A COMPARISON OF CONDITION FACTOR AND GONADOSOMATIC INDEX OF SARDINE *SARDINOPS SAGAX* STOCKS IN THE NORTHERN AND SOUTHERN BENGUELA UPWELLING ECOSYSTEMS, 1984–1999

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Time-series of condition factor (*CF*) and gonadosomatic index (*GSI*) were generated using general linear models (GLM) for sardine *Sardinops sagax* stocks in the northern and southern Benguela ecosystems over the period 1984–1999. During this period the biomass of sardine in the northern Benguela remained at relatively low levels of <500 000 tons, whereas that of southern Benguela sardine increased 40-fold to 1.3 million tons. The GLMs explained 27 and 45% of the observed variation in *CF*, and 32 and 28% of the observed variation in *GSI*, for sardine in the northern and southern Benguela subsystems respectively. Whereas the sardine *CF* in the northern Benguela remained stable over time, that for the southern Benguela stock declined steadily during the study period. Sardine *CF* showed a seasonal cycle in the southern but not in the northern Benguela. Time-series of *GSI* showed high interannual variability but no trends in either subsystem, and the seasonal pattern was similar for both stocks. The lack of coherence between the *CF* time-series for sardine in the two subsystems further suggests that sardine stocks in the northern and southern Benguela subsystems are independent.

Key words: condition factor, gonadosomatic index, northern Benguela, sardine, southern Benguela

The Benguela upwelling ecosystem lies adjacent to the south-western coast of Africa, from southern Angola (15°S) to Cape Agulhas (35°S; Fig. 1). Ecologically, it is split into separate northern and southern subsystems by a zone of intense perennial upwelling near Lüderitz (26–27.5°S; Shannon 1985). As is characteristic of upwelling ecosystems, the Benguela is highly productive and supports abundant populations of plankton-feeding clupeoids, including anchovy *Engraulis capensis*, round herring *Etrumeus* spp. and sardine *Sardinops sagax*, all of which are commercially exploited (Armstrong and Thomas 1989).

Sardine are distributed from southern Angola to KwaZulu-Natal on the north-east coast of South Africa, and despite wide-ranging migrations, there appear to be two separate stocks. The northern stock extends along the Namibian coast from the Lüderitz upwelling cell to the warm-water front off southern Angola (~15°S), and the southern stock is found from the Orange River to Kwazulu-Natal (27°S; Beckley and van der Lingen 1999). Tagging studies indicated no movement of sardine from the Western Cape to Namibia and only minimal movement in the opposite direction (Newman 1970), and genetic studies have shown no differences between the northern and southern stocks (Grant 1985). The Benguela sardine is a population

of the circumglobally distributed *Sardinops sagax*, additional populations being found in some of the other upwelling ecosystems of the world (Parrish *et al.* 1989, Grant and Leslie 1996).

Sardine have formed the basis of important fisheries in both South Africa and Namibia since the late 1940s (Crawford *et al*. 1987). Catches in both countries were high during the 1950s and early 1960s, but declined rapidly thereafter and have remained relatively low since then (Beckley and van der Lingen 1999). Off South Africa, hydroacoustic estimates of sardine biomass have shown that the stock size has grown steadily from the mid 1980s to the present (Barange *et al.* 1999). Off Namibia, signs of a population recovery in the early 1990s were followed by a decline in biomass that rendered the northern sardine population virtually commercially extinct by the end of 1995 (Boyer *et al.* 1997). Since then, the population has shown a slight increase, but it is still below the levels of the early 1990s (Fig. 2).

Large fluctuations in sardine biomass have been described in all regions of the world where the species is intensively fished (Lluch-Belda *et al.* 1989, Schwartzlose *et al*. 1999). Although variability in population size is commonly attributed to conditions affecting early life-history stages and hence recruitment vari-

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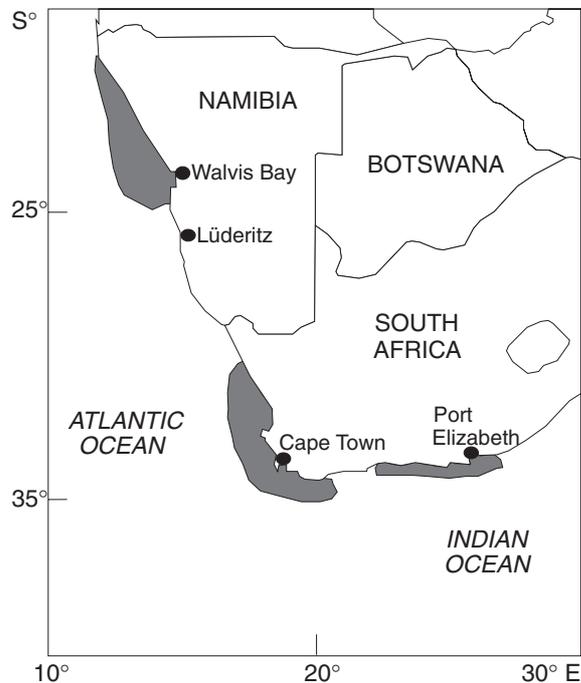‡ Institute of Research for Development, 213 Rue La Fayette, 75480 Paris Cedex 10, France

Fig. 1: Map of southern Africa showing the location of the major fishing grounds (shaded) and places mentioned in the text

ability (Bakun 1985, Chambers and Trippel 1997), processes that affect population parameters (such as growth rate, natural mortality rate, fecundity and age at maturity) of post-recruit fish have not been excluded as candidates for causality of interannual and inter-decadal variation in population size (Fréon 1989, Parrish and Mallicoate 1995). Such processes could include environmental forcing, interspecies interactions and density-dependent factors. With the exception of measurements of growth rate, however, estimating population parameters is difficult, and it requires intensive sampling and analytical effort. As a result of these difficulties, biological time-series that can be used to assess processes that could alter the population sizes of post-recruit fish, are limited. Examples of time-series that can be generated with relative ease for many fish populations are those of condition factor and gonadosomatic index.

Condition factor may be defined as an index of the physiological well-being of a fish, and can also be considered an integrator of conditions encountered during some previous period (of the order of weeks to months). Condition factor is affected by food availability, physical factors and the physiology of fish, including its gonad maturity stage. Food availability is further dependent on environmental conditions and population density (Parrish and Mallicoate 1995). Gonadosomatic index has been used as an indicator of reproductive activity of Namibian sardine (Matthews 1964), and in the absence of information on eggs and larvae, could be used to give an indication of peak spawning periods.

The objective of this paper was to derive time-series of condition factor and gonadosomatic index for sardine populations in the northern and southern Benguela over the period 1984–1999. These time-series could then be compared to assess possible co-variation between these two spatially distinct populations. The effect of various parameters (sex, fish length, etc.) on condition factor and gonadosomatic index was also studied. Finally, the condition factor time-series was compared with estimates of population biomass in order to speculate on the effect of density-dependence.

MATERIAL AND METHODS

Data sources

Biological data for sardine from both northern and southern Benguela were collected from commercial catches made during the period 1984–1999. Data were collected from a sample of 25–50 fish per landing. In the northern Benguela, samples were taken from catches landed at Walvis Bay, a total of 48 949 fish being sampled (Table I). In the southern Benguela samples were collected from commercial catches landed at several different ports (Fig. 1). In all, 62 567 fish were sampled there (Table I).

Information collected for each sample included the date (only Year and Month variables were used) and capture location (Latitude, Longitude and Depth [using class intervals 0–18.3 m, 18.3–36.6 m, 36.6–54.9 m, etc. up to 530.4–548.7 m] for the northern Benguela; and Latitude and Longitude [of the north-west corner of a 10×10 nautical mile "pelagic fishing block" in which the catch was made] for the southern Benguela). Measurements taken from individual fish included their total length (*TL*, to the nearest mm), caudal length (*CL*), wet body mass (g, to the nearest 0.1 g), sex, gonad maturity stage and gonad mass (g, to the nearest 0.1 g). Where no caudal length data were collected (for the northern Benguela from 1992 onwards), caudal
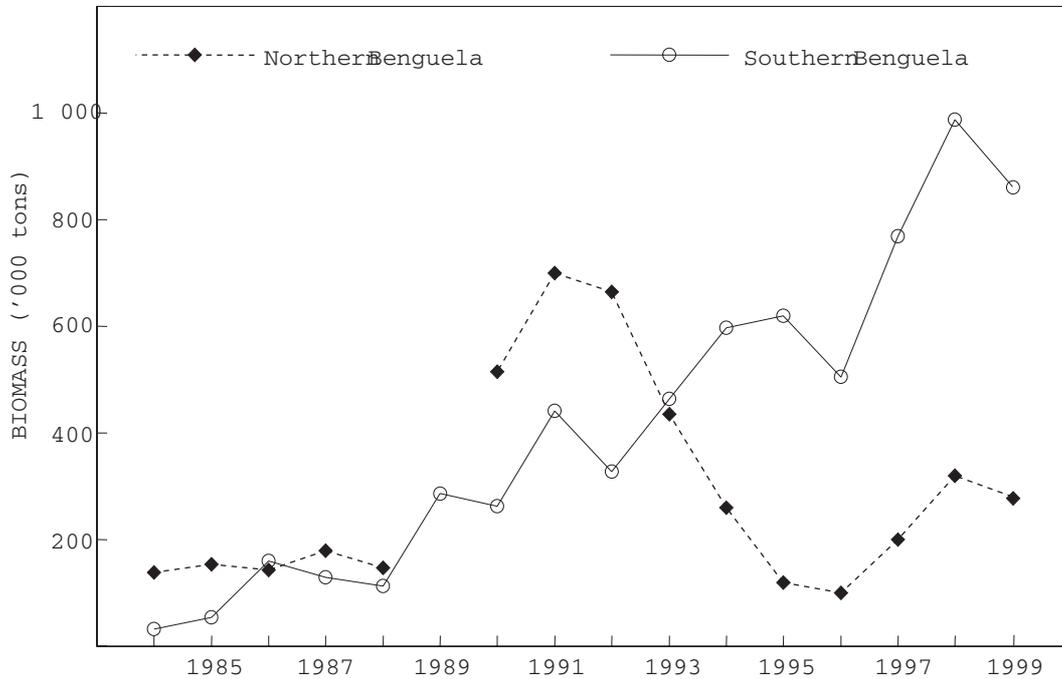
Fig. 2: Estimates of the biomass of sardine in the northern and southern Benguela derived from VPA and hydro-acoustic surveys. Data courtesy Boyer *et al.* (1997) and NatMIRC (unpublished data) for the northern Benguela, and Barange *et al.* (1999) and Marine & Coastal Management (unpublished data) for the southern Benguela

length was calculated from total length using the equation

$$CL \text{ (mm)} = 0.836328 \, TL \text{ (mm)} - 0.408755 \quad , \quad (1)$$

derived by fitting a linear regression ($r^2 = 0.984$; $n = 43\,695$) to the data points where total length and caudal length were available.

The condition factor (*CF*) of each sardine was calculated using the expression

$$CF = \frac{\text{observed wet body mass}}{\text{expected wet body mass}} \quad . \quad (2)$$

Expected mass was estimated from length/mass relationships derived separately for the northern and southern Benguela sardine populations by fitting non-linear regressions to the untransformed wet body mass and caudal length data using Marquardt's (1963) iterative algorithm:

$$\text{Wet body mass} = a \, CL^b \quad , \quad (3)$$

where *a* and *b* are estimated parameters.

Gonadosomatic index (*GSI*) was expressed as a percentage of wet body mass, and was calculated using the equation

$$GSI = \frac{\text{gonad mass}}{\text{observed wet body mass} - \text{gonad mass}} \times 100 \quad . \quad (4)$$

Data analysis

Time-series of *CF* and *GSI* were generated by fitting general linear models (GLMs) to each of the datasets for each of the regions. The SAS software package (SAS Institute Inc. 1988) was used for all statistical analyses.

The GLM fitted to the *CF* data from the northern Benguela used Year, Month, Sex (immature or mature) and Depth as independent class variables, and Latitude, Longitude, *GSI* and *CL* as independent continuous variables, plus their two-level interactions. A stepwise

Table I: Numbers of fish sampled by month and year in the northern and southern Benguela, 1984–1999

Year	Number of fish sampled												
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Northern Benguela													
1984			100	299									399
1985									100	75			175
1986	201	237	1 498	1 250	542	1 263	150	100	199	299			5 739
1987	100	100	1 547	1 797	1 241	1 330	1 174	1 004				100	8 393
1988	250	100	1 448	950	539	437	349	637	65	50			4 825
1989		339	931	1 396	997	50	2 194	798				250	6 955
1990	349	350	749	2 176	1 798	549	2 140	1 786				6	9 903
1991			10	656	569	609	499	110				10	2 463
1992		16	41	336	1 083	708	423	126					2 733
1993	20		168	487	343	334	321	63					1 736
1994		18	132	297	245	287	271	184	224				1 658
1995		63	6	370	353	172	273		201	163	106		1 707
1996		13	78	133	19	20	27	91					381
1997		45	24	114	224	87	122						616
1998	49	27	143	199	146	15	168	12					759
1999			19	144	148	150	46						507
Total	969	1 308	6 894	10 604	8 247	6 011	8 157	4 911	789	587	106	366	48 949
Southern Benguela													
1984	192	713	607	685	498	250	3			293	104		3 345
1985	501	756	631	517	630	836	550	65	17				4 503
1986	192	716	706	520	502	597	718	165	16				4 132
1987	368	592	578	519	449	314	421	316	283				3 840
1988	244	580	419	682	792	919	432	507	328	282	11		5 196
1989	372	565	940	925	1 100	764	586	275					5 527
1990	350	950	987	841	1 344	988	375	391	150	125	175	50	6 726
1991	452	852	705	1 100	699	926	172	50	148	125	75		5 304
1992	125	300	250	125	75	200	75	125	125	50			1 450
1993	75	125	150		125	50				50			575
1994	25	25	100	25	25	148							348
1995	125	175	250	166	300	350	175	625	575	688	300	175	3 904
1996	324	503	550	490	517	425	450	400	500	300	400	150	5 009
1997	50	470	639	675	550	550	750	279	275	125	75	25	4 463
1998	75	375	600	347	450	550	425	625	449	375	50		4 321
1999	150	25	499	450	650	625	525	300	350	225	100	25	3 924
Total	3 620	7 722	8 611	8 067	8 706	8 492	5 657	4 123	3 216	2 638	1 290	425	62 567

procedure was used to select manually a "sub-optimal" model. Because the number of observations is high, an optimal model (including all the significant variables) would be over-parameterized, and some parameter estimates would be biased and/or not unique estimators. As stressed by Lebreton *et al*. (1992), instead of intending to get the ideal model explaining the highest percentage of variance, it is preferable to allow some secondary and hypothetical effects in the residuals and to focus on the main effects in the model. A visual residual analysis was performed to check for normality in the distribution of residuals, and to ensure that there was no trend in the mean and variance of residuals plotted against observed values.

As the sample size was unbalanced for the different class variables, simple means are biased and were not used here. Instead, least-squares estimates of marginal means (LS means) provided unbiased estimators of the class marginal means that would be expected had the design been balanced. For northern Benguela sardine, only data collected from January to August each year were used in the analysis because of insufficient data in the last third of the year (see Table I). Owing to some wet mass data being missing, only 45 725 data points were used for the *CF* analysis.

The GLM fitted to the *CF* data from the southern Benguela used the same approach and the same dependent variables as those for the northern Benguela
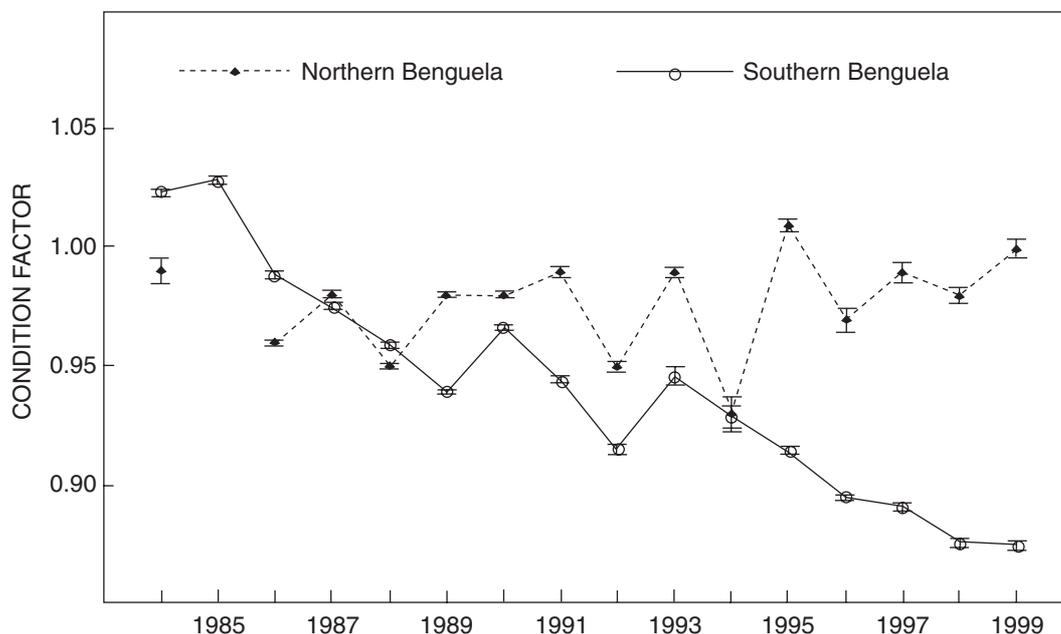
Fig. 3: GLM-derived time-series of annual LS means of condition factor for sardine in the northern and southern Benguela, 1984–1999

analysis, except for depth class, which was not available. Only data collected from January to September each year were used in this analysis because of insufficient data in the last quarter of the year (see Table I). Initial analysis of post-1996 data (years where there was good spatial coverage of sardine landings, with a significant number of samples being collected from both West Coast and South Coast fishing ports) revealed significant longitudinal effect, indicating that samples landed at Port Elizabeth had different characteristics from those landed elsewhere. Therefore, data from longitudes east of 21°E (i.e. >21°E) were excluded from further analysis, resulting in a total of 55 533 data points being used in the *CF* analysis.

The GLM fitted to the *GSI* data from the northern Benguela used Year, Month, Sex (male or female) and Depth as independent class variables, and Latitude, Longitude and *CL* as independent continuous variables, plus their two-level interactions. All fish <130 mm *CL* as well as fish with Maturity Stages <2 and >7 were excluded, because these fish were considered to be either immature or undergoing oocyte atresia. This reduced the total number of data points used for the northern Benguela sardine *GSI* analysis to 39 429.

The GLM fitted to the *GSI* data from the southern Benguela used Year, Month and Sex (male or female) as independent class variables, and Latitude, Longitude and *CL* as independent continuous variables, plus their two-level interactions. Fish <130 mm *CL* and those with Maturity Stages <2 and >7 were excluded, as for the northern Benguela data. In addition, data collected east of 21°E were excluded for the reasons described above. This reduced the total number of data points used for the southern Benguela sardine *GSI* analysis to 16 316.

RESULTS

Length-mass relationships

The length/mass relationship for sardine in the northern Benguela is described by the equation

$$\text{Wet body mass (g)} = 0.0000096 \ CL \ (\text{mm})^{3.0769}$$
$$(n = 47\ 981, \ r^2 = 0.989) \quad , \quad (5)$$

and that for sardine in the southern Benguela by
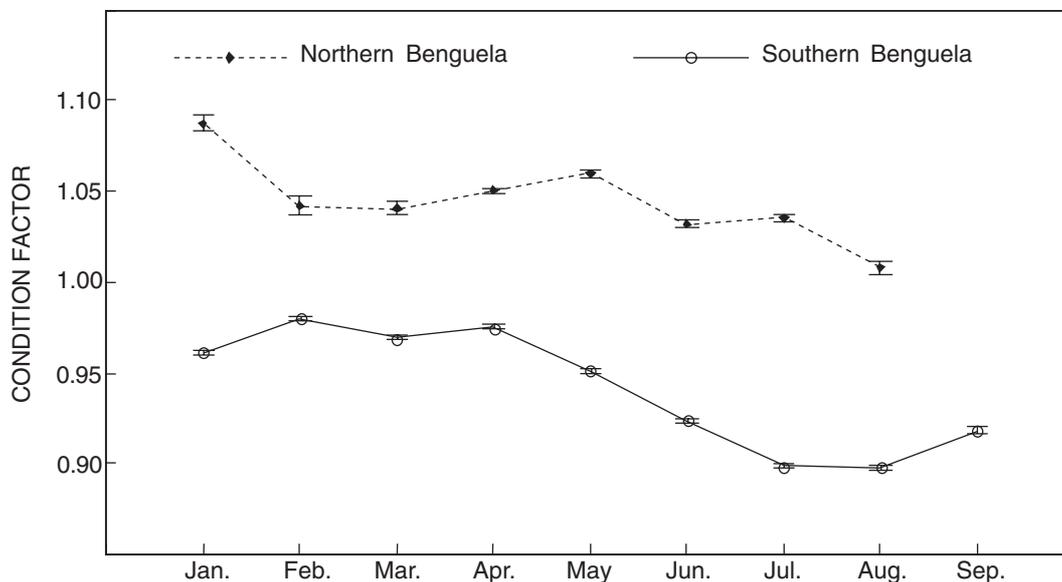
Fig. 4: GLM-derived time-series of monthly LS means of condition factor of sardine in the northern and southern Benguela, 1984–1999

Wet body mass (g) = $0.0000124\ CL$ (mm)$^{3.0194}$
($n = 62\ 452$, $r^2 = 0.988$) . (6)

Condition factor

The sub-optimal model for the northern Benguela sardine stock took into account Sex, *GSI* and *CL* effects, as well as the interaction between Year and Month. The model has the form

$$CFnorth_{Sex,\ Year,\ Month,\ i} = \text{m} + a_{Sex} + b_{Year,\ Month} + cGSI_{Sex,\ Year,\ Month,\ i} + dCL_{Sex,\ Year,\ Month,\ i} + \varepsilon_{Sex,\ Year,\ Month,\ i}\ , \quad (7)$$

where *CFnorth* is the condition factor of sardine in the northern Benguela, m a constant, *a* and *b* parameters depending respectively on the "main effects" related to the variables Sex and the interaction between Year and Month (class variables), *c* and *d* parameters related

Table II: Model outputs for sardine condition factor GLMs for the northern ($r^2 = 0.27$, $n = 45\ 725$) and southern ($r^2 = 0.45$, $n = 55\ 533$) Benguela, showing the variables used in the analysis and their associated degrees of freedom (*df*), Type III and Mean sum of squares (*SS*), *F*-value and significance (*p*-value)

Source	*df*	Type III *SS*	Mean *SS*	*F*-value	*p* (>*F*)
Northern Benguela					
Sex	1	7.59	7.59	952.55	0.0001
GSI	1	13.95	13.95	1 750.96	0.0001
CL	1	8.05	8.05	1 010.14	0.0001
Year × Month	95	101.95	1.07	134.69	0.0001
Southern Benguela					
Year	15	44.92	2.99	442.39	0.0001
Month	8	17.11	2.14	315.9	0.0001
GSI × Sex	2	72.18	36.09	5 331.66	0.0001
Year × Month	110	31.99	0.29	42.96	0.0001

Table III: Model outputs for the sardine gonadosomatic index GLMs for the northern (r^2 = 0.32, n = 31 740) and southern (r^2 = 0.28, n = 16 315) Benguela, showing the variables used in the analysis and their associated degrees of freedom (df), Type III and Mean sum of squares (SS), F-value and significance (p-value)

Source	df	Type III SS	Mean SS	F-value	p (>F)
Northern Benguela					
Sex	1	5 685.51	5 685.51	1 512.25	0.0001
CL	1	8 203.65	8 203.54	2 182.04	0.0001
Year × Month	93	49 784.24	535.31	142.38	0.0001
Southern Benguela					
Sex	1	1 488.74	1 488.74	325.59	0.0001
CL	1	4 022.99	4 022.99	879.84	0.0001
Month	8	1 775.46	221.93	48.54	0.0001
Year	12	1 438.77	119.9	26.22	0.0001
Longitude	1	7 302.48	7 302.48	1 597.07	0.0001
Year × Month	76	5 919.53	77.89	17.03	0.0001

to covariates *GSI* and *CL* respectively, observed for given Sex, Year and Month classes, with *i* repetitions, and ε is the residual. This model explains 27% of the observed variance in *CF* (Table II) and indicates that most of the variance is explained (in descending order of relative importance) by the interaction between Year and Month, *GSI* (positive effect) and *CL* (negative effect). The GLM-derived time-series of annual LS mean *CF* of sardine in the northern Benguela shows no trend and relatively high interannual variability (Fig. 3). The monthly variation looks rather high, but the maximal amplitude seems to lie during a period (August–January) where the paucity of data prevents proper estimation of the *CF* LS mean values for the period September–December (Fig. 4).

The sub-optimal model for the southern Benguela sardine stock took into account Year and Month effects, as well as the interactions between *GSI* and Sex and between Year and Month. The model has the form

$$CFsouth_{Year, Month, Sex, i} = \text{m} + a_{Year} + b_{Month} + c_{Year, Month} + d_{Sex}GSI_{Year, Month, Sex, i} + \varepsilon_{Year, Month, Sex, i} \quad , \quad (8)$$

where *CFsouth* is the condition factor of sardine in the southern Benguela, m a constant, *a*, *b* and *c* parameters, and ε is the residual. This model explains 45% of the observed variance in *CF* and indicates that most of the variance is explained by the interaction between *GSI* and Sex (*GSI* has a positive effect regardless of sex), and by Year (Table II). The GLM-derived time-series of annual LS mean *CF* of sardine in the southern Benguela shows a steady decline over the study period (Fig. 3). Monthly LS mean *CF* values show a seasonal cycle, with *CF* highest between February and April

and lowest between July and September. However, some years showed a departure from this general pattern (e.g. in 1990 and 1997 the seasonal cycle was non-existent) making it necessary to incorporate an interaction term between Year and Month in the model.

Gonadosomatic index

The sub-optimal model fitted to the *GSI* data for sardine from the northern Benguela took into account Sex and *CL* effects as well as the interaction between Year and Month. The model has the form

$$GSInorth_{Sex, Year, Month, i} = \text{m} + a_{Sex} + b_{Year,Month} + cCL_{Sex,Year, Month} + \varepsilon_{Sex,Year, Month, i} \quad , \quad (9)$$

where *GSInorth* is the gonadosomatic index of sardine in the northern Benguela, m a constant, *a, b* and *c* are parameters, and ε is the residual. The model explains 32% of the variance (see Table III) and indicates that most of the variance is explained (in descending order of relative importance) by the interaction between Year and Month and by *CL* (positive effect).

The GLM fitted to the *GSI* data for sardine from the southern Benguela took into account the Year, Month and Sex effects, the interaction between Year and Month, as well as the *CL* and the Longitude effects. The model has the form

$$GSIsouth_{Year, Month, Sex, i} = \text{m} + a_{Year} + b_{Month} + c_{Sex} + d_{Year, Month} + e{\cdot}CL_{Year, Month, Sex, i} + f Longitude_{Year, Month, Sex, i} + \varepsilon_{Year, Month, Sex, i} \quad , \quad (10)$$
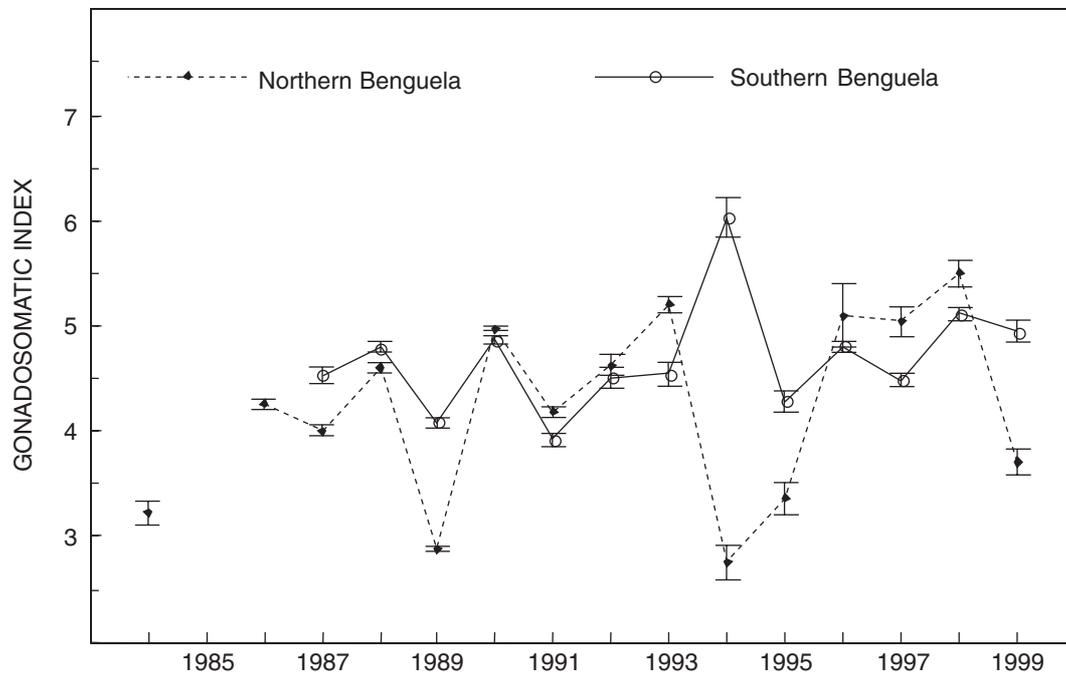
Fig. 5: GLM-derived time-series of annual LS means of gonadosomatic index for sardine in the northern and southern Benguela, 1984−1999

where *GSIsouth* is the gonadosomatic index of sardine in the southern Benguela, m a constant, *a* , *b*, *c* and *d* parameters, and ε is the residual. This model explains 28% of the observed variance in *GSI* (Table III), and indicates that most of the variance is explained (in descending order of relative importance) by Longitude (negative effect), the interaction between Year and Month, and *CL* (positive effect).

The GLM-derived time-series of annual LS mean *GSI* values for sardine in the northern and southern Benguela show high interannual variability and no annual trend over the study period in either subsystem (Fig. 5). Over the period studied, the two time-series appear to fluctuate quasi-synchronously, with the exception of 1994 where the data were out of phase; this was the lowest annual value of the time-series for the northern Benguela sardine and the highest annual value for sardine in the southern Benguela. Monthly LS mean values indicate that the *GSI* follows the same seasonal pattern for the northern and southern sardine stocks, with high *GSI* values between January and March, low values from April to June, and high values again from July onwards (Fig. 6).

DISCUSSION

The main limitation perceived in the use of the GLM approach is that it is not primarily designed to track non-linear effects of continuous variables. It is possible to overcome this limitation by categorizing continuous variables suspected of having non-linear effects when sufficient data are available, as was the case in this analysis. The non-linear effect of latitude and longitude in the northern Benguela was explored, and a slight but significant bimodal effect found in the latitude (with condition factor peaking at 19 and 22°S). However, incorporating this effect improved the percentage of explained variance by only 1%, despite an increase of 7 degrees of freedom in the model; hence, the latitudinal effect was not included. A second limitation of the analysis was the non-independence of individual observations within a subsample taken from each landing, which would have resulted in overestimation of the level of significance of the variable effects. To counter this, a very low *p*-value threshold ($p < 0.0001$) for retaining independent variables was used, and sub-
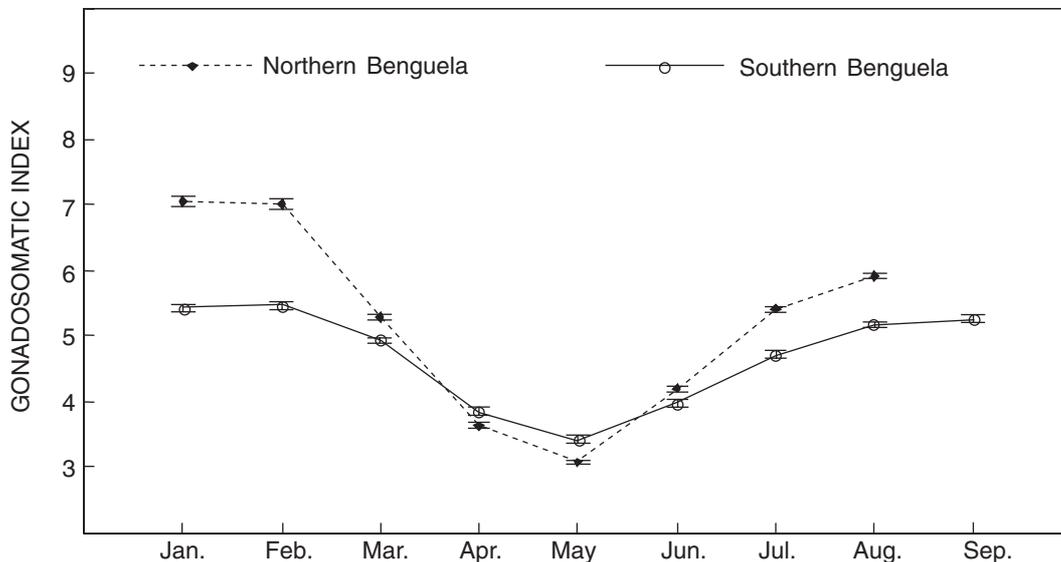
Fig. 6: GLM-derived time-series of monthly LS means of gonadosomatic index of sardine in the northern and southern Benguela, 1984–1999

optimal models, in which each independent variable accounted for at least 5% of the total explained variance, were employed to derive the time-series of LS mean values.

The length/mass relationships for sardine in the northern and southern Benguela subsystems were only minimally different, indicating that the two subpopulations have similar morphometrics.

Condition factor

Condition factor of sardine in the northern Benguela did not show a trend through time from 1984 to 1999, whereas that of sardine in the southern Benguela showed a steady decline over the same period that cannot be attributed to a negative trend in *GSI* (see Figs 3 and 5). This disparity in *CF* trends between the two subsystems suggests that the northern and southern sardine stocks are independent, and contrasts with the findings of Schülein *et al.* (1995). Those authors analysed oil-to-meal ratios of pelagic fish landings from the entire Benguela system over the period 1951–1993, and used oil content data (a proxy for fish condition) as an integrated "health" index of the fish stocks and their environment. Schülein *et al.* (1995) reported a significant degree of coherence between their data from northern and southern fishing

ports, which they attributed primarily to spatial coherence in environmental conditions, or Benguela-wide environmental signals. That conclusion is supported by the findings of Shannon *et al.* (1992), who noted periods of simultaneous change in environmental parameters throughout the entire Benguela ecosystem. The conflicting results of Schülein *et al.* (1995) and this study could be due to low frequency signals not being trapped in the same manner in both studies owing to the difference in length of the study periods (43 v. the current 16 years).

During the 16 years of the present study, the biomass of the northern Benguela sardine remained relatively constant at low levels (generally <500 000 tons). That value should be compared to estimates derived from Virtual Population Analysis (VPA) between 1950 and 1970, years when the biomass ranged between 2 and 10 million tons (Beckley and van der Lingen 1999). By contrast, estimates of the biomass of southern Benguela sardine have increased approximately 40-fold since 1984 (Fig. 2). The different trends for biomass and condition factor of sardine in the southern Benguela suggest that condition factor in that region may be at least partly density-dependent, and is reduced at high population sizes, presumably arising from intraspecific competition. Density-dependent condition factor of sardine in the northern Benguela has been previously reported by Le Clus (1987), who

observed that condition indices were low when sardine biomass was high, and high when biomass was low. Explicit statistical analysis regarding the correlation of condition factor and biomass has not yet been conducted, because this work forms part of an ongoing study using longer (50 years) time-series data.

The GLM analyses of condition factor for both the northern and southern Benguela sardine stocks showed that the Month × Year interaction term explained a significant part of the variance in each system (Table II), suggesting that seasonal patterns of condition factor varied from year to year in both systems. The amount of variance explained by this interaction was higher for the northern (78%) than for the southern (19%) Benguela, suggesting a more consistent seasonal signal in the southern Benguela data. The lack of a clear seasonal cycle in condition factor of the northern Benguela sardine has been previously reported. Matthews (1964) was unable to show a clear seasonal pattern for condition factor data over the period 1957–1960, and Le Clus (1990a) found no consistent seasonal trend in sardine condition index for data from 1965–1979. Attempts to determine the age of sardine from the region by reading annual rings on otoliths has proven to be extremely difficult because of high interannual differences (Thomas 1983, Agnalt 1995), further suggesting the absence of clear seasonal effects. Together with the results presented here, these data suggest that the seasonal effect on sardine in the northern Benguela is low and/or inconsistent. Studies in the region indicate stronger amplitude in the seasonal wind signal in the south than in the north (Taunton-Clark and Shannon 1988), but also suggest stronger occasional events in the north than in the south (e.g. Benguela *Niño*s; Shannon *et al*. 1992). These findings may indicate a high degree of variation in the seasonal pattern of food availability in the northern Benguela. If this is the case, it would imply that sardine in this subsystem have adopted an opportunistic strategy with regard to their use of energy available in the ecosystem for somatic growth and lipid storage.

For the southern Benguela sardine, condition factor is highest in summer, declines in autumn and is lowest in July/August (Fig. 4). Because of the lack of summer data (October–December is generally a closed season), the whole seasonal cycle could not be analysed for the period investigated. However, the seasonality in sardine condition factor described by the GLM analysis above agrees with the findings of Davies (1956), who showed that sardine condition factor during the years 1950–1954 was high during summer (December–February) and reached a maximum in March. From March onwards, condition factor declined through autumn and winter, reaching a minimum in August/September (Davies 1956). Using visual assessments of mesenteric fat as a proxy for total body lipid and hence an index of fish condition, Van der Lingen *et al.* (1998) also reported a strong seasonal cycle in lipid content of southern Benguela sardine, peaking between March and June and at a minimum between August and November.

Gonadosomatic index

The *GSI* for sardine in both northern and southern Benguela subsystems showed clear seasonal cycles (Fig. 6), but no trend over the study period. In the north, sardine spawn for most of the year, with peaks in summer/autumn, January/February, and winter/spring, September/October (Matthews 1964, Le Clus *et al.* 1987, Le Clus 1991). In winter (May/June) there is normally very little or no spawning, and these earlier findings are reflected in this analysis. *GSI* was low during this period for the entire study. Matthews (1964) showed, for the years 1957–1960, that gonad mass (both sexes) is lowest in May in the northern Benguela. In the southern Benguela, sardine appear to spawn year-round (Shelton 1986), but principally from August to March (Armstrong *et al*. 1989, Akkers *et al*. 1996, Huggett *et al*. 1998). The time-series of *GSI* obtained in this study confirms the winter (April–July) minimum in reproductive activity. The negative relationship between *GSI* and longitude observed for southern Benguela sardine most likely reflects the greater intensity of spawning off the West Coast than on the South Coast in recent years (Van der Lingen *et al.* in press).

A very low *GSI* was observed in 1994 in the northern Benguela system, the year before a major Benguela *Niño*, whereas in the southern Benguela a peak in the same parameter was noticeable in the same year. The low *GSI* in the north could have been a result of environmental disturbances or dispersal of food concentrations prior to the arrival of warm water (Le Clus 1990b). Le Clus (1990b) found that, prior to the onset of the Benguela *Niño* of 1984, neither sardine nor anchovy were spawning. Nevertheless, low values of *GSI* were also observed in 1989 and, to a lesser extent, in 1995 (Fig. 5), without clear interpretation.

In conclusion, the results of the GLM analyses have suggested that the two subsystems of the Benguela upwelling ecosystem displayed different and non-synchronized patterns in interannual variation in condition factor and gonadosomatic index of *Sardinops sagax* over the period 1984–1999. This finding suggests that the stocks of sardine in the two subsystems have their own short-term dynamics, probably related to

different dynamics in the environment, and confirms that, during the years of this study at least, there was little migration (if any) between the two.

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