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SEX RATIOS AND MATURATION PATTERNS OF HORSE MACKEREL (*TRACHURUS TRACHURUS*) FROM THE NE- AND SE-ATLANTIC AND THE INDIAN OCEAN -- A COMPARISON

by

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ABSTRACT

Maturity stages of 42,051 horse mackerel (*Trachurus trachurus trachurus*) of both sexes were examined in the North-East Atlantic Ocean (NEA) in 1984 and 1985. 99,157 specimens of *T. t. capensis* were staged in the South-East Atlantic (SEA) and in the Agulhas Bank (AB) region of the Indian Ocean during the period 1992-1994. Sex ratios, maturity ogives and lengths-at-sexual maturity (LM_{50}) were computed for the specimens of both areas. Sex ratios in the SEA and on the AB were in favour of males, whereas females were more abundant in the NEA in the size-classes >32cm. The relationships between sex ratio and fish length conformed with the effects of environmental sex determination and sex-specific adult mortality. In the NEA, sexual maturity occurred at higher lengths and older ages than in South African waters. Intra-regional differences among maturation rates and the LM_{50} of both sexes exceeded inter-regional differences. Sexual maturity appeared to be linked to growth rate. A comparison of the relationships between water temperature and LM_{50} of males and females suggested a more direct response of the males to changing environmental conditions, regardless of their origin from the NEA or SEA/AB. A comparison of the ogives for slope parallelism revealed that the maturation rates of males and females were, in many cases, identical in the NEA and SEA/AB, indicating stable populations with a high level of phenotypic plasticity. The possible causative relationships between changes in length-at-maturity and changes in surplus energy compartmentalization among the competing traits growth, maturation and migration were explored and served to interpret the observed maturation patterns.

INTRODUCTION

Horse mackerel *Trachurus trachurus trachurus* in the North-East Atlantic Ocean have been studied intensively with respect to their maturation (e g. Macer, 1974; Arruda, 1984), spawning periods (e.g. Borges *et al.*, 1977; Iversen *et al.*, 1989; Eltink, 1992) and fecundity (Arruda, 1986; Eltink & Vingerhoed, 1989, 1993). In this region, horse mackerel mature at lengths of 17-27cm (Polonskii, 1969; Overko, 1974; Kerstan, 1988; Lucio & Martin, 1989), which correspond to an age range of 2-5 years (e.g. Sahrhage, 1970; Overko, 1974; Kerstan, 1985). Depending on the subarea of the North-East Atlantic, mature males are smaller and younger than females (e.g. Kerstan, 1988) or of equal size (Lucio & Martin, 1989). Sex ratios rarely depart from 1:1 (Kerstan, 1991).

Previous studies on the maturation of the Cape horse mackerel *Trachurus trachurus capensis* on the Agulhas Bank off South Africa's south coast indicated a length of 33-43cm at 50% maturity (e.g. Payne, 1986; Hecht, 1976, 1990). According to an accompanying ageing study, a length of 33cm corresponded to an age of about 2 years (Hecht, 1990). However, recent studies indicate that the age at 33cm is 4 rather than 2 years (Kerstan, 1995) and that the lengths-at-maturity of horse mackerel on the Agulhas Bank were markedly smaller than previously believed (Kerstan, in prep.). On the Agulhas Bank, the sex ratios of horse mackerel varied in relation to longitude and temperature (Kerstan, in prep.).

As all maturation studies in the North-East Atlantic and off South Africa (Kerstan, 1985, 1988, in prep.) were done by the same author and were based on the same confirmed (Arruda, 1984) staging scale of Macer (1974), a comparison of the maturation patterns between these two areas can be done with confidence. The present study compares sex ratios and maturation patterns in horse mackerel from the North-East Atlantic with those from the South-East Atlantic Ocean and the Agulhas Bank in the Indian Ocean. The study investigates the observed similarities and differences in relation to the environment and to the biology of the species.

MATERIALS AND METHODS

Data for the North-East Atlantic Ocean (NEA) was collected during three research cruises conducted by FRV '*Anton Dohrn*' in 1984 and 1985. The first cruise in April 1984 covered the continental shelf areas off Great Britain and Ireland (Kerstan, 1988). The survey on the continental shelf was extended to the southern Bay of Biscay (44°30'N) during the second cruise in April/May of 1985 but ended off the northwestern tip of Ireland (Fig. 1a) at 55°30'N (Kerstan, 1988). About 52% of all specimens were collected in the Bay of Biscay. The third cruise in September 1985 commenced off South-West Ireland and ended north of Scotland (Kerstan, 1988). This survey covered an area similar in extent to the one covered in spring 1984. The depth range fished during all three surveys was 60-250m. The number of fish sampled for staging varied from <10 to >1000 per trawl, depending on the time available between tows.

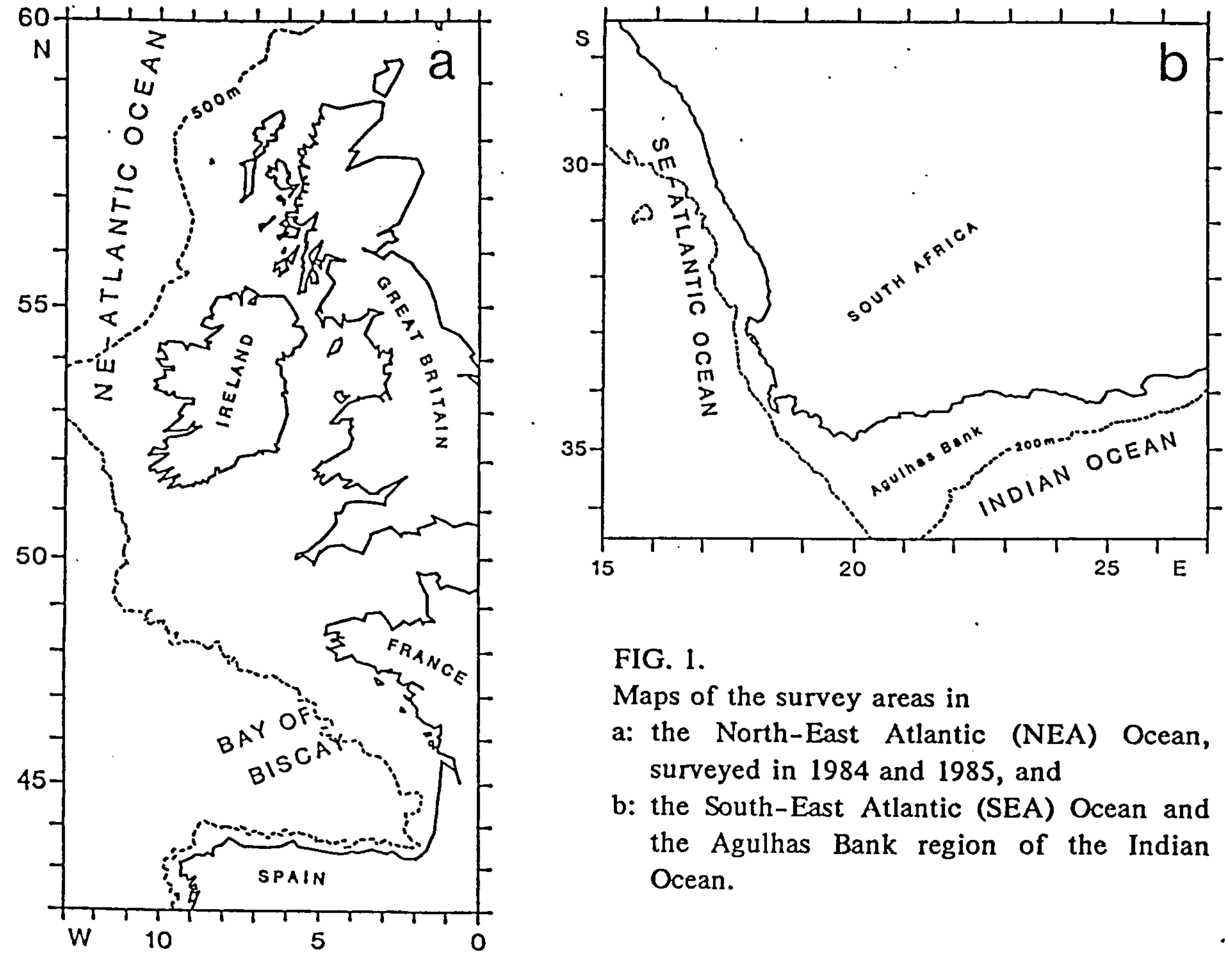

FIG. 1.
Maps of the survey areas in
a: the North-East Atlantic (NEA) Ocean, surveyed in 1984 and 1985, and
b: the South-East Atlantic (SEA) Ocean and the Agulhas Bank region of the Indian Ocean.

Maturation staging in South African waters began in early spring (September) 1992. The first survey carried out on FRV *'Africana'* covered the Agulhas Bank (AB) region of the Indian Ocean between 20° and 27°E and between 33°30' and 36°S (Fig. 1b). During the second cruise in September 1993, the survey area on the AB was extended to include the southern tip of the Bank at 36°30'S (Kerstan, in prep.). The depth range sampled during both these surveys ranged from 30 to 180m. A third cruise in January 1994 extended from the western Agulhas Bank to the west coast of South Africa (Fig. 1b). The trawl depths during this cruise ranged from 50 to 350m. During all three surveys, entire catches were staged if they contained <1500 specimens.

During all six surveys, fish lengths were measured as maximum total length (TL) to cm below. Bottom temperatures (°C) were recorded at each catch location where horse mackerel occurred. In order to detect possible effects of environmental sex determination (Charnov & Bull, 1977), sex-specific mortality (Holtby & Healey 1990), or differential growth (Davis & West, 1992) on the sex composition of the horse mackerel populations from the NEA and South African waters, the changes in sex ratios with fish size were investigated. The sex ratio was defined as the proportion of males in the population. The size-classes under 15cm were excluded, because of a potential error in macroscopic sex determination. Size-classes of the biggest fish were omitted if less than four specimens were available. Maturity stages of testes and ovaries were judged according to the macroscopic scale of Macer (1974). Because of problems concerning the distinction between resting and to an 8-stage scale (Table I). The latter scale was simplified to a 4-stage scale for the studies in South African waters (Kerstan in prep.). Critical to the classification of specimens as being sexually mature was the distinction of oocytes, which only become visible to the naked eye at the early developing stage 3/III (Macer, 1974; Hecht, 1976, 1990). Oocytes are neither visible in resting mature/recovering ovaries nor in developing virgin ovaries (Macer, 1974; Hecht, 1976, 1990).

TABLE I.

Correspondence between the original maturity stages given in Macer (1974) and its modifications (Kerstan, 1985, 1988; Lucio & Martin, 1989) and the stages developed by Hecht (1976, 1990).

Macer (1974) Stage description		Kerstan (1985) (1988)	Lucio & Martin (1989)	Kerstan (in prep.)	Hecht (1976) (1990)
Virgin	1	1	1	1	I
Developing virgin	1-3	2	2	1	II
Resting (mature fish)	2	8	2	2	II , III
Developing (early)	3	3	3	2	III
Developing (later)	4	4	4	3	IV
Ripe	5	5	4	3	V
Running	6	6	5	4	VI
Partly spent	7	7	6'	4	VII
Spent	8	7	6	4	VII
Recovering	9	8	7	2	II

Maturity data from the NEA (Kerstan, 1988) and the AB (Kerstan, in prep.) were recalculated using a unified non-linear fitting method (SPSS Inc., 1992). In addition, data from the survey off the South African west coast survey in the South-East Atlantic Ocean (SEA) in January 1994 was included. For comparative purposes, ogives using the original frequencies of mature and immature males and females staged by Lucio & Martin (1989; Table 3) in the Bay of Biscay in 1987 and 1988 were computed. Proportions of mature specimens were transformed into logits and weighted by sample size. The goodness-of-fit was judged by the sizes of the standard errors of constants (a) and slopes (b) and the residual sums of squares (SSQ). The lengths at sexual maturity (LM_{50}) were computed by substitutions of the length (l) in the standard logistic regression function

$$p(\%) = 100 / 1 + a(e^{-bl})$$

until the proportion mature (p(%)) reached 50%. In order to determine whether the regressions indicated similar rates of maturation for the NEA and South African horse mackerel populations, a Chi^2-test for slope parallelism (SPSS Inc., 1992) was used to test the slopes for significant ($P< 0.2$) differences. Ages at sexual maturity for NEA specimens were re-calculated from the combined age-length data set used by Kerstan (1991). The growth function given in Kerstan (1995) served to compute ages at maturity for SEA/AB fish.

RESULTS

Sex ratios showed opposite trends with respect to size between the NEA and SEA/AB populations. In the NEA, sex ratios decreased with increasing size from about 0.51 in the 15cm-class to 0.46 at 40cm (Fig. 2). The relationship between ratio (p) and length (l) was best fitted by a 2nd-order polynomial of the form

$$p = 0.47 + 0.0039\,l - 0.0001\,l^2.$$

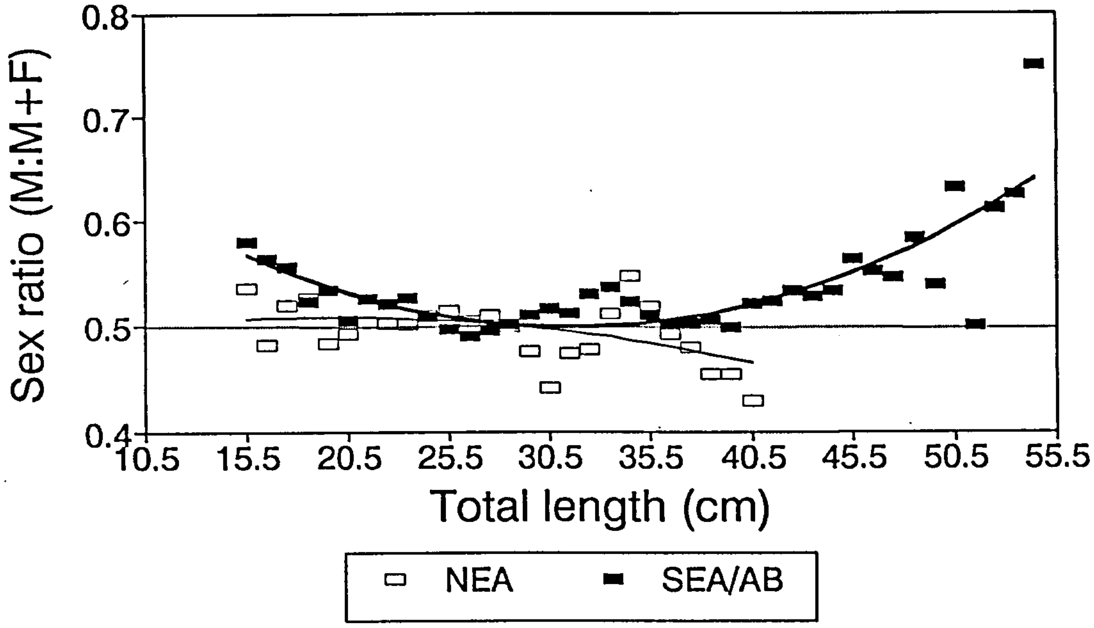

FIG. 2.

Relationship between sex ratio and length in the horse mackerel populations of the NEA and SEA/AB regions.

A fairly constant sex ratio of about 0.51 in the lower size-classes (15-28cm) indicated a balanced sex ratio until all males became mature (Table II). In South African waters, the relationship between sex ratio and fish length also followed a 2nd-order polynomial:

$$p = 0.7665 - 0.017\,l + 0.00027\,l^2.$$

Males of 15-23cm were much more abundant in the SEA/AB area than in the NEA (Fig. 2). Although proportions of about 50% were predicted for size-classes 27-37cm, males were still more numerous, reaching a maximum of 53% in the 33cm size-class. In horse mackerel larger than 40cm, the proportions of males increased rapidly with increasing size, exceeding 62% at 53cm.

Before maturation rates and LM_{50} values were compared, maturation ogives were visually inspected for their goodness of fit. The ogive calculated from the proportions of mature females collected from the AB in September 1992 gave an unsatisfactory fit to the observed slope (Fig. 3) because of a pronounced asymmetry in the size-classes above

28.5cm. The fit was visibly improved using a truncated length range of 13-28cm. The truncation had little effect on the LM_{50} but it changed the regression parameters markedly (Table II). All other ogives represented the entire size range.

TABLE II.
Maturity ogive parameters and their standard errors (s.e.) and lengths (LM_{50}) and ages at 50% and 95% maturity for male and female horse mackerel collected in the NEA and SEA/AB region.

				Regression parameters					95%-Conf. limits		Age at	
Sex	Region	Date	No.	Constant		Slope		LM 50	lower	upper	LM 50	LM 95
		(mo/yr)	staged	ln(a)	s.e.	b	s.e.	(cm)	(cm)	(cm)	(yrs)	(cm)
Male	NE-Atlantic	4 / 84	5 718	19.0071	0.8601	0.7860	0.0324	24.2	23.7	24.6	3.4	27.9
		4 / 85	11 397	7.6520	0.3604	0.3802	0.0137	20.1	17.0	22.0	2.5	27.9
		9 / 85	3 882	29.8526	2.2454	1.2150	0.0877	24.6	24.3	24.8	3.5	27.0
	Biscay **	1987/88	879	11.7046	1.2810	0.5839	0.0543	20.0	-6.9	23.9	2.5	25.1
	SE-Atlantic	1 / 94	8 237	18.6397	0.9351	0.7904	0.0352	23.6	23.2	23.9	2.2	27.3
	Agulhas Bk	9 / 92	18 902	11.5430	0.3043	0.6008	0.0137	19.2	16.8	20.7	1.5	24.1
		9 / 93	24 490	17.6596	0.4302	0.8691	0.0203	20.3	19.9	20.7	1.7	23.7
Female	NE-Atlantic	4 / 84	5 780	16.2553	0.6539	0.6039	0.0229	26.9	26.7	27.1	4.1	31.8
		4 / 85	11 766	12.0550	0.2914	0.4608	0.0108	26.2	25.9	26.4	4.0	32.6
		9 / 85	3 508	16.7100	0.9290	0.6259	0.0316	26.7	26.3	27.0	4.1	31.4
	Biscay **	1987/88	1 155	8.2306	0.8587	0.4208	0.0374	19.6	12.5	23.0	2.3	26.6
	SE-Atlantic	1 / 94	7 857	10.5886	0.3842	0.4114	0.0128	25.7	25.1	26.3	2.6	32.9
	Agulhas Bk	9 / 92	18 122	5.7397	0.1265	0.2621	0.0050	21.9	19.4	24.2	2.0	33.1
		9 / 92*	8 864	13.6195	0.3343	0.6040	0.0135	22.5	21.7	23.2	2.1	27.4
		9 / 93	21 549	15.6453	0.2510	0.6385	0.0102	24.5	24.2	24.8	2.4	29.1

*) Truncated length range (13 - 28cm).
**) Re-calculated from Lucio & Martin (1989; Table 3).

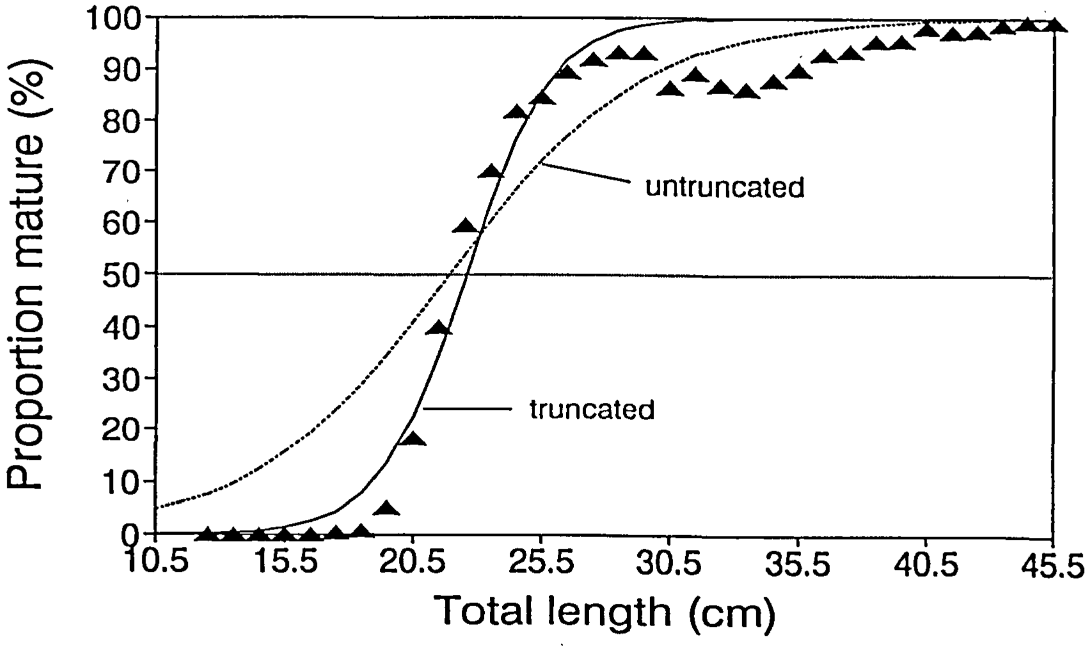

FIG. 3.
Maturity ogives calculated for horse mackerel from the AB region, using the entire length range and a truncated range of 13-28cm.

Intra-regional differences among maturation rates and the LM_{50} of males and females in the NEA and the SEA/AB equalled or exceeded the inter-regional differences between specimens from those areas, indicating an environmentally, rather than a genetically, controlled maturation process. In the NEA, males were sexually mature at 24.2cm in April 1984 and at 24.6cm in September 1985 (Table II). However, in 1985 sexual maturity was already achieved at 20.1cm, a length identical to the LM_{50} re-calculated from Lucio & Martin (1989) collections in the Bay of Biscay. 52% of all the specimens examined by Kerstan (1988) in spring 1985 were also collected in the Bay of Biscay. Length-at-maturity of horse mackerel on the AB was very similar to those from the Bay of Biscay in 1987/88 (Table II). However, the steeper slopes of the maturity ogives from the AB predicted faster maturation than in the NEA. The ogive describing the maturation process of horse mackerel in the SEA in summer 1994 closely resembled the ogive computed from the spring survey in the NEA in 1984 (Fig. 4). In general, the interannual differences among ogive slopes and LM_{50}s from corresponding sub-areas in the NEA and the SEA/AB were smaller than the differences caused by a shift of the survey area by about 300 nautical miles in both areas.

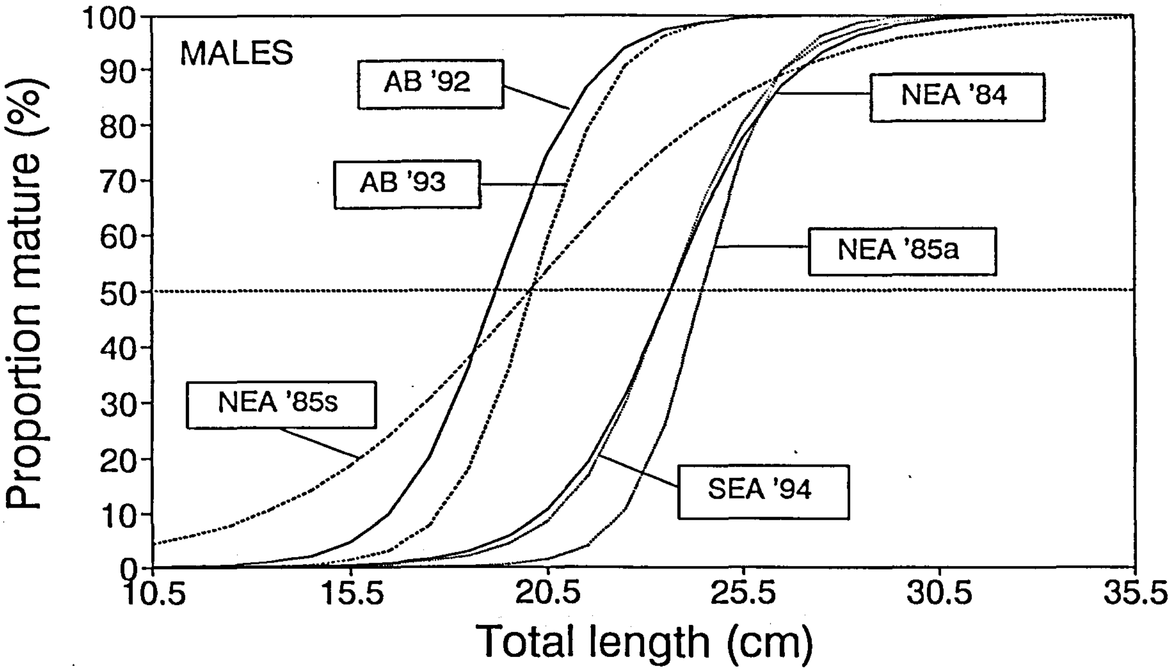

FIG. 4.
Maturity ogives of male horse mackerel computed for specimens in the NEA in spring (s) and autumn (a) of 1984 and 1985 and for fish in the SEA/AB region during the preiod 1992-1994.

The same general principle applied to the observed maturation patterns of the females in the NEA and SEA/AB (Fig. 5). However, the rates of maturation were always lower than those computed for male horse mackerel (Table II), indicating a slower process involving more age-groups. The LM_{50} computed from Lucio & Martin (1989) did not correspond with any of the values observed in the present study. The distance between the ogives of the females collected on the AB in 1992 and 1993 (Fig. 5) indicated a higher interannual variability of the onset of the maturation process than the ogives from the NEA predicted for NEA horse mackerel. The LM_{50} of 24.5cm for females from the AB in 1993 was closer to the LM_{50} of 25.7cm for females in the SEA than to the value of 22.5cm calculated for AB specimens the year before.

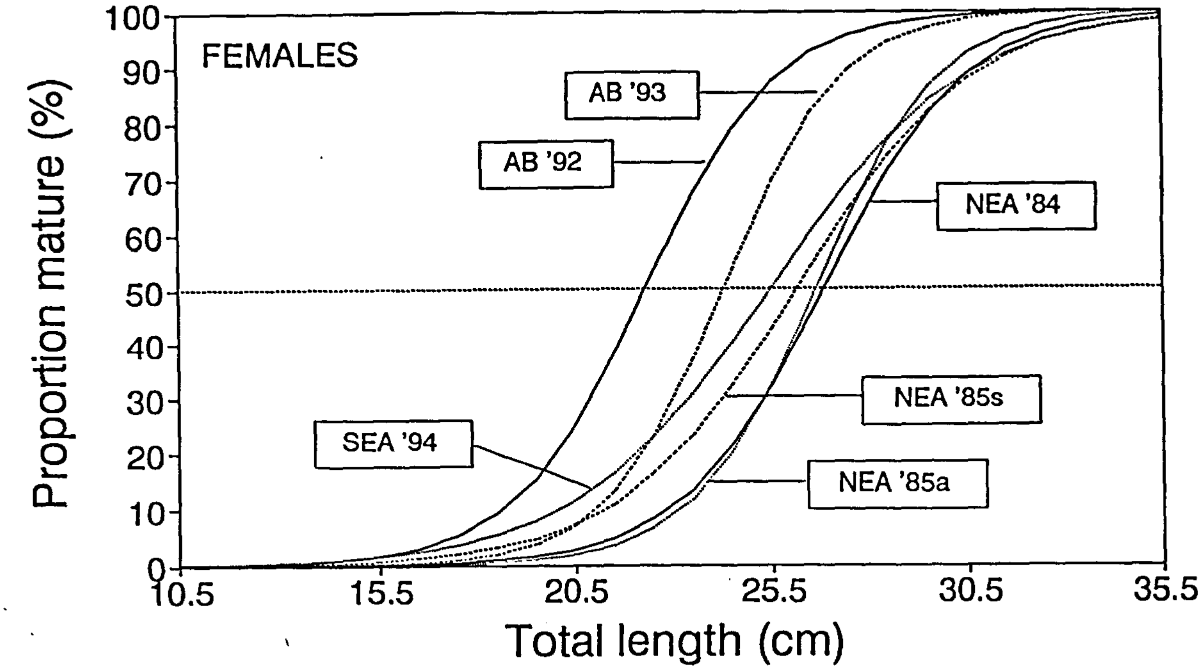

FIG. 5.
Maturity ogives of female horse mackerel computed for specimens in the NEA in spring (s) and autumn (a) of 1984 and 1985 and for fish in the SEA/AB region during the period 1992-1994.

A comparison of the ogives for significant ($P<0.2$) slope parallelisms showed that the maturation rates of both males and females were, in many cases, identical (1.00) for the NEA and SEA/AB populations, although their LM_{50} values differed by 2-4cm. The rate of maturation computed for the males from the spring survey in 1985 was identical to that given in Lucio & Martin (1989) for the Bay of Biscay specimens and for the horse mackerel collected on the AB in 1992 (Fig. 6). The slopes of the maturity ogives were also identical among males staged in the central section of the NEA in 1984 (Kerstan, 1988) and on the AB in 1993. The probability of identical slopes among males from the NEA in 1984 and the SEA in 1994 was high (58%). Identical slopes were observed among males from the AB in spring 1993/94 and the SEA in summer 1993/94.

The slopes of the maturity ogives from female horse mackerel from the northern and southern hemispheres were very similar (Fig. 6). The slope of the ogive describing the maturation process in the NEA in April 1984 was identical to those calculated for females from the AB region in 1992 and 1993 (Fig. 6). The slope for females from the AB in spring 1993 was similar to those computed for the NEA females in spring and autumn 1985 and those predicted for the AB in 1992 and the SEA in 1994. Moreover, the Chi^2-test indicated no significant differences between the slopes for females from the AB area in 1992, the SEA in 1994, and the Bay of Biscay in 1987/88 (Fig. 6). The low probability of 0.21 for identical maturation rates in the NEA in spring 1984 and 1985 is a result of the extension of the survey area into the Bay of Biscay in spring 1985.

MALES

	NEA **1984** Apr.	NEA **1985** Apr.	NEA **1985** Sept.	Biscay **L.& M. (1989)**	SEA **1994** Jan.	AB **1992** Sept.	AB **1993** Sept.
NEA **1984** Apr.		0	0	0	0.58	0	1.00
NEA **1985** Apr.	0		0	1.00	0	1.00	0
NEA **1985** Sept.	0.21	0		0	0	0	0
Biscay **L.& M.** (1989)**	0	0	0		0	0	0
SEA **1994** Jan.	0	0	0	1.00		0	1.00
AB **1992** Sept.	1.00*	0	0	1.00	0		0
AB **1993** Sept.	1.00	1.00	1.00	0	1.00	1.00*	

FEMALES

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*) Significant with truncated length range (13-28cm).

**) Source: LUCIO & MARTIN (1989).

FIG. 6.
Matrix of significant (P<0.2) ogive parallelisms for male and female horse mackerel collected in the NEA in 1984/85 and in the SEA/AB region in 1992-1994.

Bottom temperatures taken during the surveys were used as a relative index of the temperature regime in the survey areas.. LM_{50}s of males and females showed different relationships to temperature. Temperature means (t) were significantly correlated (r=0.971) with the LM_{50}s of the females regardless of the area in which they were collected (Fig. 7). The relationship was dome-shaped following the regression function

$$LM_{50} = 14.03\cdot(t\cdot e^{(-0.1664t)})^{(0.0996t)}.$$

The relationship between temperature and LM_{50} of males was best fitted (r=0.755) by a linear function of the form

$$LM_{50} = 32.578 - 0.981t.$$

The use of the LM_{50}s and temperatures from the various sub-areas of the NEA (Kerstan, 1988) as separate data points did not change the form of the regression. The positions of the LM_{50}s of the South African horse mackerel at high and low temperature extremes indicated that environmental conditions parallel or affect sexual maturity in a predetermined way, regardless of the area.

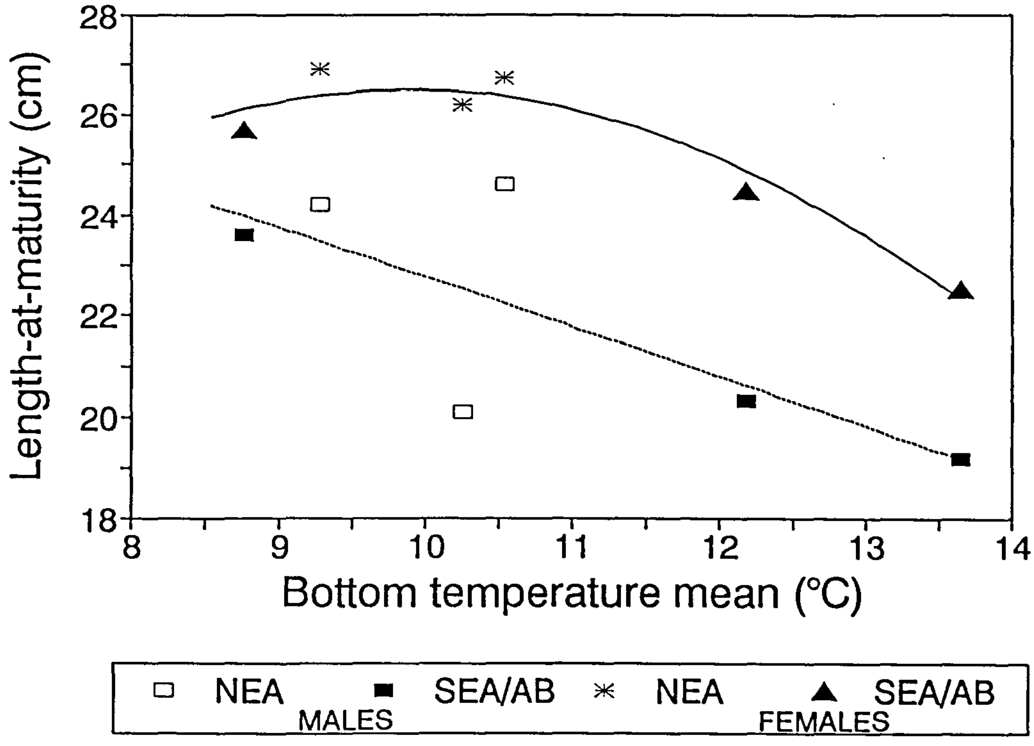

FIG. 7.
Relationship between bottom temperature and length-at-maturity (LM_{50}) for male and female horse mackerel collected from the NEA and SEA/AB.

DISCUSSION

Before the observed similarities and differences can be explained with regard to the environment and biology of the species, the general characteristics of the physical environments of the NEA and SEA/AB need to be considered.

Environmental conditions in the NEA vary on a larger scale than in the SEA/AB. The NEA area is characterised by the seasonal formation and decay of the thermocline and by the frontal gradients between tidally mixed shelf waters and stratified oceanic water masses or coastal currents (e.g. Pingree, 1975, Pingree & Griffiths, 1978; Pingree *et al.*, 1982). Upwelling is limited in the northern NEA but its intensity increases towards the southern Bay of Biscay (e.g. Simpson *et al.*, 1978; Pingree *et al.*, 1982; Littaye-Mariette, 1990). Consequently, the annual migrational cycle of horse mackerel in the NEA (Chuksin *et al.*, 1977) is strongly influenced by the hydrographic conditions (Domaschenko & Amarov, 1975; Chuksin & Nazarov, 1989). The growing season is confined to the short period between the end of the spawning season in May-July (e.g. Iversen *et al.*, 1989) and the start of the overwintering period in November/December (Nazarov & Dobrusin, 1977). Horse mackerel overwinter regularly in the deeper waters over the continental slope, which is under the influence of warmer oceanic water (Lockwood & Johnson, 1977). Environmental conditions seem to be more favourable in the Bay of Biscay because spawning is sustained there for a longer period (Lucio & Martin, 1989) than in the northern NEA.

The SEA and AB areas are characterised by a high variability of the shelf environment in the upper 200m of the water column. Specific features in the SEA include semi-permanent upwelling tongues isolated by oceanic fronts and longshore currents of different directions (e.g. Andrews & Hutchings, 1980; Nelson & Hutchings, 1983). The thermal environment on the AB is marked by the warm Agulhas Current, counter currents and eddies (Shannon, 1966; Gründlingh, 1992), variable locations of thermal fronts (Lutjeharms & Walters, 1985), upwelling, advection (Boyd *et al.*, 1985), strong shallow thermoclines, and the seasonal formation of a cold ridge (Swart & Largier, 1987). The oceanic Central Water in depths exceeding 200m is relatively homogenous but provides cooler temperatures of 6-15°C (Shannon, 1966). As a result of the growing influence of the Agulhas Current (Boyd & Shillington, 1994), lengths-at-age and the LM_{50}s of horse mackerel increase eastwards over the Agulhas Bank, indicating a dependence of growth rates on ambient water temperatures (Kerstan, 1995; Kerstan, in prep.). Spawning in South African waters seems to occur almost year-round (Hecht, 1976, 1990; Naish, 1990; Kerstan, in prep.). Overwintering, as a means of preserving energy for maintenance, growth, and reproduction during times of adverse environmental conditions, has not been reported for horse mackerel in the SEA/AB.

Sex ratios of NEA and SEA/AB horse mackerel showed opposite trends relative to length. The pattern of length-dependent change in sex ratios observed in the present study in the NEA was also observed by Lucio & Martin (1989) who investigated 12 795 horse mackerel in the Bay of Biscay in 1987 and 1988. However, they found a pronounced seasonal variation of the sex ratio. A potential bias in the analysis of the sex ratio was avoided by pooling the data from all seasons (Lucio & Martin, 1989). Accordingly, the samples from all three cruises were combined for the present study, although overall sex ratios in the research catches indicated only 2.5% more females in spring and 9.6% more males in autumn 1985. The difference to Lucio & Martin's (1989) data can be attributed to the fact that research data is less biased than commercial data. In the SEA/AB area, sex ratios were consistently in favour of males.

The dominance of males observed in the present study in the smaller size-classes in both the NEA and SEA/AB is an indicator of environmental sex determination (ESD). ESD is favoured by natural selection when environmental conditions influence the fitness of the sexes differently and when the environment cannot be chosen or is very variable or 'patchy' (Charnov & Bull, 1977; Conover, 1984). As sex ratios can be influenced by temperature during the larval stage (Conover & Kynard, 1981), changes in sex ratios between successive year-classes may be potentially large when temperatures vary greatly. Conover & Heins (1987) suggested that sex ratios should be determined by combinations of genotypic sex determination (GSD) and ESD, in order to produce a graded response which buffers the environmental fluctuations. At high latitudes, short breeding and feeding seasons lessen the advantage of early over late breeders (Bulmer, 1987), which is offered by ESD. Therefore, an increased control of GSD over ESD is an optimal adaptive strategy of fish at high latitudes (Lagomarsino & Conover, 1993), resulting preferably in a slightly male-biased sex ratio (Conover & Heins, 1987).

In the NEA, the sex ratio in horse mackerel appeared to be balanced at around 0.51 until reaching a length of 28cm at which 95% of the males attained sexual maturity. The slightly male-biased sex ratio observed in the early life phase of NEA horse mackerel agreed with the above mentioned hypothesis of Conover & Heins (1987). The different forms of relationships between environmental temperatures and LM_{50}s for both sexes shown here (see Fig. 7) are indicative of differential responses of the sexes to the environmental conditions, a necessary prerequisite of ESD (Conover & Voorhees, 1990). Consequently, the strongly male-biased sex ratios in the size-classes of 15-25cm in the SEA/AB area are caused by an increased level of ESD in a variable and 'patchy' environment.

An imbalanced sex ratio at larger sizes and older ages can be caused by differential habitat preferences (Middaugh & Hemmer, 1987), sex-specific differential mortality (Conover & Kynard, 1981; Roslyy *et al.*, 1987; Holtby & Healey, 1990; Roff, 1991) and density-dependence (Bowen *et al.*, 1991; Berglund, 1992). Differential growth, as another source of imbalance, has neither been observed in the NEA nor in the SEA/AB (Hecht, 1990; Kerstan, 1991). Bearing in mind that the reproductive effort of fish increases at older ages (Jonsson *et al.*, 1988; Roff, 1991), parallel to increased maintenance costs (Forseth *et al.*, 1994) and reduced food conversion efficiencies (Gerking, 1959), the higher energetic costs of reproduction for females (Conover, 1984; Jonsson *et al.*, 1988) can cause sex-specific differential mortality. Male survival may also be enhanced at higher temperatures (Roslyy *et al.*, 1987), which characterise the SEA/AB. Sex ratios in favour of the males at low population densities (Berglund, 1992) appear to be unlikely because estimates of the horse mackerel stock size on the AB amount to about 600,000 tons (Kerstan & Leslie, 1994).

The comparison of LM_{50}s and maturation rates between the NEA and SEA/AB was dependent on a consistent interpretation of the stages and relied on the accuracy of the observed patterns. The discrimination between sexually mature, but resting, and immature female horse mackerel is, at times, problematic (Kerstan, 1985, in prep.; Lucio & Martin, 1989) and can bias the results. Kerstan (in prep.) indicated that the misclassification of first-maturing specimens was minimal if individual oocytes could be distinguished with the naked eye (0.2-0.3mm). Ovaries of resting and recovering females were characterised by their different appearance and remaining atretic oocytes of 0.6-1.1mm in diameter (Kerstan, in prep.). Kerstan (in prep.) attributed the discrepancies between his results and those of earlier authors staging horse mackerel on the Agulhas Bank (e.g. Payne, 1986; Naish, 1990) to different interpretations of resting mature ovaries.

In both the NEA and SEA/AB, males matured at smaller sizes and younger ages than females. This is a common phenomenon in many fish species (e.g. Beacham, 1983; Jakupsstovu & Haug, 1988; Zuyev & Giragosov, 1990) and was also observed in horse mackerel during the present study. Jonsson *et al.* (1988) suggested that natural selection favours older ages and larger sizes at maturity in females because ovary development requires more energy, i.e. fat stores (Rowe *et al.*, 1991), than testis development and fecundity increases as a power function of body length in females (e.g. Roff 1982; Arruda, 1986), whereas testis weight (as a relative measure of sperm productio) increases less rapidly with length (Conover, 1984). Lucio & Martin (1989), however, observed no significant differences in length-at-maturity between male and female horse mackerel in the Bay of Biscay. An explanation of this observation relies on the prerequisites that (a) growth rates and fat stores prior to 1987/88 were higher than before the survey in 1985, and (b) that surplus energy is mainly used for reproduction, rather than growth or migration.

The observed linear relationship between the LM_{50} of males and water temperature indicated that sexual maturity responds directly to the variation of the thermal environment. The decrease of the LM_{50} with increasing temperature can be either a consequence of increased growth rates or of decreasing mortality rates, or it can be the result of a combination of both. As length-at-maturity correlates with previous growth rates (e.g. Holdway & Beamish 1985; Skilbrei, 1989; Jonsson *et al.*, 1984; Peterman, 1985), and growth rates, in turn, increase with increasing temperatures and food consumption until reaching a (species-specific) maximum (Shuter & Post, 1990, Fonds *et al.*, 1992), temperature can serve as a relative indicator of growth rate. Higher growth rates favour maturation at an earlier age (e.g. Sonina, 1981; Forseth *et al.*, 1994). The resulting reduction of the LM_{50} may equal one year's growth in length. This explains why male horse mackerel show a distinct geographical gradation in length-at-maturity in the NEA (Fig. 8). Increased survival of the smaller specimens of each year-class, which have accumulated enough fat reserves (Henderson *et al.*, 1988), will lower length-at-maturity. However, reduced juvenile mortality may not have the believed significant effect on the LM_{50} (Stearns & Koella, 1986) of the males. The mortality of the males in the smaller size-classes, as reflected in the changes of the sex ratio, is high in the SEA/AB region, despite the generally warmer thermal environment.

At temperatures below 10°C, female horse mackerel appear to invest energy into maintenance, somatic growth or migration, rather than into reproduction, thereby deferring maturity until reaching a larger size. At higher temperatures, a more direct correspondence can be expected between growth rate or metabolism and LM_{50}. Apparently, the scope for a 'decision' of surplus energy allocation to growth or one of the other competing demands is higher in female than in male horse mackerel.

Reductions in LM_{50} have often been attributed to high levels of exploitation (e.g. Beacham, 1983; Wysokinski, 1984; Armstrong *et al.*, 1989), assuming that the changes in LM_{50} correspond to density-dependent changes in growth rate. Although sexual maturity is linked to growth rate to some extent (Jonsson & Jonsson, 1993; Forseth *et al.*, 1994), growth and maturity may become competitive traits during maturation because growth slows down (Holdway & Beamish, 1985). Moreover, there is apparently no optimal size (Forseth et al., 1994), as was previously believed (e.g. Agnalt, 1989; Perrin & Rubin; 1990), which can be reached earlier at higher growth rates. As ages and/or sizes at maturity are not genetically fixed (MacKenzie *et al.*, 1983; Jonsson *et al.*, 1984), they rather depend on the amount of surplus energy, such as fat stores (Saldaña & Venables, 1983; King, 1991; Rowe *et al.*, 1991; Berglund 1992), which are accumulated by the individuals in their specific environment. High variation of surplus energy accumulation explains the variation of the LM_{50} in the same age-group (Nævdal *et al.*, 1978, 1979), among year-classes or age-groups (Rijnsdorp, 1993) and in different latitudes (Beacham, 1983; Bowering, 1983; Kerstan, 1988; Isaev & Seliverstov, 1989), as well as the similar maturation lengths of horse mackerel in the NEA and SEA/AB.

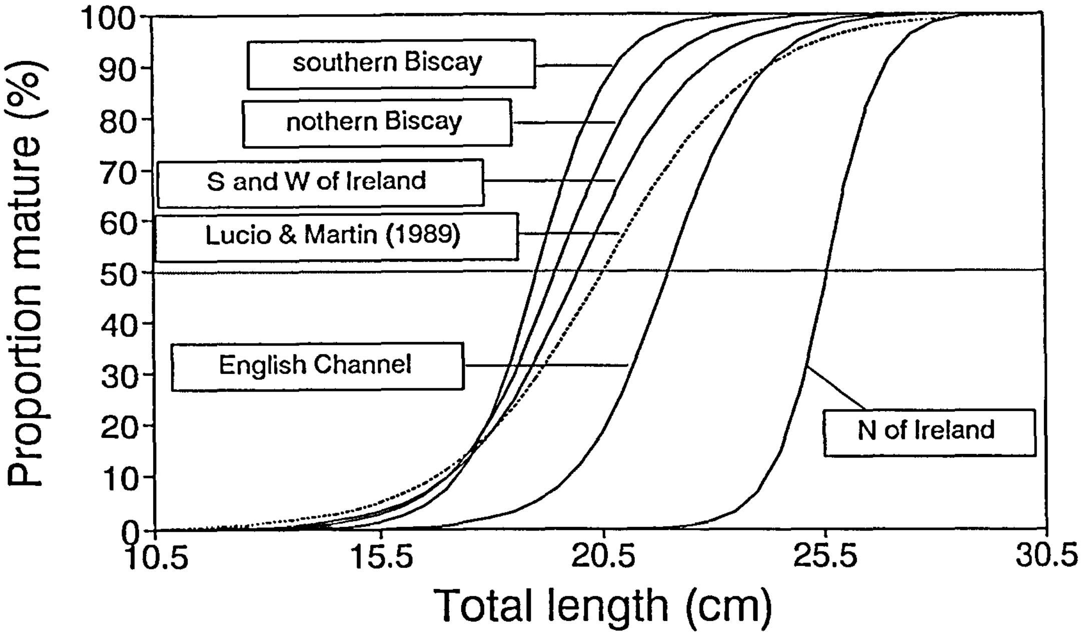

FIG. 8.
Maturity ogives for male horse mackerel collected in the NEA in spring 1985 (after Kerstan, 1988) and in the Bay of Biscay in 1987/88 (re-calculated from Lucio & Martin, 1989).

Migration is another trait competing for surplus energy (Hansen *et al.*, 1989). Whereas horse mackerel is an obligatory migrant in the NEA (Chuksin *et al.* 1977; Kerstan, 1991), migration is suspected (Hecht, 1990) but not proven for horse mackerel in the SEA/AB region (Kerstan & Leslie, 1994). The suspected genetically fixed threshold for the 'decision' to migrate (Jonsson & Jonsson, 1993) is apparently the amount of fat accumulated on the mesenteries during the previous feeding period (King, 1991; Rowe *et al.*, 1991). The possible lack of extensive annual migrations in the SEA/AB is linked to the habitat which may not necessitate migrations for survival. Migrants are dominant if population densities are high and food availability is low. The latter seems to be the case for horse mackerel in the NEA which migrates extensively (e.g. Chuksin *et al.*, 1977; Kerstan, 1991). Accordingly, density-dependent lower fat accumulation or an allocation of energy to migration may explain why lengths-at-maturity of female horse mackerel in the Bay of Biscay in spring of

1985 were much higher than two years later (Fig. 9). Most of the specimens staged in spring of 1985 belonged to the 1982 year-class (Kerstan, 1988), the strongest ever recorded in the NEA (Anon., 1990). The specimens collected by Lucio & Martin (1989) in 1987 and 1988 were younger, smaller, and from different year-classes. As males did not show a similar difference in length-at-maturity between 1985 and 1987/88 (Fig. 8), the sexes may respond differently to high population densities.

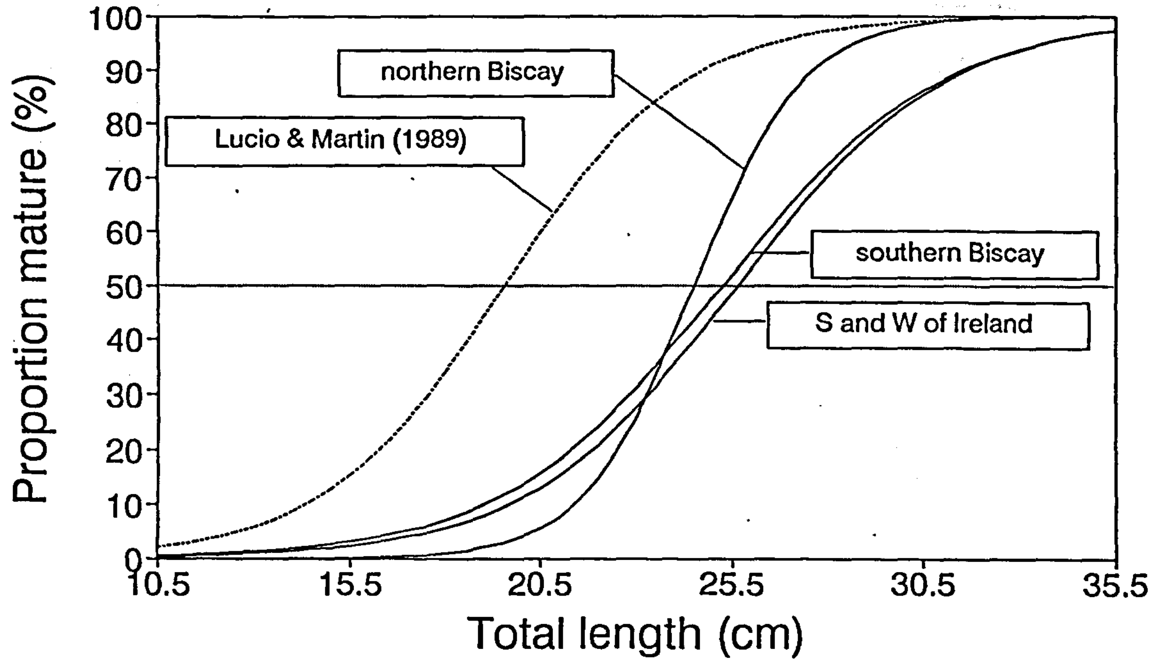

FIG. 9.
Maturity ogives for female horse mackerel collected in the Bay of Biscay and south and west of Ireland in spring 1985 (after Kerstan, 1988) and in the Bay of Biscay in 1987/88 (re-calculated from Lucio & Martin, 1989).

Size-selective mortality acting on the smallest fish in each year-class (e.g. Conover, 1984; Henderson *et al.*, 1988; Shuter & Post, 1990) will add to the variation of the LM_{50} by increasing the size-at-maturity. Therefore, survival during overwintering also competes for the surplus energy the fat stores accumulated during the previous growing season (Henderson *et al.*, 1988). The potential impact of the environment and the competitive traits on the LM_{50} renders the LM_{50} to monitor a fishery's rather useless.

Despite the observed variation of the LM_{50} among regions, ogive slopes were similar in different sub-areas of the NEA and SEA/AB (Kerstan, 1988, in prep.) and, also, differed little between the SEA/AB and the NEA. The advantage of the ogive slope over the LM_{50} as a criterion for changes in the maturation pattern is that it reflects the response of the population over the entire age and size range, and not only a particular point. As figure 3 shows, slopes can change considerably without affecting the LM_{50} much. Identical slopes for males or females in the NEA and SEA/AB imply that horse mackerel in areas about 4,500 nautical miles apart have identical population reaction norms, despite different environments and different LM_{50}s. This indicates stable populations (Jonsson et al., 1984) with a high level of phenotypic plasticity, which maximises the fitness of the species (Stearns & Koella, 1986). No changes in the slopes between areas or years indicate a high level of resistance to short-term fluctuations of the environment. If geographical populations with identical slopes but different ages or sizes at maturity mix, the slope should flatten out. This was the effect observed in the present study when specimens from the various subareas of the NEA were combined to calculate a single ogive for spring 1985. Provided that particularly strong year-classes do not steepen the slope locally (Kerstan, 1988), a change in the slope of the maturity ogives can be a reliable indicator of mixing local populations with different maturation patterns.

REFERENCES

Agnalt, A.-L. (1989). Long-term changes in growth and age at maturity of mackerel, *Scomber scombrus* L., from the North Sea. *J. Fish Biol.* **35** (Suppl. A), 305-311.

Andrews, W.R.H. & Hutchings, L. (1980). Upwelling in the southern Benguela Current. *Prog. Oceanogr.* **9**, 1-81.

Anon. (1990). Report of the working group on the assessment of the stocks of sardine, horse mackerel, and anchovy. *ICES C.M. 1977/Assess:24.* 169 pp. (mimeo.).

Armstrong, M.J., Roel, B.A. & Prosch, R.M. (1989). Long-term trends in patterns of maturity in the southern Benguela pilchard population: evidence for density-dependence? *S. Afr. J. mar. Sci.* **8**, 91-101.

Arruda, L.M. (1984). Sexual maturation and growth of *Trachurus trachurus* (L.) along the Portuguese coast. *Inv. Pesq.* **48**, 419-430.

Arruda, L.M. (1986). Fecundity of horse mackerel *Trachurus trachurus* (L. 1758) off the Portuguese coast. *Inv. Pesq.* **50**, 565-570.

Beacham, T.D. (1983). Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian Shelf in the northwest Atlantic Ocean. *Fish. Bull.* **81**, 303-321.

Berglund, I. (1992). Growth and early sexual maturation in Baltic salmon (*Salmo salar*) parr. *Can. J. Zool.* **70**, 205-211.

Borges, F., Dinis, H. & Monteiro, C. (1977). Résultats préliminaires sur la ponte, composition des tailles et état du stock du chinchard (*Trachurus trachurus* L.) de la côte continentale portugaise. *ICES C.M. 1977/J:14.* 50 pp. (mimeo.).

Bowen, S.H., D'Angelo, D.J., Arnold, S.H., Keniry, M.J. & Albrecht, R.J. (1991). Density-dependent maturation, growth, and female dominance in Lake Superior lake herring (*Coregonus artedii*). *Can. J. Fish. aquat. Sci.* **48**, 569-576.

Bowering, W.R. (1983). Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian northwest Atlantic. *Fish. Bull.* **81**, 599-611.

Boyd, A.J. & Shillington, F.A. (1994). Physical forcing and circulation patterns on the Agulhas Bank. *S. Afr. J. Sci.* **90**, 114-122.

Boyd, A.J., Tromp, B.B.S. & Horstman, D.A. (1985). The hydrology off the South African south-western coast between Cape Point and Danger Point in 1975. *S. Afr. J. mar. Sci.* **3**, 145-168.

Bulmer, M. (1987). Sex determination in fish. *Nature, Lond.* **326**, 440-441.

Chanov, E.L. & Bull, J. (1977). When is sex environmentally determined? *Nature, Lond.* **266**, 828-830.

Chuksin, Y.V. & Nazarov, N.A. (1989). Peculiarities of distribution and behaviour of horse mackerel in the Northeast Atlantic. *ICES C.M. 1989/H:7.* 20 pp. (mimeo.).

Chuksin, Y.V., Akhramovich, A.P., Mikhailov, A.J. & Arkhipov, A.Y. (1977). [Ecological factors of the seasonal distribution and behaviour of mackerel, horse mackerel and blue whiting west of the British Isles.] *Trudy VNIRO* **121**, 11-24 (in Russian.)

Conover, D.O. (1984). Adaptive significance of temperature-dependent sex determination in a fish. *Am. Nat.* **123**, 297-313.

Conover, D.O. & Heins, S.W. (1987). Adaptive variation in environemntal and genetic sex determination in a fish. *Nature, Lond.* **326**, 496-498.

Conover, D.O. & Kynard, B.E. (1981). Environmental sex determination: interaction of temperature and genotype in a fish. *Science* **213**, 577-579.

Conover, D.O. & Voorhees, D.A. van (1990). Evolution of a balanced sex ratio by frequency-dependent selection in a fish. *Science* **250**, 1556-1558.

Davis, T.L.O. & West, G.J. (1992). Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the north west shelf of Australia. *Fish. Bull.* **90**, 395-404.

Domaschenko, G.P. & Amarov, G.L. (1975). [The dependence of seasonal aggregations of horse mackerel in the Celtic Sea and Bay of Biscay on the hydrological seasons.] *Trudy AtlantNIRO* **58**, 136-140 (in Russian.)

Eltink, A. (1992). Horse mackerel egg production and spawning stock size in the North Sea in 1991. *ICES C.M. 1992/H:21.* 15 pp. (mimeo.).

Eltink, A. & Vingerhoed, B. (1989). The total fecundity of western horse mackerel (*Trachurus trachurus* L.). *ICES C.M. 1989/H:44.* 9 pp. (mimeo.).

Eltink, A. & Vingerhoed, B. (1993). The total fecundity estimate of western horse mackerel (*Trachurus trachurus* L.) in 1992. *ICES C.M. 1993/H:17.* 7 pp. (mimeo.).

Fonds, M., Cronie, R., Vethaak, A.D. & Puyl, P. van der (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature.*Neth. J. Sea Res.* **29**, 127-143.

Forseth, T., Ugedal, O. & Jonsson, B. (1994). The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. *J. Anim. Ecol.* **63**, 116-126.

Gerking, S.D. (1959). Physiological changes accompanying ageing in fishes. *CIBA Found., Colloquia on Ageing* **5**, 181-211.

Gründlingh, M.L. (1992). Agulhas Current meanders: review and case study. *S. Afr. geograph. J.* **74**, 19-28.

Hansen, L.P., Jonsson, B., Morgan, R.I.G. & Thorpe, J.E. (1989). Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). *Can. J. Fish. aquat. Sci.* **46**, 410-415.

Hecht, T. (1976). The general biology of six major trawl fish species of the eastern Cape coast of South Africa, with notes on the demersal fishery, 1967-1975. Unpubl. PhD thesis, University of Port Elizabeth, 353 pp.

Hecht, T. (1990). On the life history of Cape horse mackerel *Trachurus trachurus capensis* off the south-east coast of South Africa. *S. Afr. J. mar. Sci.* **9**, 317-326.

Henderson, P.A., Holmes, R.H.A. & Bamber, R.N. (1988). Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *J. Fish Biol.* **33**, 221-233.

Holdway, D.A. & Beamish, F.W.H. (1985). The effect of growth rate, size, and season on oocyte development and maturity of Atlantic cod (*Gadus morhua* L.). *J. exp. mar. Biol. Ecol.* **85**, 3-19.

Holtby, L.B. & Healey, M.C. (1990). Sex-specific life history tactics and risk-taking in coho salmon. *Ecology* **71**, 678-690.

Isaev, N.A. & Seliverstov, A.S. (1989). Population structure of the Hebrido-Norwegian stock of blue whiting. *ICES C.M. 1989/H:9.* 26 pp. (mimeo.).

Iversen, S.A., Eltink, A., Kirkegaard, E. & Skagen, D.W. (1989). The egg production and spawning stock size of the North Sea mackerel and horse mackerel stocks in 1988. *ICES C.M. 1989/H:16*. 22 pp. (mimeo.).

Jákupsstovu, S.H. & Haug, T. (1988). Growth, sexual maturation, and spawning season of Atlantic halibut, *Hippoglossus hippoglossus*, in Faroese waters. *Fish. Res.* **6**, 201-215.

Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Revs Fish. Biol. Fish.* **3**, 348-365.

Jonsson, B., Hindar, K. & Northcote, T.G. (1984). Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia* **61**, 319-325.

Jonsson, N., Jonsson, B. & Ruud-Hansen, J. (1988). Downstream displacement and life-history traits of whitefish, *Coregonus lavaretus*, in a Norwegian river. *Environ. Biol. Fish.* **23**, 197-204.

Kerstan, M. (1985). Age, growth, maturity, and mortality estimates of horse mackerel (*Trachurus trachurus*) from the waters west of Great Britain and Ireland in 1984. *Arch. FischWiss.* **36**, 115-154.

Kerstan, M. (1988). Year-class strength and geographical variation in the sexual maturity of NE-Atlantic horse-mackerel (*Trachurus trachurus* L.) - a case study. *Arch. FischWiss.* **38**, 133-163.

Kerstan, M. (1991). Quantitative Bedeutung und Trennung der Populationen des Stöckers (*Trachurus trachurus* L.) in den Schelfgewässern des Nordost-Atlantiks. Unpubl. PhD thesis, University of Kiel, 130 pp.

Kerstan, M. (1995). Ages and growth rates of Agulhas Bank horse mackerel *Trachurus trachurus capensis* - comparison of otolith ageing and length frequency analyses. *S. Afr. J. mar. Sci.* **15**, 137-156.

Kerstan, M. (in prep.). Variation in sex ratios and maturation patterns of Agulhas Bank horse mackerel, *Trachurus trachurus capensis*, relative to longitude, temperature, and depth. (submitted to *S. Afr. J. mar. Sci.*)

Kerstan, M. & Leslie, R.W. (1994). Horse mackerel on the Agulhas Bank - a summary of current knowledge. *S. Afr. J. Sci.* **90**, 173-178.

King, R.P. (1991). Some aspects of the reproductive strategy of *Ilisha africana* (Bloch, 1795) (Teleostei, Clupeidae) in Qua Iboe estuary, Nigeria. *Cybium* **15**, 239-257.

Lagomarsino, I.V. & Conover, D.O. (1993). Variation in environmental and genotypic sex-determination mechanisms across a latitudinal gradient in the fish, *Menidia menidia*. *Evolution* **47**, 487-494.

Littaye-Mariette, A. (1990). Rendements de la pêche sardinière (*Sardina pilchardus*) et conditions de vent, dans le nord du golfe de Gascogne. *Aquat. Living Resour.* **3**, 163-180.

Lockwood, S.J. & Johnson, P.O. (1977). Horse mackerel *Trachurus trachurus*. *Lab. Leafl., MAFF Direct. Fish. Res., Lowestoft,* **38**, 1-18.

Lucio, P. & Martin, I. (1989). Biological aspects of horse mackerel (*Trachurus trachurus* L. 1758) in the Bay of Biscay in 1987 and 1988. *ICES C.M. 1989/H:28*. 21 pp. (mimeo.).

Lutjeharms, J.R.E. & Walters, N.M. (1985). Ocean colour and thermal fronts south of Africa. In *South African Ocean Colour and Upwelling Experiment* (L.V. Shannon, ed), pp. 227-237. Cape Town: Sea Fisheries Research Institute.

Macer, C.T. (1974). The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. *J. Fish Biol.* **6**, 415-438.

McKenzie, W.D., Crews, D., Kallman, K.D., Policanski, D. & Sohn, J.J. (1983). Age, weight and the genetics of sexual maturation in the platyfish, *Xiphophorus maculatus*. *Copeia* **1983**, 770-774.

Middaugh, D.P. & Hemmer, M.J. (1987). Influence of environmental temperature on sex-ratios in the tidewater silverside, *Menidia peninsulae* (Pisces: Atherinidae). *Copeia* **1987**, 958-964.

Nævdal, G., Holm, M., Leroy, R. & Moller, D. (1978). Individual growth rate and age at first sexual maturity in Atlantic salmon. *FiskDir. Skr. Ser. HavUnders.* **16**, 519-529.

Nævdal, G., Holm, M., Leroy, R. & Moller, D. (1979). Individual growth rate and age at sexual maturity in rainbow trout. *FiskDir. Skr. Ser. HavUnders.* **17**, 1-10.

Naish, K.-A. (1990). The stock identification of the Cape horse mackerel, *Trachurus trachurus capensis* (Pisces: Carangidae). Unpubl. MSc thesis, Rhodes University, 111 pp.

Nazarov, N.A. & Dobrusin, M.S. (1977). [Some peculiarities of the dynamics of the biological and physiological characteristics of horse mackerel on the south-western Irish shelf and in the northern Bay of Biscay.] *Trudy VNIRO* **121**, 40-48 (in Russian.)

Nelson, G. & Hutchings, L. (1983). The Benguela upwelling area. *Prog. Oceanogr.* **12**, 333-356.

Overko, S.M. (1974). On peculiarities in the biology of horse-mackerel (*Trachurus trachurus*) from the Central-east Atlantic. *ICES C.M. 1974/J:13*. 13 pp. (mimeo.).

Payne, A.I.L. (1986). Biology, stock integrity and trends in the commercial fishery for demersal fish on the south-east coast of South Africa. Unpubl. PhD thesis, University of Port Elizabeth, 368 pp.

Perrin, N. & Rubin, J.F. (1990). On dome-shaped norms of reaction for size-to-age at maturity in fishes. *Functional Ecol.* 4, 53-57.

Peterman, R.M. (1985). Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. *Can. J. Fish. aquat. Sci.* **42**, 1595-1607.

Pingree, R.D. (1975). The advance and retreat of the thermocline on the continental shelf. *J. mar. biol. Ass. U.K.* **55**, 965-974.

Pingree, R.D. & Griffiths, D.K. (1978). Tidal fronts on the shelf seas around the British Isles. *J. geophys. Res.* **83**, 4615-4622.

Pingree, R.D., Mardell, G.T., Holligan, P.M., Griffiths, D.K. & Smithers, J. (1982). Celtic Sea and Armorican current structure and the vertical distributions of temperature and chlorophyll. *Continental Shelf Res.* **1**, 99-116.

Polonskii, A.S. (1969). [Growth, age, and maturity of *Trachurus trachurus* Linné in the north-eastern Atlantic.] *Trudy AtlantNIRO* **23**, 49-60 (in Russian.)

Rijnsdorp, A.D. (1993). Relationship between juvenile growth and on the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa* *Can. J. Fish. aquat. Sci.* **50**, 1617-1631.

Roff, D.A. (1982). Reproductive strategies in flatfish: a first synthesis. *Can. J. Fish. aquat. Sci.* **39**, 1686-1698.

Roff, D.A. (1991). The evolution of life-history variation in fishes, with particular reference to flatfishes. *Neth. J. Sea Res.* **27**, 197-207.

Roslyy, Y.S., Panasenko, N.M. & Kaplanova, N.F. (1987). Biological structure of hatchery stocks and reproduction of autumn chum salmon, *Oncorhynchus keta*, of the Amur river. *J. Ichthyol.* **27**, 1-11.

Rowe, D.K., Thorpe, J.E. & Shanks, A.M. (1991). Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. *Can. J. Fish. aquat. Sci.* **48**, 405-413.

Sahrhage, D. (1970). Ein Beitrag zur Biologie des Stöckers (*Trachurus trachurus* (L.)) in der Nordsee. *Ber. dt. wiss. Kommn Meeresforsch.* **21**, 122-169.

Saldaña, J. & Venables, B. (1983). Energy compartmentalization in a migratory fish, *Prochilodus mariae* (Prochilodontidae), of the Orinoco river. *Copeia* **1983**, 617-623.

Shannon, L.V. (1966). Hydrology of the south and west coasts of South Africa. *Investl Rep. Div. Sea Fish. S. Afr.* **58**, 1-52.

Shuter, B.J. & Post, J.R. (1990). Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* **119**, 314-336.

Simpson, J.H., Allen, C.M. & Morris, N.C.G. (1978). Fronts on the continental shelf. *J. geophys. Res.* **83**, 4607-4614.

Skilbrei, O.T. (1989). Relationships between smolt length and growth and maturation in the sea of individually tagged Atlantic salmon (*Salmo salar*). *Aquaculture* **83**, 95-108.

Sonina, M.A. (1981). Growth rate and sexual maturation of the haddock, *Melanogrammus aeglefinus. J. Ichthyol.* **21**, 85-97.

SPSS Inc. (1992) SPSS for Windows. Advanced statistics release 5. Chicago Ill.: SPSS Inc. 580 pp.

Stearns, S.C. & Koella, J.C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**, 893-913.

Swart, V.P. & Largier, J.L. (1987). Thermal structure of Agulhas Bank water. *S. Afr. J. mar. Sci.* **5**, 243-253.

Wysokinski, A. (1984). Length structure of the Cape horse mackerel population and changes in the sexual maturity length in the Namibian region. *Colln scient. Pap. int. Commn SE. Atl. Fish* **11**, 91-98.

Zuyev, G.V. & Giragosov, Y.Y. (1990). Reproductive biology and production characteristics of three species of croakers (Sciaenidae) along the Guinea coast. *J. Ichthyol.* **30**, 29-42.