

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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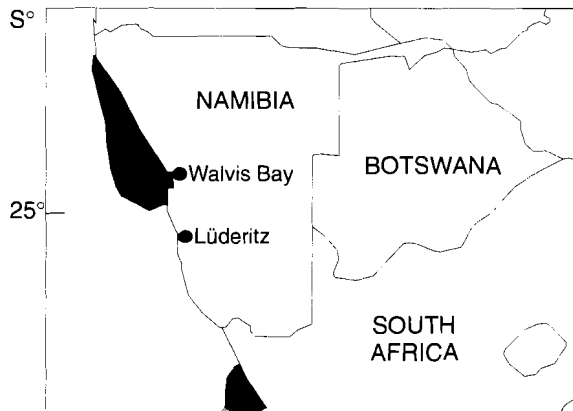
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months). Condition factor is affected by food availability, physical factors and the physiology of fish, including its gonad maturity stage. Food availability is further dependent on environmental conditions and population density (Parrish and Mallicoate 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 be-

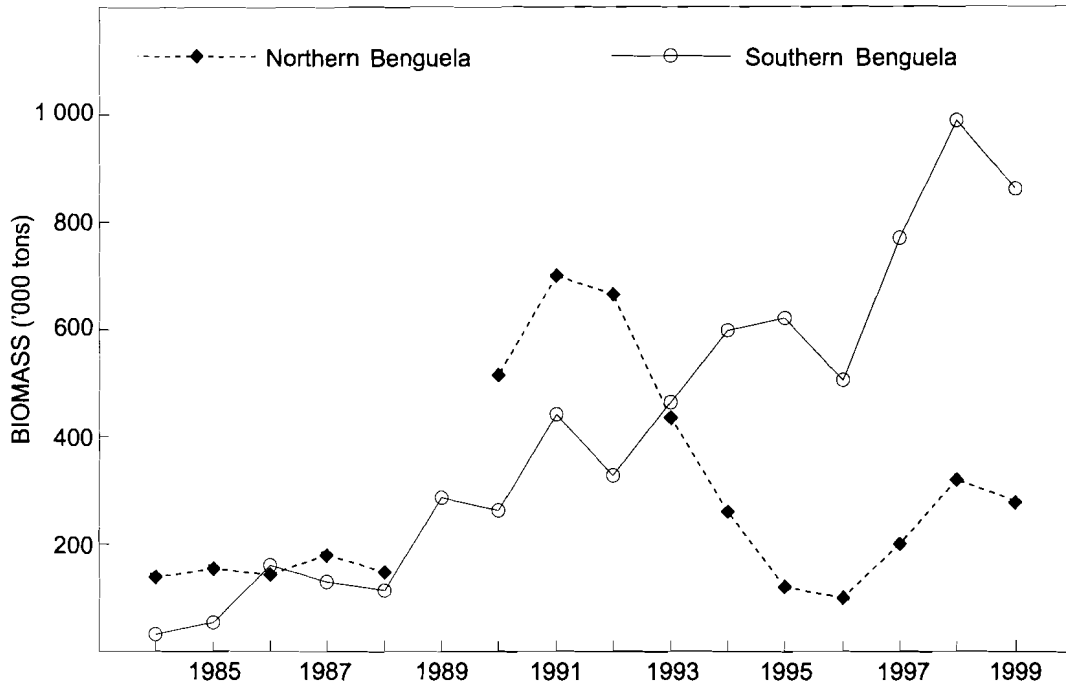


Fig. 2: Estimates of the biomass of sardine in the northern and southern Benguela derived from VPA and hydro-acoustic surveys. Data courtesy Boyer *et al.* (1997) and NatMIRC (unpublished data) for the northern Benguela, and Barange *et al.* (1999) and Marine & Coastal Management (unpublished data) for the southern Benguela

length was calculated from total length using the $L = a \cdot (1 - e^{-b \cdot TL})$ where a and b are estimated parameters.

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

Year	Number of fish sampled												Total
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	
<i>Northern Benguela</i>													
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
<i>Southern Benguela</i>													
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

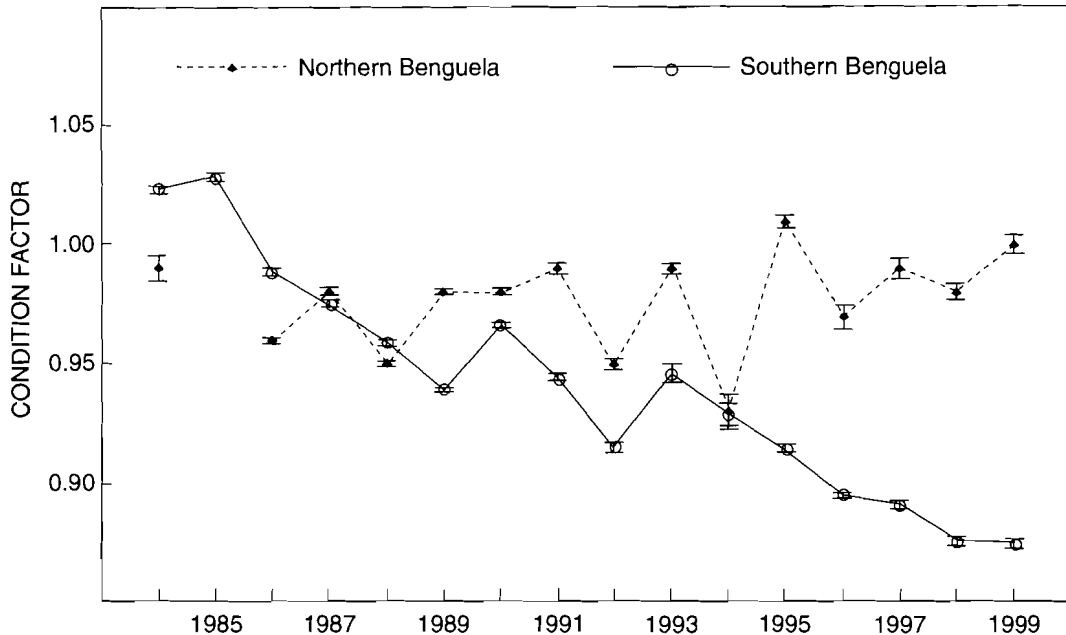


Fig. 3: GLM-derived time-series of annual LS means of condition factor for sardine in the northern and southern Benguela, 1984–1999

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

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

and that for sardine in the southern Benguela by

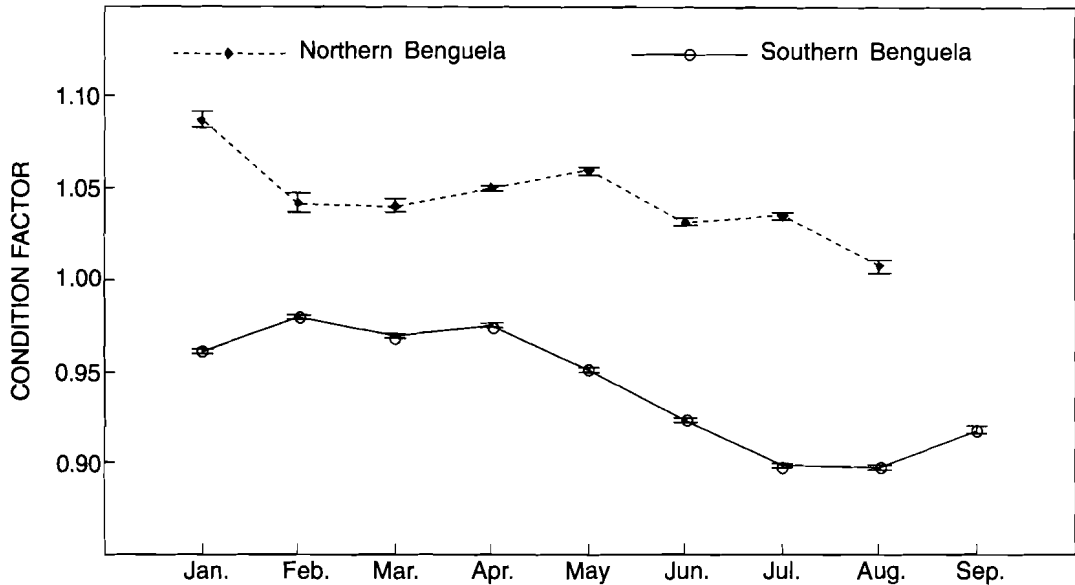


Fig. 4: GLM-derived time-series of monthly LS means of condition factor of sardine in the northern and southern Benguela, 1984–1999

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

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

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

where CF_{north} 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	$p (>F)$
<i>Northern Benguela</i>					
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 \times Month	95	101.95	1.07	134.69	0.0001
<i>Southern Benguela</i>					
Year	15	44.92	2.99	442.39	0.0001
Month	8	17.11	2.14	315.9	0.0001
GSI \times Sex	2	72.18	36.09	5 331.66	0.0001
Year \times 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)

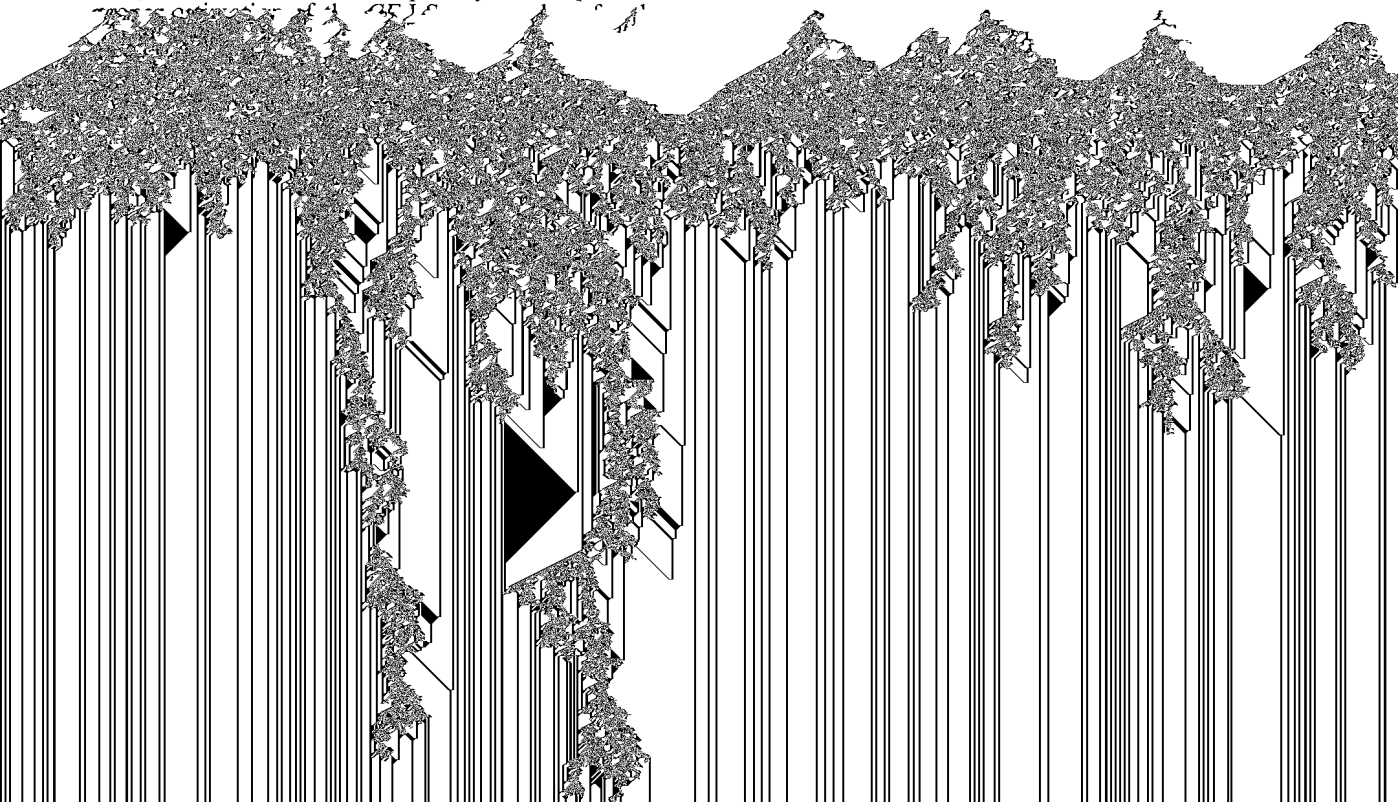
Source	df	Type III SS	Mean SS	F -value	$p (>F)$
<i>Northern Benguela</i>					
Sex	1	5 685.51	5 685.51	1 512.25	0.0001
CL	1	8 203.65	8 203.54	2 182.04	0.0001
Year \times Month	93	49 784.24	535.31	142.38	0.0001
<i>Southern Benguela</i>					
Sex	1	1 488.74	1 488.74	325.59	0.0001
CL	1	4 022.99	4 022.99	879.84	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 \times 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

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



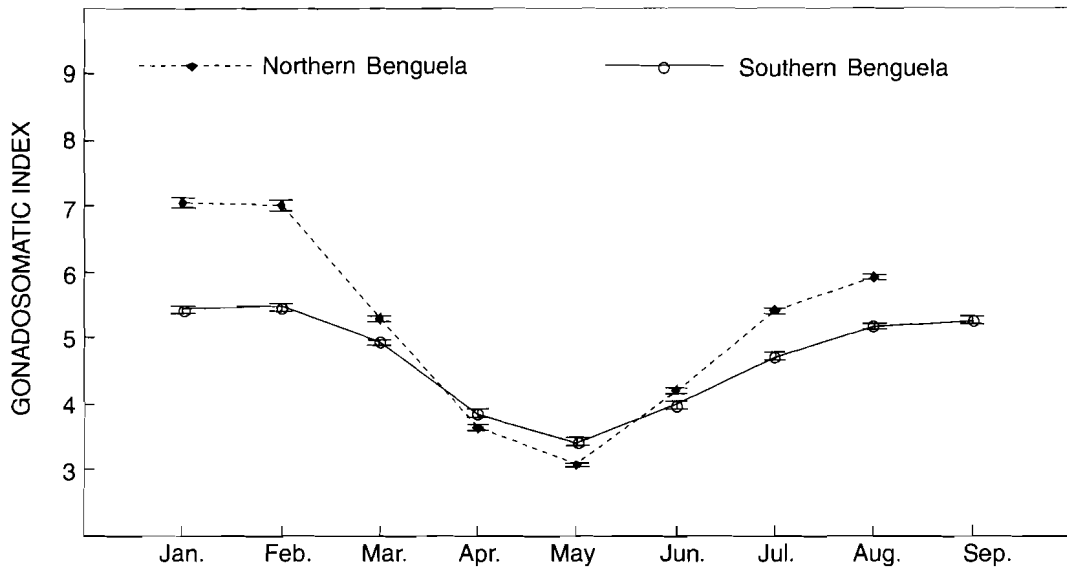


Fig. 6: GLM-derived time-series of monthly LS means of gonadosomatic index of sardine in the northern and southern Benguela, 1984–1999

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 sub-populations 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

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

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 \times 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

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

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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