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SEASONAL UNCOUPLING OF OTOLITH AND SOMATIC GROWTH IN SOUTH AFRICAN PILCHARD (*SARDINOPS SAGAX*) AND ITS APPLICATIONS

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ABSTRACT

Pilchard (*Sardinops sagax*) otoliths of the recruiting 1992/93 and 1993/94 year-classes were collected during 1993 and 1994 from commercial landings. Bimodal otolith length distributions during the second half of both years indicated two recruiting sub-cohorts. Gradual monthly changes in the fish-otolith length relationships were consistent with an increasing degree of uncoupling between otolith and somatic growth. The monthly means of individual standard length:otolith length ratios (SL:OL) were used as a relative measure of somatic growth performance. Somatic growth rates exceeded otolith growth rates until mid-summer and decreased thereafter. Minimal somatic growth was observed in August 1993 and July 1994. The times at 50%-annulus completion in the otoliths occurred in October 1993 and September 1994, presumably during the spawning season. The annual patterns of change in SL:OL ratios corresponded well with the wind velocity patterns in both years, the agreement being better in 1993. The 1993/94 year-class displayed higher SL:OL ratios in 1994, which coincided with higher wind velocities. The correspondence between SL:OL ratios and monthly sea surface temperature means was weaker than with a temperature index synonymous with upwelling intensity. Bimodal ratio distributions in several months indicated the presence of fast and slow growing pilchards. Results suggest that 1 July should be used as a starting date for management reference years if pilchard growth patterns and year-class strengths are to be assessed accurately. SL:OL ratios can be used reliably to monitor and to compare the annual growth performances of different year-classes.

-2-

INTRODUCTION

Otolith growth can be expected to correlate with somatic fish growth when environmental conditions favour growth (e.g. Volk et al. 1984, Karakiri and Westernhagen 1989, Wright et al. 1990, Bradford and Geen 1992, Moksness et al. 1995). However, if environmental conditions become unfavourable, otolith and somatic growth may diverge, a process defined as uncoupling (e.g. Wright et al. 1990). The strength of the response to suboptimal conditions depends on how differently they affect somatic and otolith growth. Starving or slow growing fish have heavier and larger otoliths than fast growing specimens of the same length (e.g. Templeman and Squires 1956, Reznick et al. 1989). The explanation for this is obvious: slower somatic growth in fish of the same size relates to an older age (Pawson 1990) and, therefore, to more daily increments (e.g. Campana and Neilson 1985). Numerous recent studies have shown that otolith growth may continue while somatic fish growth ceases (e.g. Tsuji and Aoyama 1982, Mosegaard et al. 1988, Secor and Dean 1989, Reznick et al. 1989, Secor et al. 1989, Wright et al. 1990, Mugiya and Tanaka 1992). Francis et al. (1993) showed that the otolith size-fish length relationship can vary among seasons. Kerstan (1991) separated seasonal otolith populations of horse mackerel by using otolith morphometrics. As otolith growth appears to be more consistent than somatic growth (Secor et al. 1989, Gauldie and Nelson 1990, Gauldie and Radtke 1990, Wright et al. 1991, Zhang and Runham 1992), otolith size provides a relative scale on which somatic growth performance can be measured when other data on growth performance are unreliable.

In South African waters, age and length data for pilchard Sardinops sagax is derived from commercial landings. As much, it reflects mesh selection in the recruiting year-class, seasonality in effort of the fishery (Crawford 1980) for specific target sizes, differential seasonal and regional distribution of size- and age-groups (Crawford et al. 1980, Armstrong et al. 1987), and recent shifts of catch regions and seasons (Roel et al. 1994). Stock assessment models presently operate on the assumption that the cut-off point between reference years and, thus, year-classes is 1 November. Recent doubts about the validity of this date required its validation by biologically relevant parameters. This study uses the uncoupling of otolith and somatic growth to determine the period of minimal somatic growth, which is then compared to the annulus formation period, and intends to relate changes in somatic growth to environmental parameters.

MATERIALS AND METHODS

Otoliths of the recruiting 1992/93 and 1993/94 year-classes were collected during the 1993 and 1994 fishing seasons at five field stations on the west coast of South Africa (Fig. 1). As differences in fish:otolith length (SL:OL) ratios could be expected to be most pronounced in young specimens where otolith size gain relative to fish length is highest, sampling was restricted to juvenile recruits. The sampling scheme targeted at four otoliths per 0.5cm-size-class per week and field station. All station data were subsequently pooled. Fish lengths were measured as standard length (SL) in millimetres. Whole otoliths were measured, rather than otolith radii, because the postrostral and rostral tips differed in
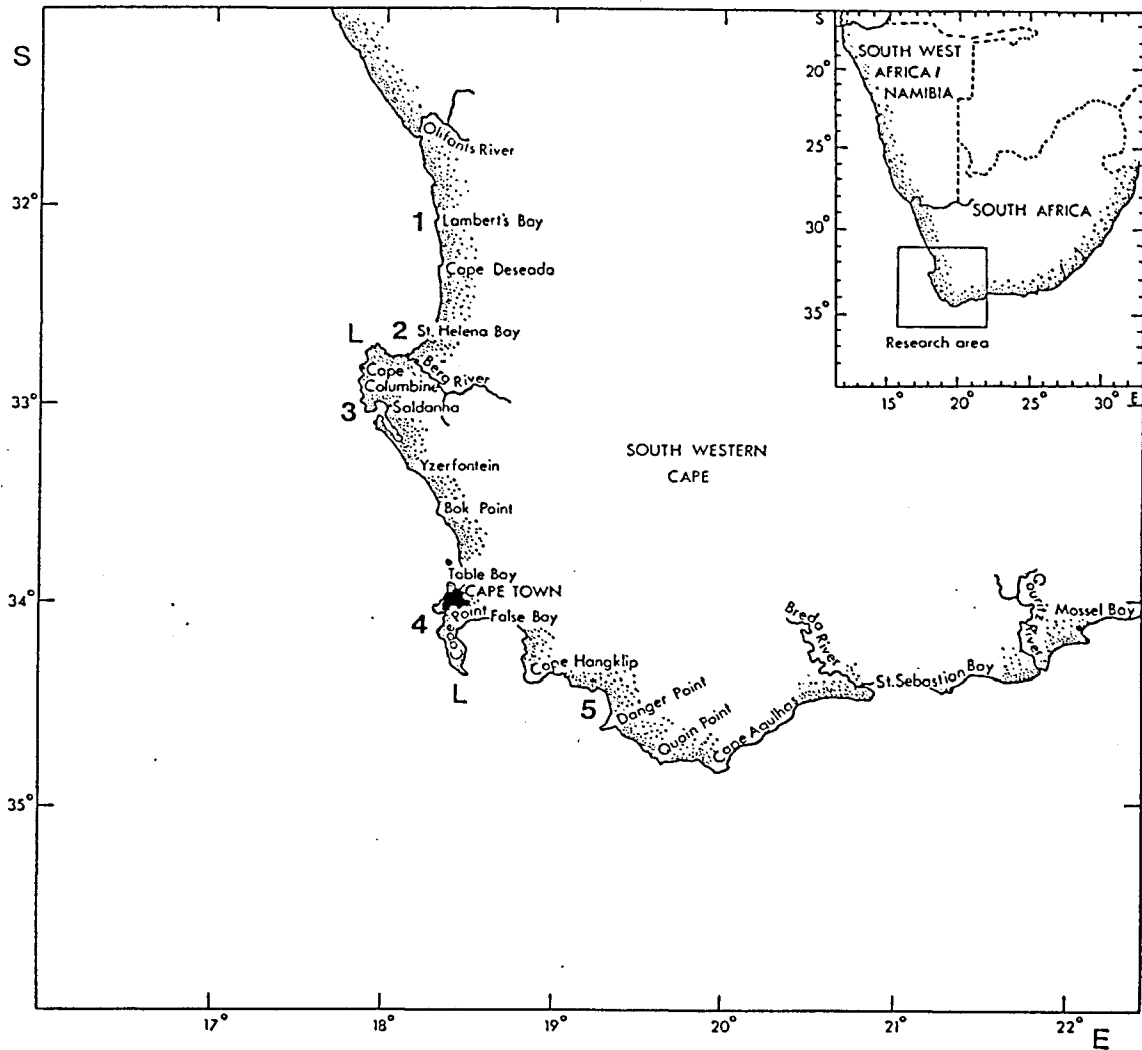
Fig. 1: Locations of the field stations (1-5) and Cape Columbine and Cape Point lighthouses (L) on the west and south coasts of South Africa.

growth synchrony during the year. In all recruits older than 1 year, lengths of the first annual growth zones and total otolith lengths including the recently deposited marginal increment were measured in eye-piece units (epu). 2.5 eye-piece units (epu) corresponded to 1mm. In order to determine the time at 50% completion (TC_{50}) of the annulus in each year-class, and to relate it to the period of minimal somatic growth, the specimens with complete and incomplete annuli in each month were counted. The proportions in each category were transformed into logits and weighted by sample size. The standard logistic function of the form

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

where p(%) is the proportion of mature fish, a is a constant, b is the regression slope and t is the month (days converted to decimals), was calculated using the non-linear regression procedure by CSS:STATISTICA (STATSOFT 1992). Monthly means of the SL:OL ratios were

calculated as arithmetic means of individual ratios. The formation and monthly progression of the marginal increments deposited after annulus completion (Fig. 2) was monitored during the entire investigation period. In order to explain seasonal changes in the SL:OL ratios with changes in the environment, monthly average wind velocities ($m \cdot sec^{-1}$) were taken from wind data recorded at the Cape Columbine and Cape Point lighthouses (Fig. 1). The longshore north and south wind components were selected, because of their importance for the generation of upwelling cells in the survey area (Nelson and Hutchings 1983). The monthly means from both lighthouse locations were then averaged to obtain a mean value for the entire area. As mean monthly sea surface temperatures (SST) from merchant ships did not show significant seasonal changes, the maximum temperature differences (°C) in a defined area ranging from Lambert's Bay to Cape Point (Fig. 1) were averaged from sea surface isotherms and used as an index of the seasonal variability in SST, which is an indicator of the strength of upwelling processes off the West Coast (Nelson and Hutchings 1983). The changes in monthly means of the SL:OL ratios were compared to the changes in wind velocity and SST.
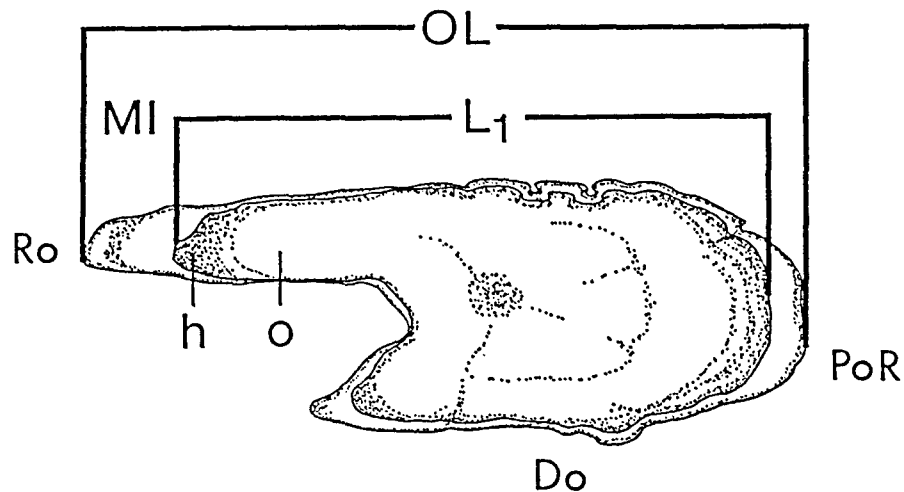

Fig. 2: Lateral view of a right-hand sagittal otolith of pilchard (OL: otolith length, L_1: length at age 1, MI: marginal increment, h: hyaline zone, o: opaque zone, Ro: Rostrum, PoR: Postrostrum, Do: dorsal side).

RESULTS

Annulus formation with subsequent marginal increment deposition started in 1993 in July and as early as May in 1994. The unimodal distribution of otolith lengths of the 1992/93 year-class in April 1993 did not indicate that any specimens were about to or had already completed their annual growth zones (Fig. 3a). Four months later, the bimodal otolith length-frequency distribution indicated that a second group of recruits with smaller otolith sizes had merged with the group of specimens which was already present in April.
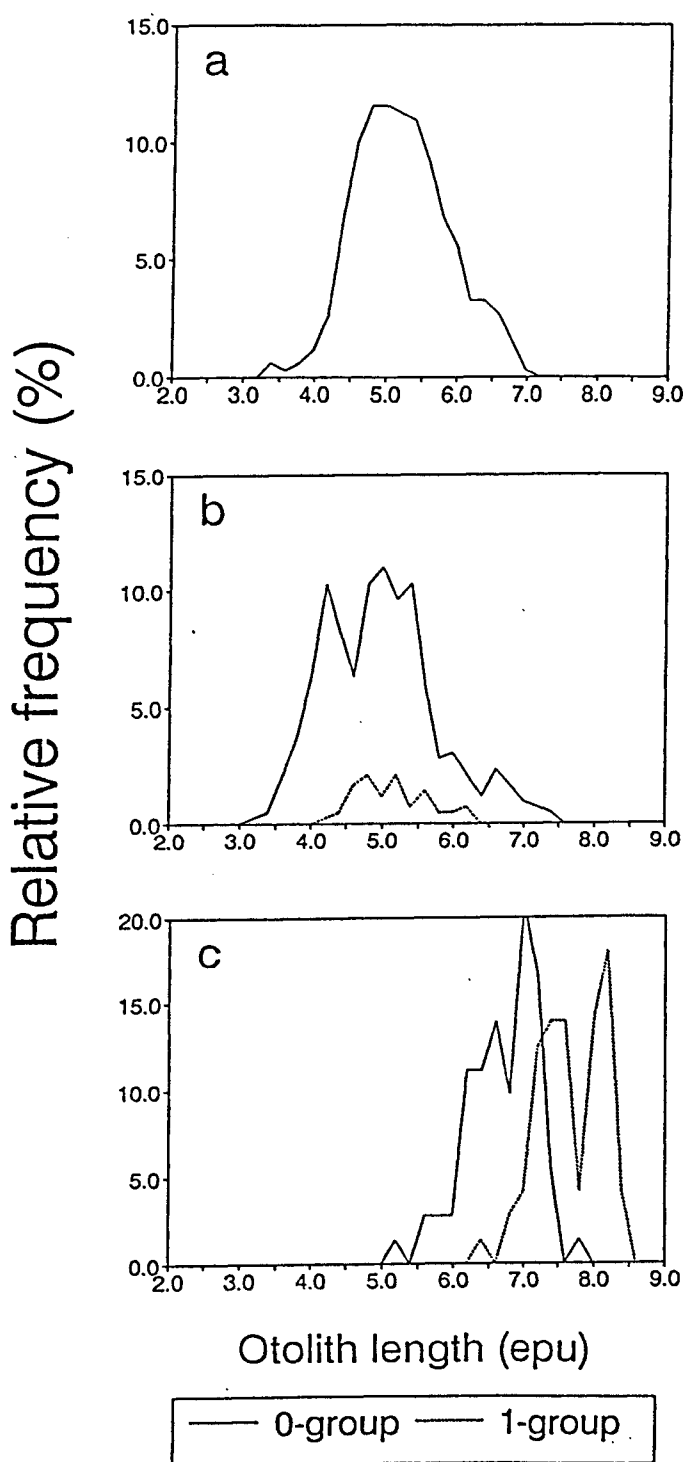
Fig. 3: Relative otolith length-frequency distributions of the 0- (——) and 1- group (- - -) pilchards of the 1992/93 year-class in (a) April (n=338), (b) August (n=427) and (c) November (n=72) of 1993.

The location of the major peak did not shift between April and August (Fig. 3b). Annulus completion in August did not start in pilchards with large otoliths but did in fish with small- and medium-sized otoliths (Fig. 3b). In November 1993, most specimens of the 1992/93 year-class had complete annuli, ranking them with the 1-group. The otolith length distribution was even more clearly bimodal (Fig. 3c). The OL distribution of the 1-group resembled the annulus distribution, indicating that growth rates were similar for all otolith specimens during the first few months of the new growing season. The completion ogives for 1993 and 1994 predicted 50% completion by mid-October and late September, respectively (Fig. 4). However, both the regression slope and the TC_{50} for 1994 were crucially dependent on the in-(1) or exclusion (2) of the September data. By omitting this data, the residual sum of squares (SSQ) decreased substantially (Table I). The increased slope of the second function suggested that in 1994 the TC_{50} occurred in the second week of September, 5 weeks earlier than in 1993. The latter calculation was more consistent with the finding that in 1994 annulus formation started two months earlier than in 1993.

Unsymmetric frequency distributions of fish and otolith lengths indicated an uncoupling of otolith and somatic growth in a substantial proportion of the recruits of each year-class in several months of both years. For example, in May 1994, the fish length-frequency distribution was positively skewed, showing a minor secondary peak at the upper end of the size range (Fig. 5a), whereas the

Table I: Function parameters, their standard errors (*s.e.*) and measures of goodness-of-fit of the annulus completion ogives for pilchard in 1993 and 1994, with (1) and without (2) the sample from September 1994.

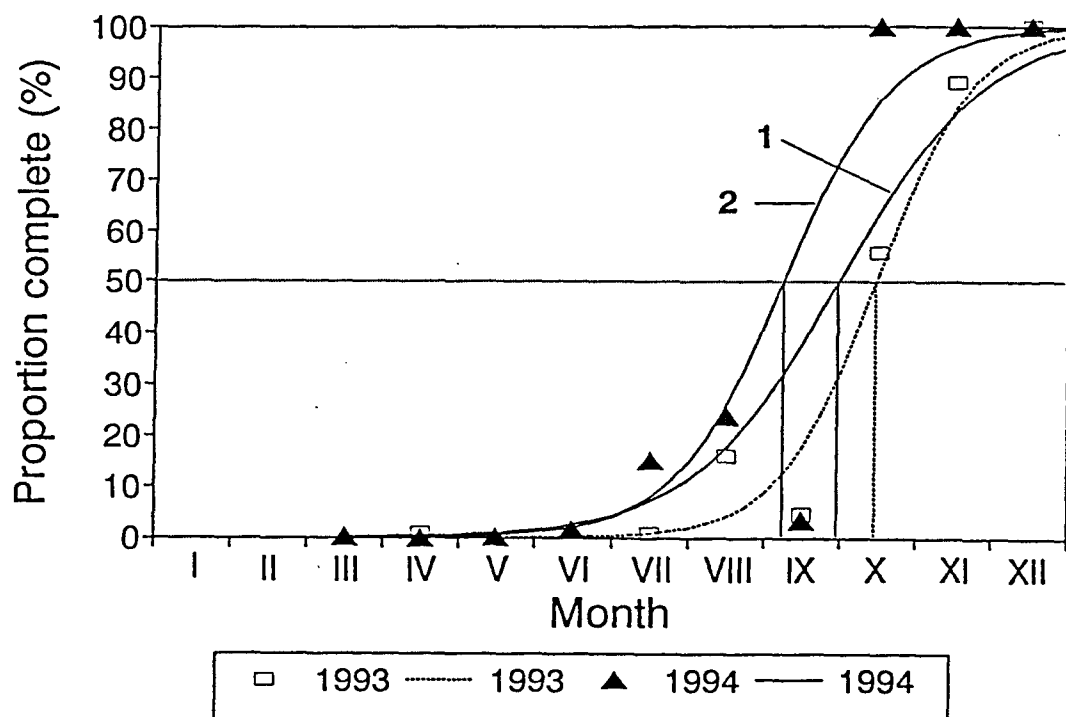| Year	Constant		Slope		Residual		No. invest.
	ln(a)	s.e.(ln(a))	b	s.e.(b)	SSQ	r	(n)
1993	15.136	1.155	1.5989	0.1234	108.8	0.699	2571
1994 (1)	9.384	0.362	1.0454	0.0422	148.1	0.662	3391
1994 (2)	11.608	0.616	1.4076	0.0807	123.5	0.723	3277

Fig. 4: Otolith annulus completion ogives for 1993 and 1994, including (1) or excluding (2) the sample from September 1994.

otolith length-frequency distribution indicated negative skewness and a minor peak at the lower end of the size range (Fig. 5b). Growth of pilchard recruits was generally faster in 1994 than in 1993. Pilchards sampled in February, May and August were 19-20% longer than those in 1993, and those collected in October 1994 were longer by 40% than the average size of the specimens analysed in October 1993 (Table II). Otolith sizes increased less markedly than fish lengths did. Gradually diverging fish-otolith length regressions
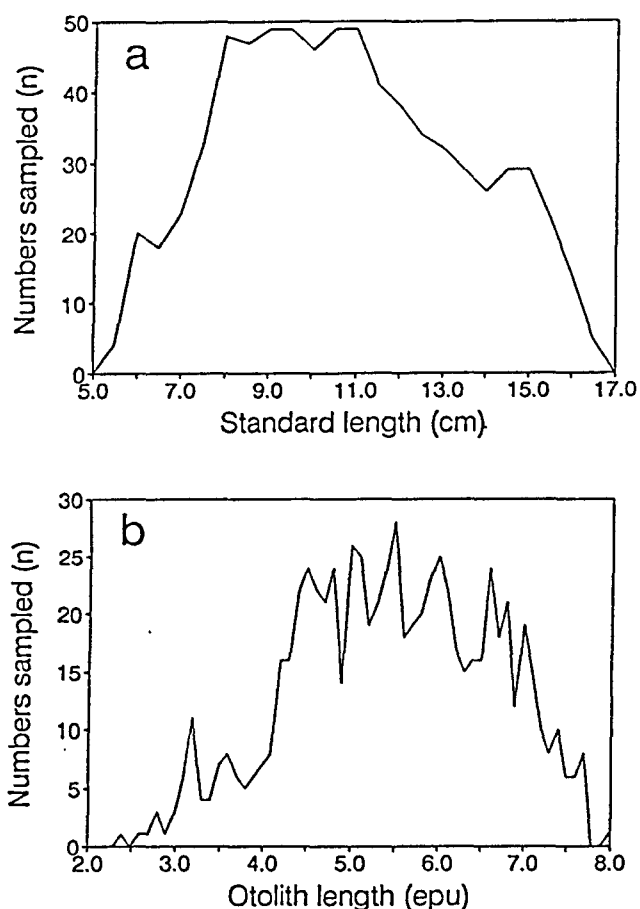
Fig. 5: Corresponding length-frequency distributions of pilchards (a) and their otoliths (2) collected in May 1994 (n=734).

between February and July were consistent with the interpretation of an uncoupling process between otolith and somatic growth (Wright *et al.* 1990). The forms of the relationships between fish and otolith length varied among months and year-classes from linear to 3rd-order polynomials and could therefore not be used to quantify seasonal changes. However, monthly SL:OL ratio means displayed a marked seasonal variation. In both years 1993 and 1994, the SL:OL ratios indicated that somatic growth was faster than otolith growth until February of each year. Somatic growth rates decreased thereafter until they reached their minima in August 1993 and July 1994 (Fig. 6). In both years, the minima appeared two months before the TC_{50}. In a number of months, bimodal SL:OL ratio frequency distributions suggested distinct sub-cohorts of slow and fast growing fish.

The monthly changes in the SL:OL ratio means corresponded well with the changes in the monthly averages of the wind velocity. The highest growth rates between December and February coincided with the highest wind velocities of 5-6m·sec⁻¹. In 1993, the decrease in wind velocity during March and the subsequent increase in April matched the decreased and increased somatic growth rates. Minimal somatic growth in August was preceded by northerly winds in July. A close correspondence between the average velocity of the southerly wind component and the SL:OL ratio was again observed during the period August-November 1993 (Fig. 6). In 1994, higher somatic growth rates coincided with generally higher wind velocities. Although the wind dropped in March 1994, as it did in 1993, a corresponding decline in somatic growth could not be detected. In 1994, minimal somatic growth coincided with low wind velocity in July. The sudden increase in wind velocity in August 1994 was paralleled by an increase in somatic growth rates. Although the wind velocity decreased again in September, somatic growth continued to exceed otolith growth until October. Somatic growth slowed down already after October 1994, one month earlier than in 1993. The relationship between monthly SL:OL ratios and average wind velocities (v) was best quantified (r=0.746) for both years by a significant (P<0.05) linear function of the form

$$ratio = 1.823 + 0.036v.$$

Table II: Monthly means of pilchard length, otolith length and SL:OL ratio for 1993 and 1994 and their differences.

Month	Year 1993				Year 1994				Interannual difference (%) 1994 - 1993		
	Fish length (cm)	Otol. length (epu)	SL:OL ratio (cm:epu)	No. invest. (n)	Fish length (cm)	Otol. length (epu)	SL:OL ratio (cm:epu)	No. invest. (n)	Fish length (cm)	Otol. length (epu)	SL:OL ratio (cm:epu)
Jan.	9.32	4.60	2.033	129	9.59	4.65	2.060	62	2.8	1.2	1.3
	0.97	0.50	0.145		1.53	0.69	0.088				
Feb.	9.60	4.71	2.041	111	11.52	5.51	2.094	189	20.0	17.0	2.6
	0.86	0.43	0.104		1.39	0.72	0.100				
Mar.	10.06	5.21	1.933	73	11.14	5.43	2.044	495	10.7	4.3	5.7
	0.93	0.46	0.102		2.17	0.96	0.107				
Apr.	9.98	5.10	1.956	338	10.34	5.21	1.965	672	3.6	2.2	0.4
	1.41	0.66	0.111		2.78	1.17	0.130				
May	8.78	4.70	1.855	330	10.46	5.41	1.921	734	19.1	15.0	3.5
	1.84	0.79	0.119		2.67	1.14	0.136				
June	9.47	5.18	1.821	239	9.63	5.16	1.848	271	1.7	-0.3	1.5
	1.65	0.73	0.106		2.64	1.20	0.113				
July	9.51	5.20	1.823	554	9.28	5.20	1.780	278	-2.4	0.1	-2.4
	1.81	0.83	0.111		1.72	0.79	0.096				
Aug.	8.79	4.91	1.789	427	10.50	5.63	1.861	442	19.5	14.6	4.0
	1.51	0.78	0.101		2.34	1.12	0.110				
Sep.	8.06	4.46	1.807	179	7.97	4.25	1.890	116	-1.1	-4.6	4.6
	1.36	0.64	0.119		1.62	0.91	0.142				
Oct.	10.65	5.85	1.818	61	14.96	7.47	2.003	27	40.4	27.6	10.2
	1.46	0.64	0.103		1.29	0.40	0.128				
Nov.	14.38	7.38	1.951	72	15.12	7.60	1.991	76	5.2	3.1	2.0
	1.21	0.62	0.098		1.02	0.49	0.096				
Dec.	14.58	7.61	1.919	42	15.69	7.80	2.012	29	7.6	2.5	4.8
	0.93	0.56	0.079		1.01	0.31	0.099				

The comparatively wider scatter of the ratios around the regression in 1994 indicated a slightly weaker correlation between somatic growth and wind velocity than in 1993 (Fig. 7).

There was no apparent correlation between monthly SST data and fish:otolith length ratios. The correspondence between the temperature indices and monthly SL:OL ratios was better in 1993 than in 1994 (Fig. 8). This was in agreement with the better correspondence between wind velocities and SL:OL ratios in 1993. The index minimum in August 1993 coincided with lowest somatic growth, but the wide scatter of the SL:OL ratios over the temperature index range indicated only a weak correlation.
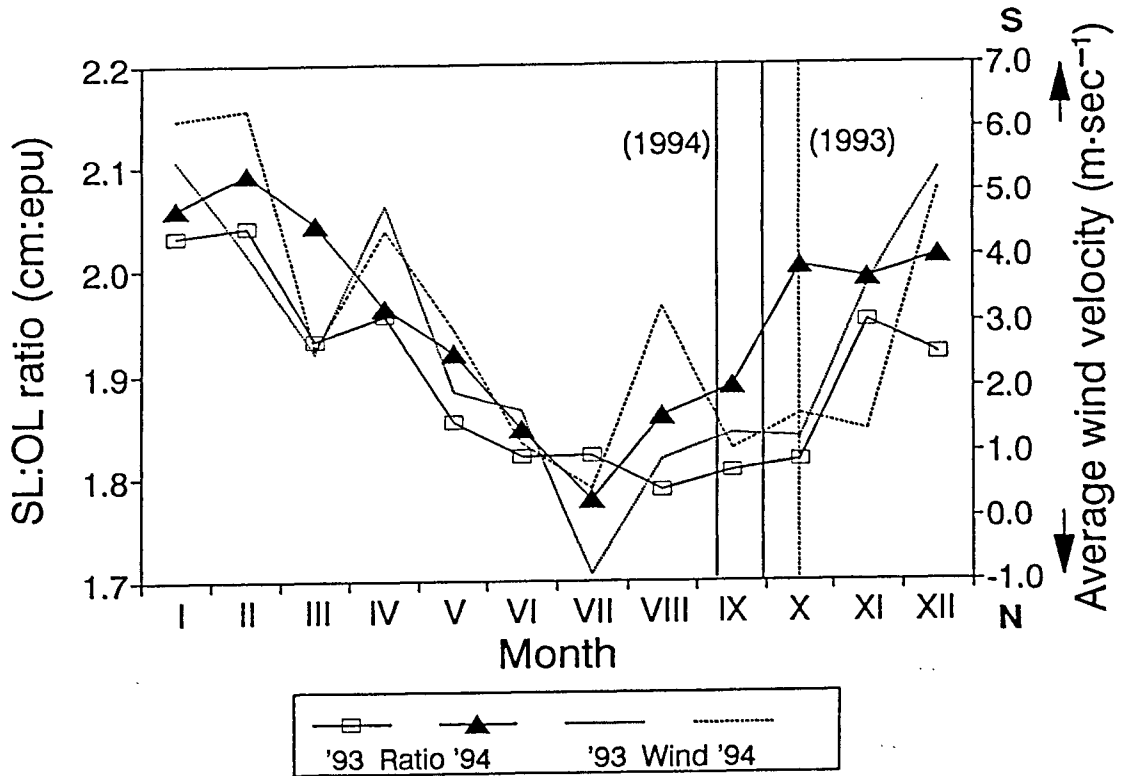
Fig. 6: Monthly changes in SL:OL ratios of pilchard and in average wind velocities in 1993 and 1994 in relation to the time of annulus completion (TC_{50}).
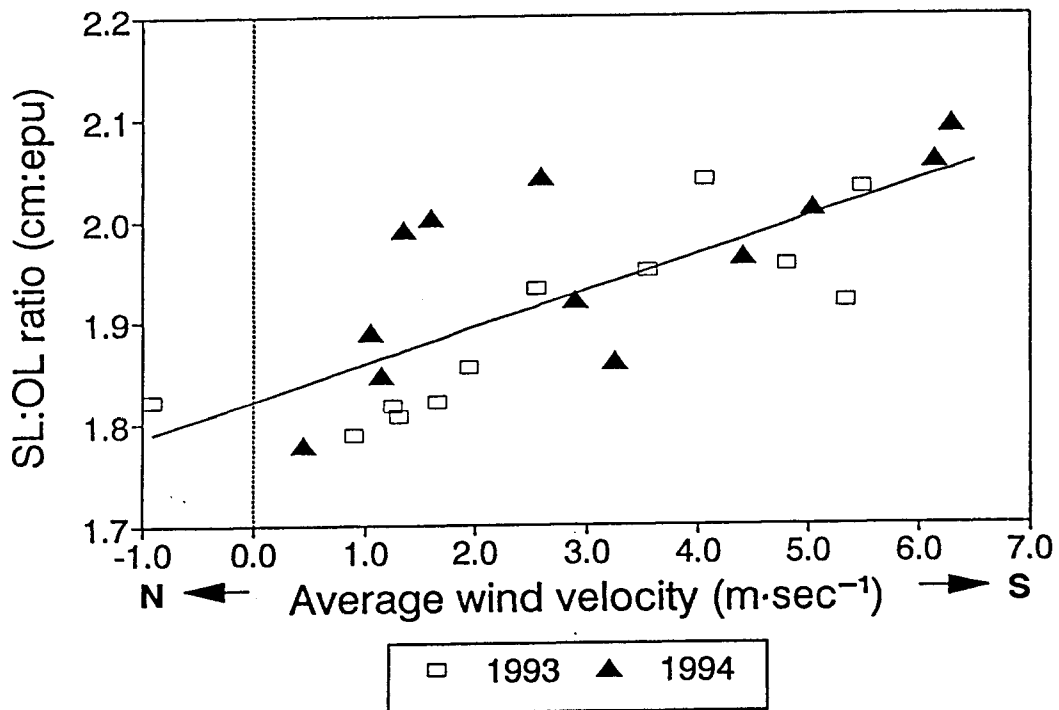

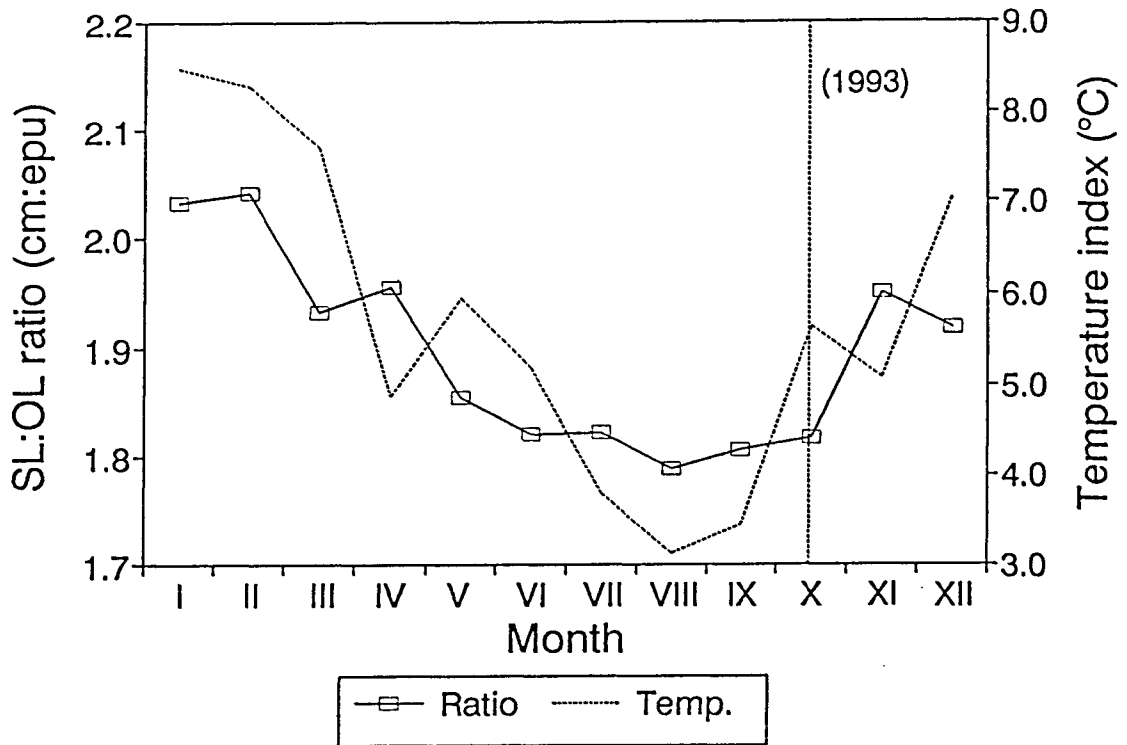Fig. 7: Relationship between average wind velocities and SL:OL ratios of pilchard in 1993 and 1994.

Fig. 8: Monthly changes in SL:OL ratios of pilchard and in surface temperature indices in 1993 in relation to the time of annulus completion (TC_{50}).

DISCUSSION

The first indication of seasonally varying fish-otolith length relationships in Namibian pilchard were given earlier in Thomas (1983). However, he did not explore the full potential of SL:OL ratios. In this study, SL:OL ratios described the seasonal growth pattern without the use of extensive series of length-frequency distributions or age-length keys. Highest somatic growth rates were observed in February and minimal somatic growth during winter in July and August. These results are corroborated by Baird (1970) who found that, during the period 1965-1967, lowest condition factors occurred in July and August. The present results indicate that the annually re-occurring period of minimal somatic growth has not shifted for about 30 years. However, small-scale interannual shifts by about one month in either direction, as shown in this study, can be expected. The similarity between Baird's (1970) work and the present study also confirms that the method presented herein provides a valid indication of seasonal somatic growth variation for all fish species, because it can be validated. Baird (1970) also stated that the highest proportions of hyaline (=translucent) otolith margins were observed in July and August. This could not be confirmed in the present study. If the subjectivity of the judgements of the optical appearance of otolith margins (Hatanaka and Kawahara 1985) is considered, Baird's (1970) data on the state of the margins have to be interpreted with caution. In this study, annuli were only regarded as

complete if bright opaque (=white) material was deposited on the, more or less, hyaline margins. Minimal somatic growth in July or August and the onset of the spawning season probably prior to August (Akkers 1995) suggest that the management reference year should commence on 1 July, rather than on 1 November, in order to determine year-class strengths correctly.

The timing of the TC_{50} in 1994 proved to be difficult because the sample in September indicated an unusually low proportion of otolith specimens with completed annuli. A similarly low proportion in September 1993 suggested that the observation made in 1994 was not a sampling artefact. A change in fishing pattern, life history stage-related migrations of certain age-groups (Crawford et al. 1980), or local concentrations of specific individuals (Armstrong et al. 1987) may have been responsible for the observed low values in September of both years. Alternatively, 100% completion in October of 1994 may have been unusual. Further surveys are necessary for a decision. Annulus completion started first among the small- and medium-sized otolith specimens, which either represented slow growing individuals or late recruits. In those otoliths, annulus deposition at age 1 coincided with minimal somatic growth and not with sexual maturity or spawning. Nevertheless, 50% annulus completion in September or October suggests that annulus formation is not linked to the periods of minimal somatic growth.

The seasonal spawning activity of pilchard indicates that spawning peaks can be expected between August and February of the following year (Crawford 1980, Akkers 1995). Therefore, the timing of the annulus completion appears to be linked to the spawning activity. The length of about 15cm SL at 50% maturity observed in recent years by Armstrong et al. (1989) corresponds well with the mean sizes attained by 1-year-old pilchards during the period October-December (see Table II). As the rapid increase of the somatic growth rate observed between July and October 1994 suggests, otolith annuli in pilchard may not be characterised by narrow but rather by wide daily increments, provided that otolith and somatic growth rates are correlated to some extent (e.g. Karakiri and Westernhagen 1989, Secor and Dean 1989). Recruitment from two peak spawning periods (Akkers 1995) would explain why otolith length distributions became increasingly bimodal after May and June. As bimodality was also observed in the SL:OL ratio in several months during the second half of each year, another two groups of pilchards are likely to exist: one with correlated otolith and somatic growth rates and the other with uncoupled growth rates. This explanation was offered by Wright et al. (1990) who analysed the bimodal length-frequency distribution of salmon (Salmo salar) parr which developed in a single population of 0-group siblings. Thomas (1985), however, showed that spring- and autumn-spawning pilchard in Namibian waters generated two sub-cohorts with apparently similar growth rates. The bimodal SL:OL ratio distributions observed in the present study, indicate that the observations by Thomas (1985) may not be typical for the South African population. It needs to be investigated whether the slower growing group will mature at age 1 and contribute to the forthcoming spawning in the following spring and summer season or not.

The close correspondence between the annual cycle of the SL:OL ratios and the wind velocity pattern was not unexpected, as abundance, migration, reproduction, recruitment success and catch sizes are related to annual wind velocity cycles in a number of sardine species (Belveze and Erzini 1983, Binet 1988, Cury and Fontana 1988, Le Clus 1990a, Littaye-Mariette 1990) and other clupeiform fishes, such as herring (Carruthers 1938) and anchovy (Peterman and Bradford 1987, Wroblewski et al. 1989). As longshore winds are the

main causative factor for upwelling processes off the west coast of South Africa (Nelson and Hutchings 1983), upwelling intensity as a consequence of sustained wind forcing, rather than wind speed *per se*, determines the life history of sardine species (Nehring and Holzlöhner 1982, Cury and Roy 1989, Cabanas *et al.* 1989, Chesney and Alonso-Noval 1989, Roy *et al.* 1989, Roy 1992). Turbulence, the depth of the mixed layer, nutrient enrichment and plankton distribution depend on wind velocity in Ekman-type upwelling systems. As the development of phyto- and zooplankton can be synchronous (Herbland *et al.* 1973 fide: Binet 1988) and rather constant in sustained upwelling areas, sardines find ample food. Sardines are microphagous planktivors (Blaxter and Hunter 1982), and *Sardinops sagax* off South Africa and Namibia is no exception (Davies 1957, Baird 1971, King and MacLeod 1976). Therefore, sardines are often most abundant at frontal divergences where chlorophyll *a* concentrations are highest (Nehring and Holzlöhner 1982). However, the annual cycle of SL:OL ratios corresponds also well with the seasonal variation of the mean zooplankton standing stock in the plume of the southernmost upwelling site off the Cape Peninsula (Andrews and Hutchings 1980), suggesting that the observed seasonal variation of somatic growth is indeed linked to food availability.

The preference of sardines for areas of strong coastal upwelling processes with frontal characteristics is underlined by the number of eggs found there (Chesney and Alonso-Naval 1989). Although the relationship between upwelling intensity and migrations, spawning or recruitment success is well-documented (Crawford 1980, Cury and Roy 1989, Roy *et al.* 1989, Roy 1992), little is known about the correspondence between seasonal changes in upwelling intensity or wind velocity and changes in growth rate. However, as sardines prefer upwelling areas, food as the basic source of growth energy should be unlimited, particularly because their filtering efficiency for very small particles (Lingen 1994) enables them to utilze, for example, flagellates. If food should be limited (Shannon and Field 1985), pilchard will switch seasonally between phyto- and zooplankton as their main food sources (Davies 1957).

Accordingly, somatic growth rates should be high when upwelling intensity and, subsequently, food abundance is high. This study indicates that the period of highest somatic growth coincided with the period of intense upwelling in the study area (Andrews and Hutchings 1980) where horizontal SST gradients of up to 10-11°C can be observed under strong south-easterly conditions (Hutchings et al. 1984). Three semi-permanent upwelling tongues isolated by strong oceanic fronts with SST gradients of 6°C in two kilometers (Andrews and Hutchings 1980, Nelson and Hutchings 1983) characterize the survey area during the main upwelling season from September to March (Andrews and Hutchings 1980). Surface waters respond immediately to changes in wind direction and intensity (Andrews and Hutchings 1980). Seasonal changes in the prevailing wind directions also cause a longshore current reversal (Andrews and Hutchings 1980) which coincides with the migration routes of pilchard recruits (Crawford *et al.* 1980). In the present study, the period of minimal somatic growth in winter coincided with decaying winds and a relaxed upwelling system and, in 1993, possibly also with reversed longshore currents. The chosen survey intervals of one month were too long to pick up the very variable nature of wind on a time scale of days and the intermittent periods of calm (Andrews and Hutchings 1980), which are most important for the rapid development of phytoplankton blooms within days (Barlow 1982, Brown and Hutchings 1987) and, thus, for the food supply of pilchard.

Whereas the influences of temperature and food availability on otolith growth have

been largely investigated (e.g. Karakiri and Westernhagen 1989, Molony and Choat 1990), the effects of wind velocity on otolith growth have rarely been studied (Maillet and Checkley 1991). Negative effects of high wind speeds or storms on otolith growth, biasing estimates of somatic growth, seem to be confined to the very early larval stage (Maillet and Checkley 1991). Therefore, high SL:OL ratios are indeed indicative of higher somatic growth and not of reduced otolith growth. In this study, highest somatic growth rates were paralleled by average wind velocities of 5-6.2m·sec^{-1}. The upwelling scenarios induced by such wind velocities agree with the conditions characteristic of optimal "environmental windows" (Cury and Roy 1989, Roy 1992). Until winds exceed these velocities, not only annual recruitment success and sardine abundances increase (Cury and Roy 1989, Littaye-Mariette 1990), but apparently also somatic growth rates. The spike in the wind speed in 1994 at the onset of the new growing period in spring, when upwelling is most intense (Nelson and Hutchings 1983), may have produced such an optimal "window", because somatic growth continued thereafter, despite decaying winds. The observed close correspondence between wind speeds and SL:OL ratios without an apparent time-lag may be explaine by the following two hypotheses: (1) lags between wind action or upwelling and subsequent somatic and otolith growth responses cannot be detected if they are shorter than a survey interval of one month, and (2) somatic growth rates increase within days after the wind velocity increased (because of the short food chain for sardines) whereas daily increment widths, the second component of otolith growth, respond with lags of two to three weeks at least (Neilson and Geen 1985, Molony and Choat 1990). In the second hypothesis, directly responding somatic growth and lagged otolith growth would result in higher SL:OL ratios corresponding almost directly with changes in wind velocity.

The poor correlation between SST and SL:OL ratios relates to a variety of factors which, most likely, act in combination. Firstly, merchant ships' temperature recordings are not very accurate and not inter-calibrated. Also, *Sardinops sagax* are highly migratory (Armstrong *et al.* 1987) and do not stay continuously within homothermic environments but prefer upwelling areas with fronts marked by steep temperature gradients. Different types of fish behaviour lead to significantly different growth rates across fronts (Brandt 1993). Moreover, increased temperatures are known to increase not only the somatic growth rates in fish (e.g. Coutant and DeAngelis 1983, Bradford and Geen 1992, Fonds *et al.* 1992, Brander 1995), but also growth rate variability (e.g. Coutant and DeAngelis 1983, Houde 1989). Finally, otolith growth rates may exceed somatic growth rate maxima with continuously increasing temperatures (Mosegaard et al. 1988) or, on the contrary, may lag behind somatic growth rates (Moksness *et al.* 1995), depending on the fish species and on whether microincrement width is coupled to the metabolism of the fish (Mosegaard *et al.* 1988) or not (Gauldie and Radtke 1990). A further complication for the interpretation of the effect of SST on the SL:OL ratio is that otolith growth responses may not relate linearly to temperature but may rather be dome-shaped (Ralston 1995). Consequently, Moksness *et al.* (1995) stated that in the marine environment decoupling of otolith and somatic growth caused by temperature alone will be of limited importance. Mendelsohn and Cury (1987) showed that SST was also not sufficient to predict catch sizes of sardines and other pelagic species. Temperature anomalies may also be only of a limited value to predict spawning distribution for pilchard (Le Clus 1990b). SST may rather be regarded·as a surrogate variable (Mendelsohn and Cury 1987) for those oceanographic and biological processes for which wind velocity is the major causative factor. Therefore, monthly SST gradients as relative indicators of upwelling processes corresponded better to the SL:OL ratio changes

than SST itself. Although annual wind speed cycles seem to correspond well with changes in somatic growth rates, upwelling indices (e.g. Roy 1992) and plankton concentrations (Andrews and Hutchings 1980) may correlate even better, because of the expected direct causative relationship.

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