REVIEW OF VARIABILITY IN BIOMASS, GROWTH, AND OTHER CHARACTERISTICS OF ANCHOVY *Engraulis encrasicolus* AND SARDINE *Sardinops sagax* IN THE BENGEULA CURRENT UPWELLING ECOSYSTEM

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INTRODUCTION

The Benguela Current ecosystem is located off the southwest coast of Africa and is divided into northern and southern sub-systems that are separated by the permanent upwelling cell at Lüderitz (26°S). The northern Benguela covers much of Namibia’s coastline and extends from the Angola-Benguela front (usually located around 15°S) to the Lüderitz upwelling cell, whereas the southern Benguela covers the South African west and southwest coasts, and extends from Lüderitz to the Agulhas Bank (Fig. 1). As is the case in the other eastern-boundary upwelling systems (Schwartzlose et al. 1999), the Benguela Current system supports large populations of small pelagic fish, principally anchovy *Engraulis encrasicolus* (formerly known as *E. capensis*; Grant and Bowen 1998) and sardine *Sardinops sagax*, which in turn support moderate to large fisheries. In addition to their economic importance, anchovy and sardine are critically important ecologically, exerting substantial predation pressure on zooplankton and being important prey items of fish, seabirds, and marine mammals. Their occupation of the mid-trophic level niche, and the significant and substantial effects on upwelling ecosystems that fluctuations in small pelagic fish populations may cause, have led to those ecosystems being termed “wasp-waist” ecosystems (Cury et al. 2000).

FISHERIES AND MANAGEMENT

Anchovy and sardine are the primary targets of well-established pelagic fisheries in the Benguela Current system, although the sardinellas (*Sardinella aurita* and *S. maderensis*), and the round herring (*Etrumeus whiteheadi*), are significant contributors to purse-seine catches in the northern and southern Benguela, respectively. Anchovy are reduced to fish meal and oil in industrial-scale factories, whereas sardine are canned or frozen for human consumption or as pet food, used for bait, or reduced to fish meal and oil.

Landings of small pelagics in the Benguela have shown considerable variability over the past five decades, particularly so in the northern Benguela. After peaking at over 1.5 million tons (of primarily sardine) in the late-1960s and sustaining levels of around 0.5 million tons between 1960 and 1980, catches of small pelagic fish in the northern Benguela have dwindled to current levels of less than 50 000 tons (Fig. 2a). The fishery was initially situated off Walvis Bay but expanded to encompass the Namibian coastline from Walvis Bay to Cape Frio during the periods of high catches. Presently however, catches are made to the north of Namibia and in southern Angola to the south of the Angola-Benguela front. Following the collapse of the sardine fishery in the 1970s, a management strategy to reduce the anchovy population was implemented in the belief that it would encourage recovery of the sardine stock, and anchovy catches averaging 170 000t per annum were taken during the 1970s and 1980s (Boyer et al. 2001). However, these decreased substantially during the 1990s and virtually no anchovy is currently caught off Namibia.
In the southern Benguela, sardine was the initial target species of the pelagic fishery and catches peaked at just over 400 000t in 1962. However, catches declined rapidly thereafter, and sardine was replaced to a large extent by anchovy between the mid-1960s and the mid-1990s (Fig. 2b) after small-meshed nets were introduced in the mid-1960s in order to target anchovy. The fishery initially targeted the inshore west coast (principally St Helena Bay to the north of Cape Columbine; see Fig. 1) but expanded southwards as it developed, and the south coast contributed a significant portion of the sardine catch by the 1990s (Beckley and van der Lingen 1999). Currently, almost no sardine is caught off the west coast and catches off the southwest and south coasts account for almost 100% of sardine landings. Additionally, each year since 1997 has seen a successive eastward shift in the mean location of sardine catches (van der Lingen et al. 2005). Sardine catches have increased steadily since the 1990s and are currently >250 000t. Anchovy are caught off the west coast primarily in St Helena Bay, with approximately 70% of fish caught being young of the year (fish of around 6 months old), which results in this fishery being highly dependent on recruitment success. Catches have remained relatively stable through time and have averaged 230 000 tonnes per annum, although peak landings of 600 000t were made in 1987 and 1988 and minimum landings of around 50 000t were taken in 1996 and 1997 (Fig. 2b).

Catches of sardine in the northern Benguela, and of anchovy and sardine in the southern Benguela, are currently regulated via the setting of total allowable catch (TAC) levels based on survey-derived estimates of population size. No TAC is presently set for anchovy in the northern Benguela, although catches may be limited if by-catch of juvenile sardine is high (Boyer and Hampton 2001). Two hydroacoustic surveys per year are used to estimate population size in both systems; in the northern Benguela a survey in autumn (February-April) estimates assesses spawner abundance and distribution, and a survey in spring (October-December) provides estimates of adult biomass and an index of recruitment (Boyer et al. 2001). In the southern Benguela recruitment of anchovy and sardine is estimated during May and spawner biomass in November (Barange et al. 1999). Population assessment models are constructed using survey data and information from commercial catches and are used to set TAC levels. In the northern Benguela the management procedure sets the sardine TAC based on a projected fishing mortality of F = 0.2 (Boyer and Hampton 2001). In the southern Benguela management is via an operational management procedure (OMP) that sets separate TACs for anchovy and sardine; because the two species school together as juveniles (see below), directed fishing for anchovy results in a by-catch of juvenile sardine. Hence catches of the two species cannot be simultaneously maximised, and the OMP represents a trade-off between catches of the two species (Cunningham and Butterworth 2005). The sardine-directed TAC is set at the beginning of the year based on the sardine spawner biomass observed during the survey conducted the previous November. Because information regarding anchovy recruitment strength is not yet available at the beginning of the year, an initial anchovy-directed TAC and an associated sardine by-catch allowance (TAB) is set that assumes recruitment is equal to the median of previous observations and is also “scaled-down” by a factor of 0.85 in case recruitment is below average. After completion of the May recruitment survey the initial anchovy-directed TAC is revised, and may be increased, or not, depending on recruitment strength. The revised anchovy-directed TAC (with associated juvenile sardine TAB) is known as the final TAC, and may be equal to or greater than the initial TAC, but is never less.

**POPULATION VARIABILITY**

Time-series of biomass estimates are available for sardine in both the northern and southern Benguela, and for anchovy in the southern Benguela. Initially these estimates were derived from
virtual population analysis based on catch data (Armstrong et al. 1983 for the southern Benguela; Thomas 1986 for the northern Benguela), but hydroacoustic surveys have been used to estimate population biomass of sardine in the northern Benguela since 1990 (Boyer et al. 2001), and of anchovy and sardine in the southern Benguela since 1984 (Barange et al. 1999). Long-term trends in sardine biomass are consistent with catch fluctuations, and show a substantial decline in the biomass of northern Benguela sardine that occurred during the late-1960s and from which the population has not recovered (Fig. 3a). A decline in the southern Benguela sardine population during the 1960s and a recovery that started in the late 1980s are apparent, with this population currently at a size similar to that estimated before the population collapsed (Fig. 3b). Southern Benguela anchovy have shown moderate interannual fluctuations in population size over most of the time-series, but exceptionally strong recruitment over the period 2000-2003 has resulted in a very large anchovy population in recent years (Fig. 3b).

**LIFE HISTORY STRATEGIES**

Life history strategies of anchovy and sardine in the northern and southern Benguela are broadly similar, but the two sub-systems differ in that spawning and nursery grounds are relatively close to each other in the former but widely separated in the latter.

Egg distributions of anchovy and sardine in the northern Benguela are currently contracted compared to when populations of these species were larger than at present. The main areas of sardine spawning in the northern Benguela were in the vicinity of Walvis Bay in spring and Palgrave Point (to the south of Cape Frio) in summer (Fig. 4c; O’Toole 1977; Le Clus 1990), but the production of eggs in the Walvis Bay region declined substantially following the collapse of the sardine stock in the early 1970s although spawning still occurred in the waters off Palgrave Point (Crawford et al. 1987). Ichthyoplankton surveys conducted in recent years have indicated that sardine egg and larval abundance in the vicinity of Walvis Bay is much lower than around Palgrave Point (Fig. 4e), consistent with the hypothesis that sardine spawning off Walvis Bay has declined in importance or possibly ceased. Anchovy eggs are also now located substantially further north than was the case in 1971/72 (Fig. 4d, f). The nursery grounds for both species occur inshore, and larvae of both species drift south close to the coast and recruit as 0-group fish into the fishery in the region of Walvis Bay, followed by a return migration of juveniles and young adults to the north (Boyer and Hampton 2001).

In the southern Benguela adult anchovy concentrate in spring and early summer over the Agulhas Bank (Fig. 5a) where they spawn (Fig 6a) during a reproductive season that extends from October to March with a major peak in November and December (Hutchings et al. 1998). Eggs and early larvae are transported to the nursery grounds off the west coast via a northwesterly-flowing shelf-edge jet current between the Cape of Good Hope and Cape Columbine (Fig. 1) that links spawning and nursery grounds. Many studies have illustrated the importance of the jet current and associated transport process to anchovy recruitment success (Roy et al. 2001; Huggett et al. 2003; Parada et al. 2003). Anchovy juveniles spend late summer and early winter utilizing the high productivity derived from upwelling off the west coast (Fig. 5b) and grow rapidly before migrating southwards onto the Agulhas Bank to spawn. In contrast to anchovy, southern Benguela sardine spawn year-round, not only over the Agulhas Bank but also occasionally off the west coast (Fig 6b; van der Lingen et al. 2001), with peaks in September/October and February/March (van der Lingen and Huggett 2003). Since 2001 virtually no sardine spawning has been observed off the west coast, the majority of eggs collected during spawner biomass surveys being found over the shelf edge of the central and eastern Agulhas Banks between Cape Agulhas and Port Elizabeth (see Fig. 1; van
der Lingen et al. 2005). The inshore region of the west coast is the principal sardine nursery area, although it has been suggested that the south coast may be an important sardine nursery ground on occasion (e.g. Miller et al. in press).

**BIOLOGY AND ECOLOGY**

1. Trophodynamics

Analysis of stomach contents of anchovy and sardine in the northern Benguela showed good correlation with the ambient plankton, and King and Macleod (1976) concluded that adults of both species were herbivorous and switched from selective feeding on zooplankton as juveniles to non-selective feeding on phytoplankton as adults. The switch between feeding regimes was attributed to a decrease in porosity of the filtering mechanism with increasing fish size. However, those authors assessed relative dietary importance using the volumetric method, which is likely to overestimate the contribution made by phytoplankton because of the low carbon : volume ratio of phytoplankton compared to zooplankton (this is even lower for nitrogen; one unit volume of copepod has almost 8 times as much nitrogen as that contained within one unit volume of phytoplankton; van der Lingen 2002).

An early study of the diet of southern Benguela sardine reported that stomach contents were dominated by phytoplankton (predominantly diatoms), with a mean annual ratio of 2:1 by volume of phytoplankton to zooplankton (Davies 1957). However, that study was subject to the same error as that of King and Macleod (1976), and consequently will have overestimated the contribution made by phytoplankton. More recently a substantial amount of laboratory and field research has been conducted to examine the trophodynamics of the anchovy and sardine in the southern Benguela. Laboratory studies have shown that both species utilise filter-feeding to capture smaller prey and selective particulate-feeding to capture larger prey, although anchovy are primarily particulate-feeders whereas sardine are primarily filter-feeders (James and Findlay 1989; van der Lingen 1994). Anchovy are unable to retain prey items <0.2mm whereas sardine can retain particles as small as 0.01mm, and the size at which anchovy switch from filter- to particulate-feeding is smaller (710-720µm) than the size (1230µm) at which sardine switch feeding mode (Fig. 7a). Anchovy show higher mass-standardized clearance rates than sardine for large (>580µm) food particles whereas sardine show higher mass-standardized clearance rates than anchovy for small food particles (Fig. 7b). Filter-feeding is energetically more expensive than particulate-feeding for anchovy, whereas filter-feeding is energetically cheaper than particulate-feeding for sardine (Fig. 8a; James and Probyn 1989; van der Lingen 1995). Both species are primarily ammoniotelic and show higher absorption efficiencies for nitrogen than carbon, and both species absorb these elements more efficiently from zooplankton than from phytoplankton, but anchovy excrete <50% of their ingested and absorbed nitrogen ration whereas sardine excrete >50% of their ingested and absorbed nitrogen ration (James et al. 1989b; van der Lingen 1998a). When feeding on zooplankton, anchovy regulate their swimming speed (and hence energetic output) according to prey size, with larger zooplankton eliciting higher swimming speeds (Fig. 8b; James et al. 1989a). In contrast, sardine regulate their swimming speed according to prey concentration, with higher concentrations eliciting higher swimming speeds (Fig. 8c-f; van der Lingen 1999). Carbon and nitrogen budget models developed for each species in the southern Benguela indicate that when filter-feeding on phytoplankton or microzooplankton, anchovy only show positive growth when concentrations of these food types are high, and scope for growth is maximized when particulate-feeding on zooplankton (Fig. 9; James et al. 1989a). Sardine show positive growth over a wide range of prey concentrations when filter-feeding on phytoplankton or microzooplankton, or particulate-feeding on...
mesozooplankton and scope for growth is maximized when filter-feeding on high concentrations of microzooplankton (Fig. 9; van der Lingen 1999).

Field studies have demonstrated that both anchovy and sardine in the southern Benguela are omnivorous plantivores, and both obtain the majority of their dietary carbon from zooplankton, although phytoplankton can be an important contributor for both species in localized regions or at particular times of the year. Whereas zooplankton is the dominant food source for both species in the southern Benguela, anchovy and sardine consume different fractions of the zooplankton and appear to partition this resource on the basis of food particle size; anchovy derive the bulk of their carbon from larger (>1.0mm) zooplankton, typically calanoid copepods and euphausiids (Fig. 10; James 1987), whilst sardine derive the bulk of their carbon from smaller (<1.2mm) zooplankton, typically calanoid and cyclopoid copepods and crustacean eggs and nauplii (Fig. 11; van der Lingen 2002). Anchovy and sardine employ different foraging strategies, with anchovy considered to be nocturnal foragers and showing marked feeding periodicity and peak feeding occurring at dusk and dawn. Feeding periodicity appears to be associated with vertical migration, with high feeding activity at night coinciding with shoal dispersal in surface waters, whereas low feeding activity during the day coincides with shoal aggregation and descent into deeper water (Fig. 12f; James 1987). Sardine >25 g wet mass appear to feed continuously and show no peaks in feeding activity throughout the diel cycle (Fig. 12a-e; van der Lingen 1998b), although fish less than 25 g do show a peak in feeding activity at or around sunset. Vertical migration by sardine appears to be highly variable, with fish being observed throughout the water column during the day (in many cases being on or near the bottom but also occasionally at the surface) but forming a scattering layer close to the surface at night.

In no other system where anchovy and sardine co-occur has such a detailed comparison of their trophodynamics been conducted, and the results summarized above provide convincing evidence that sardine and anchovy in the southern Benguela upwelling ecosystem, whilst both primarily zooplanktivorous, are trophically distinct. Sardine is a generalist planktivore, and although capable of ingesting a wide range of prey sizes, appears to have evolved its feeding ecology in order to utilize smaller zooplankton, such as cyclopoid and small calanoid copepods. Anchovy, on the other hand, have evolved a feeding ecology which utilizes larger zooplankton, principally large calanoid copepods and euphausiids. Sardine and anchovy therefore appear to minimize competition by partitioning their food resource according to prey size (van der Lingen 1999). This hypothesis is supported by studies on the size composition of the diet of juvenile sardine and anchovy from presumably mixed shoals (i.e. collected from the same trawl sample), which indicated that sardine juveniles ingested significantly smaller zooplankton prey than did anchovy juveniles (Fig. 13; Louw et al. 1998). In light of the studies described above it seems plausible that zooplankton makes a larger contribution to the diet of anchovy and sardine in the northern Benguela than previously reported. However, given the higher levels of primary production in the northern compared to the southern Benguela it is likely that phytoplankton is more important in the diet of pelagic fish in the northern Benguela.

2. Reproduction

Anchovy and sardine are indeterminate spawners, producing batches of eggs at regular intervals during the spawning season. Southern Benguela anchovy become sexually mature in their first year and have a relative fecundity of around 530 eggs.g\(^{-1}\).spawn. Southern Benguela sardine mature in their second or even third year and have a relative fecundity of around 260 eggs.g\(^{-1}\).spawn. Based on a comparison of egg distribution patterns with concurrently-observed environmental parameters, anchovy and sardine in the northern Benguela select similar spawning habitat (Tjizoo 2005; Stenevik and Kreiner in press), whereas anchovy in the southern Benguela appear to be more
selective than sardine with regard to spawning habitat, with eggs of the former generally found over narrower environmental ranges than those of the latter (Fig. 14; Twatwa et al. 2005).

3. Growth

Data on anchovy and sardine growth rates and their variability in the Benguela are relatively limited, and continuous and consistent time-series of growth rates for the two species are not available. Available sardine growth rate estimates (von Bertalanffy’s $K$ parameter) are illustrated in Figure 15. Immediately apparent are the large gaps in the time series, as well as relatively large differences in the estimates of growth obtained by different researchers.

In the northern Benguela, growth rate estimates are available for the late 1950’s, the 1970’s and early 1980’s, but no estimates of sardine growth in the northern Benguela subsequent to 1982 are available. Nawratil (1961) used scales to examine growth of northern Benguela sardine over the period 1952-1958 (a period of high sardine biomass; see Fig. 3), and derived a growth coefficient ($K$) of 0.362 (the other von Bertalanffy growth formula coefficients being $L_\infty = 29.9$cm and $t_0 = -0.245$ years). Thomas (1985) suggested that this relatively low growth rate was a function of density dependence, as sampling was conducted during a period of relatively low fishing pressure and high biomass. Newman (1970, cited by Baird, 1970), however, found that mortality estimates calculated from Nawratil’s data were unreasonably high, and suggested that Nawratil’s age determination was incorrect. Thomas (1985) used three methods to assess growth of Namibian sardine sampled over the period 1971-1983 (a period of moderate to low sardine biomass in the northern Benguela). Otolith daily increments were used to age larvae and juveniles, while growth of recruits was quantified using length-frequency analyses. Growth of adults was estimated by monitoring the progressive change in mean length of a specific group of fish (identified by means of a natural tag in their otoliths, specifically a distinct, peculiar ring) over time. The results of the three methods were pooled to generate a single growth rate estimate, which is considerably higher than any documented either before or after the work of Thomas. Thomas (1986) suggests that the slower growth rates during the 1950’s that changed to higher growth rates during the 1970’s (after the stock had collapsed) could be attributed to density dependence. Results documented by Wysokinski and Krakus (1977) for sardine collected in Namibia in 1975, however, indicated growth rates comparable to those reported by Baird (1970, 1971) for southern Benguela sardine; substantially slower than those reported by Thomas (1985). Thomas (1985) argues that this is a function of incorrect interpretation of age groups from the length-frequency data. It should be noted, however, that the von Bertalanffy parameters documented by Wysokinski and Krakus (1977) are based on age data collected from otoliths, not length frequency data.

In the southern Benguela, estimates of sardine growth are available for period spanning 1950 to about 1970, but no estimates are available for the period 1970 to 1993. Davies (1958) used scale rings to estimate the ages of sardines collected from commercial landings on South Africa’s west coast during the period 1950-1955. Although Davies did not fit growth curves to the data, estimates of $K$ (0.45) and $L_\infty$ (29.5 cm) were obtained from Davies’ results by Pauly (1978). Baird (1970, 1971) used annuli in otoliths to estimate the age of sardine collected on both the west coast of South Africa over the period 1956-1967 (Baird, 1970) and the east coast extending up into KwaZulu-Natal over the period 1951–1969 (Baird, 1971). Growth rates estimated from the data were relatively low, leading Thomas (1985) to suggest that Baird had misinterpreted false rings as annuli. Recent work by Kerstan (unpublished data) and Durholtz (unpublished data) have provided estimates for the years 1993, 1994, 1996 and 2001, but gaps in the 1990’s/2000’s time series remain to be filled.

More recently Kerstan (pers. comm. in Shin et al. 2004) provided VBGF coefficients of $K = 0.95$, $L_\infty = 21.4$cm and $t_0 = -0.17$ years, most likely for sardine sampled during the 1990s, although
this cannot be confirmed. Growth rate estimates of sardines from the southern Benguela (collected during routine November biomass surveys) have also been calculated from unpublished data recorded from the same samples (otoliths) by Kerstan and Durholtz. These preliminary data have provided estimates for 1993, 1994, 1996 and 2001 (Fig. 15b). Although the K parameters differ slightly between the two readers, the trends in the time series appear to be consistent.

An approach that may have some value when assessing changes in growth rate over time is the monitoring of otolith annual growth zone (AGZ) widths. Because of the relatively close relationship between otolith size and fish size, changes in otolith width can be considered as a proxy for fish somatic growth. Preliminary data collected from sardines sampled during November biomass surveys in the southern Benguela region are illustrated in Figure 16. Data are shown for AGZ’s 2 to 4 (i.e. 2 to 4 year old fish). The width of the first AGZ has been excluded because this is primarily related to the date of hatching, rather than growth. AGZ’s of 5+ year old fish have also been excluded due to data limitations. Apparent in Figure 16 is that growth of 2 year old sardine (i.e. width of the second AGZ) increased dramatically during the late 1980’s, remained relatively constant during the 1990’s, and is showing indications of a marked decrease subsequent to 2000. Surprisingly, the widths of AGZ’s 3 and 4 (corresponding to 3 and 4 year old fish respectively) display a different pattern. AGZ widths appeared to decline into the 1990’s, after which they showed a slight increase until the mid-1990’s. During the period 1995-1997, the growth of 3 and 4 year old sardine appears to have undergone a marked, short-term decrease, recovering by 1999/2000 and showing no signs of the marked decrease in 2001 that was apparent in the widths of AGZ 2. These data are, however, preliminary, and effort is currently being directed at extending the time series to the remainder of the 1990’s and the early 2000’s.

Growth rate estimates for anchovy in the northern Benguela region vary between K = 0.26 (Melo, 1985) and K = 1.1 (Le Clus and Melo, 1981). Wysokinski (1986) documents an intermediate K value of 0.45. Anchovy growth in the southern Benguela appears to be considerably more rapid, with K estimates of 1.586 and 1.37 being reported by Prosch (1986) and Waldron et al. (1989) respectively. Both of these studies, however, were restricted to the earlier life stages of anchovy (larvae and juveniles). The high K values may therefore merely be a function of the higher growth rates of these life stages. In both northern and southern Benguela regions, anchovy growth rate estimates appear to be restricted to the 1980’s.

4. Mortality

Very few estimates of mortality for either sardine or anchovy in the Benguela region are available. Newman and Schulein (1974, cited by Wysokinski and Krakus, 1977) document a natural mortality value of 1.1 for sardine in the northern Benguela over the period 1970-1972. Boyer and Cloete (1996) present sardine total mortality rates ranging from 0.7 to 4.1 for the years 1991 to 1994. More recently, Fossen et al. (2001) applied a simulation model to survey sardine biomass estimates in an attempt to quantify mortality over the period 1991 to 1999. Assuming a constant fishing mortality of 0.2 (Boyer et al. 2001), a total mortality (Z) of 1.44 yielded the best fit of the model to the survey data, implying that an average annual natural mortality (M) of about 1.2 is appropriate. The only estimate of anchovy mortality in the northern Benguela region appear to be that documented by Wysokinski (1986), who reported a value of M = 0.8.

Estimates of southern Benguela sardine mortality that are used in current assessment models are those documented by Cunningham and Butterworth (2004a), based on the assessment of the sardine stock conducted by De Oliveira (2003). Adult sardine mortality is relatively low (M = 0.4), whereas that of juveniles is considerably higher (M = 1.0), approaching that of sardine in the northern Benguela. Annual total mortality rate values for southern Benguela sardine were derived
for the period 1984-2004 by applying the formula suggested by Die and Caddy (1997) that uses von Bertalanfay growth parameters, the average length of fish in the catch and the size at first capture (Fairweather et al. submitted). The two available VBGF parameter sets (Baird and Kerstan) were used and the resultant time-series is shown Figure 17. Total mortality estimates derived from an Ecopath with Ecosim (EwE) mass-balanced model of trophic flow through the southern Benguela ecosystem (Shannon et al. 2003) are also shown in Figure 17. The Z values derived using Kerstan’s VBGF are substantially higher than the other two time-series for the period 1875-1995, but are more similar for the rest of the time-series, with values ranging (across all three datasets) from 0.5 to 1.3. For southern Benguela anchovy a value of M = 0.9 for both adults and juveniles and obtained from the assessment conducted by De Oliveira (2003) is employed in the assessment model (Cunningham and Butterworth 2004b).

5. Condition factor

Decadal-scale changes in morphometrically-derived (i.e. from length mass relationships) condition factor (CF) of both northern and southern Benguela sardine have been documented. Le Clus (1987) computed a CF anomaly for northern Benguela sardine over the period 1953-1984 and found a generally steady increase in this parameter through time, although low values were observed in 1963, 1965 and 1977 (Fig. 18a). Kreiner et al. (2001) used general linear modelling (GLM) to examine interannual variability in sardine CF in both the northern and the southern Benguela over the period 1984-1999, and reported that whereas CF in northern Benguela sardine remained relatively stable over time, that for southern Benguela sardine declined steadily (Fig. 17b). GLM analysis of a longer time-series (1953-2004) of CF for southern Benguela sardine showed a dome-shaped pattern through time, being initially (1953-71) low and relatively stable, then (1972-88) high but unstable, and low and continuously declining thereafter (1989-2004; Fig. 18b; van der Lingen et al. submitted). Hence sardine condition factor shows an inverse relationship to population size for both northern and southern Benguela stocks, being higher at low population size and lower at high population size. This inverse relationship provides convincing evidence for density dependence (Kreiner et al. 2001; van der Lingen et al. submitted).

6. Standardized ovary mass and length at maturity

A dome-shaped pattern (similar to that shown by the CF time-series) in standardized ovary mass (SOM) of southern Benguela sardine is apparent for the period 1953-2004. Standardized ovary mass was low over the period 1965-63 and increased rapidly thereafter to peak over the period 1972-82. A very rapid decline then followed until 1987, after which SOM has remained roughly stable (albeit with some large variation e.g. 1994; Fig. 19a; van der Lingen et al. submitted). This change in SOM has been accompanied by a change in length at maturity; Armstrong et al. (1989) documented a trend of decreasing length at sexual maturity over the period 1953-87, and attributed this to one or more of the following: density-dependence, a declining age structure, environmental change, and enhanced natural selection for early maturity under prolonged high rates of fishing mortality. Updating of this analysis has shown that length at maturity of southern Benguela sardine has increased in recent years (Fig 19b; Fairweather et al. submitted), which supports the contention of density dependence. Similarly, a decrease in the age at maturity of northern Benguela sardine following the stock collapse was reported by Thomas (1986), who also attributed this to density dependence.
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