

Density-dependent changes in reproductive parameters and condition of southern Benguela sardine *Sardinops sagax*

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The sardine *Sardinops sagax* population in the southern Benguela has undergone substantial fluctuations in size over the past 50 years, collapsing from an apparently large population in the 1950s to low levels in the mid-1960s, remaining low for the next two decades, and recovering from the late 1980s to a population size that is now similar to or larger than that which occurred during the 1950s. Marked changes in condition and reproductive parameters of sardine have also occurred during this period; condition and standardised gonad mass are higher and length-at-maturity is lower at low population size compared with high population size. The correspondence between the temporal patterns in condition,

reproductive parameters and population size are strongly suggestive of density-dependence, and indicate a compensatory response arising from reduced intra-specific competition. This is likely to have resulted from greater per capita food intake, improved body condition and hence faster growth, thus enabling fish to achieve maturation at a presumably younger age and smaller size. Biological parameters did not vary in or out of phase with time-series of sea surface temperature in the southern Benguela, weakening the hypothesis of environmentally mediated changes in these parameters and hence providing support for the hypothesis of a direct density-dependent response by sardine.

Keywords: condition, density dependence, sardine, *Sardinops sagax*, sexual maturity, southern Benguela

Introduction

Large multi-decadal fluctuations in population size are a common characteristic exhibited by small pelagic fish in upwelling and other ecosystems. Schwartzlose *et al.* (1999) showed that catches of sardine and anchovy from the Benguela, California, Canary and Humboldt currents, and off Japan and Australia, exhibited large fluctuations and were seldom maximal at the same time, and that periods of high catches of one species and low catches of the other were followed by periods of reversed species dominance. Additionally, such fluctuations in population size and changes in species dominance appear to have occurred in pre-historic times in the absence of fishing (Shackleton 1987, Baumgartner *et al.* 1996).

These long-term changes in population size of sardine and anchovy are considered driven by inter-decadal variability in climate (Klyashtorin 2001, Lehodey *et al.* 2006), which provides alternating environmental conditions that favour anchovy over sardine and *vice versa*. The processes underlying these environmental alternations are not yet well understood, but non-environmental factors linked to the dynamics of these small pelagic species and/or to other biological components of the ecosystem cannot be totally excluded as forcing factors.

The sardine *Sardinops sagax* population in the southern Benguela upwelling ecosystems has shown substantial growth over the past 20 years, attaining a size similar to or larger than that which occurred during the period 1955–1963, when sardine catches by South Africa's pelagic fishery were at their highest (Figure 1a). Sardine was the target species that led to development of the pelagic fishery in the 1940s (Beckley and van der Lingen 1999). Anchovy *Engraulis encrasicolus* became the mainstay of the pelagic fishery between 1974 and 1995 but sardine catches have since shown a steady increase.

Armstrong *et al.* (1989) reported a progressive increase in standardised mean ovary mass of southern Benguela sardine over the period 1953–1987, which equates to a decreased length at sexual maturity at low population size and was attributed to one or more of the following: a declining age structure of sampled fish, environmental change, enhanced natural selection for early maturity under prolonged high rates of fishing mortality, and density-dependence. The sardine fishery initially targeted large fish, with >90% of the fish caught during the 1950s being 20cm or longer (Armstrong 1986), which may have positively biased the length-at-maturity estimated from catch samples.

Whereas environmental forcing may impact on sardine biological processes (including maturation), Armstrong *et al.* (1989) found no relationship between sea surface temperature (SST) and sardine maturity. The imposition of sustained high fishing mortality on large sardine may have led to enhanced natural selection for early maturity in remaining smaller fish. Density-dependent effects on biological parameters of small pelagic fish may also impact on egg production and hence recruitment success, although the issue of functional stock-recruitment relationships is still debated (C Mullon, IRD, pers. comm.).

Density-dependent variability in growth rate (Thomas 1985), condition (Le Clus 1987, Kreiner *et al.* 2001) and mortality rate (Fossen *et al.* 2001) have been reported or hypothesised for sardine in both the northern and southern Benguela systems. Armstrong *et al.* (1989, p 100) suggest that the evidence for density-dependence rests '...solely upon the observation that length-at-maturity declined over a period which also saw the collapse of the stock. The rapid decline in pilchard [=sardine] abundance during the mid 1960s should have been accompanied by an immediate response in length-at-maturity if fish density was the controlling factor'.

If density-dependence does impact on sardine biological parameters, then it could be hypothesised that condition and standardised ovary mass should have decreased, and size-at-sexual maturity increased, over the recent period of recovery of the sardine population in the southern Benguela. The objective of this paper is to test this hypothesis

by examining data on sardine reproductive parameters over a longer time period than was available to Armstrong *et al.* (1989), using a similar approach and methods to that used by those authors and adding an analysis of the condition factor. In addition, we evaluate the hypothesis that environmental change was linked to changes in sardine biological parameters, through the incorporation of an SST time-series into this analysis.

Material and Methods

Biomass and SST

Estimates of sardine population size were derived from virtual population analysis (VPA) for the period 1950–1982 (Butterworth 1983) and from hydroacoustic surveys conducted since 1984 (Figure 1b). The 1983 value was estimated by linear interpolation, although there was no intercalibration between the two series. This reconstructed biomass time-series was contrasted with the extended reconstructed sea surface temperature (ERSST) (Smith and Reynolds 2004) for the $2^\circ \times 2^\circ$ area centred on 33°S and 18°E . ERSST was constructed using the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST data and improved statistical methods that allow stable reconstruction using sparse data. The selected area is the highest in density observation in South Africa and covers the West Coast upwelling area, where SSTs are inversely correlated to Ekman transport (Blanke *et al.* 2005).

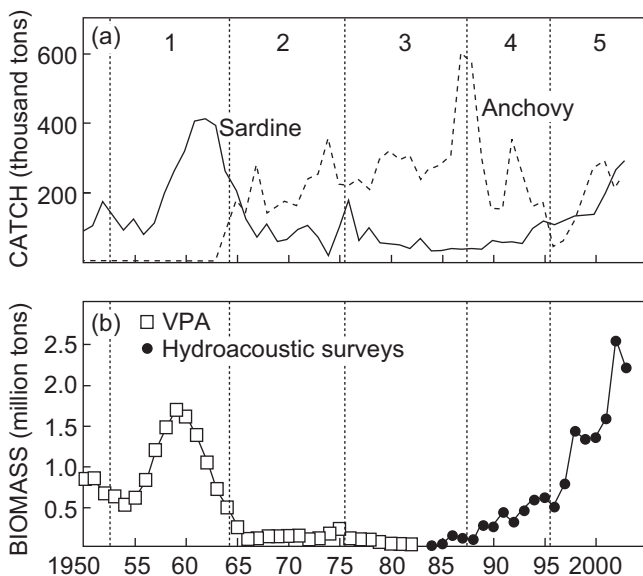


Figure 1: (a) Catches of sardine and anchovy taken by South Africa's pelagic fishery over the period 1950–2003. Vertical lines indicate Periods 1–5 differing in population levels (see text); (b) estimates of sardine biomass in the southern Benguela from estimates derived from virtual population analysis (VPA) and taken from Butterworth (1983), and those derived from hydroacoustic surveys and updated from Barange *et al.* (1999). Note that the two time-series are not strictly comparable because different methods were used to estimate biomass, but they are plotted on the same y-axis to illustrate general population trends

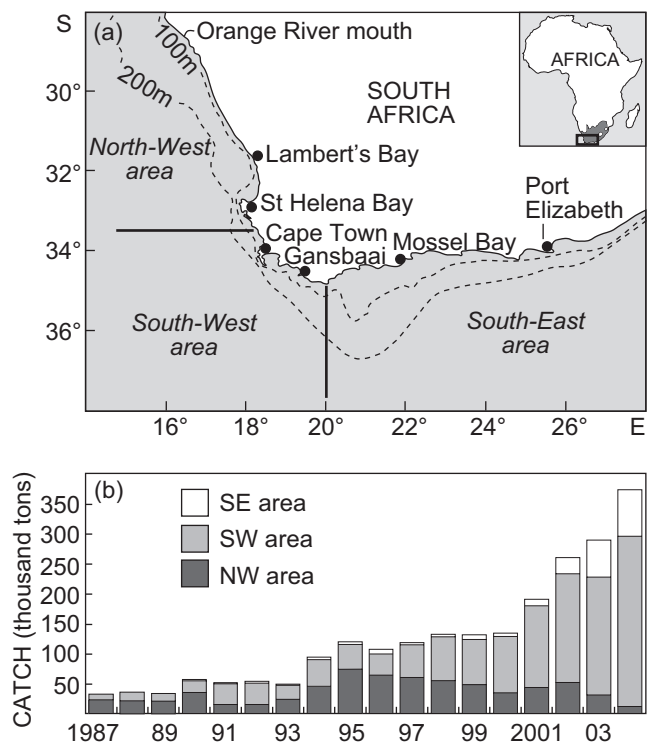


Figure 2: (a) Map of the south-western coast of South Africa showing the division of the coastline into three areas; and (b) annual landings of sardine caught in these areas from 1987 to 2004

Biological data

Biological data were collected from sardine sampled at commercial landing sites over a 52-year period (1953–2004), with 25–50 fish sampled per landing. Data from sardine commercial catches made during January–August were used for condition factor analysis and were not disaggregated by sex. Following Armstrong *et al.* (1989), data for reproductive parameters were limited to female fish sampled between January and March. Although sardine spawn throughout the year, their peak reproductive period extends between September/October and February/March (van der Lingen and Huggett 2003). Combined with the fact that a reduction in pelagic fishing operations occurs during the last quarter of the year, this means that January–March is the only period of intense sardine spawning over which samples have been available from commercial catches.

Data collected from each sample included landing date (only Year and Month variables were used), capture location (defined as Area; see Figure 2a), fish caudal length (L_c , cm; equivalent to standard length), sex (immature, male or female), gonad stage (from 1 to 10; see Table 1), ovary mass (g) and wet body mass (g). Data from catches made off both the South and West coasts were used, although Armstrong *et al.* (1989) used only data from West Coast catches. However, hydroacoustic surveys show that a substantial portion of the sardine population is found off the South Coast (Barange *et al.* 1999), with the bulk of the population found to the east of Cape Agulhas in recent

years (van der Lingen *et al.* 2005, Fairweather *et al.* 2006). This eastward shift in sardine distribution has been corroborated by recent substantial increases in sardine catches in the South-East area (Figure 2b).

Condition factor

Condition factor (CF) of each sardine was calculated using the expression:

$$CF = \text{Observed wet body mass} / \text{expected wet body mass} \quad (1)$$

Expected wet body mass was estimated from a length-mass relationship derived by fitting non-linear regressions to the untransformed wet body mass and caudal length (L_c) data using Marquardt's (1963) iterative algorithm:

$$\text{Wet body mass} = a L_c^b \quad (2)$$

where a and b are estimated parameters. CF values <0.5 or >2 were considered invalid and discarded. The numbers of individual sardine sampled from commercial landings during January–August and used to derive annual mean CF values are given in Table 2.

A general linear model (GLM) was used to examine temporal and spatial trends in CF, where CF was set as the dependent variable, and Year, Month and Area as independent categorical predictors and net standardised gonad mass (SGMn) (see below) as a covariate, and with all two-level interaction terms between these predictors. This primary

Table 1: Gonad maturity stages for the South African sardine *Sardinops sagax* (from Davies 1956)

Stage	Description	Approximate mass (g)	
		Female	Male
Stage 1	Ovaries either immature or inactive, less than half the length of the body cavity, cylindrical but thin, pale pink in colour or transparent. Testis flat and leaf-like, pink or transparent	0.2–5.5	0.2–4.5
Stage 2	Ovaries inactive generally, but with the beginnings of enlargement taking place. Slight elongation, thickening and darker colouration; mainly translucent pinkish yellow. Testis beginning to thicken and become elongated with slight white colouration	2–7	2–6
Stage 3	Ovaries elongated and filling over half the body cavity. Colour opaque yellow with discrete pigmented ova present. Testis elongated, thickened and filling over half the body cavity	3–17	2–15
Stage 4	Ovaries elongated, distended, filling approximately two-thirds of the body cavity. Colour bright yellow, gonads vascular, ova discrete and becoming transparent at posterior end. Testis further enlarged, filling approximately two-thirds of the body cavity. Colour opaque white; milkiness apparent at posterior end	6–20	5–18
Stage 5	Ovaries at maximum size, almost filling body cavity. Colour darker yellow, no longer opaque but semi-transparent due to even dispersal of ripe ova throughout the gonad. Testis at maximum size, almost filling the body cavity. Colour opaque white; posterior half of gonad milky	10–30	9–28
Stage 6	Same as Stage 5, except that perhaps greater enlargement has taken place and pressure on the belly causes extrusion of ova or milt through the vent. Fish in this condition almost in the act of spawning	12–35	10–30
Stage 7	Ovaries elongated, but flat due to recent evacuation of ova, very bloodshot, sometimes gelatinous. Testis elongated, flat, strap-like and very bloodshot	1–7	1–6
Stage 8	Ovaries much like those of previous stage, but obvious signs of recovery and reversion to Stage 1, i.e. further shrinkage, less bloodshot in appearance and beginning to become transparent. Testis — as for ovaries	2–7	2–6
Stage 9	Ovaries showing signs of having been recently spent, recovery to Stage 1 apparent, nevertheless, evident that reversion to Stage 1 is only temporary as signs of 'making' to Stage 3 already evident. Testis — as for ovaries	4–10	3–8
Stage 10	Ovaries still showing signs of having been recently spent, but evidence that gonads are about to become active almost immediately by 'making' to Stage 3. Testis — as for ovaries	2–5	2–4

Table 2: Numbers of sardine (n) sampled from commercial landings for GLM analysis of condition factor (CF, all fish) and net standardised gonad mass (SGMn, female and immature fish only) during different periods of the year

Year	Variable		
	CF		SGMn
	n (Jan.–May)	n (Jun.–Aug.)	n (Jan.–Mar.)
1953	1 714	742	393
1954	2 078	199	411
1955	0	0	0
1956	1 521	1 061	331
1957	2 977	1 393	753
1958	2 842	3 000	642
1959	1 801	1 895	227
1960	2 924	2 291	338
1961	3 037	896	1 177
1962	3 762	199	1 062
1963	2 537	1 249	540
1964	2 956	596	854
1965	3 110	1 343	871
1966	3 041	597	686
1967	831	240	111
1968	2 096	648	575
1969	1 260	187	317
1970	687	48	242
1971	1 190	297	423
1972	1 391	229	387
1973	1 688	0	657
1974	659	0	257
1975	2 874	263	960
1976	2 808	131	714
1977	544	79	95
1978	1 923	86	390
1979	2 044	0	552
1980	1 618	36	534
1981	1 833	5	538
1982	1 580	633	292
1983	2 270	84	768
1984	2 661	253	561
1985	3 016	1 446	740
1986	2 625	1 458	612
1987	2 477	1 046	745
1988	2 621	1 853	464
1989	3 882	1 621	756
1990	4 431	1 743	765
1991	3 771	1 145	623
1992	869	398	220
1993	471	49	177
1994	200	148	72
1995	1 004	1 143	0
1996	2 324	1 275	537
1997	2 383	1 579	370
1998	1 840	1 591	384
1999	1 773	1 447	241
2000	822	848	178
2001	1 123	773	322
2002	1 024	1 149	226
2003	1 647	850	452
2004	1 375	875	352
Total	103 935	41 117	24 894

GLM was fitted using SAS software (SAS Institute Inc. 1988), and included all significant predictors and their interactions. A general additive model (GAM), with the span of the LOESS local regression function set to the conservative value of 2, was applied to detect possible non-linearity between CF and the covariate SGMn, and this was incorporated in all further analyses.

A stepwise procedure was then used to remove non-significant terms from the primary GLM, or those terms or interactions that were significant, but their removal resulted in a small decrease (<7%) of the explained variance (based on Type III SS values). The resulting 'simplified' model avoids over-parameterisation while still explaining as much of the variance in CF as possible (based on r^2 values). This approach is also justified by the usual high degree of auto-correlation in the observations. Normality in the distribution of residuals of the simplified model was checked by visual examination of residual plots.

Because the CF data were not equally represented for all three categorical predictors (i.e. the dataset was unbalanced), least-squares estimators of marginal means of CF were derived. Least-squares (LS) means are predicted population margins and estimate the marginal means over a balanced population (SAS Institute Inc. 1988). Nonetheless, on account of significant interactions between Year, Month and Area, LS mean values of Year — which is the factor of major interest for this study — could not be estimated for all years. To overcome this difficulty and to limit the number of individual interaction terms that would explain >7% of the variance, LS mean values of CF by Year, Month and Area were derived separately for two seasons: January–May (high condition) and June–August (low condition).

A similar modelling exercise was also conducted where the Year effect was removed and replaced with two factors that could explain temporal changes in CF: sardine biomass and ERSST. These two continuous variables were categorised into four classes in order to be able to track possible non-linear effects, and to derive primary and simplified GLMs, as described above.

Net standardised gonad mass

Net standardised gonad mass (SGMn) was calculated for each immature and female fish using the expression:

$$\text{SGMn} = W \times 1000 / aL_c^b \quad (3)$$

where W is ovary mass (g) and L_c is caudal length (cm) and a and b are the parameters of the length-weight relationship (Equation 2).

A GAM was first applied to detect possible non-linearity between SGMn and the covariate L_c , and this GAM was incorporated in all further analyses. Then a GLM was used to examine temporal and spatial trends in SGMn in a similar way as for CF. For this analysis, SGMn was limited to non-hydrated female and immature fish, because gonad weight increases massively at hydration, which could bias the analysis; all female with Stage 6 gonads and/or with SGMn >20 were considered hydrated. The primary model set the

individual log-transformed SGMn as the dependent variable, and Year, Month and Area as independent categorical predictors and L_c as a covariate, and with all two-level interaction terms between these predictors. The incorporation of L_c in the models compensates for a possible bias in SGMn due to allometric growth. The numbers of immature and female sardine sampled from commercial landings during January–March and used to derive LS mean SGMn values are given in Table 2.

Length-at-maturity

Maturity ogives for five periods within the time-series: 1953–1964 (Period 1), 1965–1975 (Period 2), 1976–1987 (Period 3), 1988–1995 (Period 4) and 1996–2004 (Period 5) were used to assess length-at-maturity. These periods were chosen to represent different sardine biomass levels and, except for the latter period, correspond to those used in previous analyses (Armstrong *et al.* 1989, Akkers and Melo 1996). The first covers the pre-collapse period; the second and third periods when the sardine population remained at low levels; and the fourth a recovery period that led to the fifth period of high biomass. Maturity ogives were plotted for each period under the assumption that fish with a SGMn >0.25 were mature (Armstrong *et al.* 1989). Because this value was proposed as a guideline for comparing gonad masses during different time periods and is not related to well defined changes in the histological structure of the ovary (Armstrong *et al.* 1989), a sensitivity analysis was conducting by also plotting ogives for each of the periods based on SGMn values of 0.2 and 0.3. The numbers of immature and female fish sampled from commercial landings and used for the construction of maturity ogives are given in Table 3; note that hydrated fish (i.e. gonad Stage 6 and/or SGMn >20) were not excluded from this analysis, but fish <12cm were because almost all fish of this size had very low SGMn values.

Maturity ogives were plotted by calculating the predicted proportion of fish mature (\hat{p}_i) at each 0.5cm length-class (L_i) from the logistic:

$$\hat{p}_i = (1 + \exp(-(L_i - L_{50})/\delta))^{-1} \tag{4}$$

where L_{50} is length-at-50% maturity and δ is the steepness of the ogive. The likelihood (L) to be minimised is:

$$-\ln L = -\left[\sum m_i \ln \left(\frac{\hat{p}_i}{1 - \hat{p}_i} \right) + n_i \ln (1 - \hat{p}_i) \right] \tag{5}$$

where m_i is the total number of mature females and n_i the number of immature females sampled in each length-class respectively. Parameter variability was calculated using conditioned parametric bootstrapping. The pseudo-data were assumed to be binomially distributed. For each bootstrap iteration, the pseudo-number of mature fish in each size-class was a random binomial variate generated from the original number of fish sampled in each size-class, and the model predicted the proportion of mature fish in that size-class. Confidence intervals were constructed from the

Table 3: Numbers (n) of immature and female sardine (greater than or equal to 12.0cm L_c) collected from commercial landings made during January–March, which were used for construction of the maturity ogives for each of the five periods (total n = 31 973)

Year	n	Year	n
1953	512	1979	666
1954	452	1980	752
1955	0	1981	684
1956	391	1982	443
1957	1 022	1983	885
1958	852	1984	715
1959	458	1985	872
1960	848	1986	751
1961	1 301	1987	808
1962	1 526	1988	620
1963	804	1989	859
1964	1 286	1990	1122
1965	1 077	1991	797
1966	700	1992	284
1967	90	1993	211
1968	684	1994	74
1969	386	1995	0
1970	269	1996	633
1971	508	1997	598
1972	538	1998	535
1973	722	1999	352
1974	266	2000	204
1975	794	2001	343
1976	1 142	2002	297
1977	245	2003	593
1978	536	2004	466

sorted bootstrap results using the percentile method outlined by Buckland (1984).

To investigate the null hypothesis that there is no difference between L_{50} for all pairs of periods, each \hat{p}_i was simultaneously minimised by minimising the sum of their respective likelihoods (AJ Booth, Rhodes University, pers. comm.). A lambda (Δ) value was used to assess the level of significant difference (using a Chi-squared distribution table) and was calculated as follows:

$$\Delta = \ln L(\text{full}) - \ln L(\text{reduced}) \tag{6}$$

where $\ln L(\text{full})$ is the value for the simultaneously minimised sum of the likelihoods when the values for L_{50} are separate for each period, and $\ln L(\text{reduced})$ is the value for the simultaneously minimised sum of the likelihoods when the L_{50} value for Period a is set equal to that for Period b and the likelihood is minimised only on the L_{50} value for Period a in addition to the two separate δ values.

Results

Condition factor

The parameters of the length-mass relationship derived from all available observations (n = 161 600) regardless of the sex, area or season were $a = 1.1639 \times 10^{-5}$ and $b = 3.03155$, indicating a weak allometry in growth ($b \neq 3$; $p < 0.001$). These parameters were used to estimate the

Table 4: ANOVA table for simplified GLMs for sardine CF in the high condition season (January–May), showing predictors used in the models and their associated statistical indices for (a) the model including Year as a factor (see Equation 7) and (b) the model where Biomass replaces Year (see Equation 9)

Source	df	SS	MS	F	p	r ²
<i>(a) Model including Year as a factor</i>						
Model	56	485.7	8.7	1 109.4	<0.0001	0.37
Error	103 878	812	0.008			
Corrected total	103 934	1 297.7				
Year	50	285.6	5.7	730.6	<0.0001	
Area	2	95.1	47.6	6 083.4	<0.0001	
Sex	3	40.1	13.4	1 710.4	<0.0001	
SGMn	1	58.2	58.2	7 440.8	<0.0001	
<i>(b) Model — Biomass replaces Year</i>						
Model	9	286.7	31.859157	3 275.09	<0.0001	0.22
Error	103 925	1 011.0	0.01			
Corrected total	103 934	1 297.7				
Biomass	3	86.6	28.9	2 969.0	<0.0001	
Area	2	70.6	35.3	3 630.8	<0.0001	
Sex	3	33.8	11.3	1 158.8	<0.0001	
SGMn	1	81.5	81.5	8 382.2	<0.0001	

CF of sardine in the two different seasons, which explains why the average CF value for a given season is not equal to 1.

The GAM model showed a perfect linear relationship between CF and SGMn using a span value of 2, although the conventional value of 0.75 resulted in a curvilinear relationship, with a reversion of the positive relationship for the range of SGMn >15–17. The non-linear range of the function (SGMn >15) included only a small proportion of the sample for January–May (303 of 103 935) and June–August (138 of 41 117), thus the non-linearity was ignored. The simplified model for CF during the high condition season (January–May) was:

$$CF_{\text{Year, Area, Sex, } i} = m + a_{\text{Year}} + b_{\text{Area}} + c_{\text{Sex}} + d\text{SGMn} + \varepsilon_{\text{Year, Area, Sex, } i} \quad (7)$$

where m is a constant, and a , b , c and d parameters depending on the main effects related to the factors Year, Area, Sex and to the covariate SGMn respectively, and ε is the error term assumed to be normally distributed with a zero mean (i denotes individual observations). This simplified model (Equation 7) had $df = 56$ and explained 37% of the observed variance in CF (Table 4a) compared with $df = 306$ and 43% for the primary model.

The simplified model for CF during the low condition season (June–August) was:

$$CF_{\text{Year, Area, Month, } i} = m + a_{\text{Year}} + b_{\text{Area}} + c_{\text{Month}} + d\text{SGMn} + \varepsilon_{\text{Year, Area, Month, } i} \quad (8)$$

This model (8) had $df = 52$ and explained 40% of the observed variance in CF (Table 5a) compared to $df = 246$ and 47% for the primary model.

The Year LS means of both seasonal models did not show a significant linear trend ($p > 0.05$) through time, but appeared dome-shaped with the highest values during the

periods of low biomass abundance (Figure 3). After removing the Year factor and incorporating the Biomass and ERSST categorical factors (four numerically balanced categories for each), the temporal effect was captured by Biomass, which had a negative and significant effect in the simplified models for the high (January–May; Equation 9) and low (June–August; Equation 10) condition seasons respectively:

$$CF_{\text{Biomass, Area, Sex, } i} = m + a_{\text{Biomass}} + b_{\text{Area}} + c_{\text{Sex}} + d\text{SGMn} + \varepsilon_{\text{Biomass, Area, Sex}} \quad (9)$$

$$CF_{\text{Biomass, Area, } i} = m + a_{\text{Biomass}} + b_{\text{Area}} + c\text{SGMn} + \varepsilon_{\text{Biomass, Area}} \quad (10)$$

where a is a parameter depending on the main effect related to the factor Biomass, and the other parameters follow the notation used earlier. The simplified model (Equation 9) had $df = 9$ and explained 22% of the observed variance in CF (Table 4b, Figure 4) compared with $df = 40$ and 24% for the primary model. The categorical variable ERSST had a significant but very low contribution (<0.03 that explained by the factor Biomass; primary model not shown) and that variable was therefore removed from the simplified model.

Similarly, the simplified model (Equation 10) had $df = 6$ and explained 25% of the observed variance in CF (Table 5b, Figure 4) compared with $df = 22$ and 31% for the primary model. Again, the categorical factor ERSST had a significant but extremely low contribution in the primary model (only explaining almost three orders of magnitude less than Biomass), and adding interactions with this factor did not improve the model. Therefore, ERSST and Month were not retained in the simplified model.

Plots of monthly LS mean CF in Figure 5 show a clear seasonal pattern, with highest values from January to May and lowest from June to August. Although these corresponding LS mean values were derived from two different

Table 5: ANOVA table for simplified GLMs for sardine CF in the low condition season (June–August), showing predictors used in the model and their associated statistical indices for (a) the model including Year as a factor (see Equation 8) and (b) the model where Biomass replaces Year (see Equation 10)

Source	df	SS	MS	F	p	r ²
<i>(a) Model including Year as a factor</i>						
Model	52	150.7	2.9	529.8	<0.0001	0.40
Error	41 064	224.7	0.005			
Corrected total	41 116	375.4				
Year	47	59.0	1.3	229.3	<0.0001	
Area	2	37.8	18.9	3 450.9	<0.0001	
Month	2	8.8	4.4	806.4	<0.0001	
SGMn	1	39.1	39.1	7 143	<0.0001	
<i>(b) Model — Biomass replaces Year</i>						
Model	6	97.8	16.3	2 413.4	<0.0001	0.26
Error	41 110	277.6	0.007			
Corrected total	41 116	375.4				
Biomass	3	27.2	9.1	1 342.5	<0.0001	
Area	2	30.9	15.5	2 290.9	<0.0001	
SGMn	1	46.8	46.8	6 932.6	<0.0001	

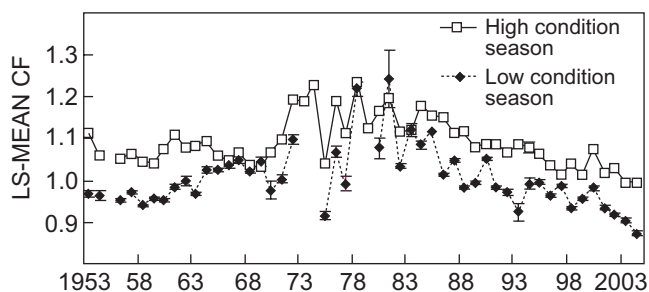


Figure 3: Yearly least-square (LS) means of sardine condition factor (CF) from 1953 to 2004 for the high condition season (January–May) and low condition season (June–August) from GLMs (Equations 7 and 8 respectively). Error bars denote SE

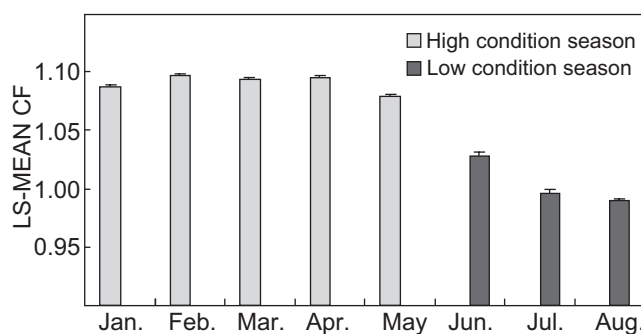


Figure 5: Monthly least-square (LS) means of sardine condition factor (CF) for the high condition season (January–May) and low condition season (June–August) from GLMs (Equations 7 and 8 respectively). Error bars denote SE

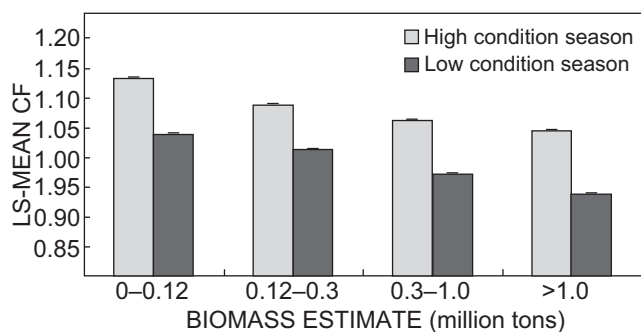


Figure 4: Least-square (LS) means of sardine condition factor (CF) by biomass category for the high condition season (January–May) and low condition season (June–August) from GLMs (Equations 9 and 10 respectively). Error bars denote SE

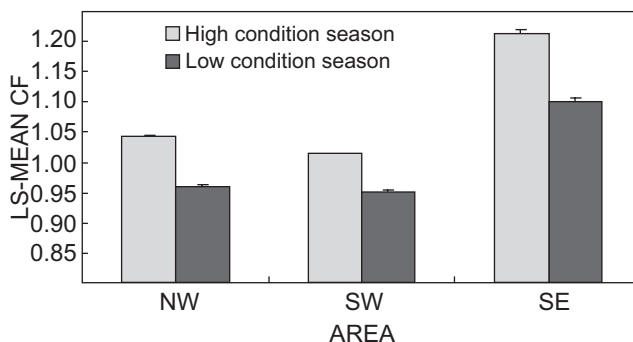


Figure 6: Least-square (LS) means of sardine condition factor (CF) by area (NW = North-West; SW = South-West; SE = South-East) for the high condition season (January–May) and low condition season (June–August) from GLMs (Equations 7 and 8 respectively). Error bars denote SE

models, a plot of the true mean values also shows a steady increase in CF from August to January (not shown). Spatial effects on LS mean CF were obvious, with medium values in the West and South-West areas and high values in the South-East area (Figure 6).

Table 6: ANOVA table for simplified GLMs on log(SGMn) for female sardine, showing predictors used in the model and the associated statistical indices for (a) the model including Year as a factor (see Equation 11); and (b) the model where Biomass replaces Year (see Equation 12)

Source	df	SS	MS	F	p	r ²
<i>(a) Model including Year as a factor</i>						
Model	54	3 243	60.1	348.4	<0.0001	0.43
Error	24 839	4 282	0.2			
Corrected total	24 893	7 525				
Year	49	750.4	15.3	88.8	<0.0001	
Month	2	300	150	870.1	<0.0001	
Area	2	598.1	299.1	1 734.7	<0.0001	
L _c	1	840.5	840.5	4 875.5	<0.0001	
<i>(b) Model — Biomass replaces Year</i>						
Model	8	2 746.9	343.4	1 788.3	<0.0001	0.37
Error	24 885	4 778.1	0.2			
Corrected total	24 893	7 525				
Biomass	3	254.4	84.8	441.6	<0.0001	
Month	2	438	219	1 140.6	<0.0001	
Area	2	586.4	293.2	1 527	<0.0001	
L _c	1	879.9	879.9	4 582.8	<0.0001	

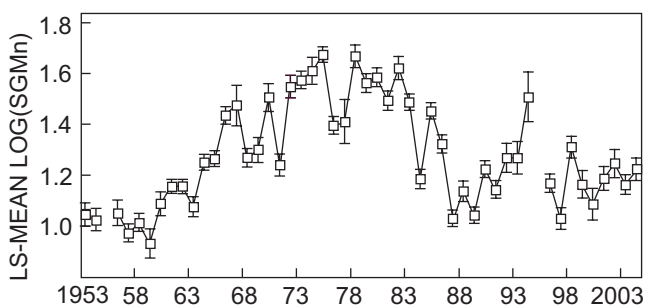


Figure 7: Annual least-square (LS) means of sardine log(SGMn) for 1953–2004 from GLM model (Equation 11). Error bars denote SE

Net standardised gonad mass

The GAM model showed a linear relationship between SGMn and L_c using a span value of 2; when using a span of 0.75 the relationship was curvilinear for smaller (<13cm L_c) fish but only for <400 of the 41 117 sardine analysed. Interestingly, nearly all of these small fish that had a SGMn that was higher than expected from the linear relationship were sampled during 1967 and 1975. This marginal non-linearity was ignored in the simplified GLM model for SGMn which had the form:

$$\log(\text{SGMn})_{\text{Year, Month, Area, } i} = m + a_{\text{Year}} + b_{\text{Month}} + c_{\text{Area}} + dL_c + \varepsilon_{\text{Year, Month, Area, } i} \quad (11)$$

where m is a constant, and a , b , c and d are parameters depending on the main effects related to the factors Year, Month, Area and to the covariate L_c respectively, and ε is the residual.

The simplified model had $df = 54$ and explained 43% of the observed variance in log(SGMn) (Table 6a) compared with $df = 242$ and 50% for the primary model. Most of the variance in log(SGMn) was explained by Year and to a lesser extent by Area. The Year LS means did not show a

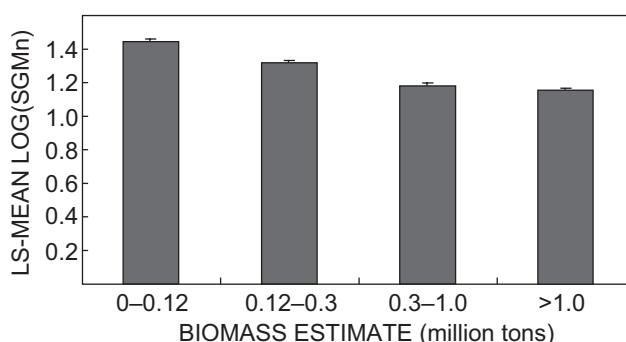


Figure 8: Least-square (LS) means of sardine log(SGMn) by biomass category from GLM model (Equation 12). Error bars denote SE

significant linear trend ($p > 0.05$) but a dome-shaped one, with the highest values during the period of low biomass (Figure 7). As for CF, this temporal effect on SGMn was captured by the incorporation of a Biomass factor, which was found to have a negative and significant effect on SGMn. The simplified model had the form:

$$\log(\text{SGMn})_{\text{Biomass, Month, Area, } i} = m + a_{\text{Biomass}} + b_{\text{Month}} + c_{\text{Area}} + dL_c + \varepsilon_{\text{Biomass, Month, Area, } i} \quad (12)$$

in which $df = 8$ and explained 37% of the observed variance in log(SGMn) (Table 6b, Figure 8) compared with $df = 23$ and 38% for the primary model. The categorical variable ERSST was not retained in the simplified model because, although it was a significant factor, it contributed very little to explaining the observed variability (<0.3% of that explained by the factor Biomass; model not shown).

GLM-derived plots of monthly LS mean SGMn (Figure 9) show a steady decrease from January to March. Spatial effects in LS mean SGMn were obvious, decreasing steadily from west to east (Figure 10).

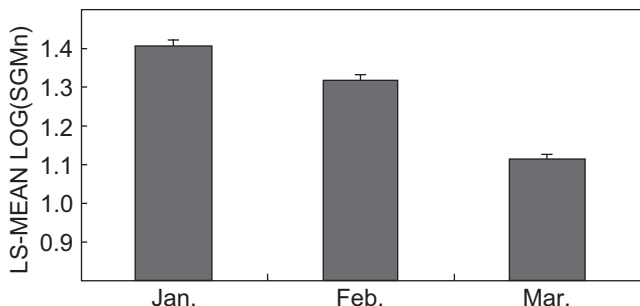


Figure 9: Monthly least-square (LS) means of sardine log(SGMn) from January to March resulting from GLM model (Equation 11). Error bars denote SE

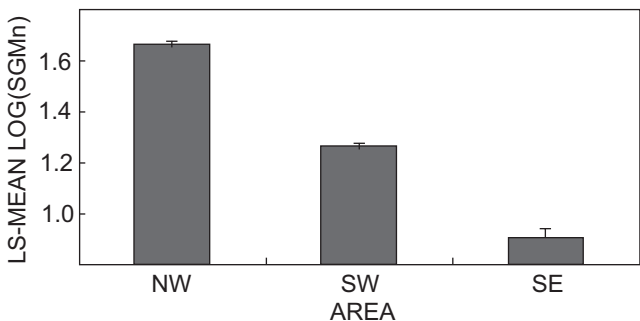


Figure 10: Least-square (LS) means of sardine log(SGMn) by area (NW = North-West; SW = South-West; SE = South-East) resulting from GLM model (Equation 11). Error bars denote SE

Length-at-maturity

Length-at-50% maturity (L_{50}) from ogives plotted using SGMn values of 0.2 and 0.3 were minimally different to those plotted using a value of 0.25, with ogives shifting uniformly by about 3mm to the left or the right of the 0.25 ogive respectively. Maturity ogives plotted using a SGMn of 0.25 as indicative of sexual maturity for the five periods are shown in Figure 11. The L_{50} value was high during the pre-collapse period (Period 1 [1953–1964]) but had decreased substantially by the time the population had collapsed (Period 2 [1965–1975] and Period 3 [1976–1987]). Length-at-50% maturity increased in the recovery period (Period 4 [1988–1995]), and in the recovered period (Period 5 [1996–2004]) was at a level similar to that seen during the pre-collapse period. Significant differences between L_{50} values were apparent for all pair-wise comparisons except for Periods 1 and 5, the pre-collapse and recovered periods respectively (Table 7).

Discussion

Over the past 50 years, the southern Benguela has been characterised by two periods of high sardine biomass separated by a long period of low biomass (Figure 1), and the present data show that both the condition factor and the net standardised gonad mass display an opposite pattern, suggestive of a density-dependent response. However,

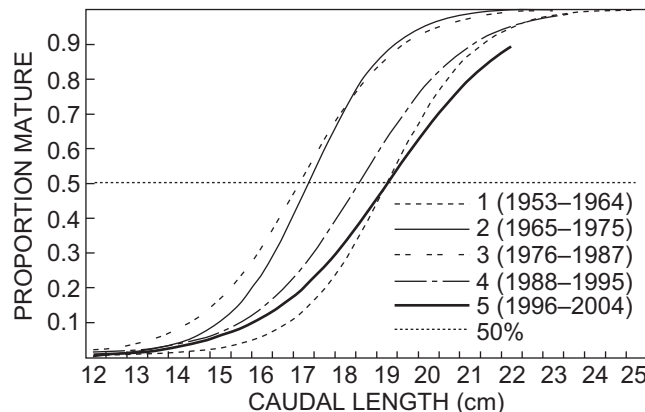


Figure 11: Maturity ogives for immature and female sardine (maturity criterion was SGMn >0.25) for the five periods analysed

Table 7: Mean (and standard deviation) of length-at-50% sexual maturity (L_{50}) for immature and female sardine for the five periods analysed

Period	Time	Mean	Standard deviation
		L_{50} (cm)	L_{50} (cm)
1	1953–1964	19.1	0.03
2	1965–1975	17.2	0.04
3	1976–1987	17.0	0.03
4	1988–1995	18.4	0.05
5	1996–2004	19.1	0.05

density-dependence is not the only possible causal factor impacting on biological parameters of exploited fish populations such as sardine. Factors such as a declining age structure, selection for early maturity under prolonged rates of high mortality or changes in the environment were proposed by Armstrong *et al.* (1989).

We lack data to assess whether the age structure of the southern Benguela sardine population has changed over the period examined, but information on the length frequency of catches are available. In the early 1950s, >90% of the sardine landed were >20cm, but smaller fish (15–20cm) became dominant from the late-1950s to the mid-1960s, and from the mid-1960s to the mid-1980s the vast majority of sardine in the catches were <15cm (Armstrong 1986). This pattern has persisted since 1987, with >95% of fish landed being <20cm (Fairweather *et al.* 2006). Armstrong *et al.* (1989) suggested that the decline in L_{50} could have been an artefact of a changed population age structure on account of the absence of large (i.e. old) fish after the collapse in 1964. Given that the population has recovered and yet the size structure of landings has not changed, this suggests that the temporal change in sardine biological parameters is not related to changes in population size (and presumably age) structure.

The similarity in sardine sexual maturation characteristics between pre-collapse and recovered population levels indicates that an evolutionary change related to the selection for early maturity under prolonged rates of high mortality was not a significant factor in the sardine stock. Had this

been the case, then a more persistent change in maturation characteristics would have been expected. By contrast, changes arising from phenotypic plasticity are expected to be readily reversible should conditions revert (e.g. Law 2000, Heino and Godo 2002).

If patterns in female sardine CF and SGMn are linked to environmental conditions, it could be hypothesised that the period of higher levels of these biological parameters should correspond to a period of increased productivity in the southern Benguela. Unfortunately, except for the ERSST data used here, long-term datasets of the environment of the southern Benguela that cover the entire period examined here are scarce. Shannon *et al.* (1992) showed a steady increase in an upwelling index off the West Coast (and by implication production) from 1950 to 1989, which roughly paralleled the increase in CF and in SGMn of female sardine up to around 1980. However, this trend did not match the declines in these parameters from 1980 onwards. The ERSST dataset explained very little of the observed variance in sardine CF and SGMn, and the lack of correspondence between these parameters and available environmental time-series reduces support for an environmentally induced causal relationship.

Density-dependence in reproductive and other biological parameters of sardine in the Benguela system has previously been argued by Le Clus (1987, 1990), Thomas (1985, 1986) and Fossen *et al.* (2001). Recent data show a reduction in the lipid content of anchovy recruits in the southern Benguela during years of exceptionally high recruitment (van der Lingen and Hutchings 2005). Density-dependence has also been reported for sardine in other systems. Age-at-maturity of Pacific sardine *S. sagax* was reduced at low population size (Butler *et al.* 1996). Japanese sardine *S. sagax melanostica* shifted the location of their major spawning area southwards and their migratory range was substantially extended at increased population size (Li *et al.* 1993), whereas their growth increased during a period of stock decline (Morimoto 2003). Kawasaki and Omori (1995) reported a decrease in sardine lipid content at high biomass levels, which led to recruitment failure arising from the production of low quality eggs. Wada and Jacobson (1998 p 2459) hypothesised that '...density-dependent effects on recruitment are typical of *Sardinops* stocks, but that they could only be measured using long-time series of data with large changes in abundance'. However, Jacobson *et al.* (2001) considered it likely that environmental effects contributed more variance than density-dependent effects.

A recent attempt to disentangle density-dependent effects (via phenotypic plasticity) from fisheries-induced genetic change (via selection for early maturing phenotypes) in regulating age- and length-at-maturation of Norwegian spring spawning herring *Clupea harengus* indicated that density-dependent effects dominated (Engelhard and Heino 2004a). Further analysis of maturation reaction norms (which describe the probability of an immature individual of a given age and size to become mature) provided only ambiguous evidence for a genetic change in maturation tendencies (Engelhard and Heino 2004b).

Reports of compensatory responses by fish to fishing, including reductions in age-at-maturity and/or length-at-

maturity, faster growth and increased fecundity for commercially exploited fish populations, are becoming increasingly common (Trippel *et al.* 1997, Rochet 1998, 2000). This phenotypic plasticity is considered to result from high adult mortality attributable to fishing (Rochet 1998), and counteracts the effect of fishing mortality on population growth rate by maintaining the reproductive potential of the population (Rochet 2000). Given that the onset of maturity is sensitive to energy intake during the juvenile phase, fish may mature at a smaller size if they can acquire the nutrition necessary to support gonadal maturation (Trippel 1995). Evidence of a relatively high condition factor of sardine, likely to be indicative of increased energy intake, was observed in the southern Benguela from the early 1970s to the mid-1980s (Figure 3). This corresponds to the periods of reduced length-at-maturity (Figure 11) and lowest abundance (1965–1975 and 1976–1987), and supports the hypothesis that the observed decrease in L_{50} was linked to an abundant food supply and an increased proportion of smaller sardine joining the spawning population. The question of whether a decrease in L_{50} corresponds to an earlier age-at-maturity is unlikely to be answered, given the paucity of age studies on sardine in the southern Benguela.

The slightly higher value of CF in the South-East area compared with the North-West and South-West areas was unexpected, because the former area supports lower primary production. However, phytoplankton is not the primary food source for sardine, which derive most of their dietary carbon from zooplankton (van der Lingen 2002), and copepod biomass is higher east of Cape Agulhas (20°E) (Hutchings *et al.* 1995). The significant decline of CF in winter can be related to lower productivity in the North-West and South-West areas as a result of a decrease in upwelling-favourable winds (Shannon and Nelson 1996). But this explanation does not hold for the South-East area, where there is increased primary production from January to July (Demarcq *et al.* 2003). An increased lipid content of sardine in the east compared with those in the west was also reported by de Goede and van der Lingen (2005).

The decrease in SGMn values between January and March can be ascribed to the fact that this period comprises the latter half of the peak reproductive season, hence a decrease in relative gonad size is to be expected. In addition, there was a west-to-east decrease in SGMn. Both these results corroborate findings of Kreiner *et al.* (2001) who reported that gonadosomatic index (GSI) values for southern Benguela sardine (females and males >13cm L_C) decreased from January to March, and that longitude explained most of the spatial variance in a GLM-derived time-series of GSI over the period 1984–1999, with GSI decreasing from west to east.

Conclusions

Values of CF, SGMn and L_{50} for southern Benguela sardine display a clear interdecadal pattern correlated to the estimated biomass. During periods of high abundance CF and SGMn were low, whereas L_{50} was high, and this combination

is expected to result in lower reproductive success. In contrast, during periods of low abundance the situation was reversed. A high CF allows efficient energy transfer to gonad development (by including SGMn as a covariate in the CF GLM in this study, the two effects were disentangled), and a high SGMn is expected to result in more eggs spawned per female and/or bigger eggs with a higher probability of survival (e.g. Trippel 1998). The present results, using a 52-year time-series and a large number of observations, support the hypothesis of density-dependent auto-regulation of the southern Benguela sardine population. Such a finding is expected from obvious theoretical considerations (Beverton and Holt 1957), but is seldom observed owing to many other sources of variability, up to the point that the existence of a functional stock-recruitment relationship is debated (C Mullon, pers. comm.). The addition of the environmental variable ERSST did not contribute to the model, suggesting that the environment is not the primary factor influencing the long-term variability of biological parameters, although we cannot reject the hypothesis that there is another environmental signal, unrelated to SST, which plays a major role.

Additionally, if density-dependence impacts on recruitment success, as has been hypothesised for the sardine stock off Japan (Li *et al.* 1993, Kawasaki and Omori 1995), then the current low SGMn values for female sardine reported here, and the reduction in sardine condition factor in recent years, indicate an increased likelihood of a decline in the southern Benguela sardine population in the near future. Recent years (2004 and 2005) of low sardine recruitment have resulted in such a decline (Coetzee *et al.* 2005).

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References

- Akkers TR, Melo YC (1996) Spawning seasonality in the South African pilchard. In: Barange M, van der Lingen CD (eds) *Workshop on Southern African Sardine: Proceedings and Recommendations. Benguela Ecology Programme Report 29*: 22–25
- Armstrong MJ (1986) Assessments of appropriate yield for the pilchard resource in ICSEAF Division 1.6. *Collection of Scientific Papers of the International Commission of the Southeast Atlantic Fisheries 13*(1): 25–44
- Armstrong MJ, Roel BA, Prosch RM (1989) Long-term trends in patterns of maturity in the southern Benguela pilchard population: evidence for density-dependence? *South African Journal of Marine Science 8*: 91–101
- Barange M, Hampton I, Roel BA (1999) Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds) *Benguela Dynamics: Impact of Variability on Shelf-Sea Environments and their Living Resources. South African Journal of Marine Science 19*: 367–391
- Baumgartner T, Soutar A, Riedel W (1996) Natural time scales of variability in coastal pelagic fish populations of the California Current over the past 1500 years: Response to global climate change and biological interaction. *California Sea Grant Report 1992–1995*, California Sea Grant College, La Jolla, pp 31–37
- Beckley LE, van der Lingen CD (1999) Biology, fishery and management of sardines (*Sardinops sagax*) in southern African waters. *Marine and Freshwater Research 50*: 955–978
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. *Fisheries Investigations, London 2*: 1–533
- Blanke B, Speich S, Bentamy A, Roy C, Sow B (2005) Modeling the structure and variability of the southern Benguela upwelling using QuikSCAT wind forcing. *Journal of Geophysical Research 110*, C07018, doi:10.1029/2004JC002529
- Buckland ST (1984) Monte Carlo confidence intervals. *Biometrics 40*: 811–817
- Butler JL, Granados ML, Barnes JT, Yaremko M, Macewicz BJ (1996) Age composition, growth, and maturation of the Pacific sardine (*Sardinops sagax*) during 1994. *Report of the Californian Cooperative Oceanic and Fisheries Investigations 37*: 152–159
- Butterworth DS (1983) Assessment and management of pelagic stocks in the southern Benguela region. In: Sharp GD, Csirke J (eds) *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983. FAO Fisheries Report 291*: 329–405
- Coetzee JC, Merkle D, Twatwa N, Rademan J, van der Lingen CD (2005) Results of the 2005 spawner biomass survey. Unpublished Report, Marine and Coastal Management, South Africa, **SWG/DEC2005/PEL/03**, 11pp
- de Goede J, van der Lingen CD (2005) Application of a fat staging technique to examine temporal and spatial variability in lipid content of southern Benguela sardine *Sardinops sagax*. *African Journal of Marine Science 27*(3): 671–675
- Demarcq H, Barlow R, Shillington FA (2003) Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as observed by satellite imagery. *African Journal of Marine Science 25*: 363–372
- Engelhard GH, Heino M (2004a) Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. *Fisheries Research 66*: 299–310
- Engelhard GH, Heino M (2004b) Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Marine Ecology Progress Series 272*: 245–256
- Fairweather TP, van der Lingen CD, Booth AJ, Drapeau L, van der Westhuizen JJ (2006) Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. *African Journal of Marine Science 28*(3&4): 661–680
- Fossen I, Boyer DC, Plarre H (2001) Changes in some key biological parameters of the northern Benguela sardine stock. In: Payne AIL, Pillar SC, Crawford RJM (eds) *A Decade of Namibian Fisheries Science. South African Journal of Marine Science 23*: 111–121
- Heino M, Godo OR (2002) Fisheries induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science 70*: 639–656
- Hutchings L, Verheye HM, Mitchell-Innes BA, Petersen WT, Huggett JA, Painting SJ (1995) Copepod production in the southern Benguela system. *ICES Journal of Marine Science 52*: 439–455
- Jacobson LD, De Oliveira JAA, Barange M, Cisneros-Mata MA, Felix-Uraga R, Hunter JR, Yeong Kim J, Matsuura Y, Niqen M, Porteiro C, Rothschild B, Sanchez RP, Serra R, Uriarte A, Wada T (2001) Surplus production, variability, and climate change in

- the great sardine and anchovy fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1891–1903
- Kawasaki T, Omori M (1995) Possible mechanisms underlying fluctuations in the Far Eastern sardine population inferred from time series of two biological traits. *Fisheries Oceanography* **4**: 238–242
- Klyashtorin LB (2001) Climate change and long term fluctuations of commercial catches: the possibility of forecasting. *FAO Fisheries Technical Paper* **410**: 86pp
- Kreiner A, van der Lingen CD, Fréon P (2001) A comparison of condition factor and gonadosomatic index of sardine *Sardinops sagax* stocks in the northern and southern Benguela upwelling ecosystems, 1984–1999. In: Payne AIL, Pillar SC, Crawford RJM (eds) *A Decade of Namibian Fisheries Science. South African Journal of Marine Science* **23**: 123–134
- Law R (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57**: 659–668
- Le Clus F (1987) Reproductive dynamics of female pilchard *Sardinops ocellatus* in the northern Benguela system, with particular reference to seasonality, the environment and fish condition. PhD Thesis, University of Port Elizabeth, South Africa, 430pp
- Le Clus F (1990) Spatial variability in the seasonal trends of ovary weight in the Namibian pilchard population, 1965–1979. *South African Journal of Marine Science* **9**: 69–83
- Lehodey P, Alheit J, Barange M, Baumgartner T, Beaugrand G, Drinkwater K, Fromentin J-M, Hare SR, Ottersen G, Perry RI, Roy C, van der Lingen, CD, Werner F (2006) Climate variability, fish and fisheries. *Journal of Climate* **19**(20): 5009–5030
- Li X-Y, Kawasaki T, Honda H (1993) A mechanism to explain fluctuations in population size of the Far Eastern sardine (*Sardinops sagax melanosticus*). *Asian Fisheries Science* **6**: 51–71
- Marquardt DW (1963) An algorithm for least-squares estimation of non-linear parameters. *Journal of the Society of Industrial and Applied Mathematics* **11**: 431–441
- Morimoto H (2003) Age and growth of Japanese sardine *Sardinops melanosticus* in Tosa Bay, south-western Japan, during a period of declining stock size. *Fisheries Science* **69**: 745–754
- Rochet M-J (1998) Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science* **55**: 371–391
- Rochet M-J (2000) May life history traits be used as indices of population viability? *Journal of Sea Research* **44**: 145–157
- SAS Institute Inc. (1988) *SAS/STAT User's Guide, Release 6.03 Edition*. SAS Institute Inc., Cary, North Carolina, 1028pp
- Schwartzlose RA, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, Lluch-Belda D, Lluch-Cota SE, Maccall AD, Matsuura Y, Nevarez-Martinez MO, Parrish H, Roy C, Serra R, Shust KV, Ward MN, Zuzunaga JZ (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science* **21**: 289–347
- Shackleton LY (1987) A comparative study of fossil fish scales from three upwelling regions. In: Payne AIL, Gulland JA, Brink KH (eds) *The Benguela and Comparable Ecosystems. South African Journal of Marine Science* **5**: 79–84
- Shannon LV, Crawford RJM, Pollock DE, Hutchings L, Boyd AJ, Taunton-Clark J, Badenhorst A, Melville-Smith R, Augustyn CJ, Cochrane KL, Hampton I, Nelson G, Japp DW, Tarr RJQ (1992) The 1980s — a decade of change in the Benguela system. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) *Benguela Trophic Functioning. South African Journal of Marine Science* **12**: 271–296
- Shannon LV, Nelson G (1996) The Benguela: large scale features and processes and system variability. In: Wefer G, Berger WH, Siedler G, Webb DJ (eds) *The South Atlantic Past and Present Circulation*. Springer Verlag, Berlin, Heidelberg, pp 163–210
- Smith TM, Reynolds RW (2004) Improved extended reconstruction of SST (1854–1997). *Journal of Climate* **17**: 2466–2477
- Thomas RM (1985) Growth rate of the pilchard off South West Africa, 1971–1983. *Investigational Report of the Sea Fisheries Research Institute of South Africa* **128**: 41pp
- Thomas RM (1986) The Namibian pilchard: the 1985 season, assessment for 1952–1985 and recommendations for 1986. *Collection of Scientific Papers of the International Commission of the Southeast Atlantic Fisheries* **13**(2): 243–269
- Trippel EA (1995) Age at maturity as a stress indicator in fisheries. *BioScience* **45**: 759–771
- Trippel EA (1998) Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of the American Fisheries Society* **127**: 339–359
- Trippel EA, Kjesbu OS, Solemdal P (1997) Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA (eds) *Early Life History and Recruitment in Fish Populations*. Chapman and Hall, London, Fish and Fisheries Series **21**, pp 31–62
- van der Lingen CD (2002) Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African Journal of Marine Science* **24**: 301–316
- van der Lingen CD, Coetzee JC, Demarcq H, Drapeau L, Fairweather T, Hutchings L (2005) An eastward shift in the distribution of southern Benguela sardine. *GLOBEC International Newsletter* **11**: 17–22
- van der Lingen CD, Huggett JA (2003) The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In: Browman HI, Skiftesvik AB (eds) *The Big Fish Bang. Proceedings of the 26th Annual Larval Fish Conference*. Institute of Marine Research, Bergen, Norway, pp 303–343
- van der Lingen CD, Hutchings L (2005) Estimating the lipid content of pelagic fish in the southern Benguela by visual assessment of their mesenteric fat. *African Journal of Marine Science* **27**(1): 45–53
- Wada T, Jacobson LD (1998) Regimes and stock-recruitment relationships in Japanese sardine (*Sardinops melanosticus*), 1951–1995. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 2455–2460