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DISTRIBUTION PATTERNS, STOCK SIZE AND LIFE-HISTORY STRATEGIES OF CAPE HORSE MACKEREL *TRACHURUS TRACHURUS CAPENSIS*, BASED ON BOTTOM TRAWL AND ACOUSTIC SURVEYS

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Research surveys of Cape horse mackerel *Trachurus trachurus capensis* abundance on the south coast of South Africa are complicated because changes in the species' vertical and horizontal distribution limit the value of stock assessments based a single survey method. Annual bottom trawl surveys conducted in spring provide estimates of the abundance of fish close to the bottom over trawlable grounds. Between 1991 and 1994, hydro-acoustic surveys conducted in spring have been used to estimate the pelagic portion of the stock, as well as the portion over untrawlable grounds. These two research datasets, as well as data from purse-seine, midwater and bottom trawl commercial landings, are reviewed to elucidate distribution patterns of horse mackerel and their migratory and spawning strategies. The problems and advantages of bottom trawl and acoustic surveys are discussed in the context of fluctuations in estimates of the size of the stock between 1991 and 1994 and the prevailing environmental conditions. It is concluded that combined acoustic and bottom trawl surveys are the only effective means of surveying horse mackerel, and that effort should be concentrated east of 22°E to assess the spawner stock. It is suggested that research effort directed at improving understanding of exchanges between West Coast (including Namibia) and South Coast population of horse mackerel, as well as of the role of vertical migrations in modulating these exchanges, would be beneficial.

The Cape horse mackerel *Trachurus trachurus capensis* fishery off South Africa started in the mid-1940s, mainly by purse-seiners operating off the West Coast. Since then, purse-seine catches of horse mackerel have declined gradually, and since the 1970s the species has become a by-catch of the pelagic fishery (Tilney 1995). The South Coast demersal trawl industry began targeting horse mackerel in the 1960s, as did foreign (mainly Japanese) trawlers. Between 1967 and 1975, horse mackerel contributed some 40% of the landings of the South Coast demersal inshore fishery (Hecht 1990). Since the gradual phasing out by foreign trawling from 1982, their contribution to the South Coast landings has declined to 20% (Tilney 1995). However, research surveys have indicated that the species is potentially the largest single fishery on the Agulhas Bank (Japp *et al*. 1994). Furthermore, a midwater trawl fishery, which developed in the 1990s on the South Coast, was believed at that time to have had the capacity to exceed the maximum sustainable yield (*MSY*) of the resource (Payne 1990). This prompted Sea Fisheries (SF) to commence modelling studies of the dynamics of the horse mackerel population in order to provide sound scientific management advice.

Initially, assessments of horse mackerel were hampered by the lack of reliable long-term datasets. Catch data on per unit effort (*cpue*) were available from four sources: the South African inshore and offshore demersal fishery, the midwater fishery and the Japanese fleet. However, these data were potentially flawed and were regarded as unusable for stock assessment (Kerstan and Leslie 1994). The only direct biomass index available was provided by SF demersal trawl surveys, which targeted primarily the Cape hakes *Merluccius capensis* and *M. paradoxus* and South Coast sole *Austroglossus pectoralis* (Badenhorst and Smale 1991). However, because large areas of the outer shelf, where horse mackerel can be abundant, are untrawlable, this index was also considered to be inaccurate (Kerstan and Leslie 1994). Nevertheless, stock assessments were made for the years 1989 and 1991, using a Schaefer form of the Butterworth-Andrew observation error estimator to allow for multiple *cpue* series and bottom-trawl biomass estimates (Punt 1989). However, the output from the model had to be treated with caution because of the perceived biases in the data. In order to overcome some of these uncertainties, a study into the feasibility of estimating the biomass of horse mackerel acoustically was initiated by SF in 1991. Four acoustic assessment cruises, extending from near Mossel Bay to East London were carried out in

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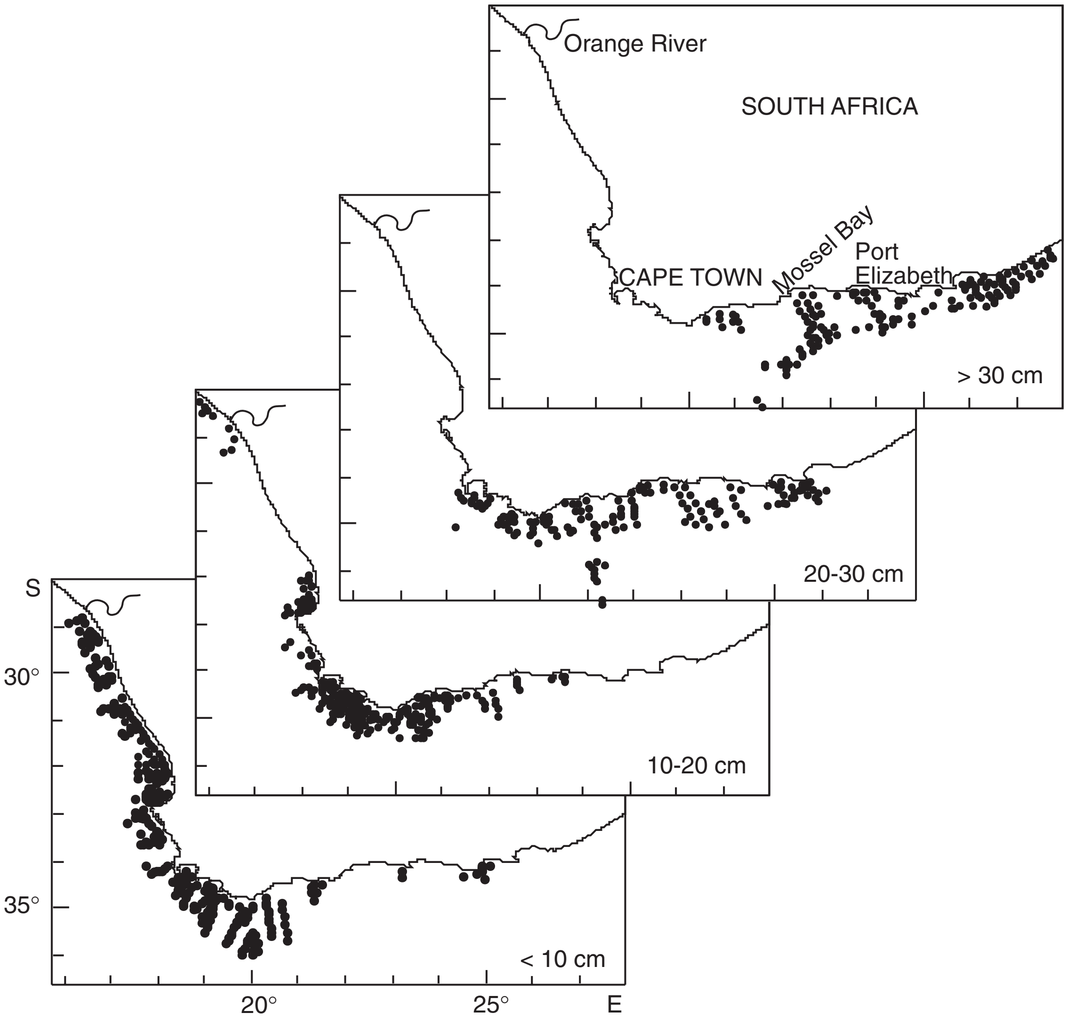

Fig. 1: Distribution of Cape horse mackerel by size derived from all acoustic/midwater trawl surveys carried out in South African waters for the period 1984–1996

October of 1991, 1992, 1993 and 1994. The results of the first two surveys indicated that a surplus-production model could be substantially underestimating the resource. Consequently, a Beddington and Cooke approach was implemented to estimate a precautionary upper limit for 1993 (Butterworth and Raubenheimer 1992).

In the present study, data from the four above-mentioned acoustic cruises, as well as from commercial and bottom trawl surveys, have been analysed to describe spatial and temporal patterns in the distribution of horse mackerel around South Africa. The comparability of abundance indices between acoustic and bottom trawl surveys are investigated, and suggestions are provided on developing a much-needed robust survey for this resource.

MATERIAL AND METHODS

Horse mackerel acoustic surveys

Acoustic surveys directed at horse mackerel were

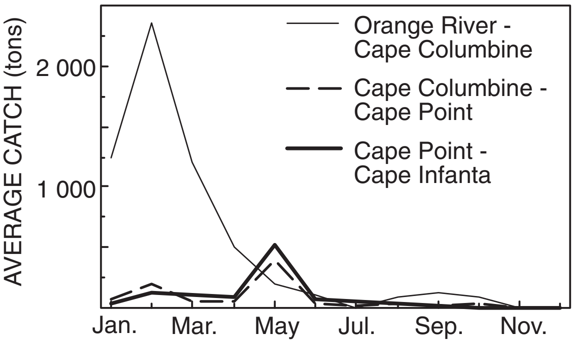

Fig. 2: Seasonal trends in the average purse-seine catches of Cape horse mackerel during the period 1987–1994 in three regions off South Africa

carried out annually between 1991 and 1994 aboard F. R. S. *Africana* between Mossel Bay (22°E) and East London (28°E) In 1993, the survey started from Cape Agulhas (20°E). In October 1991 and 1992, data were collected along parallel and equidistant cross-shelf transects running from within five miles of the coast to a depth of approximately 500 m. Sampling was continuous, except for intermittent breaks for trawling to identify acoustic targets by means of an Engels 308 midwater trawl fitted with a codend liner of 8-mm mesh, and for CTD casts. Acoustic data were collected using a sphere-calibrated Simrad EK400 38-kHz echo-sounder, transmitting 43 × 1-ms pulses per minute on a range of 300 m. Only echo signals exceeding a pre-set amplitude (generally 0.05 V) for more than 1 ms within the selected depth range were logged, using a digital data-logging and echo-integration system (Anon. 1986). Digitized echo-voltages were squared and averaged over 1-m depth channels between the range limits, and were stored on magnetic tape for further

Table I: Purse-seine catches of Cape horse mackerel on the West Coast

Year	Catch (thousand tons)
1987	2.80
1988	6.30
1989	25.50
1990	7.20
1991	0.50
1992	1.90
1993	11.64
1994	8.21
1995	1.98

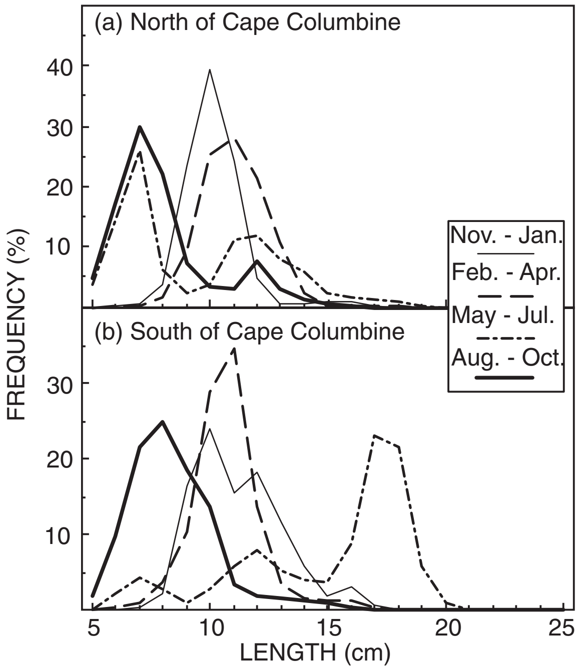

Fig. 3: Three-monthly mean of the length distributions of Cape horse mackerel taken in purse-seine catches (a) north and (b) south of Cape Columbine

analysis. The 1991 survey showed that night-time acoustic records of horse mackerel were substantially larger (3.63 times) than those made during daylight, probably as a result of a proportion of the stock residing too close to the bottom during the day to be detected acoustically. Consequently, only data collected at night were processed from the 1992 survey.

In 1993 and 1994, the acoustic surveys of horse mackerel were carried out at night during bottom trawl surveys. Acoustic sampling was conducted along transects, starting in the evening at the last bottom trawl station of the day and ending at, or near, the designated first trawl station of the following morning. This design introduced an element of randomness in the acoustic survey, a prerequisite for the unbiased estimation of survey variances (Jolly and Hampton 1990). Acoustic data were collected using a PC-based echo-integrator interfaced to a sphere-calibrated EK400 echo-sounder, and integrated as described earlier. Sampling was continuous, except for *ad hoc* intermittent breaks to identify acoustic targets.

For all surveys, back-scattering strengths were apportioned between the different pelagic resources on the basis of the species and size composition in the

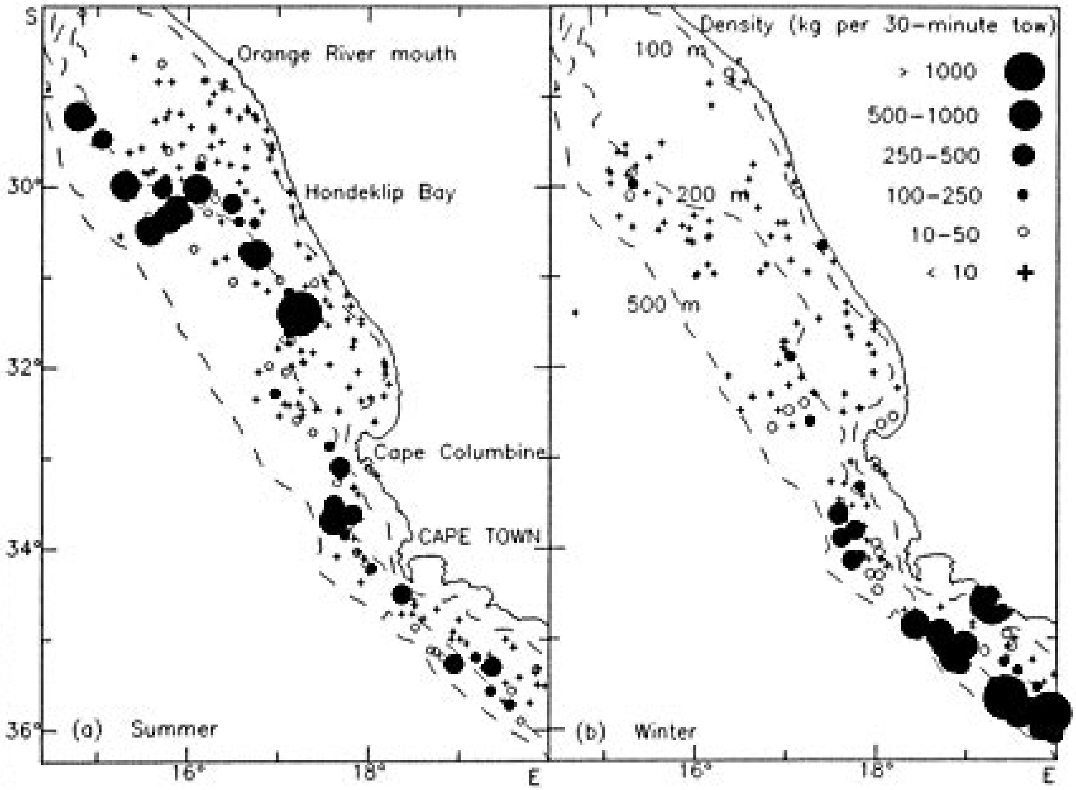

Fig. 4: Mean catch rates of Cape horsin bottom trawl research surveys in (a) summer and (b) winter on the West Coast for the period 1987–1991

midwater trawl samples. Previously, data had been transformed into fish densities using the same published relationship between target strength (*TS)* and length for all species. However, a more appropriate *in situ* target strength expression for *T. t. capensis,* derived by Barange *et al*. (1996), has recently been used:

$$TS(\text{dB/kg}) = -15.44 \log TL - 7.75 \quad ,$$

where *TL* is the total length in cm. Densities have now been recalculated using this expression.

Pelagic acoustic surveys

Acoustic data on horse mackerel have also been collected since 1984 during routine acoustic/midwater trawl surveys carried out by SF for the assessment of pelagic fish resources (mainly anchovy *Engraulis capensis* and sardine *Sardinops sagax*) over the South African continental shelf. The surveys covered the peak recruitment (May–June) and spawning (November–December) seasons of those fish. The recruitment surveys covered the inner shelf between the Orange River mouth (28°30′S) on the West Coast and Cape Infanta (21°E) on the South Coast (prior to 1996), extending to Port Alfred (27°E) in recent years. The spawner biomass surveys generally covered most of the shelf between Hondeklip Bay (30°30′S) and Port Elizabeth (25°30′E). The methods are detailed in Hampton (1987, 1992).

Demersal swept-area surveys

Additional data on distribution and abundance of horse mackerel are available from bottom trawl research surveys carried out since 1983. These

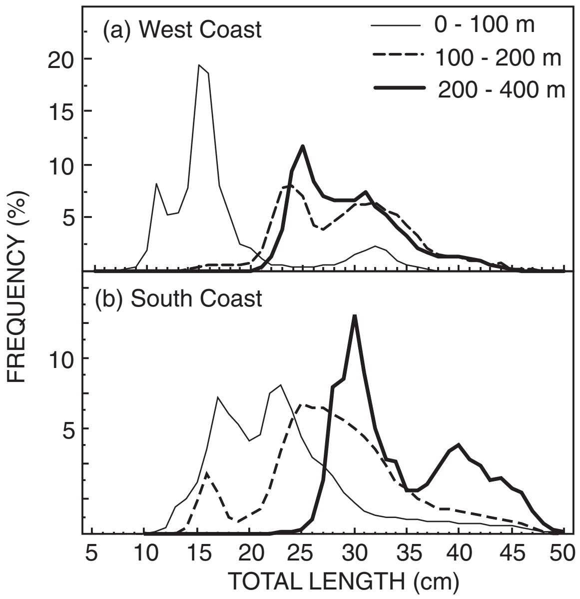

Fig. 5: Length distribution of Cape horse mackerel by depth stratum derived from bottom trawl research surveys on (a) the West and (b) the South coasts for the period 1987–1991

surveys were designed to assess the abundance of Cape hakes and other demersal fish, and have been carried out regularly off the west and south coasts of South Africa aboard F. R. S. *Africana*. The surveys extend from the Orange River mouth to Port Alfred to a depth of 500 m. The methods used and the areas surveyed are described in detail by Payne *et al*. (1984) and Badenhorst and Smale (1991). Briefly, a 180-ft German bottom trawl (vertical opening of 2–3 m) is towed for 30 minutes at each station during daylight, according to a stratified random design. Surveys have been conducted in January/February and July/August on the West Coast and in April/May and September on the South Coast. The July/August survey on the West Coast was discontinued in 1992.

Commercial catch data

Three sources of commercial catch data were used to investigate the horizontal migratory patterns of horse mackerel over the South African shelf. First, purse-seine landings between 1987 and 1994 from the West Coast were examined. The data were divided into three areas: Orange River to Cape Columbine, Cape Columbine to Cape Point, and Cape Point to Cape Infanta. From these, the seasonality in the distribution and size composition of the catches was determined. A second source of data was the reported landings of the South Coast inshore demersal fishery, which operates mainly between Mossel Bay and Port Elizabeth at depths shallower than 110 m. Such data were useful in elucidating seasonal and interannual patterns of the abundance of horse mackerel in that region between 1987 and 1995. A third source was the catch statistics from a midwater trawl fishery (between 1991 and 1996), which were used to support the evidence of interannual patterns in resource abundance obtained from the other two time-series.

Table II: Estimates of Cape horse mackerel biomass from swept-area surveys on the South Coast by depth stratum

Date	Biomass estimate (thousand tons)	
	< 100 m	100–200 m
September 1986	49	89
September 1987	149	159
May 1988	62	53
May 1989	85	52
May 1990	64	57
September 1990	210	299
June 1991	218	119
September 1991	212	363
April 1992	144	173
September 1992	140	336
May 1993	182	213
September 1993	112	199
June 1994	122	207
September 1994	210	147
May 1995	68	118
September 1995	103	178
May 1996	106	121

RESULTS

Spatial and temporal patterns in pelagic horse mackerel

Data obtained from SF pelagic surveys on the South and West coasts showed differences in the distribution of horse mackerel by size-class (Fig. 1). Recruits (<10 cm) were generally limited to the area between the Orange River and Mossel Bay, whereas the majority of adults (>30 cm) were east of Mossel Bay, particularly along the shelf edge. Fish of 20–30 cm, which are about 2 years old and are sexually mature (Kerstan 1995),

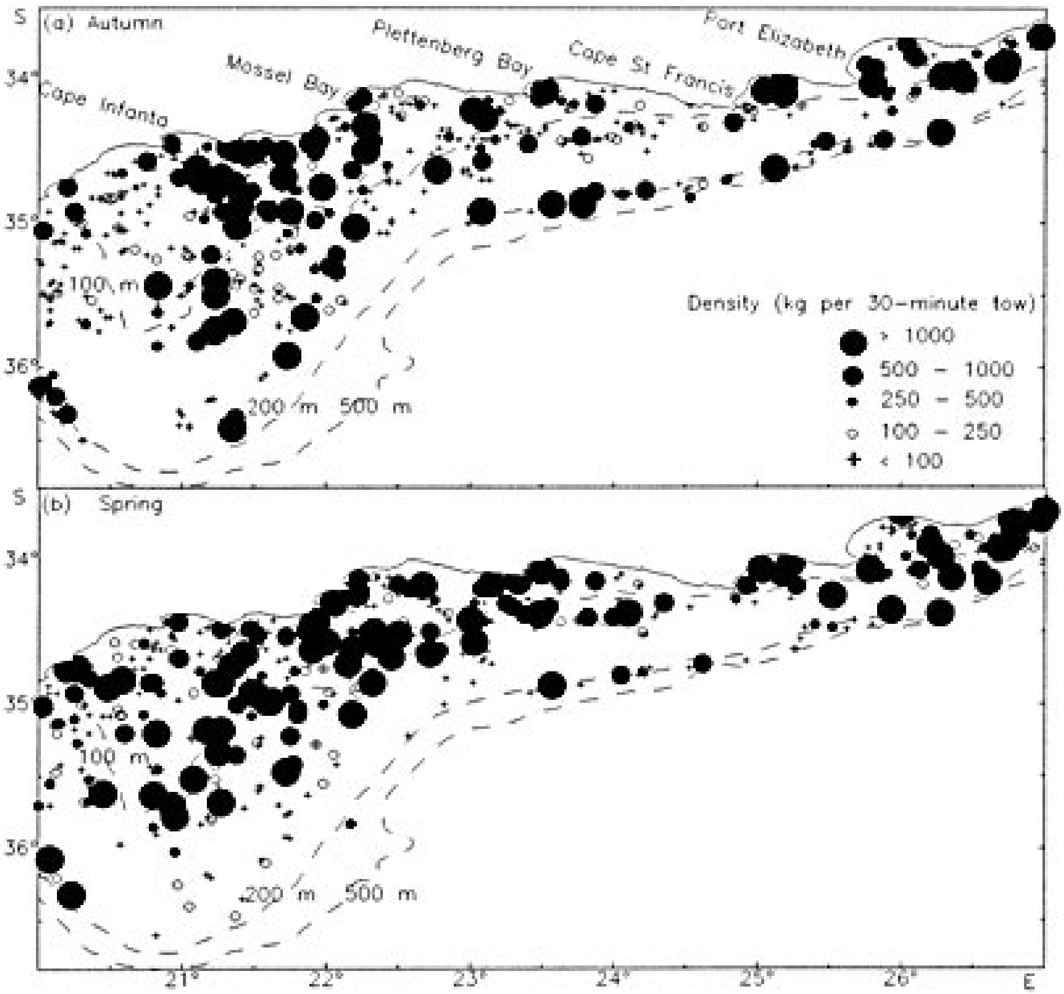

Fig. 6: Catch rates of Cape horse mackerel derived from bottom trawl research surveys on the South Coast in (a) autumn and (b) spring for the period 1987–1996

occurred over the whole South Coast shelf. Juvenile fish (10–20 cm) were concentrated inshore along the coasts of the Western and Southern Cape. It should be noted, however, that the pelagic surveys did not extend beyond the shelf and were generally restricted to the inner shelf on the West Coast. Consequently, they did not cover the entire habitat range of the resource. Nevertheless, the results suggest an eastward migratory pattern, with recruits concentrating more on the West Coast, juveniles over the central Agulhas Bank and adults farther east.

Information on temporal shifts in the distribution of horse mackerel can be obtained from West Coast pelagic purse-seine catches. Trends indicate that most fish were caught between the Orange River and Cape Columbine in the first quarter of the year (Fig. 2). These were mainly young recruits (approximately 10 cm long and 6 months old, Fig. 3). South of Cape Columbine, most fish were caught in May (Fig. 2), consisting of 1-year old fish (Fig. 3).

Purse-seine catches indicate that availability of horse mackerel on the West Coast was greatest during the years 1988–1990 and 1993–1994 (Table I), which suggests that recruitment was largest before and

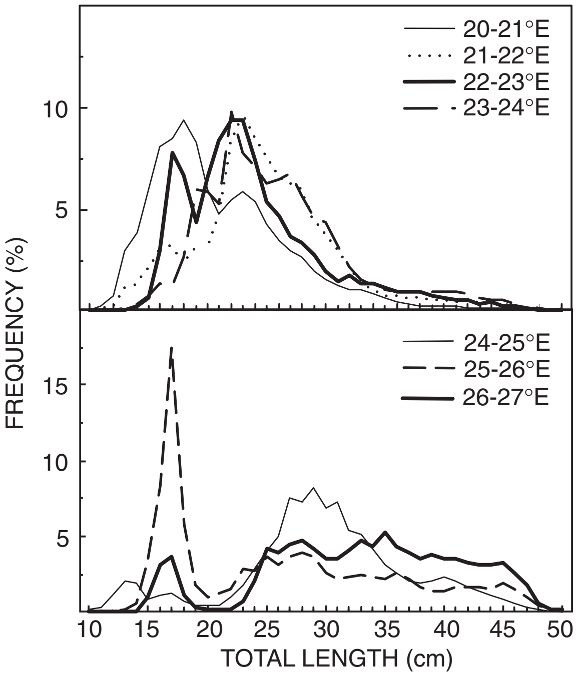

Fig. 7: Length distribution of Cape horse mackerel by degree of longitude derived from bottom trawl research surveys on the South Coast for the period 1987–1996

immediately after the *El Niño*-Southern Oscillation event, which had an impact on the pelagic resources of the Benguela between 1991 and mid 1993 (Boyd *et al*. 1997).

Spatial and temporal patterns in demersal horse mackerel

Summer and winter catches of horse mackerel during the bottom trawl surveys on the West Coast indicate that the species concentrates at the shelf-break, along the 200-m isobath (Fig. 4). Horse mackerel appear to be more widespread in summer than in winter, when they tend to move south, although the size composition did not differ markedly between seasons (data not shown). However, there is a clear spatial separation between size-classes on the West Coast, with larger (>25 cm), older (2+ year-olds) horse mackerel distributed farther offshore than smaller and younger fish (Fig. 5a).

The time-series of biomass estimates of horse mackerel from the South Coast demersal surveys is shown in Table II. There is a significant trend of larger estimates of biomass in spring than in autumn (ANOVA, $p < 0.05$) in the 100–200 m stratum. This may be indicative of a seasonal inshore-offshore migration. Alternatively, it could indicate that the fish are closer to the sea bed and more available to bottom trawling in spring than in autumn. It is not apparent why there is no such trend in the inshore (< 100 m) stratum.

Demersal research catches off the South Coast (Fig. 6) show that horse mackerel are widely distributed over the Agulhas Bank during both autumn and spring. Averaging catch rates by longitudinal degree identifies a minimum in abundance between Plettenberg Bay and Cape St Francis, where the shelf narrows and the 100-m isobath is closest to the coast. Length distributions of horse mackerel are markedly different on either side of this region (Fig. 7), where

Table III: Spring biomass estimates and coefficient of variation (CV) of Cape horse mackerel from hydro-acoustic and demersal trawl surveys east and west of 22°S (Mossel Bay). Modified from Leslie (1995) using the new target strength expression (see text)

Year	Bottom trawling		Hydro-acoustics
	West of 22°E	East of 22°E	East of 22°E
1991	337 (23)	243 (27)	270 (23)*
1992	370 (30)	97 (21)	261 (17)*
1993	209 (25)	111 (22)	50 (50)
1994	205 (24)	169 (21)	75 (43)
Arithmetic mean	280	155	164

**CV* not strictly valid because the survey was systematic

Table IV: Total reported catch of Cape horse mackerel by the South Coast inshore demersal fishery and the "targeted" midwater fishery, 1987–1995

Year	Catch (tons)	
	Demersal	Midwater
1987	4 081	*
1988	2 218	*
1989	1 470	*
1990	2 310	15 526
1991	5 435	15 301
1992	4 933	11 637
1993	2 196	10 549
1994	1 523	5 508
1995	1 008	4 889

*No directed midwater trawling

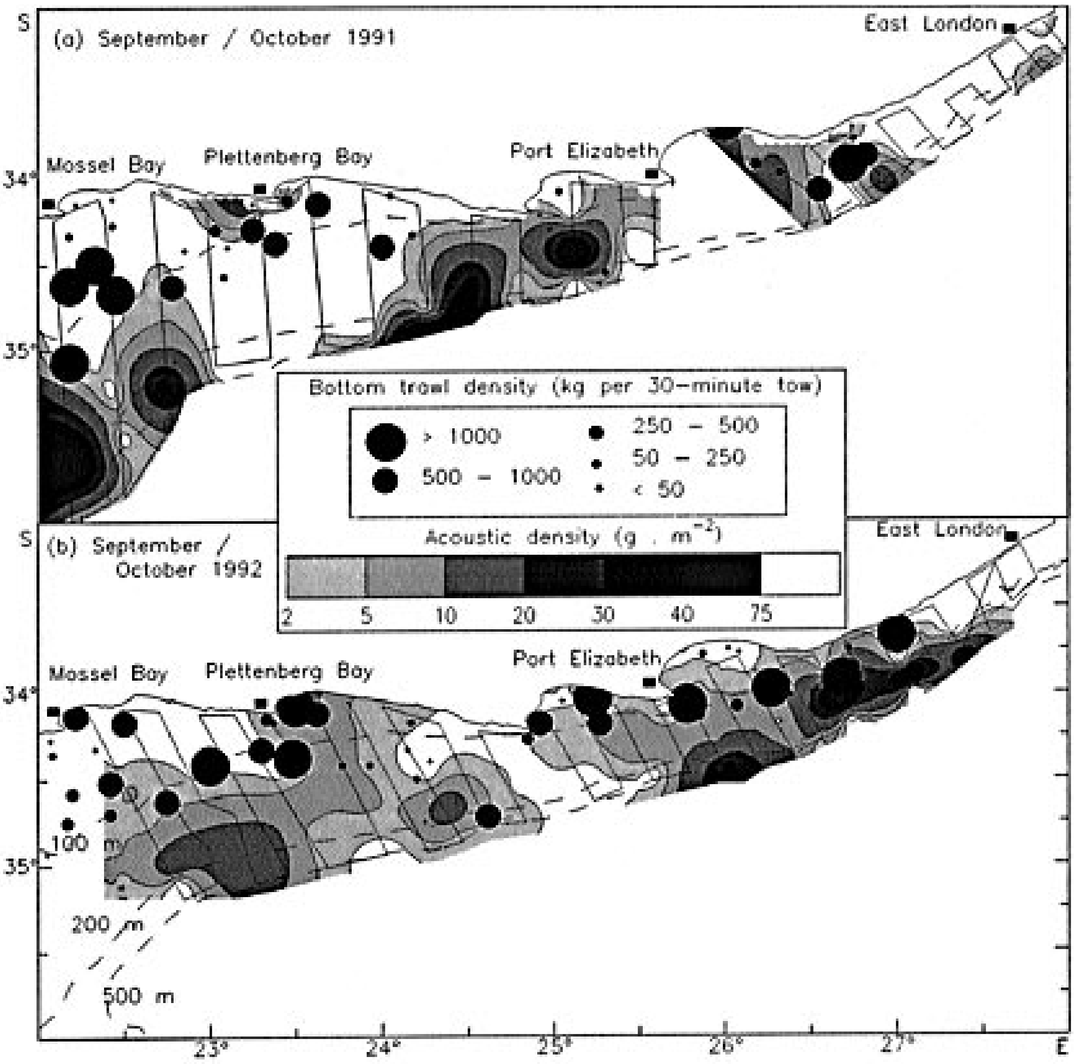

Fig. 8: Catch rates of Cape horse mackerel derived from bottom trawl research surveys (daylight only) and acoustic surveys during (a, b) September/October 1991 and 1992 respectively and (c, d) September 1993 and 1994 respectively. The acoustic survey tracks are indicated

upwelling is prevalent (M. Roberts, SF, pers. comm.). West of 24°E, fish were mostly <30 cm long (younger than 3 years), whereas east of that region they were generally >25 cm long. The peak of small fish between 25 and 26°E is a result of a strong cohort of 1-year-olds in winter 1993, coincident with good catches of juveniles on the West Coast early the same year (Table I). As on the West Coast, large fish were distributed farther offshore on the South Coast (Fig. 5b). Generally, 1- and 2-year-olds were found in shallow (<100 m) water, 3- and 4-year-olds over the shelf, and older fish at the shelf-break and beyond (Fig. 5b).

Stock assessment cruises 1991–1994

The distribution of horse mackerel on the South

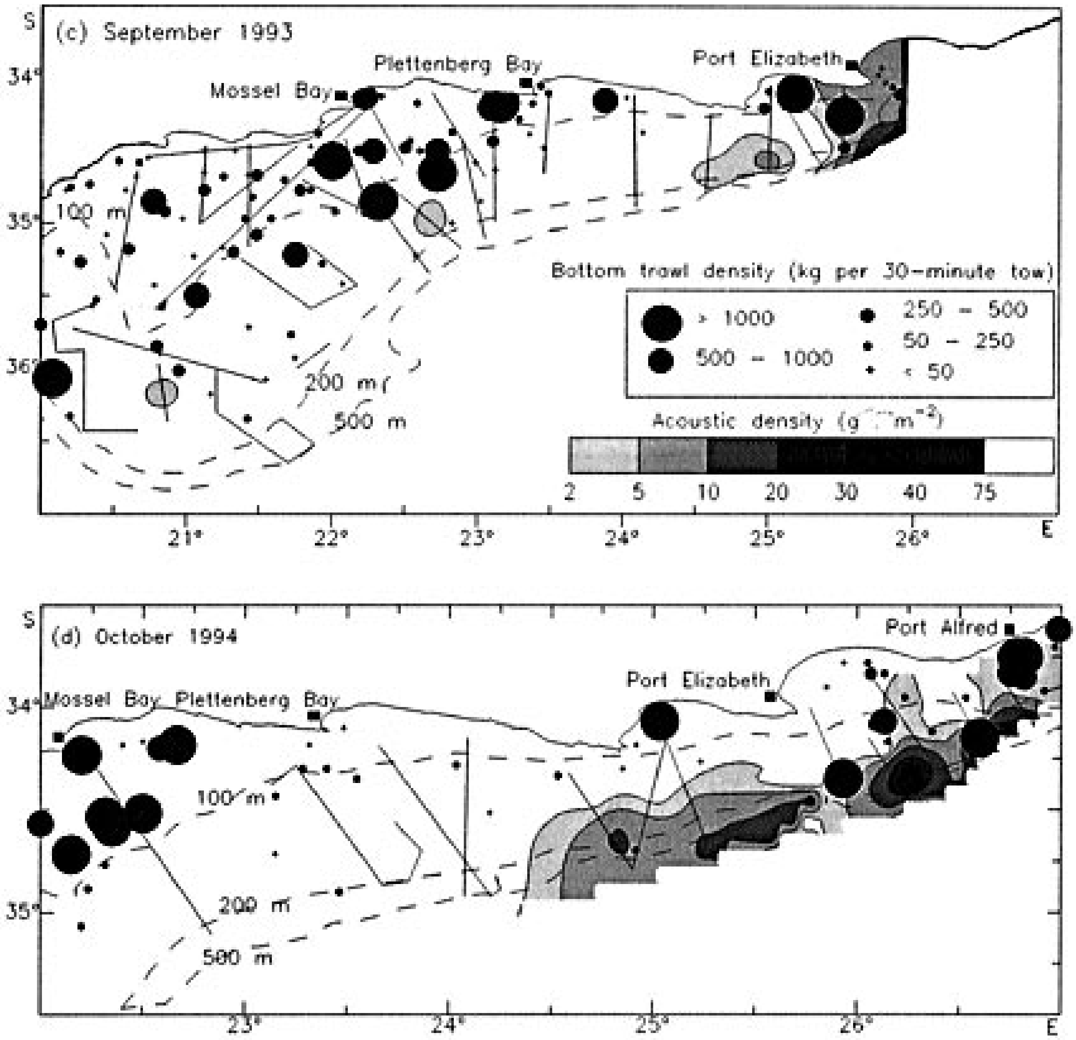

Fig. 8 *(continued)*

Coast in spring 1991–1994, determined by acoustic and bottom trawl surveys, is presented in Figure 8. It is clear that the stock distributions inferred from the two survey methods are poorly correlated. In 1991 (Fig. 8a), bottom trawl catches showed high concentrations of fish over the shelf between Mossel Bay and Plettenberg Bay, but no pelagic targets were recorded acoustically in that area one month later. However, it should be noted that acoustic sampling in 1991was round-the-clock and therefore subject to bias as a result of diel changes in the vertical distribution of horse mackerel. Nonetheless, the larger concentrations of horse mackerel recorded acoustically around the shelf-break were not detected in the bottom trawl survey, particularly west of Port Elizabeth, where the offshore stratum was poorly sampled. In 1992 (Fig. 8b), the correlation between the two survey methods was better. However, as in the previous year, poor sample coverage by the bottom trawl survey failed to show the high concentrations of fish recorded acoustically at the shelf-break. Conversely, substantial demersal catches were recorded on the inner shelf, particularly west of Plettenberg Bay where there were no pelagic targets. In 1993

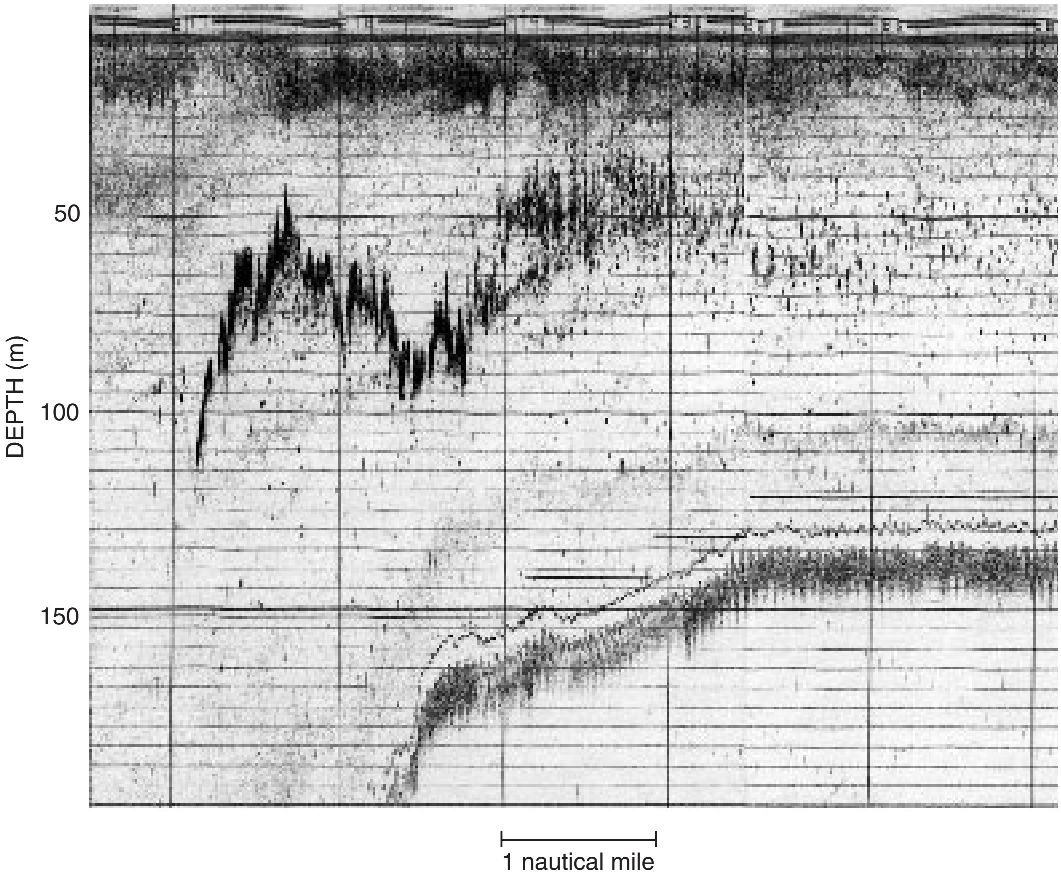

Fig. 9: Acoustic echo-chart showing the night-time (00:00 GMT) vertical distribution of Cape horse mackerel over the shelf-break approximately 35 miles south of St Francis Bay (25°12′E) in October 1991

(Fig. 8c), when the two sampling methods were combined on the same cruise (acoustic sampling taking place each night after the last bottom trawl of the day), very few pelagic targets were recorded (except off Port Elizabeth), despite the bottom trawl survey again showing fairly high concentrations of fish between Mossel Bay and Plettenberg Bay. In 1994 (Fig. 8d), although the acoustic coverage was poorer than in 1993, horse mackerel were again not detected in regions of good catches by bottom trawl, e.g. in shallow water off Mossel Bay and St Francis Bay (25°E). Also, as in 1991 and 1992, high abundances were recorded acoustically near the shelf-break. An example of a target off the shelf-break is presented in Figure 9. Typically, horse mackerel form undulating, high-density concentrations in midwater for several miles, moving closer to the sea bed during the day (Pillar and Barange 1998).

An important finding is the difference in size between horse mackerel taken in bottom and midwater trawls. In all four surveys, fish caught close to the bottom were smaller than those caught in midwater (Fig. 10). However, most midwater trawl catches were made farther offshore, where horse mackerel tend to be larger (Fig. 5b). Also, trawl selectivity may be partially responsible for the differences in size composition. Nevertheless, the present results suggest that old fish tend to display a more pelagic behaviour, indicating that bottom trawl and acoustic surveys may be targeting different portions of the population.

The bottom trawl and acoustic estimates of the abundance of horse mackerel of the western and

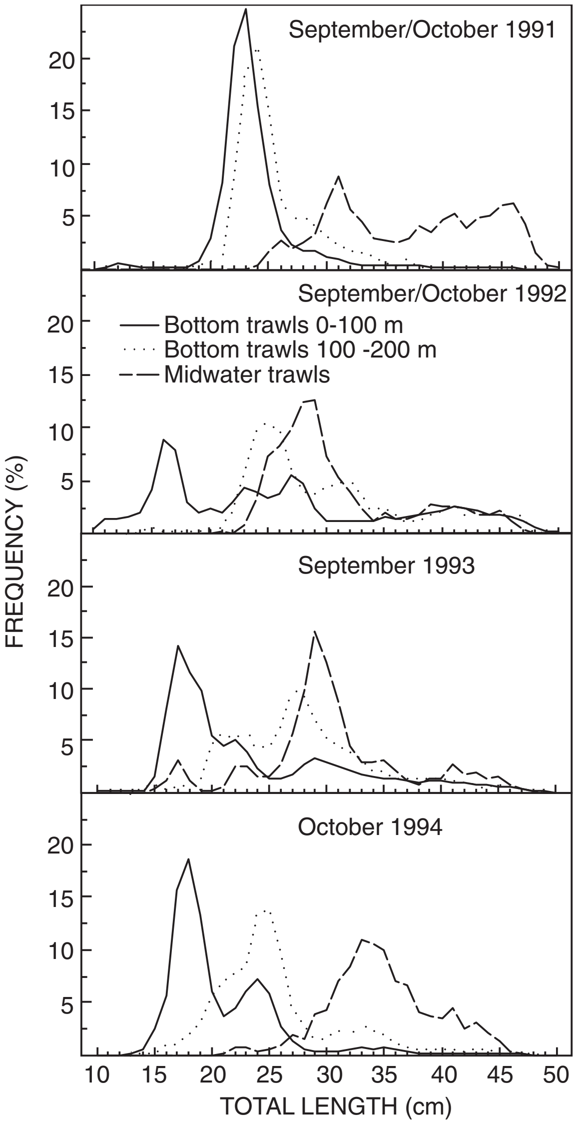

Fig. 10: Length distributions of Cape horse mackerel derived from research bottom trawls (by depth stratum) and midwater trawl surveys during spring for the period 1991–1994

eastern Agulhas Bank for the years 1991–1994 are shown in Table III. In 1993, when acoustic measurements were also made on the western Bank (Fig. 8c), echo-traces of horse mackerel were scarce, despite the relatively high estimate of biomass from the demersal trawl survey. With the exception of 1991, there is poor agreement between the two survey methods, with no consistent pattern in the differences. Surprisingly, the coefficients of variation for the acoustic surveys were greater than those for the bottom trawl surveys, despite the larger volume sampled acoustically as a result of the continuous nature of the survey.

DISCUSSION

Survey strategies

Although the time-series of abundance estimates presented here is relatively short, the results clearly show that neither bottom trawl nor acoustic indices can be treated as reliable, independent estimates of abundance of the horse mackerel on the South Coast. It is evident that bottom trawling during the day was successful in detecting horse mackerel in some areas (particularly the inner shelf around Mossel Bay), but that it was ineffective in the shelf-break, where a substantial proportion of the population extends beyond the routine survey area and over untrawlable grounds. Conversely, it is clear that acoustic surveys failed to detect a large portion of the horse mackerel stock over the shelf. Combined bottom trawl and acoustic surveys appear to be the only effective means of assessing the total abundance of horse mackerel. Such surveys should lead to improved (or at least more accurate) estimates of abundance, as has been the case for other semi-pelagic fish worldwide, e.g. walleye pollock *Theragra chalcogramma* (Karp and Walters 1994, see review by Godø 1994). Ideally, the two methods should be conducted concurrently, using acoustics to assess the abundance of fish above the headline of the bottom trawl (presently 2–3 m above the sea bed) and employing the swept-area method to assess fish close to the bottom. This differs from the strategy followed in 1993 and 1994, when the acoustic assessment was confined to night and bottom trawling to daylight. It also deviates from the method used for walleye pollock (Karp and Walter 1994), in which the acoustic and bottom trawl assessments are not done concurrently. However, those surveys are conducted in a narrow, seasonal window, when migratory activities are believed to be minimal, a compromise that does not appear to be appropriate for horse mackerel.

An important consideration that supports combining bottom trawl and acoustic techniques is the fact that the proportion of demersal to pelagic horse mackerel

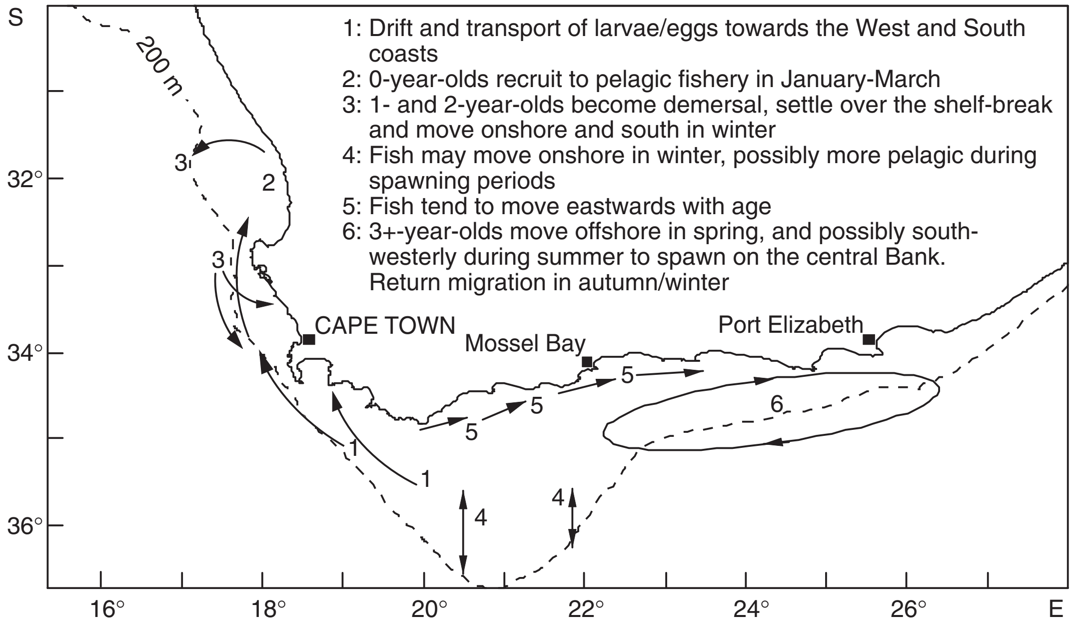

Fig. 11: A conceptual model postulating migration and spawning strategies of Cape horse mackerel

is variable. This is evident from the differences in the ratios between the acoustic and trawl estimates in the 1991/92 and 1993/94 surveys. The lack of acoustic targets in the latter period could be attributed to a change in the vertical migratory patterns of horse mackerel, whereby fish remained close to the bottom throughout the survey (Barange 1995). Because *El Niño* conditions dominated the southern Benguela from 1991 to mid-1993 (Boyd *et al.* 1997), it is tempting to speculate that the unusual environmental conditions at that time increased the availability of horse mackerel to acoustic surveys. However, as both research bottom trawl estimates (Table II) and demersal and midwater commercial catches (Table IV) increased during that period, it appears that the warm conditions improved the availability of demersal as well as pelagic horse mackerel. *El Niño* years are typified by an increased incidence of westerly winds, which causes the intrusion of warm oceanic water over the shelf (Goschen and Schumann 1990). Such conditions could have forced horse mackerel into the fishing and survey areas, as well as changing their vertical distribution pattern. With a return to normal environmental conditions in mid 1993, horse mackerel could have assumed a more demersal behaviour, possibly spreading over a larger area and beyond the survey limits.

Horse mackerel life history

Major gaps still exist in knowledge of important aspects of the basic ecology of horse mackerel, such as the direction and timing of their migrations and reproductive time-scales and periods. Ignorance of these behavioural aspects hampers the design of an effective survey programme. Based on the surveys presented here, salient features of the life history of horse mackerel can be postulated (Fig. 11). These features should be seen as working hypotheses, around which a survey programme can be framed.

Horse mackerel appear to have two major spawning peaks in South African waters, although the timing seems to vary between the eastern and western Agulhas Bank. On the eastern Bank, peak spawning was documented in June and November (Hecht 1990), whereas Naish (1990) reported August and February as the main spawning period on the western Bank. However, in inshore waters along the Western and Southern Cape, larval of horse mackerel were most numerous between June and October (Shelton 1986), perhaps indicating that winter spawning on the western Bank is closer inshore than in summer. Geldenhuys (1973) reported an onshore migration of horse mackerel in winter, which could be related to their

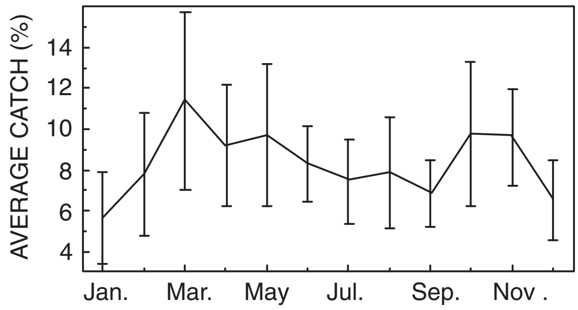

Fig. 12: Seasonal trends in catches of horse mackerel derived from landings by the South Coast inshore demersal industry for the period 1987–1995. Vertical lines denote standard deviations

spawning behaviour, as reported for mackerel *Scomber japonicus* (Baird 1978). Geldenhuys (1973) also postulated that horse mackerel could become more pelagic as a result of their spawning migrations into midwater. This behaviour could account for the seasonal differences in bottom trawl abundance indices shown in Table II.

It is likely that horse mackerel recruit in the numerous bays on the South Coast (Hecht 1990). However, during summer, a substantial proportion of the eggs and larvae from the western and central Agulhas Bank would be transported northwards in the shelf-edge jet current along the West Coast, as demonstrated for the reproductive products of sardine and anchovy (Fowler and Boyd 1998). The arrival of horse mackerel recruits on the West Coast is reflected in the purse-seine landings, which peak from January to March (Fig. 2). The fish move offshore as they mature, before recruiting to the demersal fishery on the West Coast as 1–2 years of age (Figs 4, 5). The southward shift in the distribution of fish in summer and winter (Fig. 4) suggests that a portion of that population migrates south in winter, probably assisted by the poleward flow of near-bottom water at the shelf-break along the West Coast (Shannon and Nelson 1996).

On the South Coast, juveniles recruit to the inshore demersal fishing grounds, mainly west of 24°E. As they grow older, they move offshore and eastwards (Figs 5, 7). This eastward migration, which may take more than a year to complete, is probably enhanced in winter by the prevailing easterly flow (Boyd and Shillington 1994, Tilney *et al*. 1996). After two years of age, they mature (Kerstan 1995) and enter the spawning cycle. As indicated above, fish may become more demersal between spawnings, perhaps as a strategy to build up energy reserves. Although there is no evidence of this behaviour in South African horse mackerel, there is a seasonality in the vertical distribution of horse mackerel off Namibia, believed to be related to feeding (Andronov 1985). If such behaviour also exists in South African waters, it may explain the seasonality found in the landings of the inshore demersal trawl industry (Fig. 12), which shows smallest catches during May–September and December–February, roughly coinciding with the periods of peak spawning of horse mackerel.

Horse mackerel older than 3–4 years seem to have an affinity for the shelf-edge region of the eastern Agulhas Bank (Fig. 8). This may be a seasonal feature. Results of a survey on the South Coast shelf-break region in January 1992 did not show acoustic targets of horse mackerel east of Mossel Bay, whereas in October of 1992 and 1993, strong targets were found there (Fig. 8). It could be that horse mackerel move offshore in spring to benefit from the abundant food supply (mainly copepods) concentrated at the inshore edge of the Agulhas Current (Barange 1994). Fish there are likely to be transported westwards along the bathymetry by the strong south-west flowing current. As a result, these older fish may contribute to the spawning population on the central Agulhas Bank in summer. Large populations of horse mackerel recorded in the outer-shelf region west of Mossel Bay in January 1992 (SF unpublished data) would support this hypothesis. Alternatively, they may move onshore to spawn on the eastern Bank. These two hypotheses may not be exclusive.

The distribution patterns of horse mackerel described here suggest that migratory routes may take several years to complete, with old fish migrating more extensively than juvenile fish. The ecological significance of such migrations can be explained in terms of spawning and foraging success, which can be influenced by environmental conditions. The specific characteristics of the migrations are useful for delimiting the core sampling area of any survey programme. If the emphasis is on estimating the spawner stock, i.e. fish of 2+ years and >22 cm long, sampling should concentrate east of 21°E (Fig. 7), using mainly bottom trawls. However, acoustics should be used farther east of this, especially where the shelf narrows. The biomass of horse mackerel on the West Coast is approximately five times smaller than that on the South Coast, so the West Coast is less important in assessing the total size of the stock. However, the level of interchange of fish between the two coasts needs careful examination. On the basis of catch distributions, Crawford (1980) assumed that the West and South coast populations of horse mackerel formed separate stocks, an hypothesis supported by Hecht (1990). However, on the basis of mitochondrial DNA analysis, Naish (1990) concluded that South African west and south coast populations were part of a single stock, genetically separated from the Namibian stock by the environmental barrier of the Lüderitz upwelling cell. Naish (1990) also concluded that there was a limited exchange of fish stocks between the Namibian and South African stocks. The question of integrity of stocks is important, because changes in the population on the West Coast could be linked to stock fluctuations in the northern Benguela. It is possible that the increase in the size of the South African stock from 1993 to 1996 on the West Coast may be a result of southward migration of fish from Namibian waters (E. Klingelhoeffer, National Marine Information and Research Centre, Namibia, pers. comm.).

Improved knowledge of the exchanges between populations of horse mackerel in the different regions of the Benguela system, as well as better insight into the factors that control and modulate their vertical distribution (Pillar and Barange 1998), is needed before the relationships between environmental conditions, fish availability and fish vertical distribution can be elucidated. Until such time, interpretations of catch and *cpue* indices will remain questionable.

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