of the entire study region (the total area of which was known).

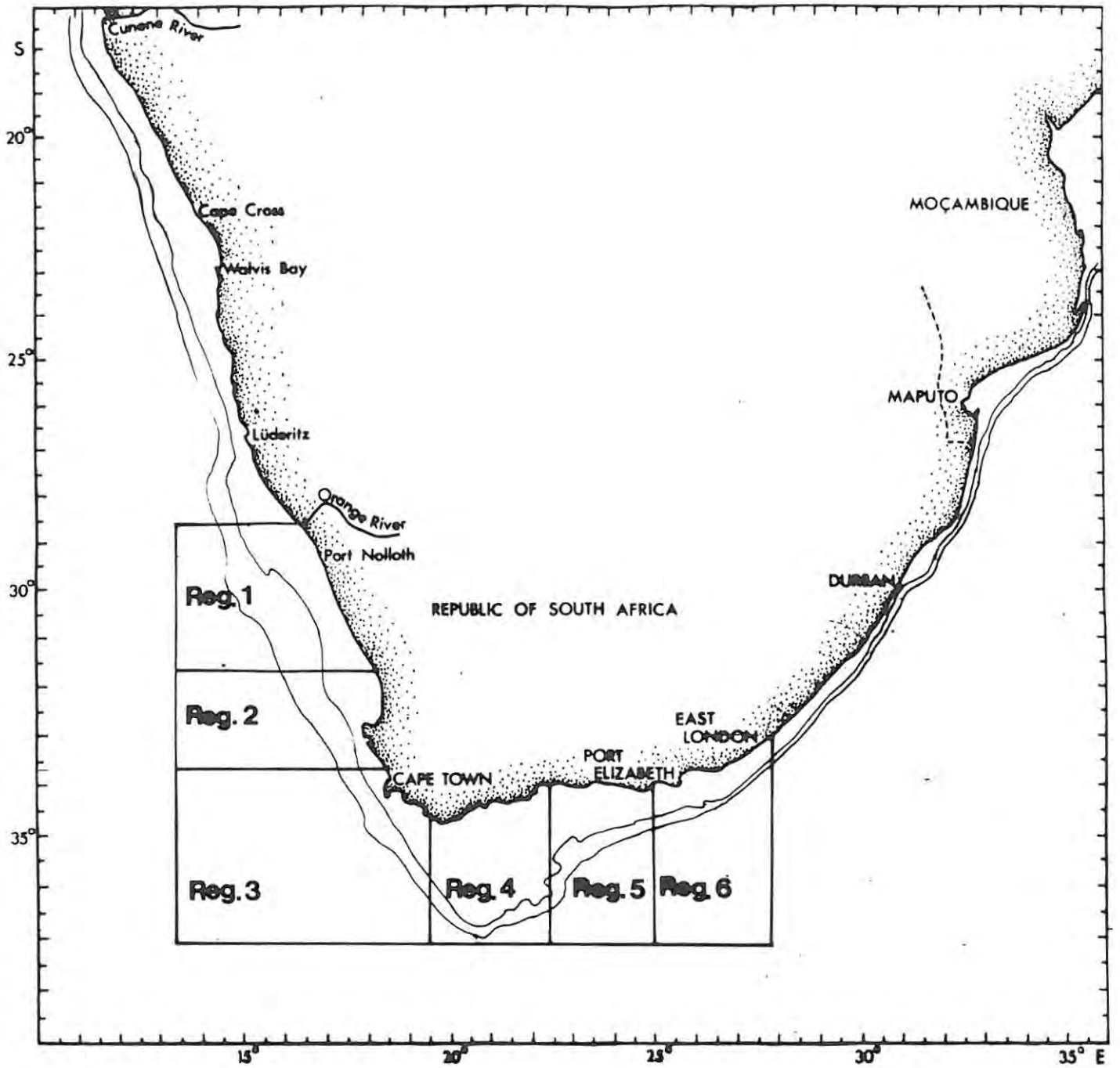


FIGURE 2.1: Map showing the division of the study area into regions which were used to calculate trends in catch-per-unit-effort of horse mackerel from the demersal industry

RESULTS

1. Catch Data Analyses

The trends in CPUE per month per region are shown in Figure 2.2 for the inshore industry and Figure 2.3 a-b for the offshore industry. Despite the large variance for each point, certain trends were noted to exist. There was no notable spatial discontinuity in the catch distribution of horse mackerel as shown by the inshore and offshore graphs. CPUE values were highest over the Agulhas Bank (regions 4 to 6, Figure 2.1), with a decline in values noted north of Cape Town off the West coast (regions 1 to 3). A seasonal trend was reflected by the inshore data (Fig. 2.2). During the months May to November, a decline in the CPUE values in the east (region 6) is accompanied with an increase of the values obtained over the Agulhas Bank (region 4). Such a result was not evident in the offshore data of regions 4 and 6 (Fig. 2.3b). This may have been a reflection of abundance or, more likely, availability. A seasonal trend was, however, apparent in the offshore data from regions 1,2 and 3. CPUE values increased slightly from July to December (Fig. 2.3a).

The statistical significance of the data set is discussed briefly in this section. The large variance which was noted in the CPUE graphs may be attributed to several factors. First, all data from trawl squares in which catches of horse mackerel was recorded were used. Alternately, the data from trawl squares in which no horse mackerel were caught was not used. This had the effect of elevating the biomass estimate in regions of low abundance, since the "dampening" effect of zero abundance was not recorded. However, in regions such as the Agulhas Bank, the high biomass estimate of the inshore region was affected by the low biomass estimate of the offshore region. Since a mean of all CPUE's in the region was evaluated, the value of the inshore region was decreased and a large variance was recorded. Second, the fishery may have been either hake- or sole-directed. The

distribution of the target species does not necessarily coincide with that of horse mackerel. Should horse mackerel constitute a small by-catch of the aforementioned fisheries, it would have been included in the calculations performed here. This low biomass estimate would have decreased the estimate of regions of the preferred range of horse mackerel and introduced a large variance. Third, although CPUE did not vary with effort (X^2 ; $P < 0.05$), effort in any given month may have been directed either in offshore regions where the density of horse mackerel was lower, or inshore where density was higher. This had the effect of increasing or decreasing the biomass estimate. Fourth, correction of effort according to fishing vessel size may introduce error to the data set. The variation in vessel size in the offshore fleet is far greater than the inshore fleet. This factor might have rendered the latter data set more reliable than the former. Finally, human error is introduced in the collection of the original data set. Catch weight is estimated by the captains of the vessels and some may be more conscientious than others in maintaining an accurate record. Despite the large variance of the data set, a seasonal distribution of inshore catches of horse mackerel does seem to occur (R. Human, I&J, Mossel Bay, pers. comm.; pers. observation).

2.Length frequency distribution

The maps of the length frequency distributions obtained from the research cruises are shown in Figs 2.4 a-f. Three length categories were recognized using the age curve described later in this study (Chapter 3). Fish with a total length (TL) less than 35cm were deemed as immature (on the basis of maturity curves described in Chapter 3). Mature fish were placed in two size categories; 35 to 42 cm TL and fish larger than 42cm TL.

The West Coast cruises of January 1987 and February 1988 realized a low biomass of horse mackerel (Figs 2.4a and 2.4c); horse mackerel was found in small numbers south of Cape Columbine ($32^{\circ}40'S$). A second population was noted in the north of the study area ($29^{\circ}30'S - 30^{\circ}30'S$). In comparison, the distribution during July 1987 (Fig 2.4b) reflects more horse mackerel in the south of the study region (along the 100m contour line of the Agulhas Bank) than in January of the same year. Few horse mackerel were found north of Cape Columbine during July, 1987. In August 1988 (Fig 2.4d), a concentration of juveniles (<35cm) was found at a station north of St Helena Bay ($32^{\circ}40'S$), and a second off the Cape Peninsula ($34^{\circ}20'S$), a distribution similar to that of February of the same year. Fewer individuals were caught than in February 1988, but northern and southern populations were apparent. Large fish (>42cm TL) were not noted in large quantities during any of the West Coast cruises. The biomass of horse mackerel was much greater on the South Coast cruises than on the West Coast and interesting distribution patterns were noted. Juveniles (<35cm TL) were located west of Mossel Bay (from $20^{\circ}E$ to $22^{\circ}E$) over the central, shallow Agulhas Bank in both 1987 and 1988. Fish larger than 35cm TL were spread fairly uniformly over the whole study region during September, 1987 (Fig. 2.4e), with a predominantly offshore distribution. The numbers of fish larger than 42cm TL increased eastwards. In contrast, distribution of horse mackerel larger than 35cm TL in May 1988 was patchy (Fig. 2.4f), with concentrations of individuals occurring inshore, west of the capes Infanta, Francis, Recife and Padrone. The graph of the biomass estimate obtained from each cruise is shown in Fig. 2.5. Values obtained from the Agulhas Bank exceeded those from the West Coast. Additionally, an increase in biomass was apparent in July, 1987 as compared to January 1987. However, the trend was not repeated in 1988: biomass in February was greater than in August.

CPUE PER 25 KM SQUARED
(Thousands)

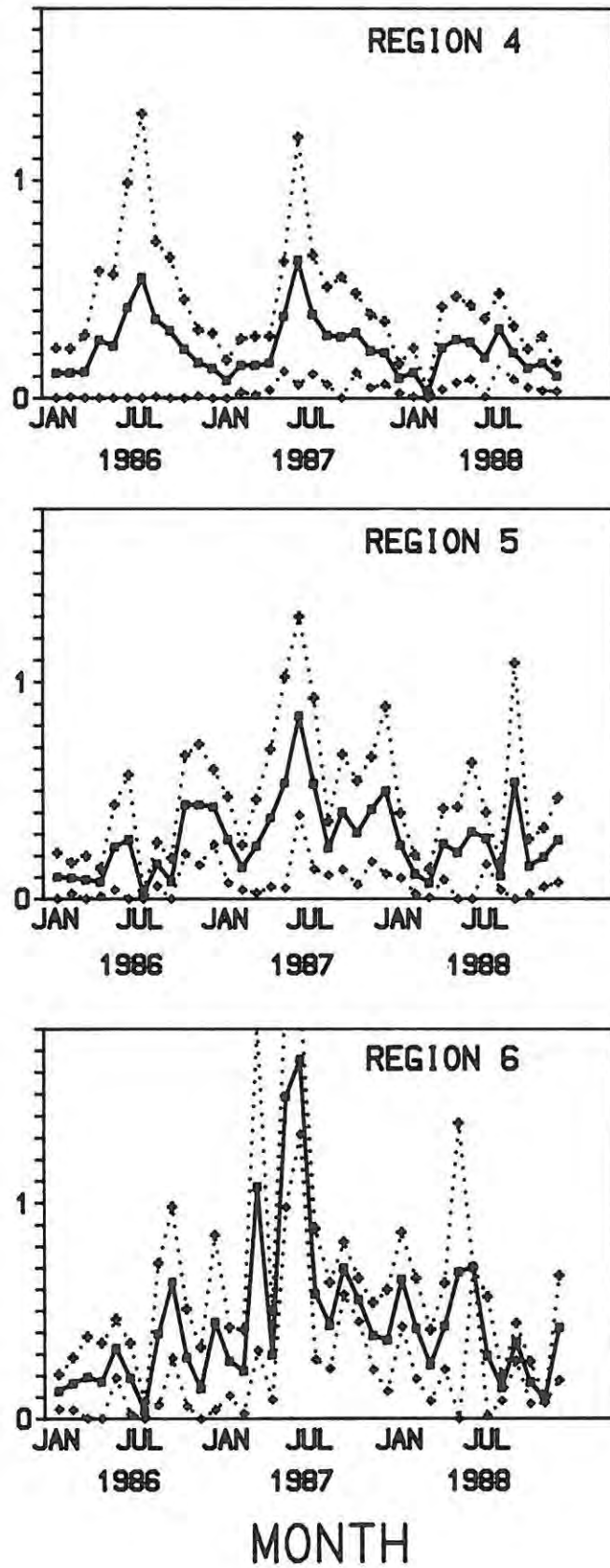


FIGURE 2.2: Trends in catch-per-unit effort of horse mackerel in the inshore demersal trawling industry during the years 1986-1988.

CPUE PER 25 KM SQUARED

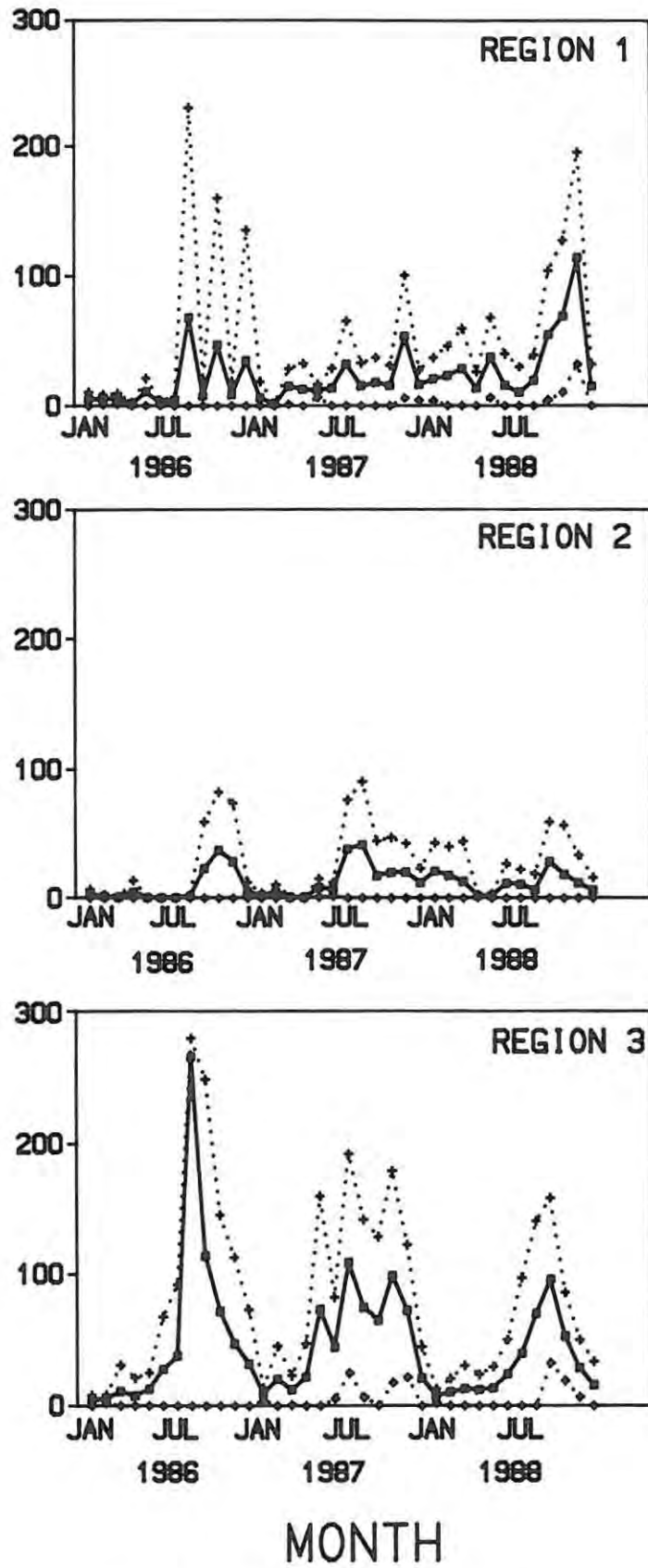
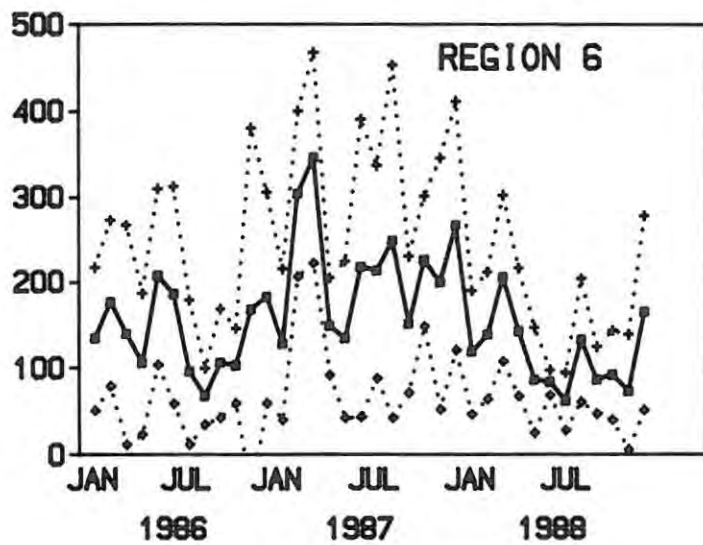
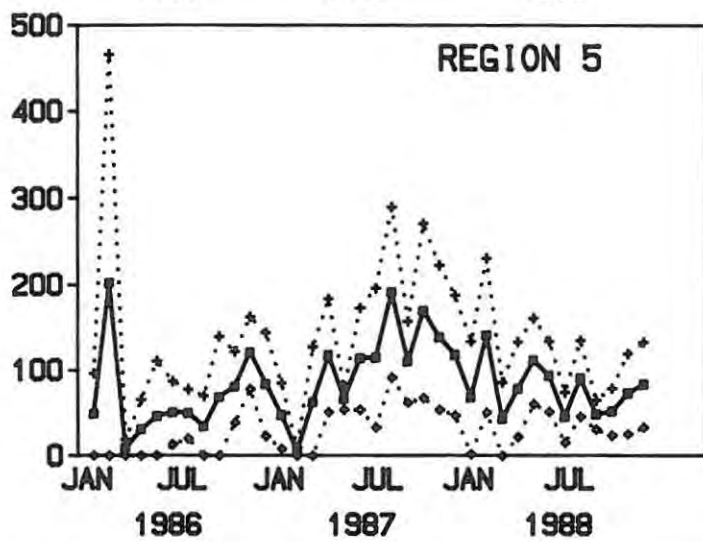
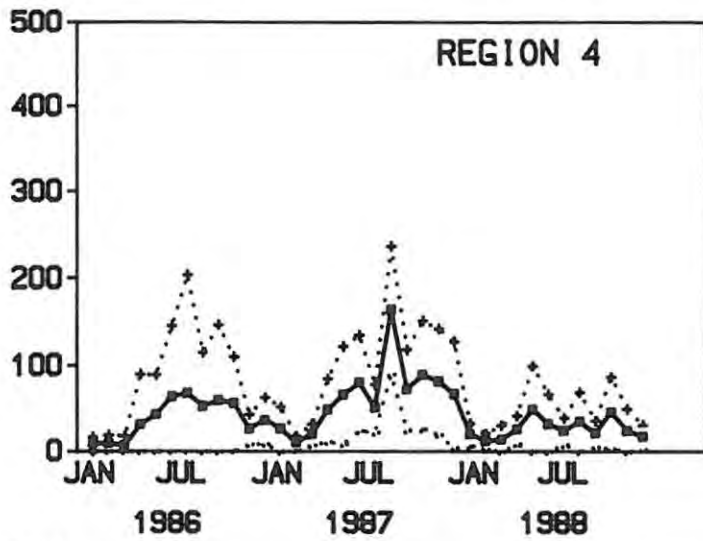


FIGURE 2.3a: Regions 1-3

FIGURE 2.3: Trends in the catch-per-unit-effort of horse mackerel in the offshore demersal trawling industry during the years 1986-1988. Standard deviation is denoted by a dotted line.

CPUE PER 25 KM SQUARED



MONTH

FIGURE 2.3b: Regions 4-6

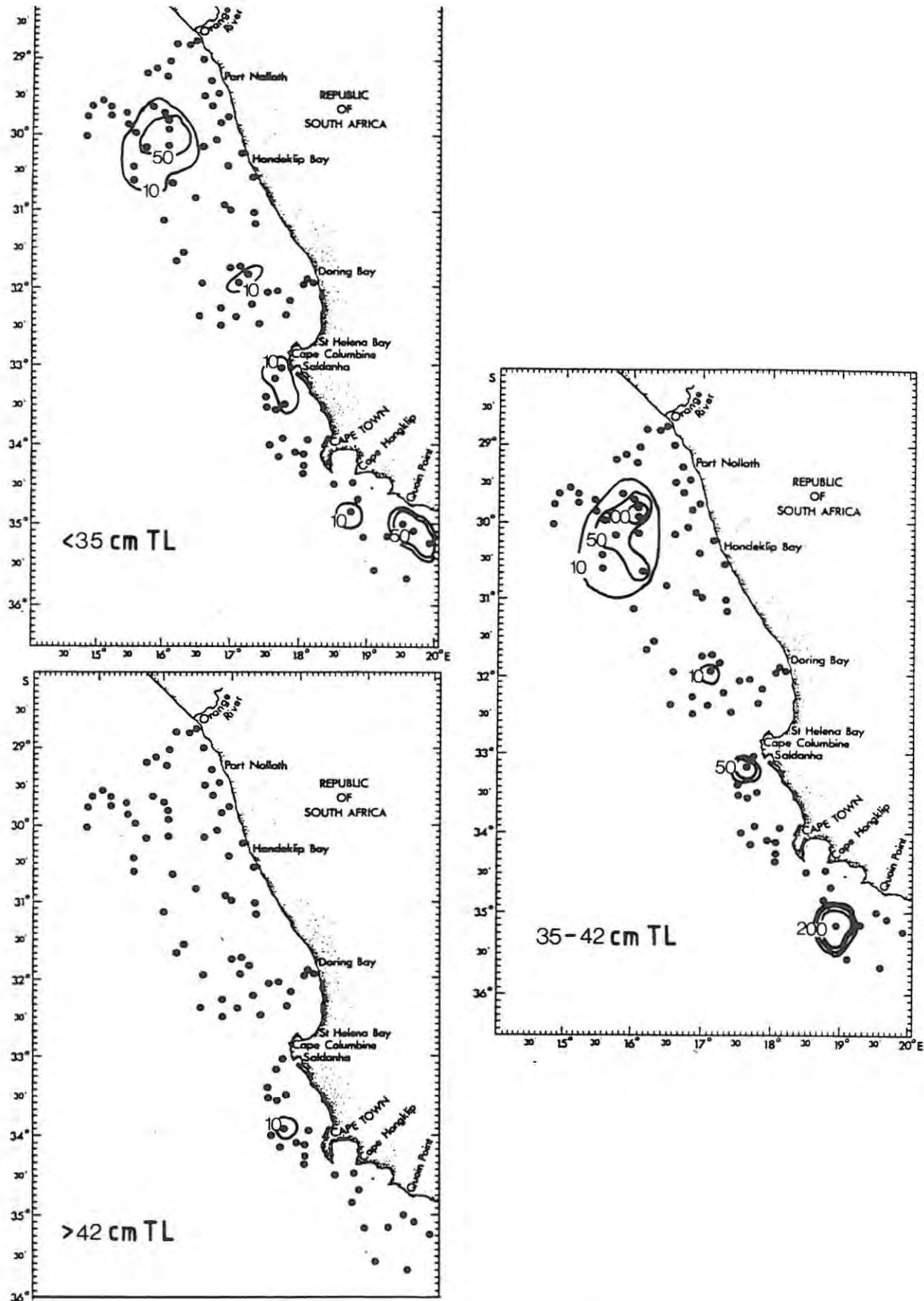


FIGURE 2.4a: January 1987

FIGURE 2.4. Maps of length frequency distributions of three size classes of horse mackerel, using results of biomass surveys in 1987 and 1988. Contour lines show the boundaries for the number of fish in an area.

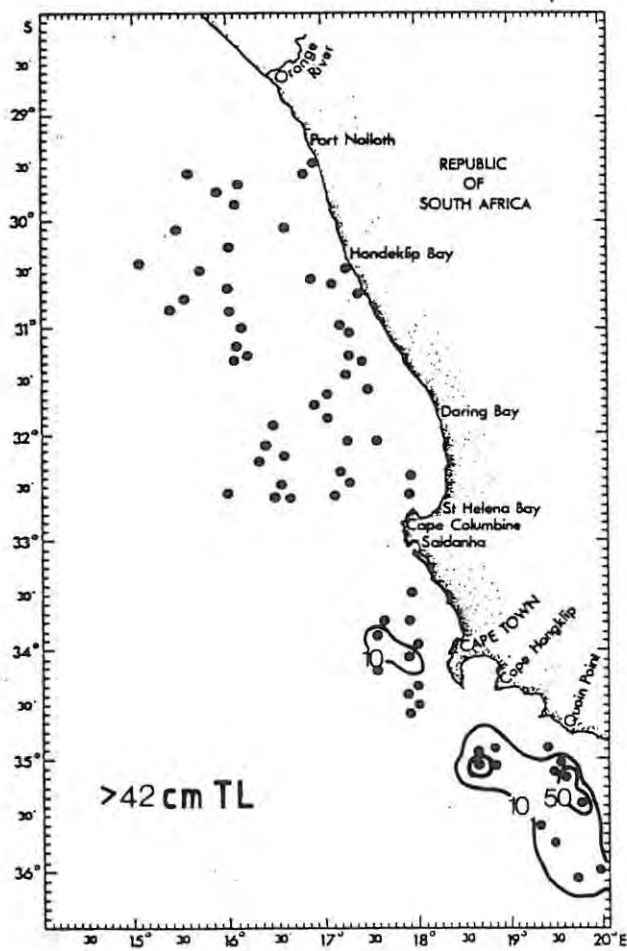
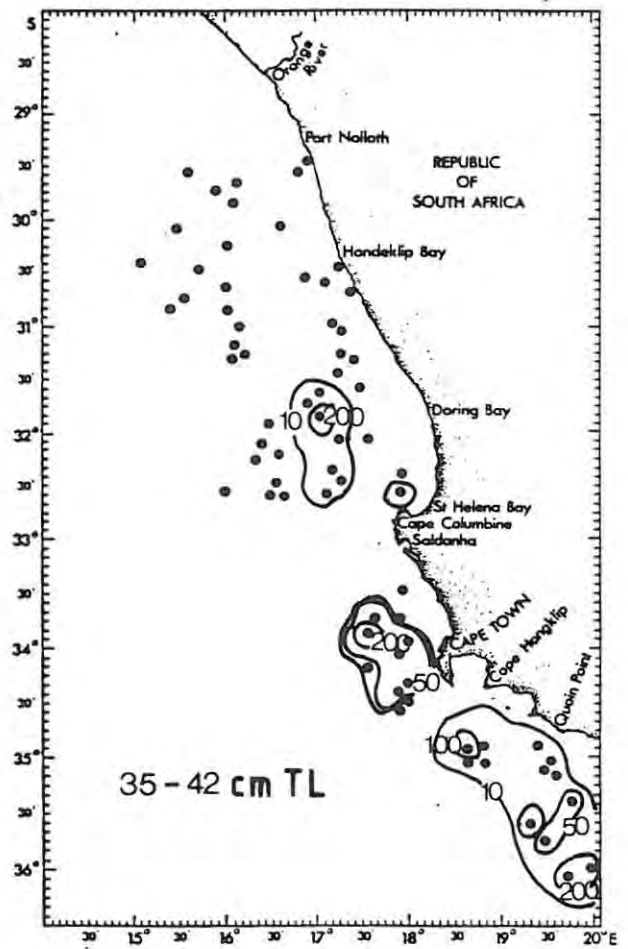
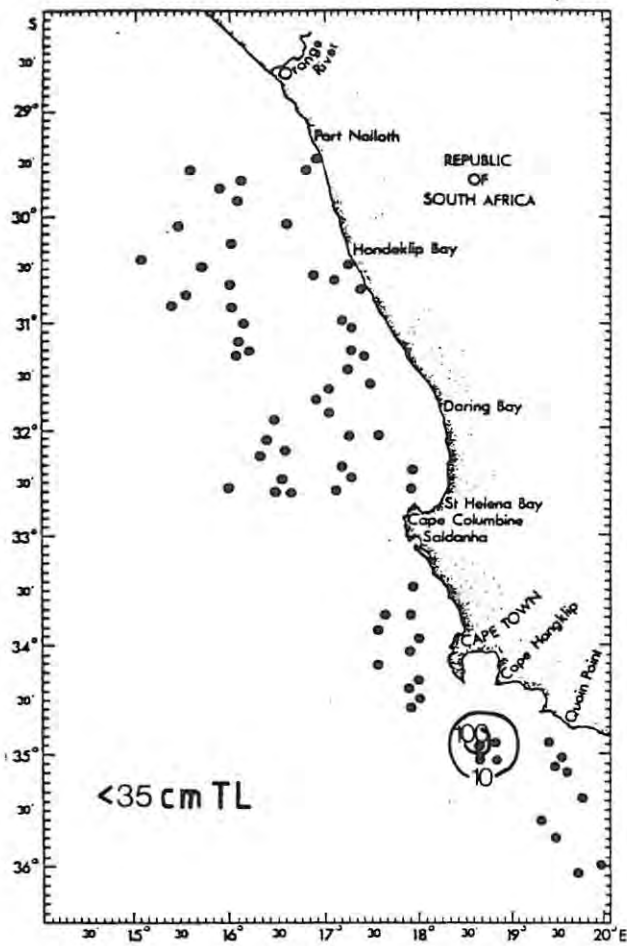


FIGURE 2.4b: July 1987

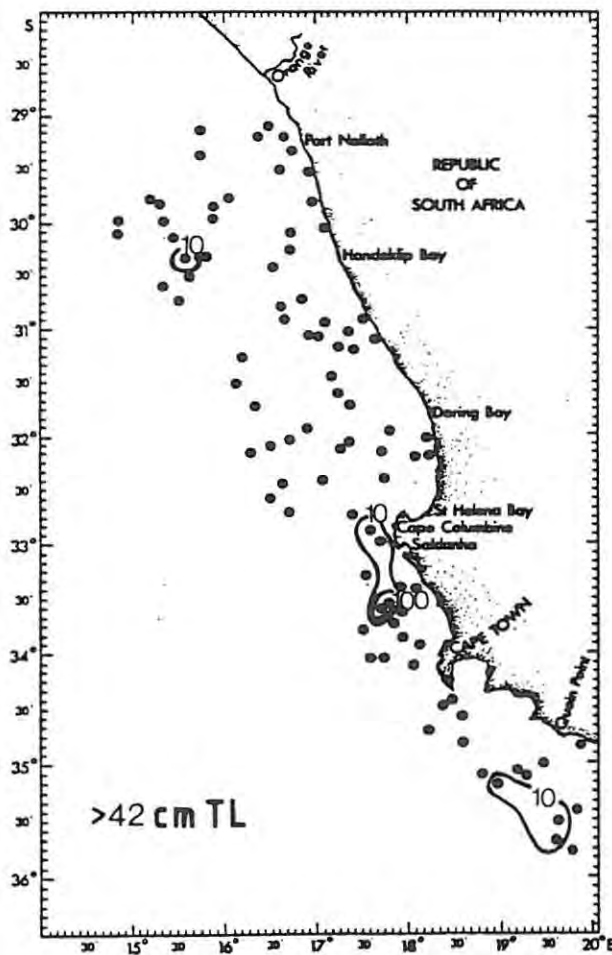
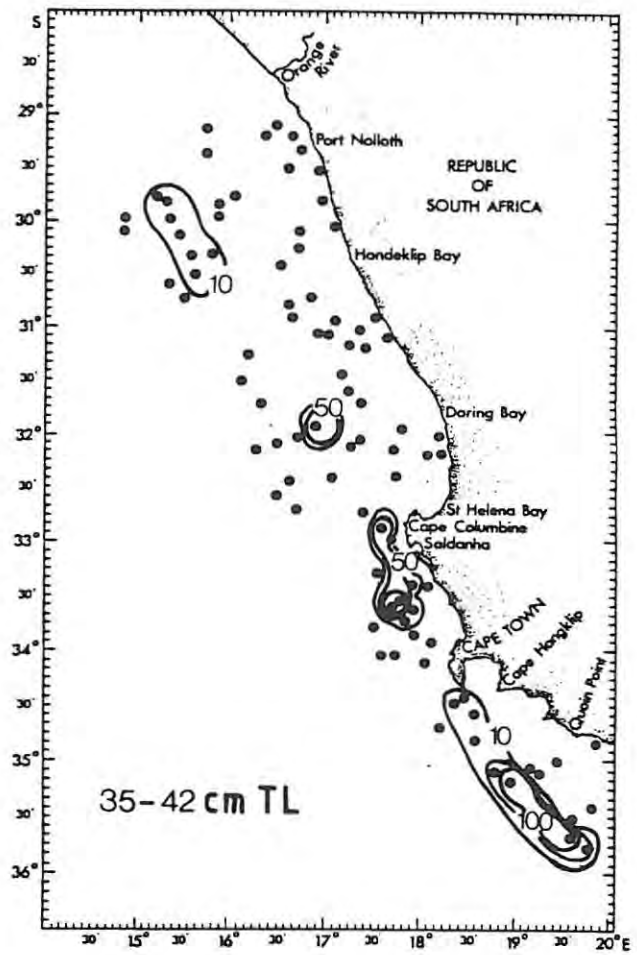
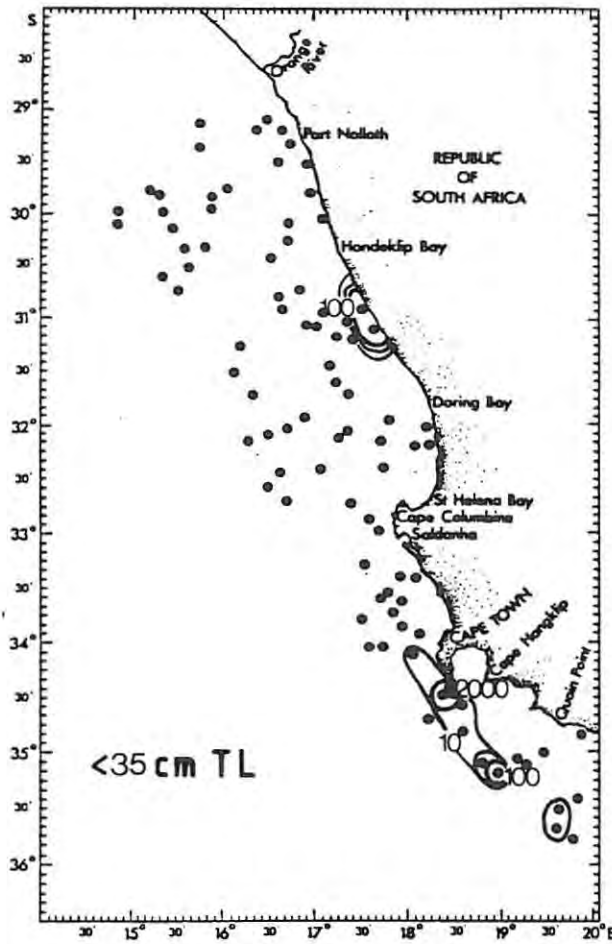


FIGURE 2.4c: February 1988

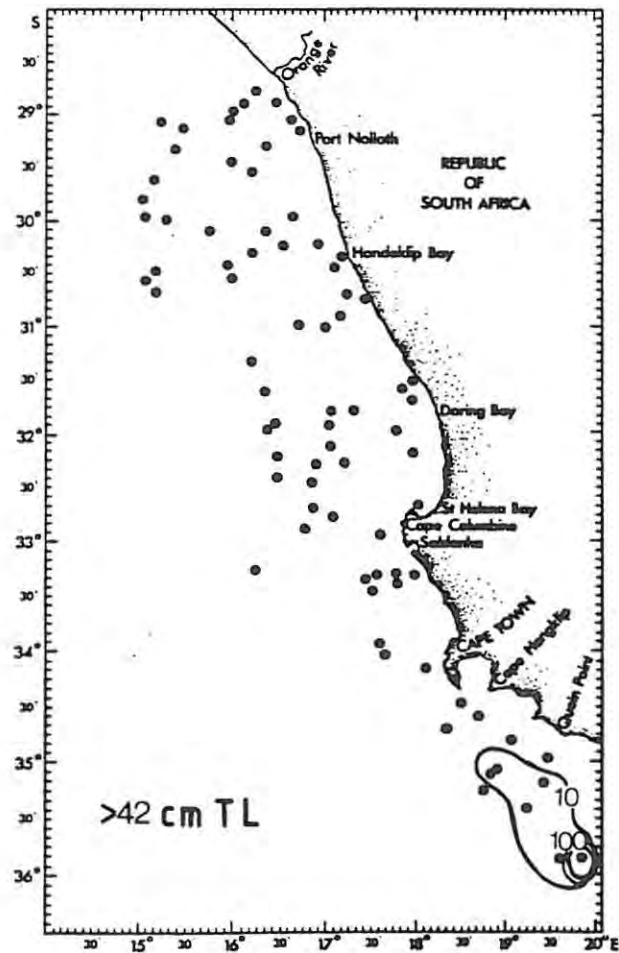
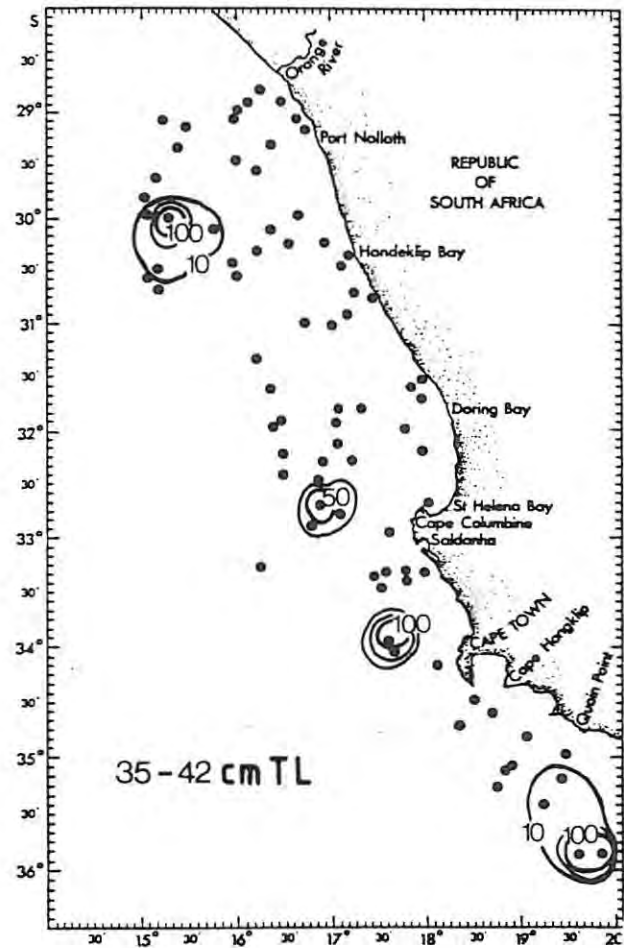
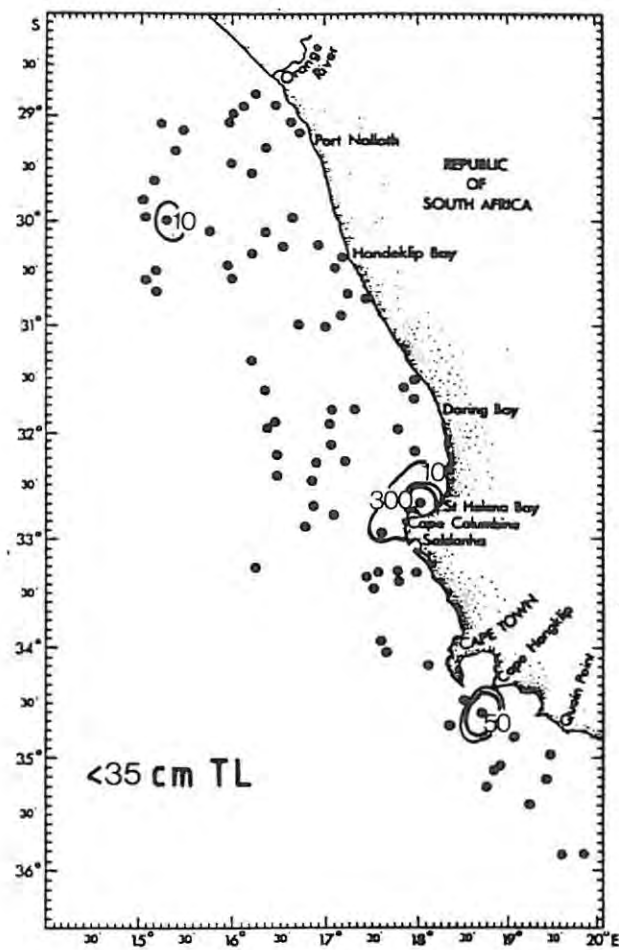


FIGURE 2.4 d: August 1988

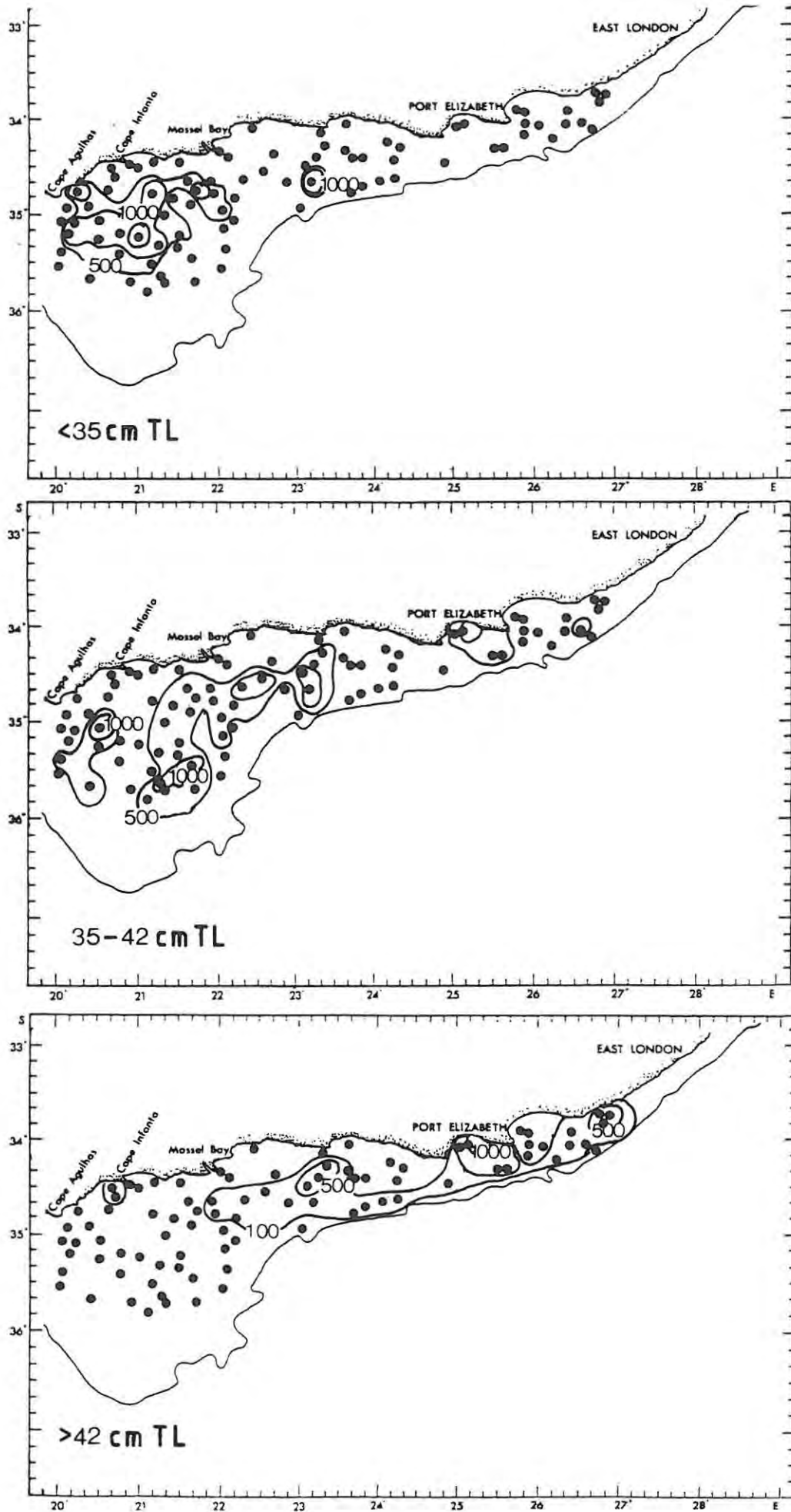


FIGURE 2.4e: September 1987

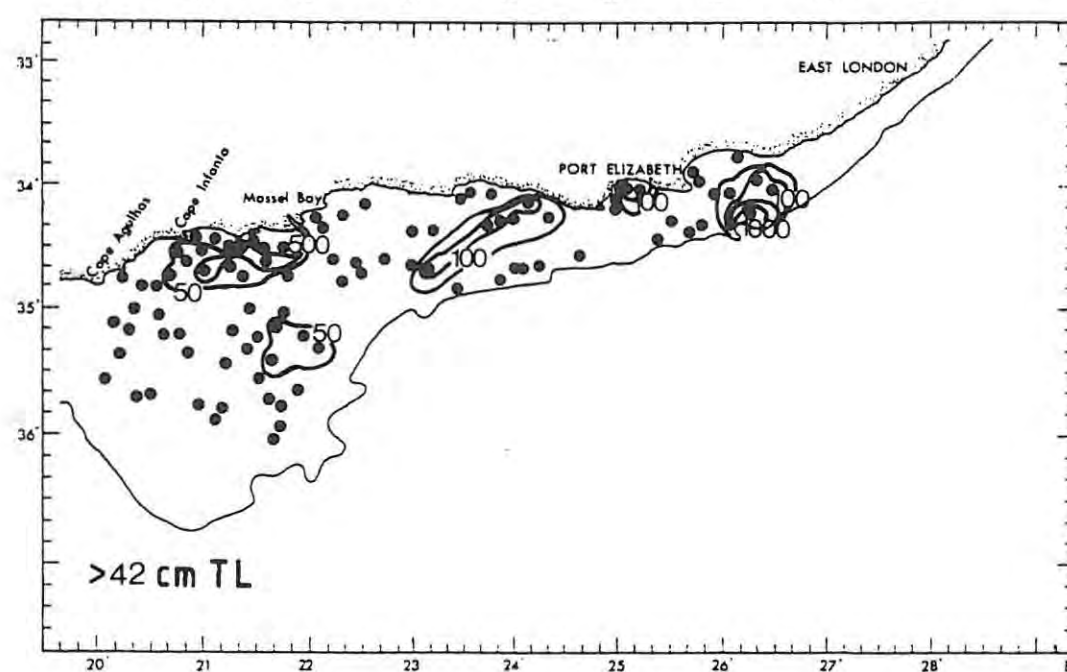
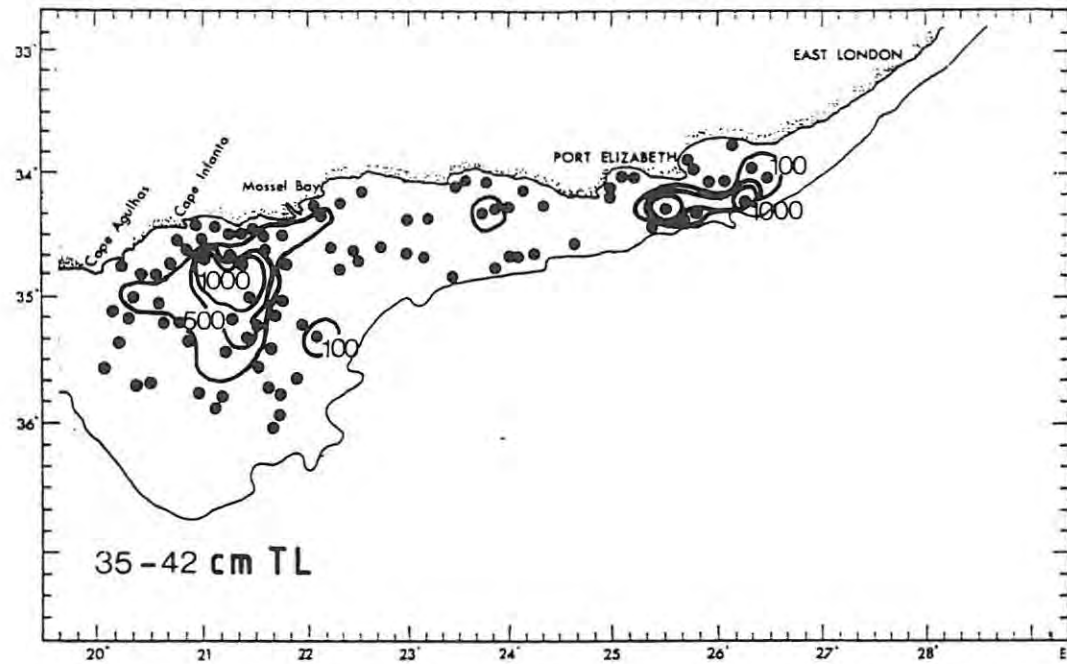
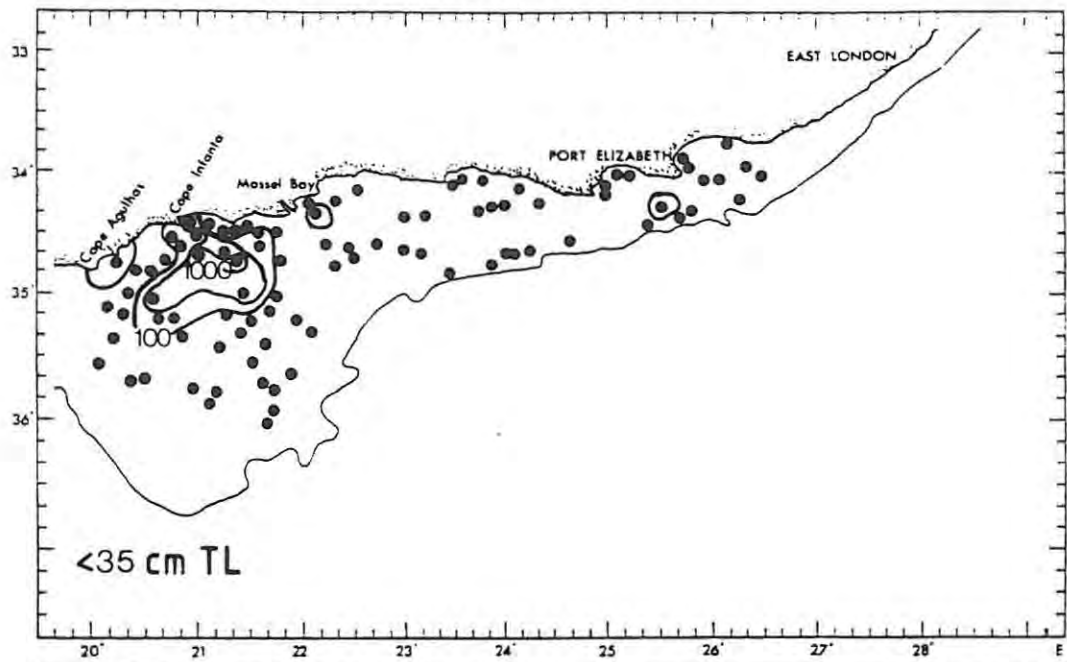


FIGURE 2.4f: May 1988

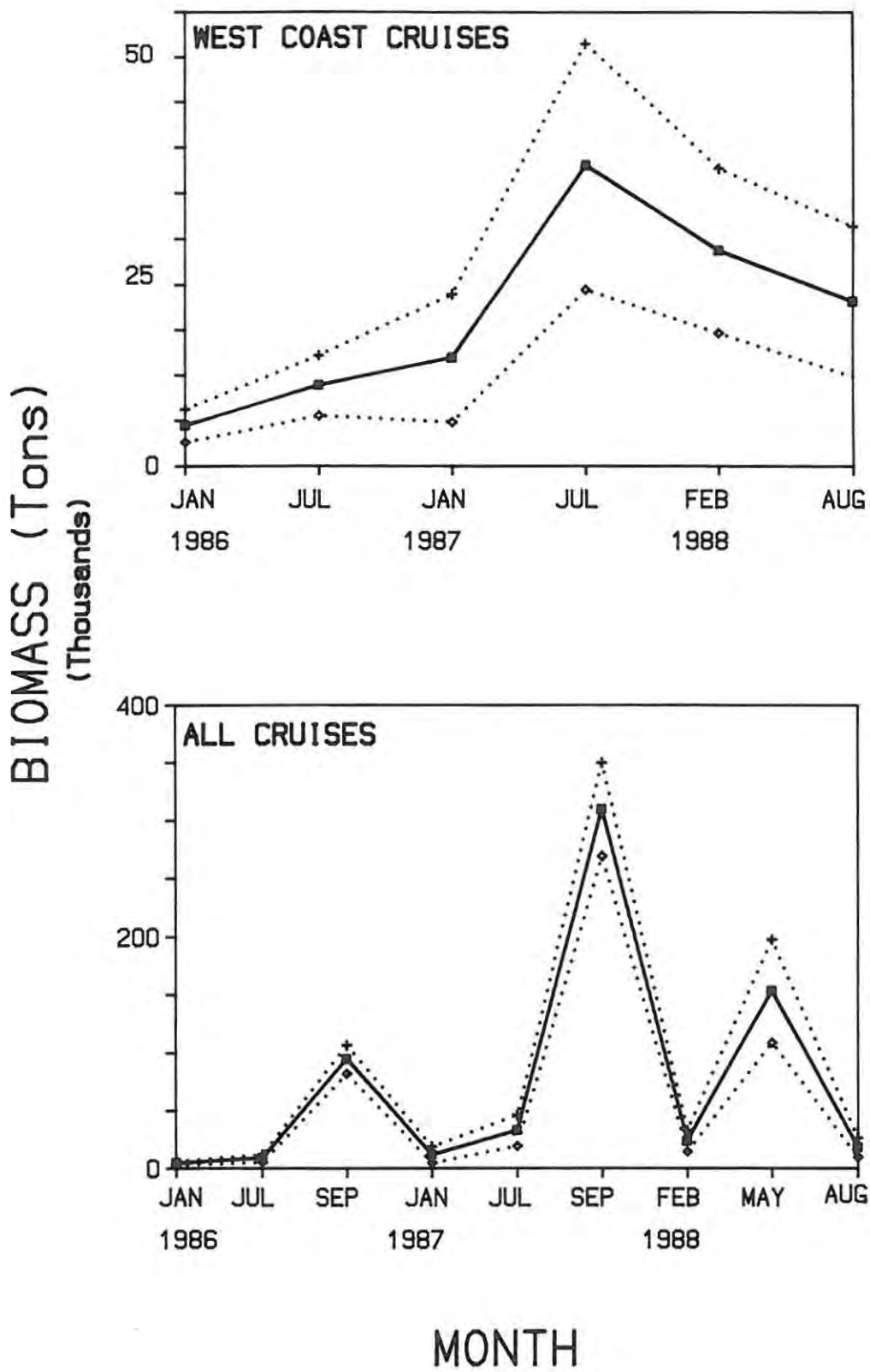


FIGURE 2.5: Biomass estimates obtained from demersal biomass cruises during the years 1986-1988, derived from aerial expansion methods. Dotted denotes standard deviation.

DISCUSSION

It is possible to draw a few salient points from the results presented and, further, from the literature. A composite picture of horse mackerel distribution may be created, leading to a tentative idea about migrations during the life history of the species.

First, horse mackerel were distributed fairly evenly over the Agulhas Bank, but there was a distinct decrease in biomass over the West Coast, north to the Orange River. In support of this statement, Payne (1986) showed that 80% of horse mackerel caught by the demersal industry during the 1970s was caught over the Agulhas Bank. The largest landings were recorded at Port Elizabeth (Sea Fisheries Research Institute, unpublished data). Draganik (1977) noticed a decrease in catches of horse mackerel northward from the Orange River (in ICSEAF Div. 1.5), but catches increased again in the north of the Benguela system (ICSEAF Div. 1.3 and 1.4)

The length frequency distribution showed interesting and consistent trends; juveniles were found in the shallower waters of the central Agulhas Bank, and the mean length frequencies of fish increased offshore and eastwards. Such a finding is supported by cruises conducted during the years 1975-1978 (Payne, 1986) and 1980 to 1982 (Hatanaka *et al.*, 1983; Uozumi *et al.*, 1984; 1985). The distribution of juvenile horse mackerel was seen to be shared with juvenile hake and the area over the Agulhas Bank has been designated a possible nursery area for both species (Uozumi *et al.*, 1985).

Significantly, a seasonal trend has been reported by several authors. For example, Hecht (1976 ; 1989) reported a decline in catches landed at Port Elizabeth during winter. Similarly, Payne (1986) noted a

decrease in the numbers of adult fish in medium depths during the same months and Uozumi *et al.* (1985) saw an inshore migration of adults during winter from their summertime offshore distribution. The results presented here also show that the catches made inshore focused less on Port Elizabeth and more in the Mossel Bay vicinity during July to December. Of interest are the biomass estimates of the West Coast cruises conducted during 1986-1988 and by the CPUE graphs for regions 1 to 3; all show an increase in biomass during July (as compared to January of the same year) along the western Agulhas Bank, a finding which seems to support the east - west movement postulated here.

It is proposed that the apparent seasonal movement is a spawning migration; horse mackerel were found in a spawning condition from June to December (Hecht, 1976; 1989; this study, chapter 3). During January to June, horse mackerel appear to be concentrate inshore and in the east. Then, during July to December, they seem to aggregate over the central and western regions of the Agulhas Bank where spawning presumably takes place. A similar seasonal distribution associated with spawning has been noted in the horse mackerel population off northern Namibia (Kolarov, 1980; Macpherson *et al.*, 1982; Konchina, 1986; Assorov *et al.*, 1988). There, adults were found in the far north (17°S to 19°S) during the summer spawning months, thereafter they moved south and offshore as the fishing season commenced, to be quite widespread over their distribution range (17°S to 23°S) during the non-spawning period. Additionally, the mean size of fish in the north was larger during the spawning months than at any other period (Macpherson *et al.*, 1982).

It is important to note that the 'juveniles' in the present study were in their second year of life (average total length, 25-26 cm) and were

larger than the individuals traditionally fished by the pelagic fishery on the West Coast (3-16cm, TL), studied by Crawford (1980, 1981). The 'adults' of the latter study were, in fact, juveniles; the age curve of Geldenhuys (1973), utilized by Crawford (1980) placed fish of 27.9cm (fork length) at an age of seven years, whereas for this study (Chapter 3) and that of Hecht (1989) those fish would be considered to be in their second year of life. It is very likely, given the distribution patterns mentioned already, that juvenile horse mackerel behave similar to other juvenile pelagic fish, being transported onto the West Coast by a frontal jet current to the nursery grounds north of St Helena Bay (32°S - 33°S) (Shelton and Hutchings, 1982, in press), to return to the Agulhas Bank before maturation. Pelagic catches of horse mackerel during 1984 to 1989 have been almost exclusively in the vicinity of St Helena Bay (SFRI, unpublished data). The effect of exploitation of the pelagic horse mackerel off the West Coast on recruitment to the demersal fishery of the South Coast is little understood, given that there was no demersal fishery for horse mackerel at the time of the decline in purse-seine catches after the peaks in the late 1950s and early 1960s (Geldenhuys, 1973). It should be noted, however, that pelagic catches remained low until 1989, when 25 000 tons were caught (SFRI, unpublished data). The possible existence of nursery grounds other than the West Coast cannot, however, be ruled out, because the adult population has been exploited at high levels since the 1970s (Kinloch *et al.*, 1986; Payne, 1986). Lasiak (1981) reported juvenile horse mackerel (2.9-9.8 cm TL) in Algoa Bay at Port Elizabeth, suggesting that juveniles may seek sheltered bays along the South Coast during the first year of their life.

A pattern of distribution is apparent from the discussion thus far; fish in their first year of life definitely live off the West Coast and in their second year over the central Agulhas Bank west of Mossel Bay. With maturation (35-38cm TL; Chapter 3.), these fish move eastwards over the Agulhas Bank to recruit to the adult stock, which is found mainly between 100 and 220m depth (Payne, 1986). In turn, these fish migrate westwards during July to December. An explanation for this distribution, with an oceanographic basis, will be attempted.

It is apparent that *T.t.capensis* has a preference for the warmer, temperate waters of the Agulhas Bank as opposed to the colder, upwelling features of the West Coast (see Shannon, 1985, for a review of the oceanographic features of the Benguela system). The tendency of the species to be found in warmer waters may explain the decrease in biomass of horse mackerel northward on the West Coast, where upwelling is persistent, and their reappearance in the northern Benguela system where mixing between the warmer Angolan water and the cooler Benguela waters occurs. Agenbag and Shannon (1988) use physical data to explain the existence of a 'biological barrier' at 24°30'S in ICSEAF Division 1.5, a barrier which seems to affect the distribution of several pelagic species (O'Toole, 1977; Agenbag, 1980; Cruickshank, 1983; Cruickshank and Boyd, 1985; Crawford *et al.*, 1987). This 'barrier' may serve as an isolating mechanism (although it is assumed to be breached on occasion, Hewitson, 1988) and helps to explain the occurrence of northern and southern stocks of horse mackerel.

The occurrence of localized upwelling along the south coast has been described by Schumann *et al.* (1982), primarily off Capes Recife (25°40'E), St Francis (24°50'E), Seal (23°20'E) and Blaize (22°E). An explanation for the concentrations of horse mackerel along the capes of the South Coast during months of no spawning activity may be

offered by this phenomenon. It has been suggested by Talbot (1974) that the high numbers of zooplankton, which forms the largest component of the diet of horse mackerel (Hecht, 1989), off Port Elizabeth are supported by intermittent upwelling in this region. Further, Schumann and Beekman (1984) have shown that the water over the Agulhas Bank is well mixed during winter and strongly stratified during summer. The stratification of the water column may create favorable conditions for spawning (Shelton and Hutchings, in press) and therefore a westward movement of adult spawners during the spring months.

Nelson and Hutchings (1987) postulated a longshore transport system from the Agulhas Bank to St Helena Bay on the West Coast. Such a system would facilitate the northward movement of planktonic components to St. Helena Bay by means of the following mechanism. The jet current flowing from the Agulhas bank towards Cape Columbine would passively transport spawning products, which would be swept into the bay by the cyclonic gyre and eddies associated with the region. The populations then reside in the region for a significant time (Shelton and Hutchings, 1982; in press). Considerable numbers of horse-mackerel eggs and larvae were found offshore around Cape Point between 1951 and 1965 (Haigh, 1972). The inshore movement of adults may serve to place such spawning products in a position to be transported northward, or alternatively, to the sheltered bays around which upwelling occurs.

Finally, it has been shown by Boyd *et al.* (1987) that juvenile horse mackerel off Namibia show a preference for the mixed waters of the Angolan intrusion front. It is remarkable, therefore, that individuals in the second year of their life are found south of Cape Infanta and Agulhas, an area designated a 'transition region' by Schumann and

Beekman (1984), consisting of mixed waters throughout the year. It is possible that the individuals from the West Coast actively swim to this region.

From the preceding discussion it could be concluded that *Trachurus trachurus capensis* is a species clearly distributed according to age structure. The 'stock' found on the West Coast is, most likely, a component of the adult stock on the Agulhas Bank. However, it is recognized that the results presented here are incomplete and serve merely as a tentative assessment of stock integrity to be ascertained by further studies.

CHAPTER 3 : ANALYSIS OF PHYSICAL AND BIOLOGICAL CHARACTERISTICS

INTRODUCTION

If a stock is conceptualized as a "population of fish that behaves as a cohesive unit whose members exhibit common responses to environmental conditions within its geographic boundaries" (Casselman *et al.*, 1981), it follows that several ecological and biological characteristics may be used to differentiate such stocks. Should the variation of a suite of characters among groups of fish be deemed to be adaptive, then those characters may prove effective in detecting differences between populations (Ihssen *et al.*, 1981). While it is often postulated that such characters reflect an underlying genetic influence, it is recognized that they may be epigenetic, thus influenced by environmental history such as food availability and temperature variation (Lindsey, 1981; Clayton, 1981; Ihssen *et al.*, 1981). However, since the fisheries manager is interested in the adaptation of different stocks to different environments, characters reflecting ecological responses will be used herein to determine the stock integrity of horse mackerel.

The methods used may be placed under the following categories; population parameters, physiological characteristics and morphological characteristics. The first, population parameters, includes growth and length-at-maturity. Ihlsenn *et al* (1981) caution the use of population parameters; they are effective only with sympatric stocks and show no clear relationship with the genetic character of a stock. If, however, a stock is recognized as a production unit, then the use of population parameters is justified in stock identification. The second category, the use of morphological characters (body morphometrics and zonation in otoliths) has proved effective in isolating stocks in several studies (e.g. Berst *et al.*, 1980; Casselman *et al.*, 1981) despite a

poor understanding of the influence of genetic and environmental conditions of the phenotype (Clayton, 1981; Todd *et al*, 1981). The final category, the study of the reproductive characteristics of a stock, reflect the adaptive significance of differing characteristics among stocks. Here, the reproductive life history of horse mackerel will be studied.

METHODS

Since the distribution of stocks may vary both temporally and spatially, it is deemed wise by Ihssen *et al.* (1981) to sample a population when it is least dispersed; for example, at the time of spawning (Casselman *et al.*, 1981). Segregation by age, sex or size is therefore reduced. Therefore, individuals were studied during the spawning period where relevant. A further source of error lies in the unequal vulnerability of different sizes of fish to fishing gear; this may be reduced by matching the gear used in sampling (Ihssen *et al.*, 1981). Samples were drawn from the inshore fishery, from the "Cape" class of boats operated by Irvin and Johnson (Pty) Ltd. Generally, these are wet-fish, side trawlers of average size 21m. The fishing gear deployed is a 30.4m otter trawl with wing nets, 6ft V-type trawl doors, and a net with a cod-end section of 75mm mesh size. The nets are adapted by different skippers towards the target species; for example, a chain footrope is used for sole-directed catches and floats are used on the headrope for horse mackerel-directed catches. The average trip is set at 7.5 days, with 4 drags a day of duration 3.5 hours (Mr. P. Sims, Sea Fisheries Research Institute, pers. comm.).

The study area was divide into three regions ; the East Agulhas Bank (ICSEAF Division 2.2), the central Agulhas Bank (Div. 2.1) and the West Coast north of Cape Town (Div. 1.6), (Fig. 1). Generally, monthly samples of horse mackerel (approximately 150 kg) were taken from ships operating from ports representing each division (Port Elizabeth, Div. 2.2; Mossel Bay, Div. 2.1; Saldanha Bay; Div. 1.6). All samples were taken within a week of each other at the beginning of each month, each from approximately the same monthly locations. Sampling commenced from Port Elizabeth and Mossel Bay in May, 1988 and from Saldanha Bay in

February, 1989. All sampling ended in June, 1989. Additional samples were obtained from the West Coast during cruises of the R.S. *Africana* in August, 1988 and January, 1989. A detailed description of data collection and analysis follows.

1. Population parameters.

The growth rate was determined using 645 sagittal otoliths collected from each of the three locations. Fifty otoliths per month were measured from Subarea 2 during the months July to December, and 125 measured from Division 1.6 during August. A relationship between otolith length and fork length was determined by measuring the anterior-posterior axis with vernier calipers. Care was exercised in selecting the otoliths with unbroken rostra. The findings of previous workers rendered the separation of otoliths according to sex unnecessary (ICSEAF, 1986, Hecht, 1989). The data was subjected to multiplicative regression analysis. The relationships obtained for each of the locations were compared to each other using a three-way analysis of variance. This method of comparison was deemed more effective than assigning age groups by counting annual growth rings, since it was not subject to personal interpretation. Additionally, for greater accuracy, fork length in millimeters was used; throughout the rest of the study, the total length of individuals will be used, thereby adopting the convention applied by ICSEAF (ICSEAF, 1986). A relationship between fork length and total length was determined by least squares linear regression.

Size at sexual maturity was determined by examining the gonads of fish during the spawning season. A maturity index was assigned to individuals using the seven stage international maturity scale (Ehrenbaum, 1930), the adaptation of which is shown in Table 3.1. All

individuals with gonads in stages I, II and III were deemed immature while those with gonads in stages IV-VII were considered mature. The percentage of mature individuals was plotted against total length in centimeters. Where the percentage of mature fish equaled or exceeded 50%, the concomitant total length was assigned as the length-at-maturity. The values obtained from each of the three locations were compared by means of a three-way analysis of variance.

Once the temporal nature of the zones of the otolith were validated (described later in this section), the rings were counted and an age was assigned to individual fish, using the recommendations made by ICSEAF (1986). Appropriate growth models were fitted to the data using the curve fitting and statistical tests recommended by Hughes and Punt (1989).

2. Morphological characteristics

Fish used for morphometric analyses were collected on board the R.S. *Africana* during May, 1989 (South Coast) and July, 1989 (West Coast). Fourteen conventional morphometric characters (Fig. 3.2) were measured to the nearest millimeter using freshly-caught fish. The data were analyzed by principal component analysis (PCA) using a correlation matrix. The choice of this method over other statistical analyses was affected by the fact that PCA provides an effective means of producing a size-free measure of characters (Winans, 1987). Shape measures are deemed to be dependent on size due to allometric relationships and measures with larger sizes can be expected to dominate the analysis. Multivariant analyses such as discriminant function (DFA) and principal component analyses circumvent such difficulties by removing size influences in the analysis of shape. Humphries *et al* (1981) reject DFA in favor of PCA since the latter method has the advantage

of not assigning individuals to groups *a priori*, allowing "group differences to be discovered". Further, they argue that the coefficients obtained by DFA are difficult to interpret in a biological context, while PCA coefficients are amenable to biological interpretation.

A further means of measuring morphological variation between locations was obtained by studying the temporal formation of opaque and hyaline zones on the outer edge of the saggital otoliths. Monthly samples of otoliths for all regions were placed in xylene and were viewed under a stereo microscope using reflected light against a black background. Under these conditions, the opaque zone is seen as white and the hyaline zone, dark. The optical nature of the edge was established using the otoliths of younger individuals, since the otoliths of older individuals were calcified and therefore difficult to interpret. Edge interpretation was validated by burning the otoliths. The monthly frequency of otoliths with an opaque edge was expressed as a percentage of all otoliths studied during that month and the results from the three locations were compared.

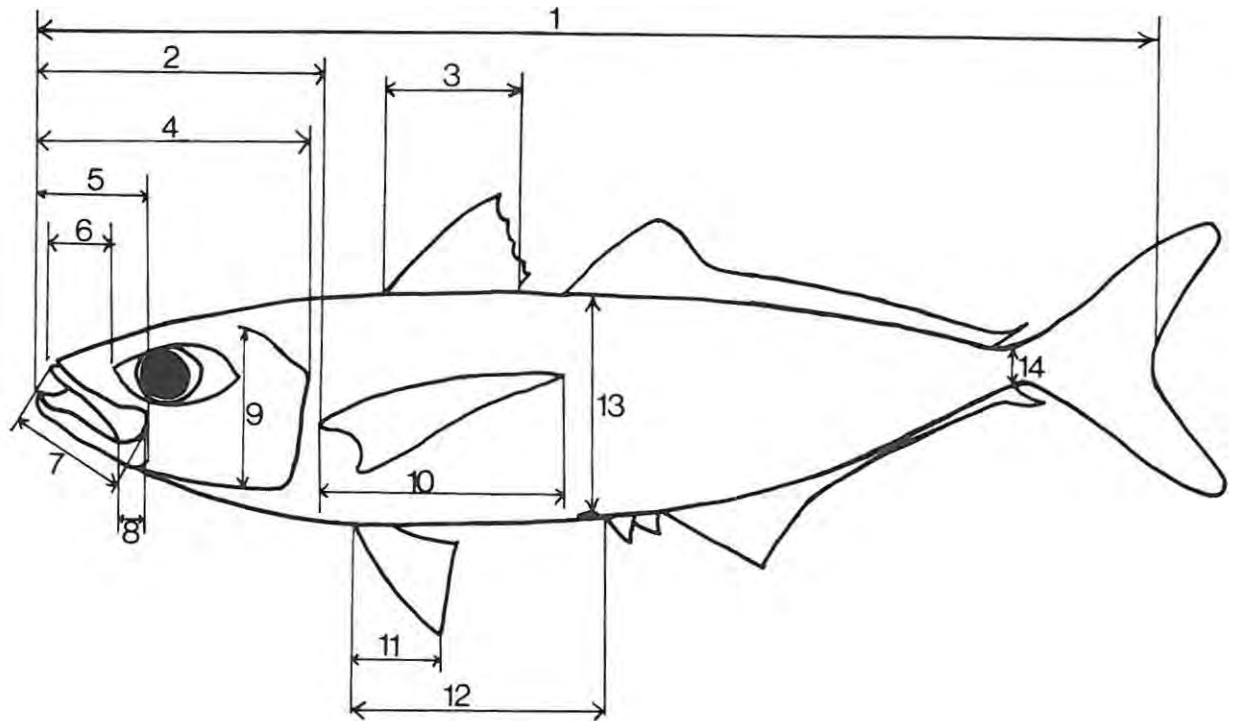
3.Reproductive characteristics

The reproductive life history of horse mackerel was studied by determining the monthly gonadosomatic index (GSI) of individuals of from each location (approximately 150 per month), where $GSI = \text{Gonad weight} / \text{Body weight} * 100$. Seasons of maximum and minimum gonad activity were compared between each of the three locations. A significant amount of fatty tissue was found attached to gonads during the quiescent stages while nematode and cestode parasites were seen to infect gonads in the post spawning stage; the tissue and parasites were removed before weighing the gonads. It was noticed that older

fish had a higher GSI value than younger fish; samples containing a greater number of the former size category had a higher weighted GSI than those containing smaller fish. It was deemed prudent to separate individuals according to three size categories, determined using the relationship between age and length derived in this study. In an attempt to test any correlation between the spawning season and the migratory movements postulated in the previous chapter, monthly length frequencies were obtained by measuring the total length of fish at Port Elizabeth and Mossel Bay, with the aim of tracing temporal movements of different size classes.

TABLE 3.1 The maturation stages in the horse mackerel (adapted after Ehrenbaum, 1930 and Macer, 1974)

MATURITY STAGE	OVARY EXTERNAL APPEARANCE	TESTIS EXTERNAL APPEARANCE
I Virgin	Rounded, 1-2mm broad, translucent, less than a quarter of length of body cavity. No oocytes visible.	Flattened, 1-2mm broad, less than a quarter of length of body cavity.
II-III Developing virgin	Rounded, 2-4mm, pink, about a quarter of length of body cavity.	Flattened, 2-4mm, grey, quarter of length of body cavity.
II Resting (Mature Fish)	Rounded, about 5mm broad, pink, about a third of length of body cavity. No oocytes visible.	Flattened, 5mm broad, grey about third of length of body cavity.
III Developing (early)	Yellow, a third to a half of length of body cavity; oocytes visible.	Becoming fatter, off white a third to a half of body cavity.
IV Developing (late)	Yellow, half to whole length of body cavity. Large oocytes visible.	Firm, becoming whiter, half to whole length of body cavity
V Ripe	Orange: Almost fills body cavity. Hyaline oocytes may be present, giving ovary a speckled appearance.	Pure white, parts becoming soft, almost fills body cavity.
VI Running	Oocytes are hydrated and run from vent on slight pressure. Ovary may have patches of red where no oocytes are visible.	Milt runs from vent on slight pressure. Gonads soft, may have grey patches.
VII Spent	Flaccid, dark red; less than half of body length. Few large oocytes may be visible.	Flaccid, grey-brown, may be residual milt.



- | | |
|------------------------------------|---|
| 1. fork length | 8. upper jaw width |
| 2. snout to origin of pectoral fin | 9. gill depth |
| 3. first dorsal fin base length | 10. pectoral fin length |
| 4. head length | 11. ventral fin length |
| 5. lower jaw length | 12. ventral fin origin to anal fin origin |
| 6. snout length | 13. body depth |
| 7. upper jaw length | 14. caudal peduncal depth |

FIGURE 3.2 The morphometric characters of horse mackerel used for analysis.

RESULTS

a. Population parameters

The relationship between otolith length and fork length of fish from each study region was obtained by means of multiplicative regression. Assuming an exponential relationship between otolith length and fork length;

$$OL = a*FL^b$$

where OL = otolith length

FL = fork length

a and b are constants

natural logarithms were used to derive a linear relationship;

$$\ln(OL) = b*\ln(FL) + \ln(c)$$

and a graph of $\ln(OL)$ versus $\ln(FL)$ produced a y intercept, $\ln(c)$, and a gradient, b.

The results of the regressions are shown in Table 3.3 and in figure 3.4 Using the values obtained by regression, the final relationship for each location was determined;

Division 1.6; $OL = 0.09039*FL^{0.816001}$

Division 2.1; $OL = 0.15761*FL^{0.71691}$

Division 2.2; $OL = 0.16057*FL^{0.71627}$

TABLE 3.3. The results of the linear regression of the natural logarithm of otolith length versus the natural logarithm of fork lengths of fish taken from ICSEAF Divisions 2.2, 2.1 and 1.6. The values obtained from the y intercept and the gradient of the regressions are shown. All models were acceptable at $P < 0.001$ (T-test).

LOCATION	Y INTERCEPT	STANDARD DEVIATION INTERCEPT	GRADIENT	STANDARD DEVIATION GRADIENT	R SQUARED VALUE
DIV. 1.6	-2.40367	0.05679	0.81600	0.02160	0.94142
DIV. 2.1	-1.84745	0.05451	0.71691	0.02105	0.84744
DIV. 2.2	-1.82933	0.05656	0.71627	0.02872	0.74317

The three way analysis of variance revealed no significant difference between the parameters obtained from Divisions 2.1 and 2.2 ($P < 0.001$), but those obtained from Division 1.6 were found to differ from the former two regions ($P > 0.05$).

The growth rate of fish from all areas was assumed to be the same, based on the above results. Therefore, all the age data was combined and a single age curve was calculated. A total of 243 fish were used in the calculation. The data satisfied the requirements for randomness of residuals and homoscedasticity (Hughes and Punt, 1989) and the parameter estimates obtained from the relative error model showed that the three-parameter von Bertalanffy model (Pauly, 1981) could be used to describe the growth of horse mackerel (Figs. 3.5 and 3.6), by the equation

$$L(t) = 487.989 * (1 - e^{-0.556 * (t - 0.229)}) \text{ mm}$$

The standard errors for the curve parameters were calculated using the jack-knife re-sampling method (Hughes and Punt, 1989). The standard error was found to be 3.132 for L infinity, 0.069 for t and 0.023 for k . A relationship between weight (g) and total length (mm) was derived by multiplicative regression (Fig. 3.7) ($n = 881$, $r^2 = 0.969$) and is described by the equation

$$W = 3.011 * TL^{7.8} \exp^{-6}$$

Therefore, weight-at-age may be described as follows;

$$W(t) = 1469.33 * (1 - e^{-0.556 * (t - 0.229)})^{0.000008} g$$

Finally, fork length (mm) was found to be related to total length (mm) as follows; $FL = 0.906 * TL - 2.337$ ($r^2 = 0.996$, $n = 881$).

The results of the study to determine length-at-maturity are shown in Figures 3.8 a-b. Female horse mackerel were shown to reach 50% maturity at 35cm TL in Division 1.6, 36cm TL in Division 2.1 and 37cm TL in Division 2.2. Three way analysis of variance revealed no

significant difference between the values for each study region ($P < 0.05$). In contrast, male horse mackerel were found to reach 50% maturity at 36cm, 37cm and 40cm in Divisions 1.6, 2.1 and 2.1 respectively. The value obtained for division 2.1 was different from those of Divisions 1.6 and 2.1 ($P > 0.05$).

2. Morphological characteristics.

The results of the principal component analysis of the morphometric data obtained from horse mackerel throughout the study region are shown in Figure 3.9. A plot of the first two principal components reveals no apparent biological grouping. All components were strongly correlated with the first principal component and the first two components explained 83.2% of all variability. Despite the fact that the data was transformed with logarithms to reduce the effect of size, an analysis of the data set revealed that all negative components were small fish (<32cm) and all positive components were large fish. Small fish were sampled inshore in Div. 2.1 and large fish offshore in all regions.

The temporal nature of the zonation of the outer edge of otoliths obtained from each of the three locations is shown in Figure 3.10. The opaque zone was deposited on otoliths from all study regions during August to January, with the hyaline zone being deposited during February to June.

3. Physiological characteristics.

The results of the monthly GSI values are shown in Figures 3.11 and the monthly length frequencies in Figures 3.12 a-b. Three size categories were recognized in calculating the monthly GSI values; small fish (35-42cm), medium fish (42-44cm) and large fish (>44cm). The GSI trends of the males followed that of the females, although

only the values of the females are used here for illustrative purposes.

Generally, a spawning season falling between July 1988 and February 1989 was noted in all regions. However, maximum spawning activity differed between different size groups and between regions. The maximum GSI value of large fish in Div. 2.1 occurred in August with a second, smaller peak occurring in February. GSI values of fish from Div. 2.2 reached maxima in September and December. An interesting trend was shown in the rate of maturity of large fish in each of the regions; fish in Div. 2.2 matured earlier than those in Div. 2.1. In contrast, the GSI values of Div. 2.1 decreased at a slower rate after December than those of Div. 2.2. The GSI values of medium sized fish showed the same trends as those of large fish. The GSI of small fish in Div. 2.1 and 2.2 realized maximum values in August and September respectively, with a decline thereafter. Fish from the West Coast were not sampled regularly and conclusive trends cannot be examined. However, GSI values in August exceeded values obtained from January to June 1989.

The length frequencies obtained from Port Elizabeth and Mossel Bay show no significant differences throughout the study period, with three exceptions (Fig. 3.12 a-b). In August, large fish dominated the Div. 2.1 catches while small dominated those in Div. 2.2, a similar result was noted in February and March. In May 1989, large fish dominated catches in Div. 2.2 with smaller fish being caught in Div. 2.1.

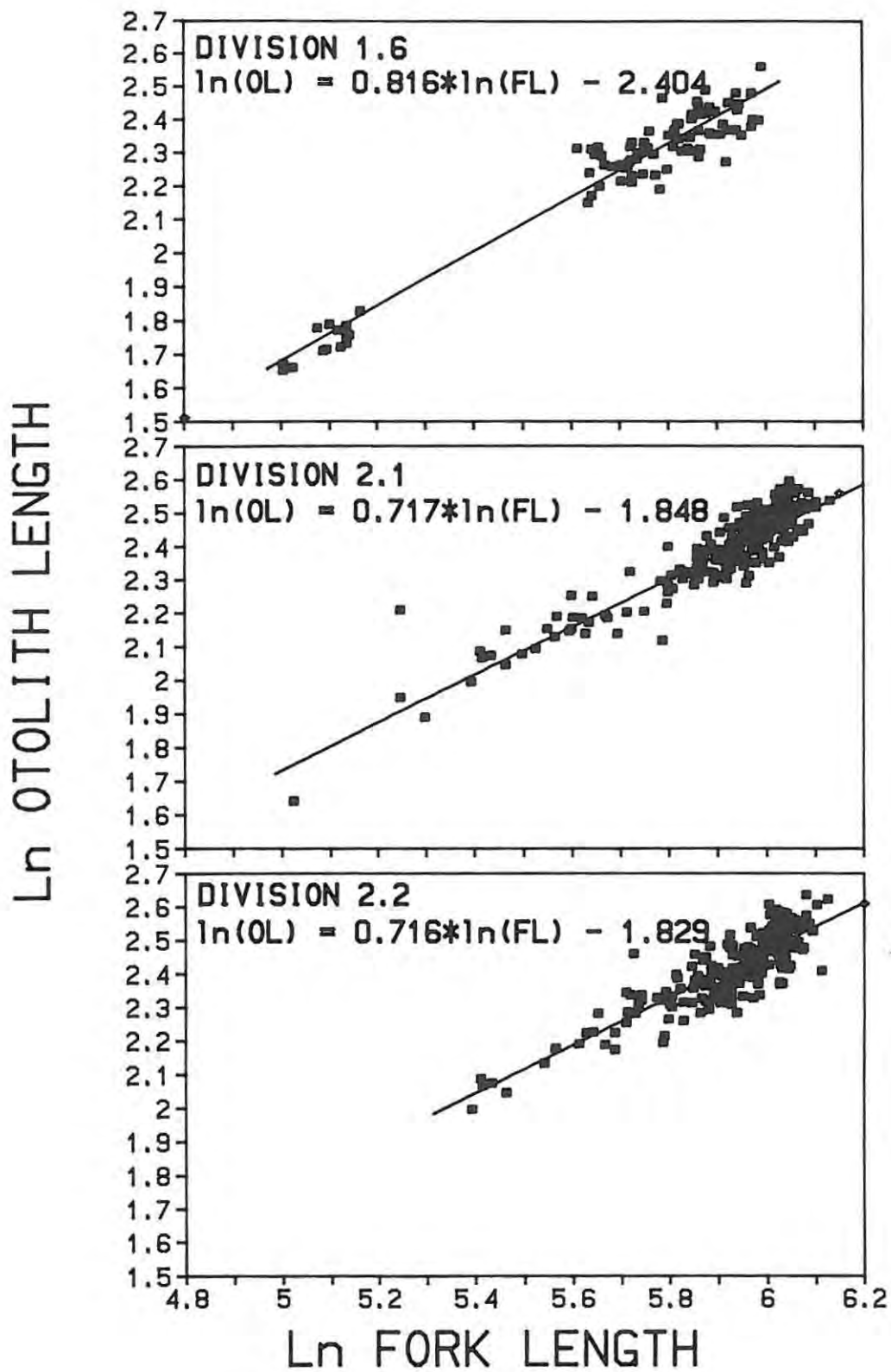


FIGURE 3.4. Graphs showing the results of the regression of fork length against otolith length for horse mackerel from ICSEAF Divisions 1.6, 2.1 and 2.2.

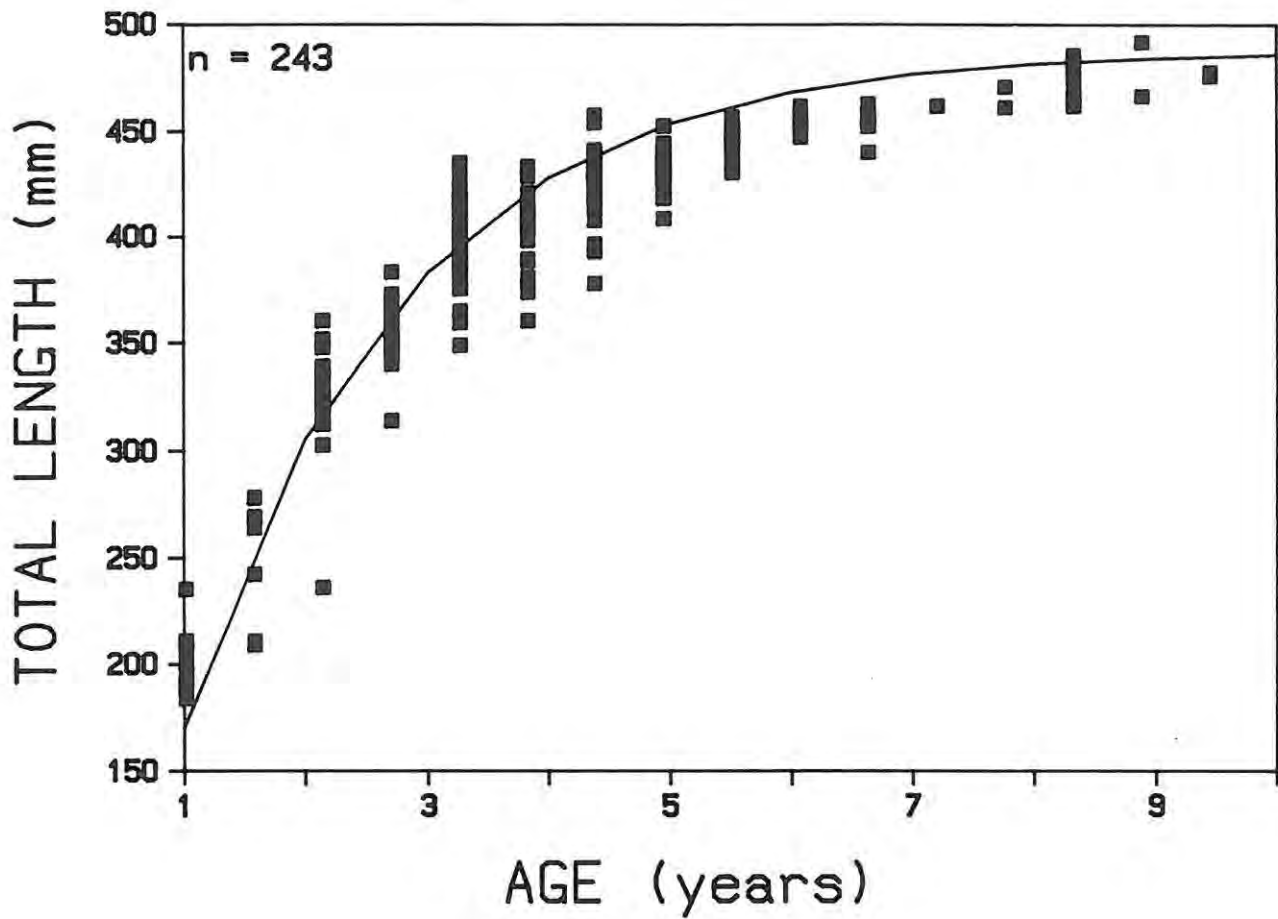


FIGURE 3.5: Graph showing the fit of the von Bertalanffy growth curve to the data obtained from reading the number of rings on the otoliths of horse mackerel of known total length.

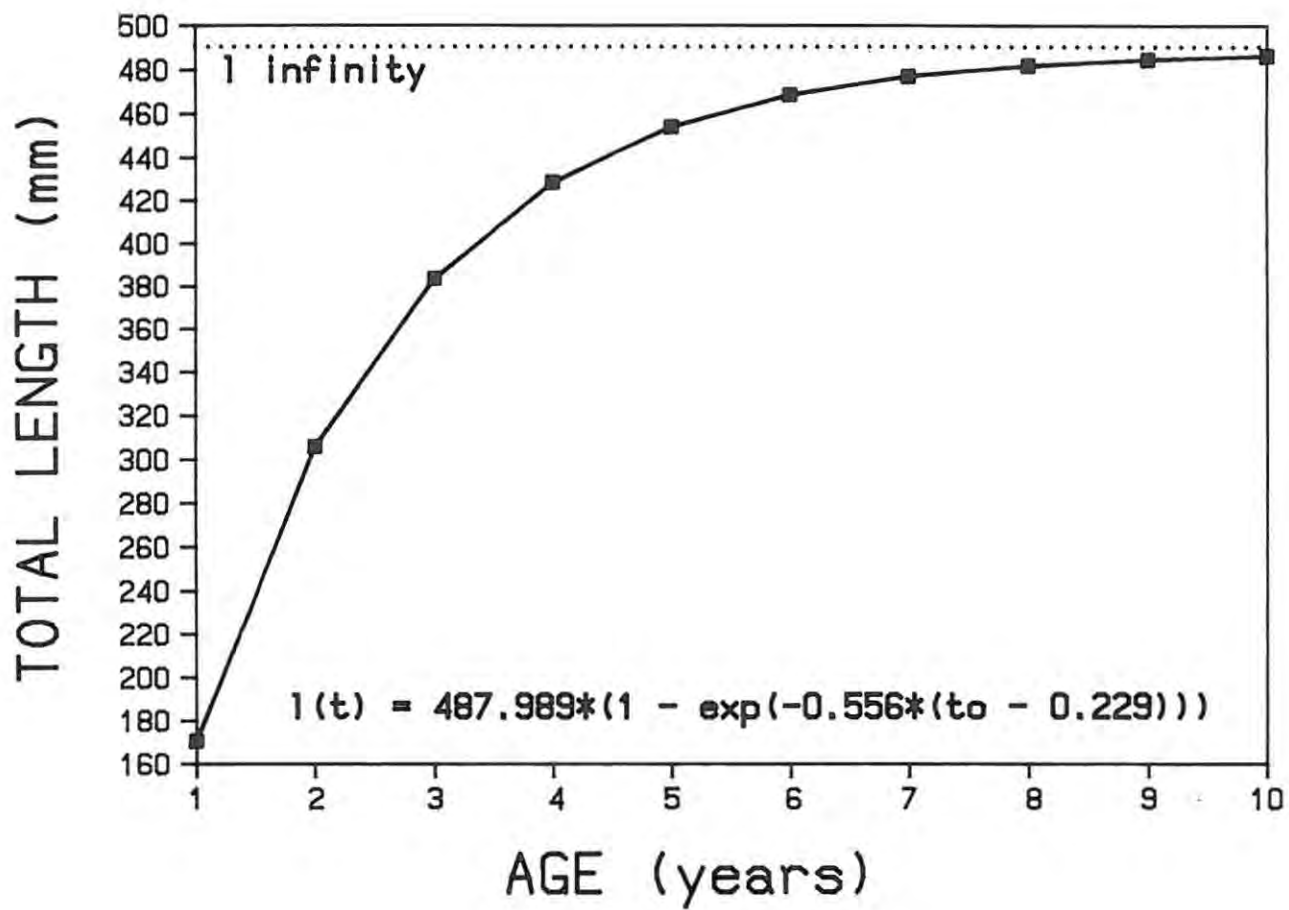


FIGURE 3.6 Graph showing the lengths-at-age of horse mackerel and the values of the von Bertalanffy parameters.

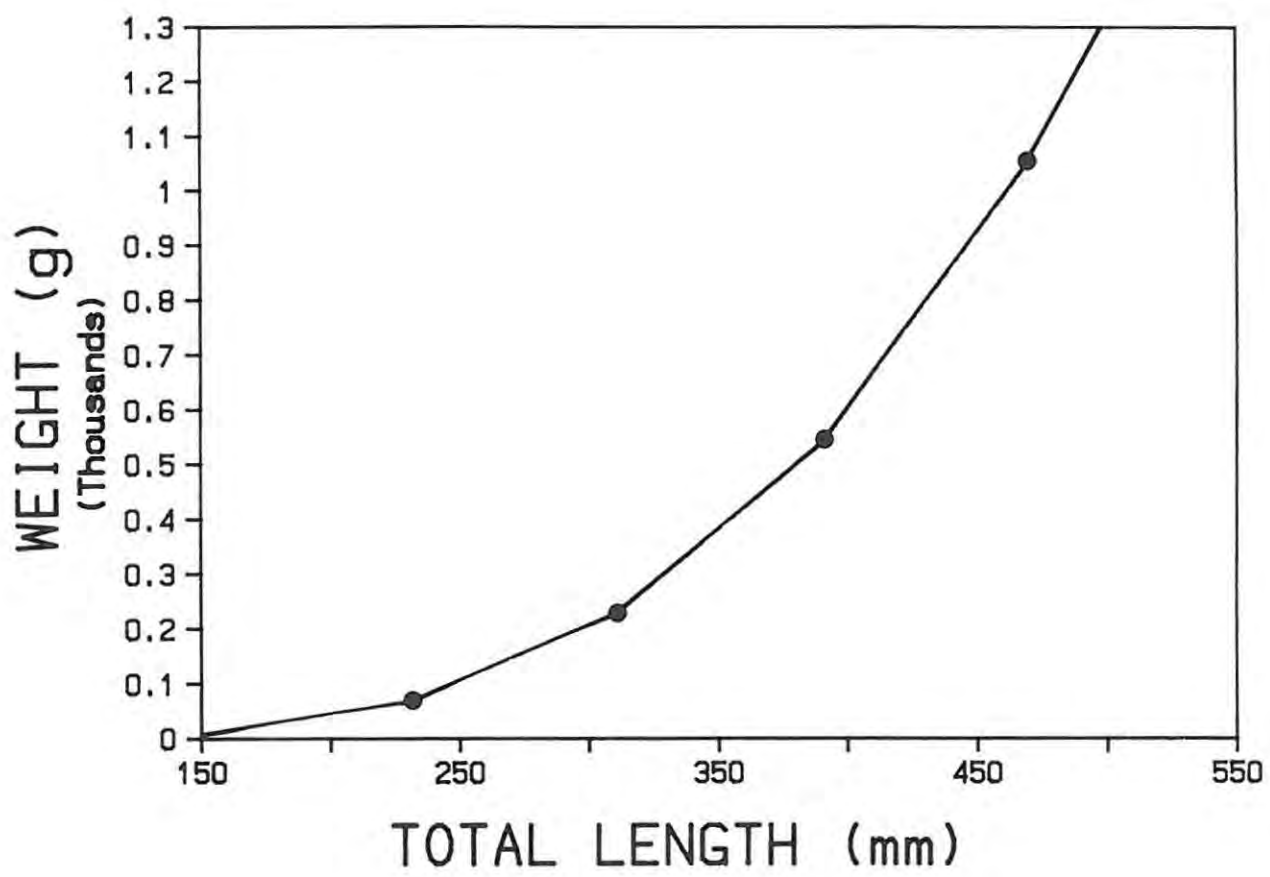


FIGURE 3.7. Figure showing the total length/weight relationship for horse mackerel.

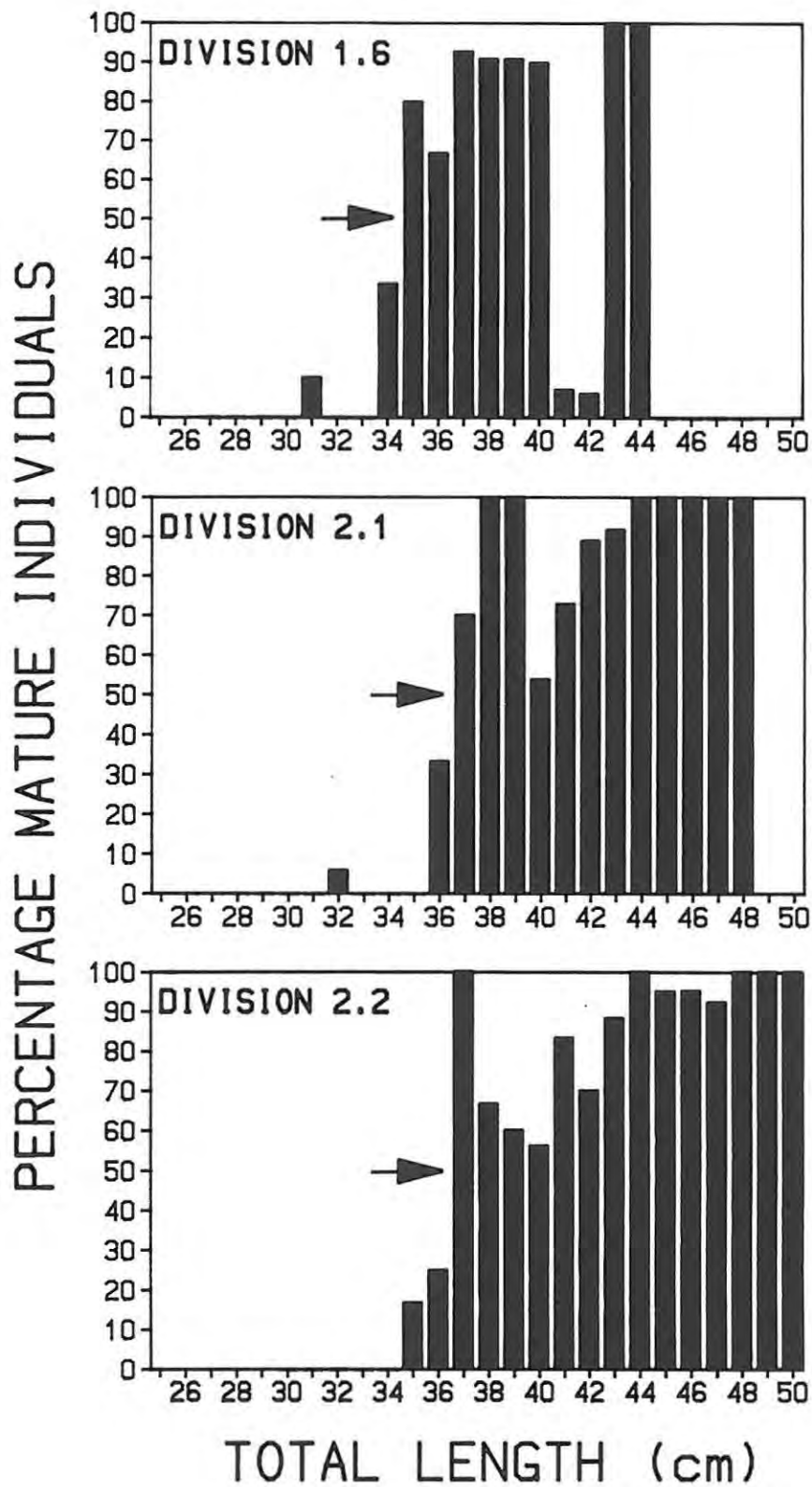


FIGURE 3.8a: Length-at-50%-maturity of female horse mackerel

FIGURE 3.8: Graphs showing the values obtained for Length-at-50%-maturity.

PERCENTAGE MATURE INDIVIDUALS

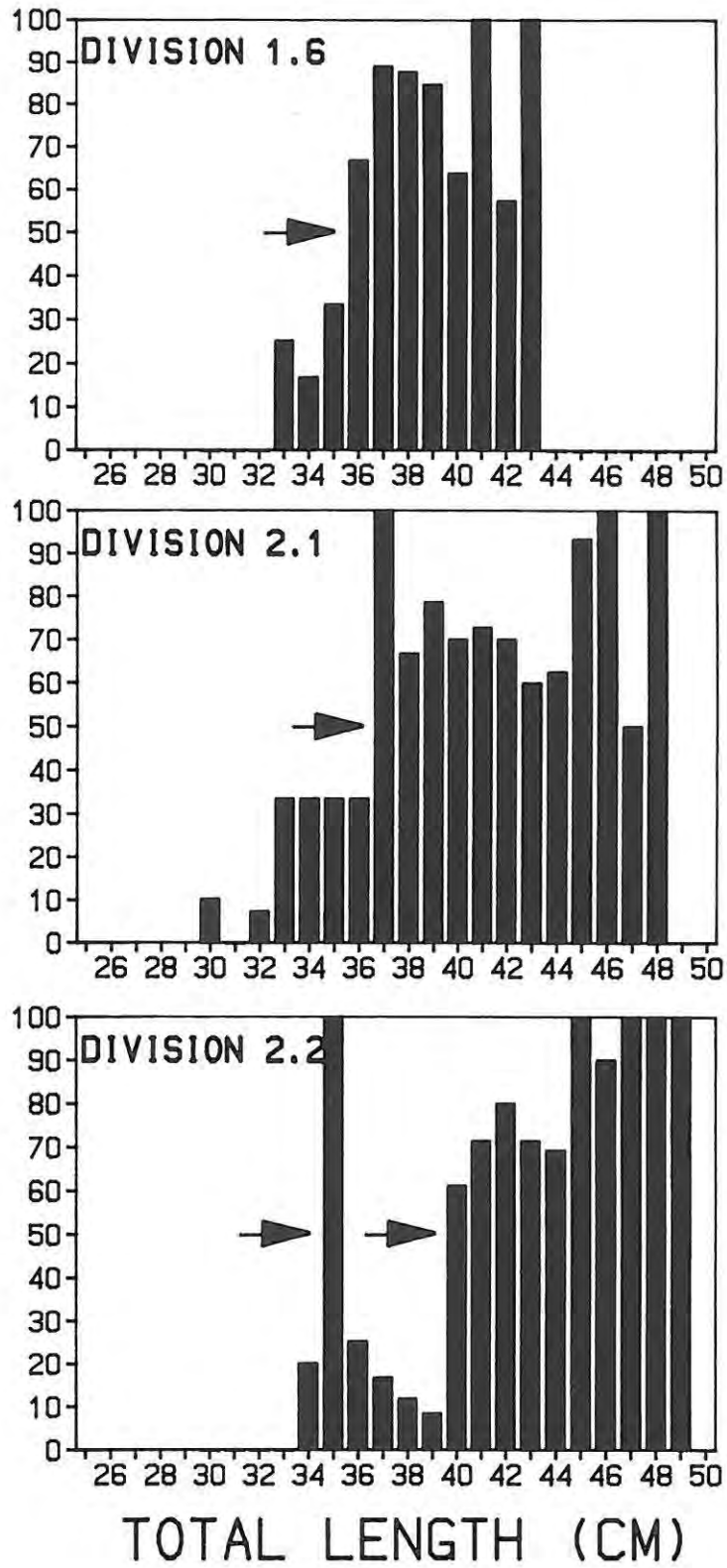


FIGURE 3.8b. Length-at-50%-maturity for male horse mackerel.

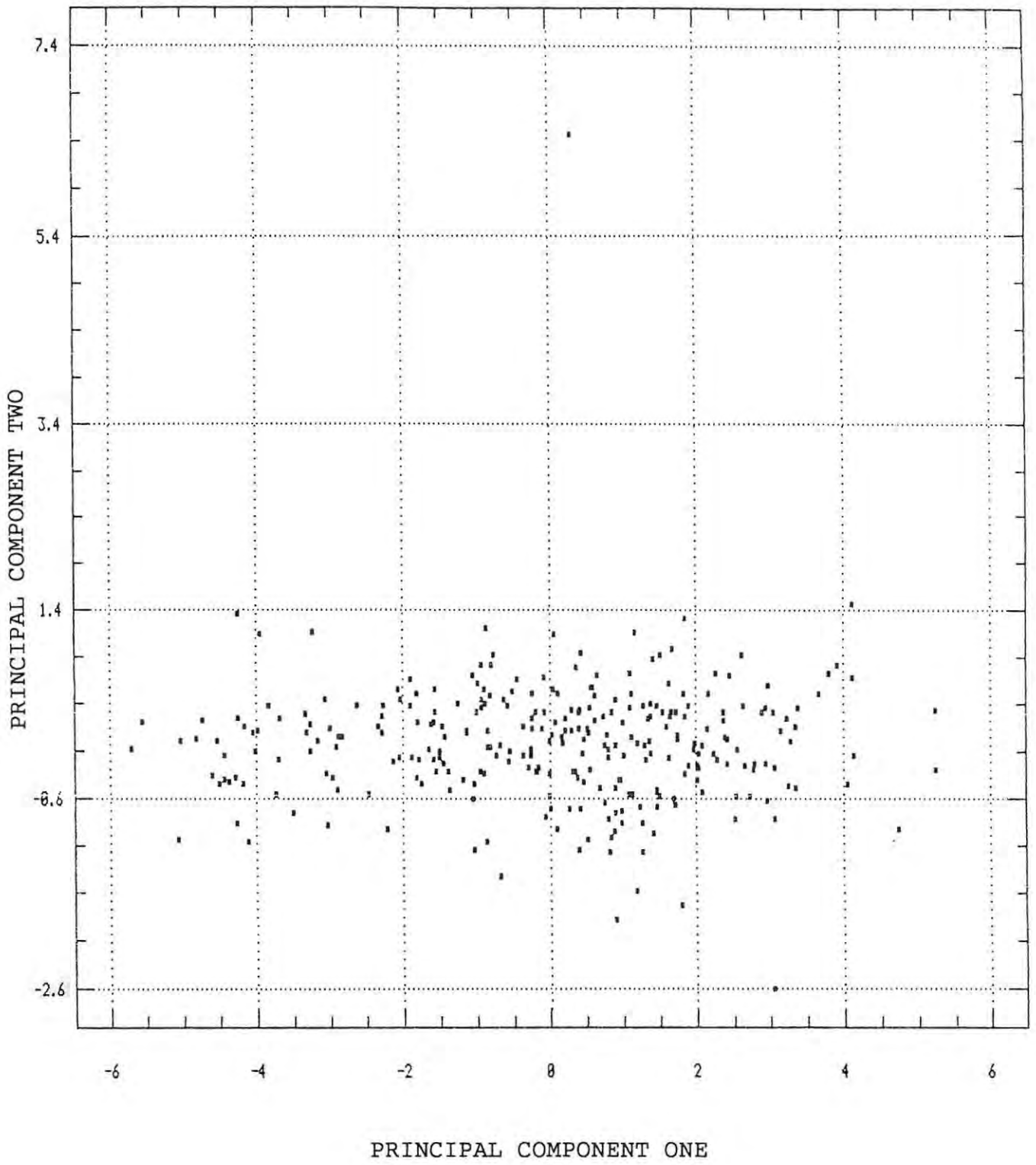


FIGURE 3.9: Plot of the first two principal components derived from the analysis of the morphometric characters of horse mackerel.

PERCENTAGE OTOLITHS WITH OPAQUE EDGE

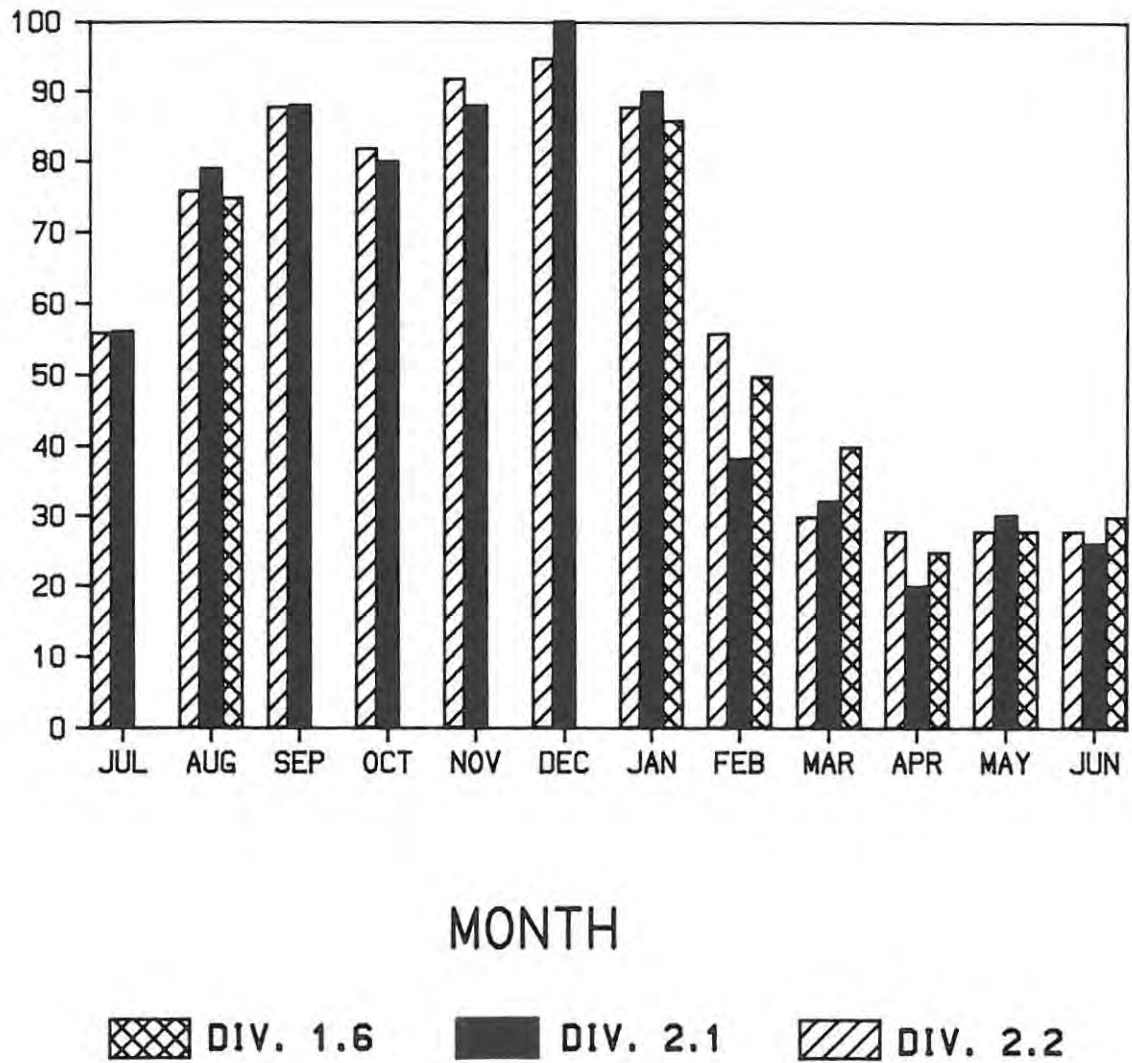


FIGURE 3.10. Graph showing the season of opaque ring formation in the otoliths of horse mackerel from ICSEAF Divisions 1.6, 2.1 and 2.2 during July, 1988 to June, 1989.

AVERAGE G.S.I.

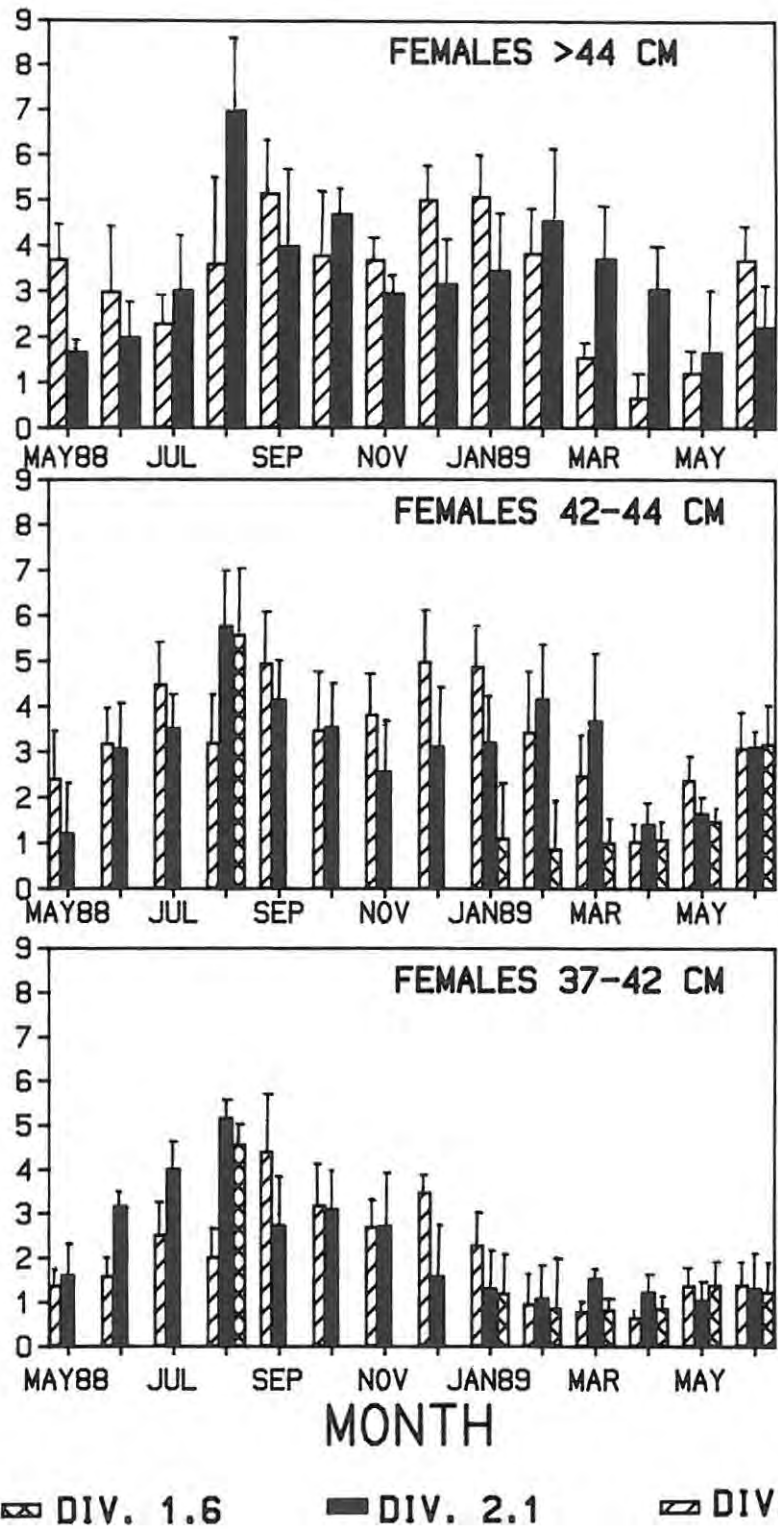


FIGURE 3.11: Graphs showing the monthly gonadosomatic indices obtained for three size classes of female horse mackerel from ICSEAF Divisions 1.6, 2.1 and 2.2 during May 1988 to June, 1989.

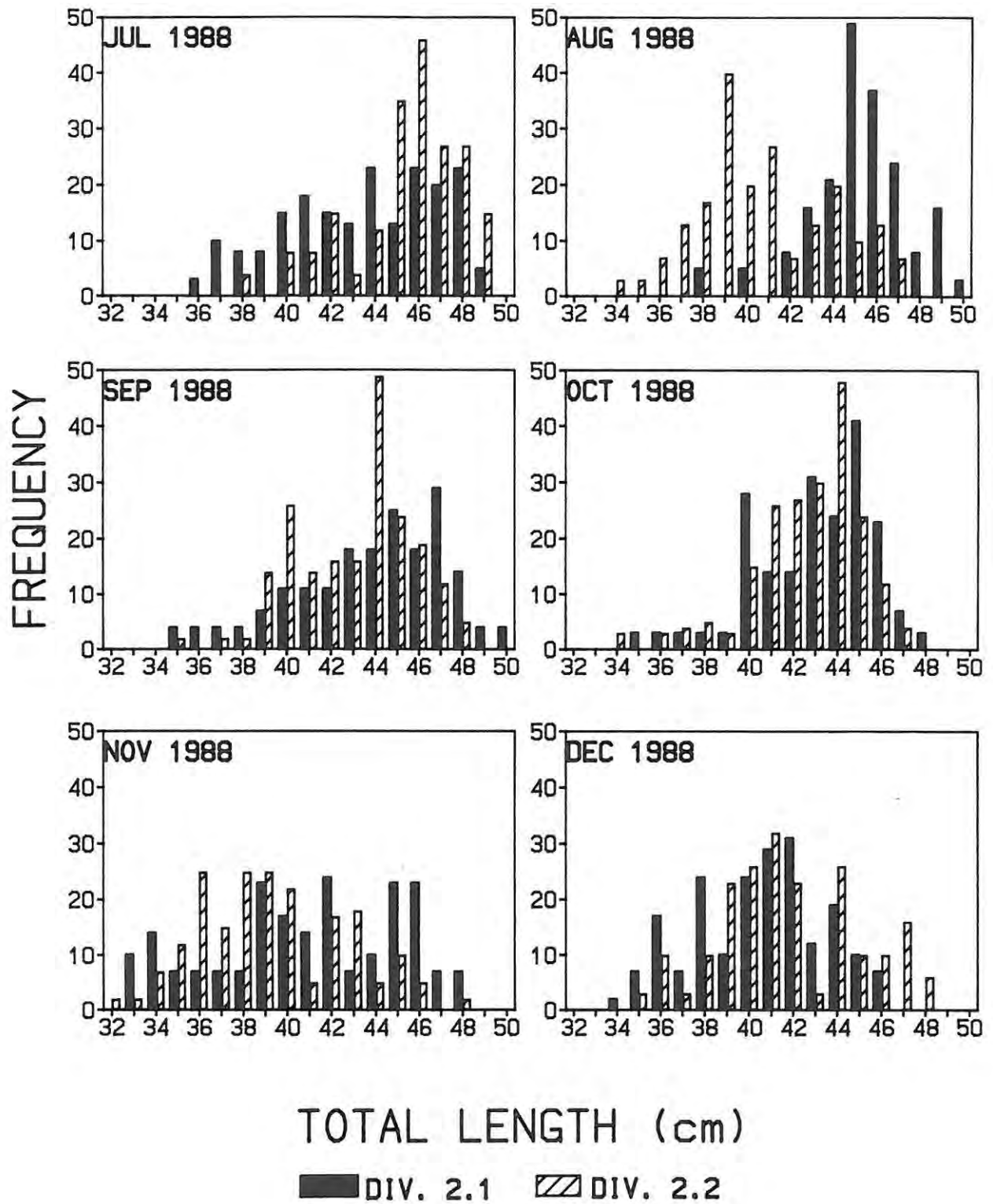


FIGURE 3.12a: July, 1988 to December, 1988.

FIGURE 3.12: Length frequency distributions of the inshore, demersal trawl catches of horse mackerel, July, 1988 to June, 1989.

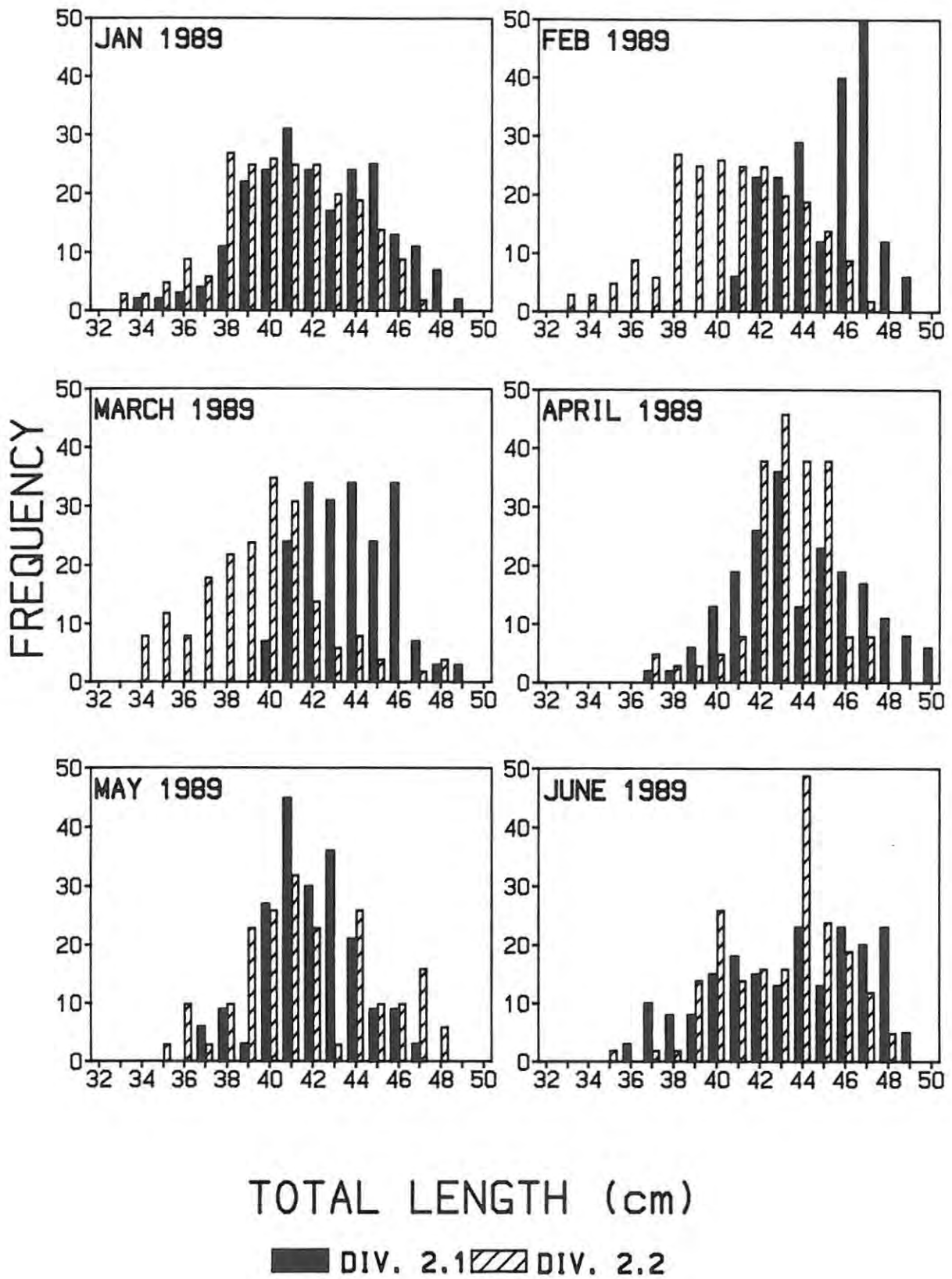


FIGURE 3.12b: January, 1989 to June, 1989

DISCUSSION

The wide variety of characteristics examined in this study reveal a consistent trend; variation of the phenotype of *Trachurus trachurus capensis* between regions south of the Orange River is minimal.

Constants obtained from the relationship between otolith length and fork length were remarkably similar for fish from ICSEAF Subdivision 2. The variation in parameters obtained from the West Coast may reflect an adaptation by fish to the different environmental conditions of Division 1.6. However, it is likely that such a result reflected a difficulty encountered in sampling. The majority of fish from the West Coast were smaller (<400mm TL) than those from the Agulhas Bank (350-500mm TL). It has been shown that the otoliths lengths of smaller fish are more closely correlated to body length than older fish (ICSEAF, 1986). Comparison of the present results with earlier studies off Namibia are difficult; a quadratic relationship was derived for fish in ICSEAF Divisions 1.3 and 1.4.

The values obtained for lengths-at-age from the growth model were comparable to those derived by Hecht (1989), but the values for the von Bertalanffy parameters L_{∞} , t_0 and k differed. Horse mackerel sampled in Div. 2.2 during 1974 and 1975 were larger than those of the present study (Hecht, 1989) and it is probable that this factor resulted in a decreased value for L_{∞} for the present model. A comparison of the growth curve presented here with those of previous studies will not be attempted, since assessment of annual growth rings varied greatly before the interpretation was standardized in 1986 (ICSEAF, 1986).

The length-at-sexual maturity values were consistent throughout the study region. Values obtained from Div. 2.2 were slightly higher than those of other regions (in the case of males, significantly higher). Again, this may reflect a response to environmental factors but the growth rate of horse mackerel from this region was found to be the same as those over the central Agulhas Bank. Since there were few fish smaller than 38cm TL sampled in Div. 2.2, a significant result could not be expected. Interestingly, Hecht (1989) reported a lower 50% length-at-maturity value of horse mackerel during 1974-1975 (318mm) than that reported here. This result reflects a different interpretation of the seven stage maturity scale or a change in conditions during the fourteen year lapse between the two studies. Wysokinski (1984) showed a decrease in length-at-maturity of horse mackerel off northern Namibia during 1977-1983 as a result of increasing fishing pressure. Fish matured at approximately 29.6cm in 1977/1978, but matured at 23.5cm in 1983. Similarly, Kuderskaya (1989) reported a decreasing maturity value of horse mackerel off Namibia during 1973-1987. It is noteworthy that the lowered maturity values in the north of the Benguela system has not been mirrored in the south. It must be assumed, therefore, that the increased fishing pressure off Namibia has no affect on the stock off South Africa. This strongly supports the hypothesis of a separate northern stock in Div. 1.3 and 1.4.

The data gathered for morphometric analysis has proved inadequate for the purpose of discovering differences between populations of the southern stock. Whether the data set itself was insensitive, or whether there are no differences to be detected is unclear. Winans (1987) encourages the use of "truss" measurements which are more sensitive than "conventional" measurements in detecting stock

differences. It should be noted, however, that the variability of morphometric characters is not directly inherited. Such variability may be related more to environmental restraints than to genetic differences (Bock, 1980; Lindsey, 1981; Todd *et al*, 1981).

The season of otolith ring formation reported here for horse mackerel occurring in ICSEAF Divisions 1.6, 2.1 and 2.2 is similar to that reported by Geldenhuys (1973) and Hecht (1989). Opaque zones were formed when growth is minimal - during the spawning season - while the hyaline zone was formed during the period of rapid growth. The opaque zone was deposited in the majority of otoliths during December. In comparison, deposition of the opaque zone in the otoliths of horse mackerel from Namibia was reported to occur during May by Hatanaka and Kawahara (1985), during May to October by Wysokinski (1985) and during April to August by Kuderskaya (1983).

Hecht (1989) postulated a possible spawning migration of horse mackerel on the basis of decreased catches in Div. 2.2 during the spawning season and a distinct absence of individuals in the ripe-running condition in the same region. Examination of the monthly gonadosomatic values of the present work reveals differing spawning maxima between the central and eastern Agulhas Bank which may support the theory for existence of two stocks. Spawners may well aggregate in separate regions in an attempt to facilitate the movement of spawning products to protected areas. There is little evidence, however, of any environmental barrier over the Agulhas Bank to prevent crossbreeding between populations (Schumann and Beekman, 1984) and it is noteworthy that horse mackerel in all regions spawned between July and January. A closer examination of the trends in GSI values reveals certain points of interest. Although larger fish in Div. 2.2 started maturing earlier

than those in Div. 2.1, a maximum was reached in August in Div. 2.1, earlier than in Div. 2.2, precisely the month when larger fish dominated the catch in Div. 2.1. The maximum GSI value reached during August was the highest value obtained in all size groups during the study period. Additionally, the highest percentage of ripe-running individuals was noted during this period in Div. 2.1. Thereafter, the GSI value of larger fish (>420mm TL) decreased. A subsequent increase in values was seen in both regions and a second peak was reached in December in Div. 2.1 and in February in Div. 2.2. The GSI of the younger fish declined steadily after the maxima in August and September. During September to December, the length frequency histograms reveal a mixture of all size classes throughout Subarea 2. During February and March, larger fish dominate the Div. 2.1 catches while smaller fish are found in the catches of Div. 2.2. GSI values of fish in Div. 2.2 decreased after December, but those of fish in Div. 2.1 decreased slowly after February. Finally, during May, 1989, the larger fish are found in the catches in Div. 2.2. Wysokinski (1984) reports a rapid transition of spent Cape horse mackerel gonads collected from northern Namibia to a renewed mature stage. Macer (1974) observed a 'partly spent' stage during the spawning season of horse mackerel *Trachurus trachurus* in the North Sea and English Channel. Fish with gonads in the 'partly spent' condition were observed to reach a spawning condition within a short period. The presence of hyaline oocytes in the ovary is deemed indicative of serial spawners by Macer (1974). Hyaline oocytes lend a 'speckled' appearance to the external surface of the gonad and are therefore easy to characterize. Hyaline oocytes first appeared in Cape horse mackerel gonads in September and persisted until the end of the spawning season (February). It is likely that the maximum GSI value shown during August in Div. 2.1, coinciding with a length frequency peak, reflects

a movement of mature adults from Div. 2.2 to the central Agulhas Bank. The decrease thereafter may be explained by the mixing of 'partly spent' and mature adults, with a possible return to Div. 2.2 by fish of the former category - thereby explaining the wider range of length frequencies of horse mackerel in both areas. The second peak in February in Div. 2.1 is preceded by one in Div. 2.2, again suggesting a second migration. It is evident that the late spawners remain in Div. 2.1 at the conclusion of the season while spent adults move back to Div. 2.2. This may explain the higher GSI values after January in Div. 2.1 as compared to 2.2. While the results obtained herein may be seen as a sampling artifact, it is significant that Hecht (1989) reported two spawning peaks for horse mackerel in Div. 2.2 during 1974-1975. In this study, horse mackerel in Division 1.6 spawned during the same period as those in Subarea 2. Similarly, Geldenhuys (1973) and Crawford (1980) report a May to October spawning maximum coinciding with an increase in catches of horse mackerel in 1.6. These findings support the hypothesis of a spawning migration undertaken by horse mackerel. Finally, it is significant to the manager of the horse mackerel resource that the smaller fish (35-42cm) spawn for a limited period; should the average length be reduced to first-time spawners, a recruitment failure is likely. The likelihood of such an event occurring is probable; the length frequencies of this study are considerably lower than that conducted during 1974-1975 (Hecht, 1989).

The spawning season for Cape horse mackerel off Namibia (Div. 1.3 and 1.4) is reported as falling between September and May, with maximum activity occurring between December and April. Similarly, O'Toole (1977) and Olivar and Rubies (1983) found a maximum in larval abundance for this species during the same months. While there is a slight overlap between the spawning season of the "Namibian" stock and

that of the "South African" stock, it can be claimed that the differing seasons between the two stocks is indicative of assortive mating and a reduced gene flow and supports the theory of a northern and single southern stock of *T.t.capensis*.

Serial spawning may be seen as an adaptation by a species towards maximizing the recruitment success of juvenile fish. Spawning seasons are timed to avoid disturbances in the environment conducive to a failure in recruitment (Parrish *et. al*, 1983). Shelton and Hutchings (in press) describe a "window" of stability in the southern Benguela system from late spring to early autumn which favor anchovy *Engraulis capensis* spawning and larval survival. Like horse mackerel, anchovy prefer regions close to warm water regimes ; the Angolan and Agulhas systems (Shannon, 1986). Anchovy spawning coincides with the period of increasing stratification of the water column (Shannon, 1986) ; off northern Namibia this is in summer after the upwelling season and on the Agulhas Bank this is in spring after the strong winter mixing. Such a finding may be extended to the spawning habits of horse mackerel, and provides a clear explanation for the evolution of two separate spawning stocks of *T.t.capensis*.

While results presented by this study strongly indicate a single stock of *T.t.capensis* south of the Orange River, caution must be exercised in drawing firm conclusions. Ihssen *et al.* (1981) state that phenotypic variations are not directly related to differences in the genome. Phenotypic characters provide little information on assortive mating and genetic discreteness, and may change with environmental changes. It is important, therefore, to study the genetic characteristics of a stock before the integrity of a stock can be confirmed.

CHAPTER 4 : THE DETERMINATION OF THE GENETIC STRUCTURE OF THE STOCKS

INTRODUCTION

Genetic discreteness between populations is inherent in the term 'stock'. A shared informational source (DNA) coding for a range of phenotypes within a population is expected to differ from those of other populations due to an isolating mechanism (Ricker, 1972; Booke, 1981). It therefore follows that a genetic comparison between populations should identify component stocks within the range of a species. Such a comparison would render an identification independent of environmental factors (Ferris and Berg, 1987), which have been shown to affect conventional morphological methods (Lindsey, 1981; Clayton, 1981; Bookstein, 1982).

The use of molecular methods in fisheries biology is increasing (Ryman and Utter, 1987). The first advances were made by geneticists studying the applicability of protein studies to differentiation of populations above and below the species level (Wilson *et al.*, 1985; Allendorf *et al.*, 1987). First, it was shown that the accumulation of amino-acid substitutions during species divergence had little effect on the functions of the organism, thereby leading to the 'neutrality hypothesis' (Anfinsen, 1959; Kimura, 1968; King and Jukes, 1969; all in Wilson *et al.*, 1985). Such substitutions were deemed 'free' from selection pressures and were therefore expected to persist and to be transmitted to subsequent generations. Second, substitutions were shown to accumulate at a steady rate in certain proteins, leading to a 'biological clock' concept which allowed the construction of phylogenetic trees and the estimation of evolutionary rates (Wilson *et al.*, 1977; Wilson *et al.*, 1985). Protein electrophoretic patterns are indicators of allelic variation and therefore reveal genetic variation pertinent to studies of population differentiation. Such a method is

easily applied, proving a rapid means of collecting a clear data set (Hartl, 1980; Allendorf *et al.*, 1987), but has proved inadequate in stock differentiation in certain cases (Lewontin, 1974; Grant, 1985; Utter, 1987; Ferris and Berg, 1987, Becker *et. al.*, 1988). As the proteins isolated are merely indicators of base changes in the genome, they are believed to be removed from the actual information source - DNA - and therefore allow for masking in mutational events. All base changes do not necessarily result in an amino-acid change (Lewontin, 1974; Utter, 1987). Interest has thus turned to the DNA constituting one percent of the total cell DNA (Ferris and Berg, 1987), the mitochondrial DNA (mtDNA).

Mitochondrial DNA has certain properties which have rendered the study of its base sequences a powerful tool for evolutionary studies of recent events (Brown *et al.*, 1979; Wilson *et al.*, 1985; Ferris and Berg, 1987; Harley, 1988). Vertebrate mtDNA is a closed, circular molecule of 16 000 to 18 000 base pairs. Being small, there is considerable ease in its characterization, a task further aided by the absence of complicating features of nuclear DNA (introns and repetitive sequences). Mutations in the genome are relatively simple and are in the form of base substitutions and length mutations, the greatest mutation rate occurring in the 'D loop' region involved in replication; mtDNA is believed to evolve five to ten times more rapidly than nuclear DNA (Brown *et al.*, 1979). Wilson *et al.* (1985) ascribe this rapid evolutionary rate to two main factors. First, mtDNA has an inefficient repair system, and second, it does not code for proteins used in its own replication, transcription and translation; it is "freer to be inaccurate" than the conventional translation apparatus.

Three properties of mtDNA are of importance to population studies. First, the entire mtDNA genome is transcribed as a unit during translation; in short, the maternal genome is inherited by the offspring with little or no paternal contribution (Hecht *et al*, 1984; Avise *et al*, 1984; Gyllesten *et al*, 1985). There is no recombination in mtDNA (Olivo *et al*, 1983) and therefore an absence of masking of any mutations occurring in the genome. Second, individuals are homoplasmic for one type of mtDNA ; heteroplasmy is rarely encountered (Wilson *et al.*, 1985). Third, closely related taxa exhibit mutational differences of the silent site transition type; they are selectively neutral (Brown *et al.*, 1982; Kimura, 1983) and therefore persist, given successful transmission, through the population. Effectively, mtDNA exhibits considerable variation between individuals both above and below the species level and has proved a powerful tool in probing population structures and their geographical patterns of distribution (Harrison, 1989). Pertinent to this study, mtDNA characterization has been proposed as a means to evaluate stock identification and genetic diversity (Ferris and Berg, 1987; Avise, 1987).

Restriction endonuclease analyses have proved an efficient and rapid means of characterizing mtDNA (Brown *et al*, 1979; Ferris and Berg, 1987; Avise, 1987; Harley, 1988). Restriction enzymes, each recognizing a characteristic base sequence, are used to digest purified mtDNA, thereby producing fragments of variant lengths. These are separated by means of gel electrophoresis, forming a pattern. Single-base mutations change restriction enzyme recognition sites; related DNA will share some sites and differ in others. A comparison of fragments produced will highlight differences between the genomes of individuals studied.

The aim of this study, therefore, is to utilize restriction endonuclease analysis of the mtDNA of individuals of *Trachurus trachurus capensis*, sampled throughout the species distributional range, in an attempt to identify the number of existing stocks.

METHODS

Mitochondrial DNA has been described as having a great resolving power (Ferris and Berg, 1987); it is therefore unnecessary to collect a large sample size for analysis. Individuals from the same locality show homogeneous mtDNA distribution (Awise and Saunders, 1984); it is therefore a preferred strategy, statistically, to sample from as many different locales as possible. Sampling positions are shown in Fig. 4.1 .

Isolation and purification of mtDNA was achieved by means of the following extraction protocol, modified from Brown *et al.* (1979) and Cummings *et al.* (1987). Fresh and frozen tissue (gonads, liver, heart and red muscle tissue) was chopped finely at 4°C and suspended in extraction buffer (sucrose - sodium chloride - tris - EDTA) at a ratio of 5ml buffer to 1g tissue. The tissue was homogenized with a blender (disrupting the cell membranes) for 15 seconds and then passed through two low-speed centrifugations (1000 g for 10 min at 4°C), separating intact mitochondria from nuclei, the latter remaining suspended in the supernatant. The supernatant was filtered through cheesecloth to remove surface particles, and the mitochondria were collected as a crude pellet after three high-speed spins (10 000 g for 15 min at 4°C). The pellet was resuspended in 30ml of buffer at 4°C and was spun once more (20 000 g for 15 min at 4°C). The pellet was resuspended in buffer (saline - tris - EDTA) at room temperature, the mitochondrial membranes were lysed with 1% sodium dodecyl sulphate and proteins and membranes were precipitated by making the solution 1M with caesium chloride and incubating the solution for 15 min at room temperature. The suspension was centrifuged at 10 000 g for 15 min at 20°C and the supernatant was saved. The mtDNA was separated from

contaminating nuclear DNA by means of a centrifugation in a caesium chloride density gradient (50 000 g for 18 h at room temperature). Ethidium bromide was added before the spin to aid visualization of the resultant mitochondrial and nuclear DNA bands under ultra-violet light. Further, ethidium bromide intercalates more readily with the supercoiled structure of nuclear DNA than with the simple structure of mtDna, lending a higher bouyant density to the former molecule. This factor facilitates the separation of the nuclear DNA from the mtDNA with centrifugation. A thin, low-density mtDNA band was seen below the nuclear band after the spin; this was extracted by means of a pump (when not visible, the region in which the band was expected was extracted). Ethidium bromide was dissolved and removed with a salt-saturated solution of isoamylalcohol. MtDNA was precipitated from the solution using a mixture with a ratio of 1 vol. solution to 2 vols. distilled waster to 6 vols. 100% ethanol. The solution was left for 1 h at -20°C). The DNA was precipitated from solution by spinning the suspension at 10 000 g for 10 min at 10°C . The pellet was washed with 70% ethanol and respun. After drying, the mtDNA pellet was resuspended in 200ul of Tris-EDTA buffer and stored at -20°C .

Differences in the sequences of mtDNAs from individuals were determined by means of the following analysis. A restriction enzyme, recognizing a known sequence of six base pairs, was used to digest the purified mtDNA (2 h at 37°C). The fragments were then end-labelled with a radioactive nucleotide to aid visualization, using two steps. Large fragment polymerase (Klenow) was added to the digested fragments. Klenow cleaves individual nucleotides off the chain in the absence of free nucleotides, thereby creating 'exposed ends' of nucleotides to which bonding can take place. The second step was the addition of free deoxynucleotides (dATP, dTTP, dGTP and dCTP) one

class of which was radioactively labeled (dCTP, with the isotope ^{32}P). In the presence of free nucleotides, Klenow rebuilds the chain, binding nucleotides to the free ends. Labeled fragments were formed as a result and they were then separated by electrophoresis using a 1.2% Agarose gel suspended in Tris - Acetate - EDTA buffer. The gels were dried and fragments were visualized by autoradiography.

Fragment patterns of individuals were evaluated by means of an adaptation of the formulae derived by Nei and Li (1979), (Harley, 1988; Essop and Harley, in prep.). Using computer-generated iterations, the proportion of shared fragments was related graphically to the number of nuclear substitutions per site (Fig. 4.2). The proportion of shared fragments (S) was derived using the following ratio:

$$S = \frac{\text{total number of shared fragments}}{\text{total number of fragments produced}}$$

The corresponding value for nucleotide substitutions per site was read from the graph, using the curve obtained for enzymes which cut six bases. The sequence divergence (SD) between individuals of differing genotypes was calculated using the formula

$$SD = \frac{-(\ln S)}{r}$$

where r = number of base pairs recognized by the restriction enzyme.

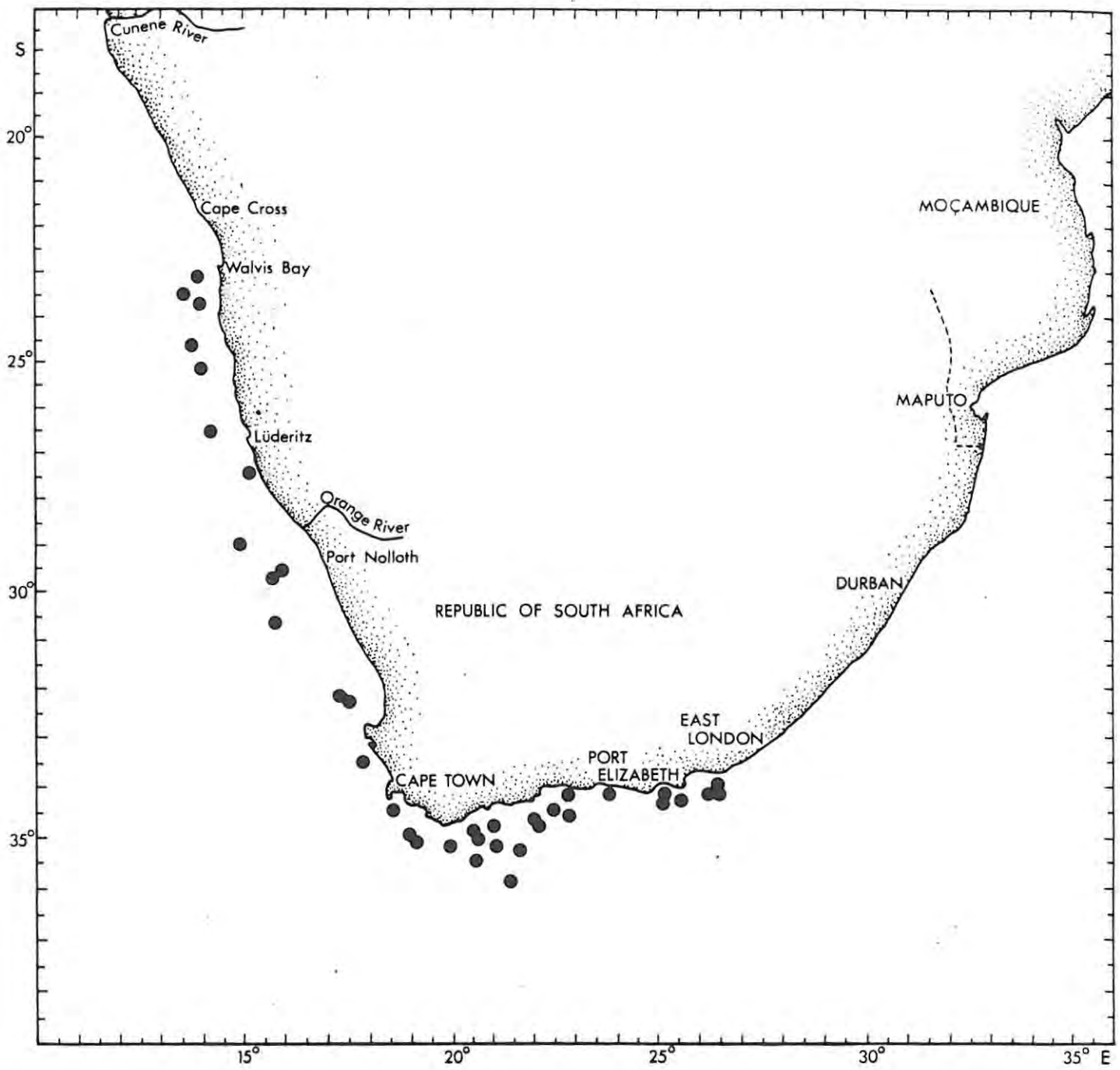


FIGURE 4.1: Map showing the sites from which samples of horse mackerel were taken.

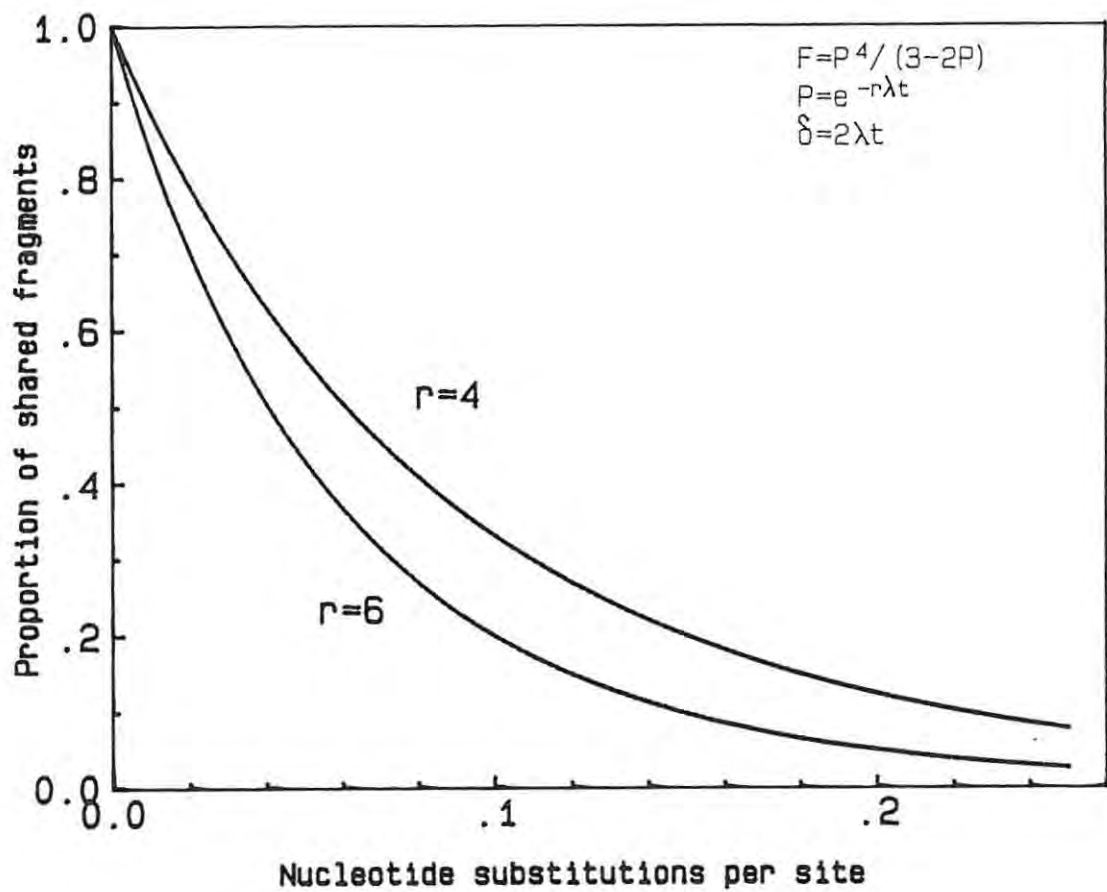


FIGURE 4.2: Graph showing the relationship between the proportion of fragments shared and the number of nucleotide substitutions per site. r is defined as the number of base pairs the restriction enzyme recognizes, in this experiment $r = 6$. (After Essop and Harley, in prep.)

RESULTS

Fragment patterns were obtained for 37 fish using 12 restriction enzymes. Two genotypes were revealed in this study; one was common to all samples taken from South African waters (ICSEAF Divs. 1.5, 1.6, 2.1 and 2.2) and one was common to samples taken off Namibia (ICSEAF Div. 1.4), the distribution shown in Fig. 4.3. The restriction enzyme patterns are shown in Fig. 4.4. A photograph of a gel showing the homogeneous nature of samples taken from South African waters is shown in Plate 4.5.

The sequence divergence between the Namibian genotype and the South African genotype was calculated using the formulae described earlier. The number of nucleotide substitutions per site was determined to be 0.022 and the sequence divergence was calculated as being 0.07, values expected for closely related taxa (Nei and Li, 1979). No polymorphism was noted in the South African samples, whereas the Namibian samples were inadequate, numerically, to determine intrapopulation variation.

It was noted during the extraction process that fresh, red muscle tissue (approx. 80g) maintained at 4°C gave significantly high yields of mtDNA; frozen tissue gave very low yields and the nuclear DNA tended to break down and contaminate the mtDNA band at CsCl centrifugation. DNA was obtained, however, from certain frozen red-muscle tissue used soon after collection, although at reduced yields. Other tissues proved high in nuclear DNA content, which inevitably contaminated mtDNA. Such a result was reflected in cichlid fish in the same laboratory (D. De Villiers, J.L.B. Smith Institute, pers. comm.). This is in sharp contrast to findings for mammalian and bird tissue; the freezing process (E. Harley, U.C.T., pers. comm.) aids the extraction of mtDNA. It must be stressed that samples from Namibian

waters were frozen and results, in many cases, were difficult to interpret. While differences between the Namibian samples and the South African were apparent, the exact results were unclear.

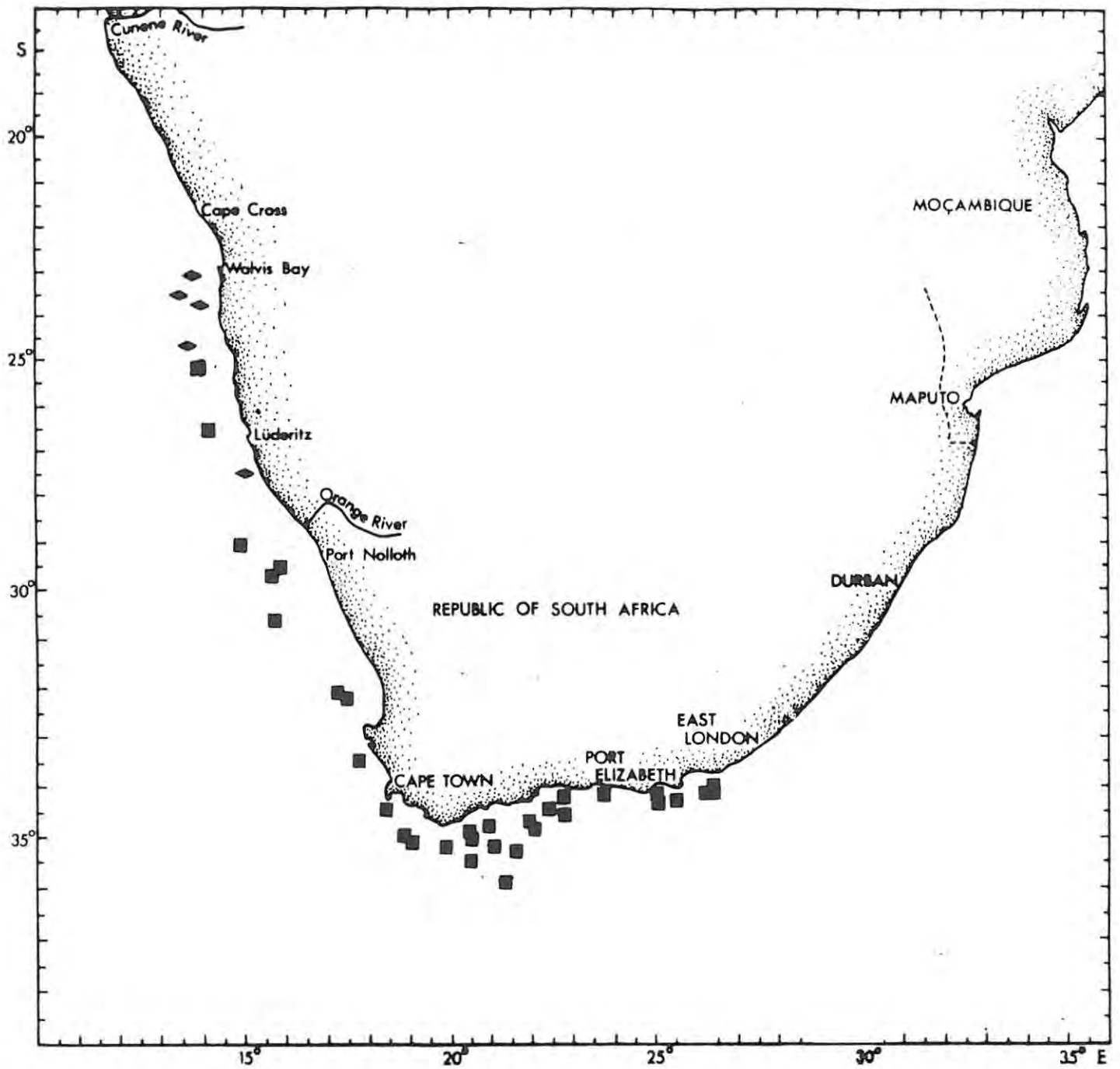


FIGURE 4.3: Map showing the distribution of horse mackerel with the two Mitochondrial DNA genotypes found by restriction enzyme analysis. Triangles denote the **Namibian** genotype and squares denote the **S.African** genotype.

FIGURE 4.4. Diagrammatic representation of the fragment patterns resulting from the digestion of horse mackerel Mitochondrial DNA by restriction enzymes recognizing a known base sequence of six base pairs. A standard marker, λ Hind III, was used to determine the size of fragments produced by digestion. The number of base pairs of the fragments of the marker were known. The number of bases pairs of horse mackerel Mitochondrial DNA should total approximately 16 000. Fragment patterns were compared and the ratio of shared fragments to total fragments calculated. Two genotypes were revealed. S = South African genotype and N = Namibian genotype.

λ HIND III	BAM HI		BCL I		BGL II		DRA I		ECO RI		HIND III	
	S	N	S	N	S	N	S	N	S	N	S	N
23.1												
9.4	—	—	—	—	—	—	—	—	—	—	—	—
6.6							—	—				
4.4			—	—		—	—			—		
2.3			—	—								
2.0							—	—			—	—
0.6					—		—	—			—	—
TOT. NO. FRAGMENTS	2		6		4		8		3		6	
NO. FRAG. SHARED	2		6		0		2		0		6	

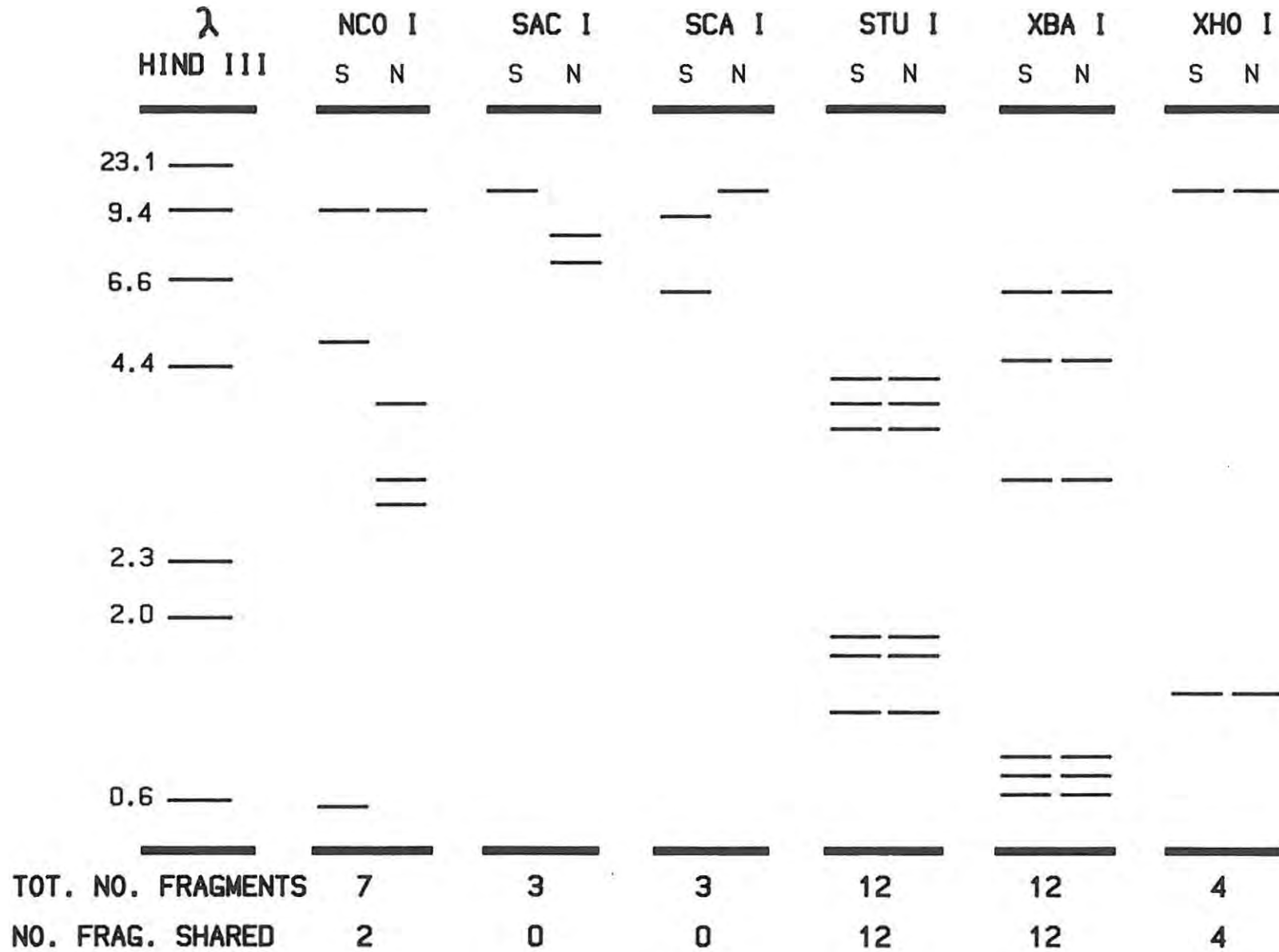
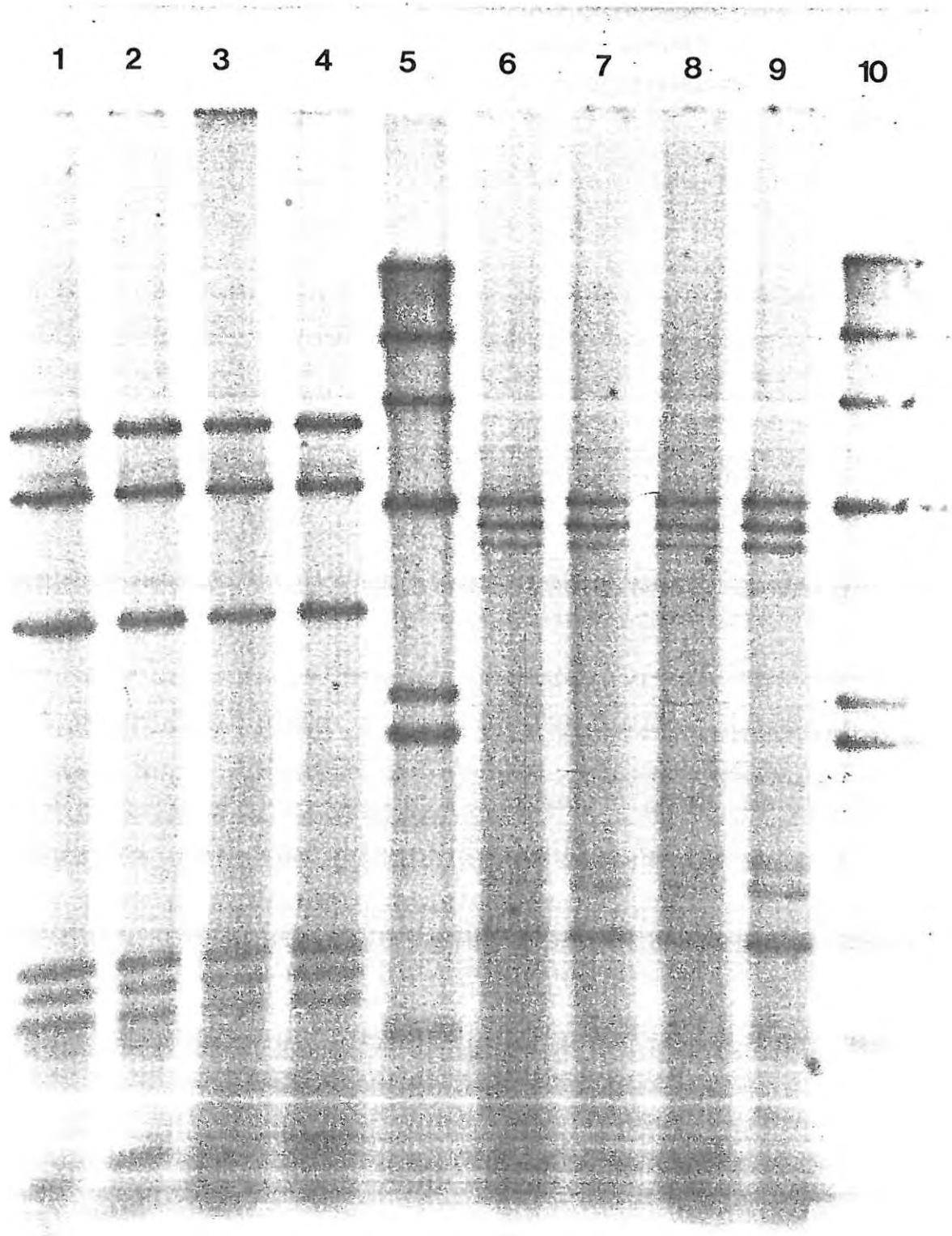


PLATE 4.5. Photograph of a sample gel which shows the homogeneity of the genotype of horse mackerel from South Africa. Mitochondrial DNA in lanes 1-4 were digested with XbaI and in lanes 6-9 with StuI. The standard marker is in lanes 5 and 10. Samples were taken from the Orange River region (lanes 1 and 6), off Cape Town (2 and 7), off Mossel Bay (3 and 8) and off Port Elizabeth (4 and 9).



DISCUSSION

Avise (1987a) cautions the interpretation of mtDNA differences in attempting to delineate marine stocks. Ideally, mtDNA lineages would reflect a reduced gene-flow between structured populations within a species range, thereby identifying mtDNA stocks significant to management. However, given the female lineage of mtDNA and the non-recombinant nature of the structure, it is possible for widely divergent mtDNA types to exist in a population; either persisting from polymorphic origins or through non-transmission of allopatrically evolved mtDNA. Further, controversy exists over whether or not marine species with a continuous distribution will show geographic variation of the mtDNA genotype. Studies on skipjack tuna (Graves *et al.*, 1984), marine catfish (Avise *et al.*, 1987), Atlantic herring from separate spawning regions (Kornfield and Bogdanowicz, 1987), Atlantic salmon with differing spawning behaviors (Birt *et al.*, 1986) and Cape hake (Becker *et al.*, 1988) have all failed to show geographically correlated variation. It is important to note, however, that the conventional methods of stock differentiation had also failed when applied to the aforementioned examples. The sensitivity of mtDNA in detecting intraspecific differences has been demonstrated in terrestrial and freshwater species (e.g. Brown and Simpson, 1982; Ferris *et al.*, 1983; Avise *et al.*, 1984; Cann *et al.*, 1987; Harrison, 1989) and certain marine species (Saunders *et al.*, 1986; Avise *et al.*, 1986). The meaning and significance of mtDNA stocks is brought into question with these considerations, leading to the suggestion that each individual case be evaluated in relation to the zoogeography, biology and life history of the species studied (Avise, 1987).

Trachurus trachurus capensis has a continuous distribution south of the Orange River (ICSEAF Divs. 1.6, 2.1, 2.2) and off Namibia (ICSEAF Divs. 1.3 and 1.4), (Chapter 2), with a biomass hiatus between the two populations (in Div. 1.5) attributable to the environmental barrier in the vicinity of Luderitz, set at 24°30'S by Agenbag and Shannon, 1988. The populations spawn during different seasons (Chapter 3), with a possible spawning migration occurring in both regions. Therefore, two isolating mechanisms serve to restrict gene-flow between the northern and southern populations of *T.t.capensis* and it is not surprising that two different genotypes have been identified.

A similar study of Namibian and South African anchovy, a pelagic fish also expected to be affected by the aforementioned barrier, showed insignificant geographic variation (Grant, 1985), although this was determined by means of protein electrophoresis. From that study, it was contended that the genetic stock concept was less applicable to marine fish than to freshwater fish, because fewer barriers to interchange exist in the marine environment and only a few migrants would be required to maintain genetic homogeneity (13 individuals in the case of Cape anchovy). It was of interest that the barrier region (Div. 1.5) contained both Namibian and South African genotypes of *T.t.capensis*. Although biomass of horse mackerel in Div. 1.5 was very low during the collection of the samples used in the present study, this finding does suggest a degree of interchange between the two populations. It further challenges the setting of the barrier at a precise location (Agenbag and Shannon, 1988); both genotypes crossed the latitude 24°30'S. The timing of the spawning activity of the Namibian and South African populations of horse mackerel was seen as a response to local oceanographic conditions (Chapter 3) which are

optimal for spawning at different months within a year. It is likely that the evolution of two separate stocks has been due to reproductive isolation, rather than a separation by a physical barrier in Div. 1.5.

In comparison, protein electrophoresis methods was used to identify a northern and southern population of *T.t.capensis* (Zenkin and Komarov, 1981). Homogeneity was established in the northern population, leading to the surmise that the Namibian individuals formed a unit stock. The homogeneous nature of the mtDNA genotypes encountered in the present study has two implications; first, morphological stocks found south of the Orange River are not detected by mtDNA analysis or second, there is only one South African stock. If the latter is correct, it can be assumed that the northern and southern populations have been separated recently or that the southern population has passed through a 'bottleneck' (a period of reduced numbers and therefore reduced genotypes). 'Bottleneck' effects have been reported for several species (e.g. Ferris *et al.*, 1982, 1983, 1984; Helm-Bychowski, 1984, cited by Wilson *et al.*, 1985), in time periods as recent as the 1930s and 1940s. Carr (1984) found that genotype variation in the Cape platanna *Xenopus laevis* was severely reduced when females of the species were used for pregnancy testing! (In Wilson *et al.*, 1985). The decline in the catch rates of the pelagic fishery for *T.t.capensis* after the 1950s (Geldenhuys, 1973) may well have reflected a decline in the spawner biomass, therefore producing a 'bottleneck' effect in this species.

Given the conclusions reached in the preceding chapters, it can be assumed that the mtDNA genetic stocks correspond to the biological stocks identified. The use of studies of the life history, migration and biology of the species has verified, in this example, the accurate

application of mtDNA. There is little reason to suspect discontinuities within the northern and southern populations identified.

CHAPTER FIVE: GENERAL DISCUSSION AND CONCLUSIONS

THE STOCK CONCEPT - A MANAGEMENT PERSPECTIVE

Royce (1972) correctly observed that there exists "a bewildering array of semantic problems because there is little agreement on the meaning of the words used to define groups in the hierarchy with the rank of subspecies and below". Many authors favor a defining fish stocks on a genetic basis (e.g. Kutkuhn, 1981; Clayton, 1981; Ferris and Berg, 1987). In an attempt to provide a working definition of fish stocks, Booke (1981) redefined the generalized definition - "a stock is a species group, or population, of fish that maintains and sustains itself over time in a definable area" - to one with a precise genetic measure. He claims a genotypic stock to be "a population of fish maintaining and sustaining Castle - Hardy - Weinberg equilibrium". He also argues that the latter definition quantifies the genetic stock structure of a stock, despite the limitations the Castle - Hardy - Weinberg law imposes on evolution; it depends on the constraints of no mutation, natural selection, immigration and emigration. Further, Booke (1981) claims that, because both genetic and environmental effects contribute towards the expressed character of a fish, the definition may be extended towards a phenotypic one: "a group, or population, of fish maintaining characteristics which are expressed in one or more ways depending on the type of environment or domicile". It is contended here that the stock unit defined by a biologist is not necessarily that which a manager seeks.

Shomura (1987) expressed concern over the use of genetic delineation for stocks of skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean. Electrophoretic studies had revealed distinct boundaries in the distribution of that species (Fujino, 1970, in Shomura, 1987), but tagging studies conducted later revealed

considerable movement throughout the region, regardless of pre-defined distributions (Kearney, 1983, in Shomura, 1987). Additionally, Winans (1980) found a low degree of genetic diversity in the milkfish (*Chanos chanos*) of the central and western Pacific. That species occupies estuarine and lagoon habitats, which are conducive to the development of several discrete population units. Low genetic diversity was attributed to larval dispersal between locations. A manager would be expected to recognize smaller units than those shown by the electrophoretic study. Similarly, Grant (1985) found a low genetic diversity between two supposedly separate breeding populations of anchovy (*Engraulis capensis*) in the Benguela system off the southwestern coast of Africa. He concluded that a migratory rate of as few as thirteen individuals per generation would maintain the homogeneity found. Again, separate management of the two populations could be anticipated and does, in fact, take place.

In several cases, the use of phenotypic characters has proved inadequate (Lindsey, 1981; Clayton, 1981), a feature ascribed to the plasticity of morphological structures in response to the environment. Combined with the apparent insensitivity of genetic methods to management units, the practical definition of stocks appears a disparaging task. It is proposed that the difficulty lies in the conflicting methods of stock identification used by the biologist and by the manager. The biologist aims to delineate a stock spatially and temporally by tracing interactions between individuals. The genetic stock displaying homogeneity over a wide distribution range is therefore a stock in the true sense; genetic flow occurs within that unit, thereby maintaining the genetic integrity. The manager seeks to quantify the genetic flow between two or more components of the genetic stock. Should one component of a population be overexploited,

it is important to assess whether the gene-flow between the populations would suffice to repopulate the region. Rolon (1987) claims that the terms "management unit" and "gene pool" are incorrectly interchanged.

The belief that stocks should be exploited in such a manner as to maintain genetic diversity may not be of primary concern to management decisions (Bert, 1987). The aim of management is to maintain all components of the stock and to harvest them at an optimal rate. The management of a low-diversity population, sharing similar growth, mortality, maturation and reproductive patterns may be the preferred strategy (Awise, 1987). Of importance is the definition of stock differences in terms of a time-scale (Scott, 1987). The effect of fishing mortality on natural mortality in evolutionary terms is little understood. If evolution is a stochastic process, then the extinction of a genome is of little consequence because it is likely that a replacement genome will arise. If, however, evolution is deterministic, then the extinction of a genome may have serious implications for the evolution of a species.

Should the purpose of management be the identification of components with population parameters of growth, mortality and productivity distinct from other components of a species, then phenotypic methods of stock identification may, in some examples, be preferable to genotypic differences. Regions of differing environmental conditions may be expected to contain characteristic phenotypes distinct from other regions, despite an underlying genetic homogeneity (with the assumption that individuals remain in these regions). Such differences may reflect the productivity of each phenotype, the unit of relevance

to the manager. Such a postulation may explain the success of morphological methods in certain examples of 'stock' identification (e.g. Winans, 1987). The argument that genetic and environmental effects on phenotypic characters should be regarded together, as interchangeable definitions in attempts at stock identification (Booke, 1981), is disputed here; each may not contribute equally to the phenotype, the unit generally managed in fisheries.

In conclusion, the stock concept is a nebulous one. It should be applied with practical management in mind and manipulated according to the individual case studied. Evidently, a wide range of techniques of stock identification would be a preferable strategy.

THE HORSE MACKEREL RESOURCE - MANAGEMENT RECOMMENDATIONS

It is clear from the arguments presented in this chapter that the biologically defined stock is not necessarily the unit that a manager may find relevant for the development optimal exploitation strategies. It is therefore of importance to identify the management units pertinent to the exploitation of the Cape horse mackerel resource.

The hypothesis proposing the existence of three stocks of *Trachurus trachurus capensis* in the ICSEAF convention region (Draganik, 1977; Crawford, 1980) is rejected herein. While the evidence examined in this study strongly supports the separation of *T.t.capensis* into northern 'Namibian' and southern 'South African' stocks, there is no basis for a separation, either phenotypically or genotypically, of the southern stock. In short, two stocks are deemed to exist in the ICSEAF convention region.

The two biological stocks identified here are found off Namibia (ICSEAF Divisions 1.3 and 1.4) and off South Africa (Divisions 1.6 and Subarea 2). A limited interchange is believed to occur between the two regions (Division 1.5). Should overexploitation of either stock take place, it can be safely assumed that migration from the other stock (if that is underexploited) would not provide a means of repopulating the region. Both stocks are genetically distinct and are reproductively isolated, a result of different spawning seasons. It is of socio-political relevance that the resource is not shared by the two countries, namely Namibia and South Africa, off which the two stocks are found. Therefore it is a preferred strategy to assess the two stocks separately.

The management of the southern stock poses interesting questions. Given that the stock has a distribution range extending from the warmer waters of the south-East Coast to the colder upwelling waters of the South-West Coast, environmental conditions may result in phenotypic variation. The stock has been shown to be genetically homogeneous and, while there may be morphological variations, none have been found in this study. Growth rates, reproductive seasons and maturity rates vary little between each coast. Such homogeneity should be attributed to migration throughout the region and the use of age-specific habitats by the horse mackerel (St Helena Bay as a nursery ground, the central Agulhas Bank as an adult spawning ground, the offshore shelf regions as an adult feeding ground). Therefore, the stock should be managed as a single entity using the same population parameters.

Further, the southern resource is utilized by different components of the fishery: as juveniles, they are taken by pelagic purse-seiners, and as adults, they are caught by directed midwater trawling and non-directed bottom trawling. The effects of each fishery on the total resource has been a subject of considerable debate, but from this study, it is clear that they are exploiting the same resource. Therefore, if a Total Allowable Catch (TAC) is to be set for the southern stock as a whole, it should be assigned to the fishery as a whole. Unfortunately, the effect of the West Coast purse-seine catches on the succeeding years' adult catches is still unclear; apart from some small horse mackerel in a few bays on the South Coast (Payne, 1986), no other nursery grounds of consequence have been identified. Also, the importance of St Helena Bay as a nursery ground has not been quantified, although purse-seine catches there in some years are large. It would thus seem prudent to manage the total stock with caution,

particularly in limiting catches of juveniles, at least until more is known about the whole life history of horse mackerel off South Africa.

Clearly, an adult horse mackerel, destined for direct human consumption or as bait in the rock lobster fishery, may be expected to command a higher market price than many juveniles, almost all of which are used to manufacture fish meal. There is therefore some economic benefit in reducing the rate of exploitation of juveniles. In the use of the adults, the main fishing companies have been investigating improved means of marketing horse mackerel. It is a fish which is difficult to market as a convenience food (it has small fillet size and is difficult to scale, because of the scutes covering the lateral line), and therefore it is not readily accepted into the higher income market. However, its present low price per kilogramme renders it an attractive fish to the lower income market. At present, the price per kilogramme of horse mackerel on the retail market is priced at R1.90 and the cheapest category of hake, 'baby hake' is priced at about R2.60 per kilogramme (Pers. observation). Any increase in the rate of exploitation, and particularly a concomitant increase in production costs, may result in the fish being too expensive for the lower income market, while it may take some time for it to reach full potential in the higher income market.

Finally, it is fortunate that, in the case of the Cape horse mackerel, management units and biological stocks are the same. From the results presented in this dissertation, there is clearly no relevance in dividing the southern stock of *Trachurus trachurus capensis* on a phenotypic or genotypic basis.

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