A Decade of Namibian Fisheries Science
Payne, A. I. L., Pillar, S. C. and R. J. M. Crawford (Eds). *S. Afr. J. mar. Sci. 23: 111–121*
2001

CHANGES IN SOME KEY BIOLOGICAL PARAMETERS OF THE NORTHERN BENGUELA SARDINE STOCK

*I. FOSSEN**, *D. C. BOYER*† *and H. PLARRE*†

During the past 50 years, more than 15 million tons of sardine have been harvested from the northern Benguela ecosystem. The sardine population has undergone changes in abundance estimated to range over more than two orders of magnitude, but for the past two decades it is estimated to have remained at less than 10% of former levels of abundance. Some key changes in biological parameters, notably age composition and rates of natural mortality, are discussed in relation to the changes in abundance. Literature values for the period before the 1990s are compared to values calculated from acoustic survey population estimates thereafter. Although these recent data are potentially biased, and often lack estimates of precision, it is argued that they are sufficient to demonstrate general trends. The likelihood of the sardine stock recovering is seemingly reduced owing to the recent high rate of adult natural mortality.

Key words: biological parameters, exploitation, mortality, northern Benguela, sardine, *Sardinops sagax*

Traditionally, sardine *Sardinops sagax* has been the backbone of the Namibian pelagic fishing industry. In the 1950s, soon after commercial fishing started, estimates put the size of the region's sardine stocks at around 5 million tons (Butterworth 1983). Successive years of good recruitment during the late 1950s and early 1960s caused the population to increase to more than 10 million tons by the mid 1960s (Crawford *et al.* 1987), after which a series of stock crashes resulted in a biomass of only a few thousand tons by 1996 (Boyer *et al.* 2001). Catches have fallen concomitantly from a peak of 1.4 million tons in 1968 to a low of 2 400 tons in 1996 (Fig. 1). During that period more than 15 million tons of sardine were harvested from the northern Benguela (Boyer *et al.* 2001).

Following the halcyon years of the 1960s and mid 1970s, the sardine fishery has been managed in a manner intended to enhance recovery. Total allowable catches have been kept relatively low and bycatches of juvenile fish have been strictly limited. Since Namibian Independence in 1990, a constant proportion of the adult stock, 18%, has been used as the basic criterion for setting catch levels (Boyer *et al.* 2001). This equates to a fishing mortality of approximately 0.2 year^{-1}.

Changes in fish stock abundance have resulted in alterations in biological parameters of several fish stocks worldwide (Blaxter and Hunter 1982, Wootton 1990, Cury *et al.* 2000). As a general rule, teleosts react to high adult mortality by decreasing age at maturity (Rochet 1998), although Murphy (1977) reported that density-dependent changes in growth are less clear in clupeiforms than in many other teleosts. Nevertheless, Armstrong *et al.* (1989) reported a decreased length at maturity for South African sardine coinciding with a collapse in the biomass of the stock. Any changes in key biological parameters might significantly influence stock behaviour and production. In some situations, populations may be reduced to such an extent that changes in fecundity, mortality or growth are of such character that the stock may not be able to recover. An understanding of such changes is clearly of importance to the management of any stock, especially where that stock has been heavily depleted, as in the case of the northern Benguela sardine.

This study focuses on changes in key biological parameters of the northern Benguela sardine stock since exploitation started. These changes are discussed in relation to fluctuations in stock abundance.

MATERIAL AND METHODS

Values from the literature have been used for parameters prior to the 1990s. Data from surveys and commercial catches form the basis of estimates of parameter values for the past decade. Since 1990, three acoustic surveys of abundance have been conducted on average each year, most in autumn (February–April) or spring (October–November). Those surveys targeted the fishable stock and pre-recruits respectively.

---

* Formerly Institute of Marine Research, Bergen, Norway; now Møre Research, Section of Fisheries, P.O. Box 5075, N-6021, Ålesund, Norway. E-mail: if@als.moreforsk.no
† National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources, P.O. Box 912, Swakopmund, Namibia

Manuscript received February 2001; accepted May 2001

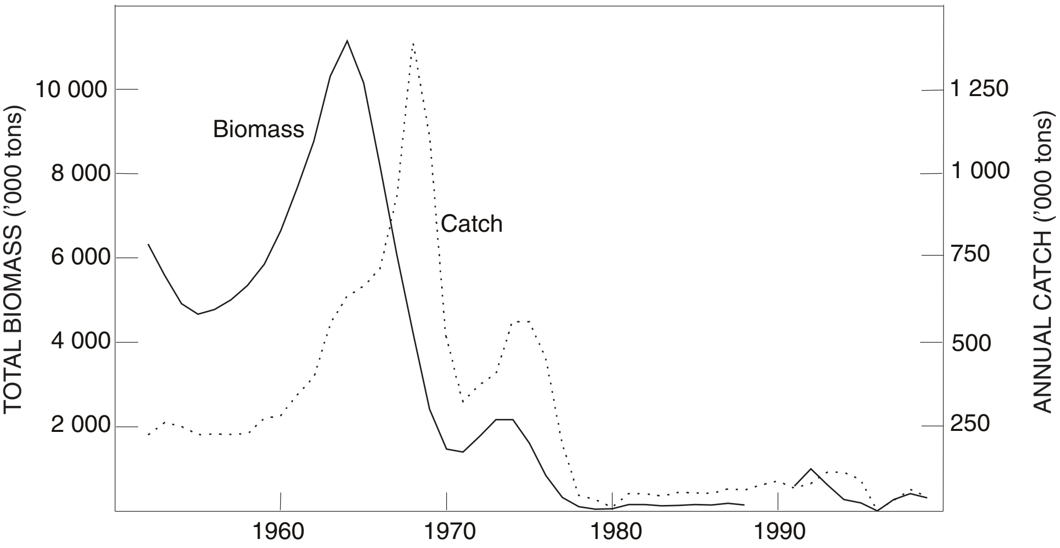

Fig. 1: Total biomass of northern Benguela sardine estimated by VPA (1952–1988, after Le Clus *et al.* 1988) and acoustic surveys (1990–2000), and annual catches, 1952–1999

In addition one sample of fish per 500 tons of commercial catch has been collected from landings. Details and procedures of surveys and sampling are given in Boyer *et al.* (2001).

During the period investigated, data collection and assessment were conducted primarily for immediate management purposes rather than to describe biological processes (Boyer *et al.* 2001). The data are therefore not always ideal for the latter purpose. Consequently, simple methods have been chosen for the analysis rather than sophisticated ones more demanding of data. In an attempt to validate the results, several methods, using different sources of input data, have also been used.

Age distribution

At present there is no validated age determination method for the northern Benguela sardine, largely because a lack of seasonality in the northern Benguela marine system results in a lack of clear annuli in the hard structures of sardine (Kerstan 1997, Waldron 1998). Age determination based on otolith zonation pattern seems, however, to be precise and in line with length frequency analyses for the youngest age-classes (Baird 1970, Thomas 1985, Kerstan 1997, 2000, Waldron 1998). To be able to compare the age distribution and other population parameters with values found in the literature, catch and survey data from the 1990s were divided into age-classes deduced from length frequencies. Studying length frequencies from individual commercial catches from consecutive months gave a good indication of the different cohorts present in the stock. The cohorts were also found during the scientific surveys, although the length frequency in one area often differed from that in another, indicating spatial separation of the cohorts. Techniques normally used to decompose length distributions were not suitable when dealing with composite length frequencies from surveys. Also, the existence of two peak spawning periods during a single spawning season complicated the use of such methods. For some of the areas, however, the Bhattacharya method (Sparre and Venema 1992) could be used to separate cohorts using the FISAT (FAO-ICLARM Stock Assessment Tool) software.

Based on this, the total length frequencies from each survey were divided by eye into three age-classes, using the abundance of fish and the length frequency within separate areas together with the results from the Bhattacharya method as a guide (Fig. 2). The length frequencies from the different areas were of considerable help when dividing what appeared to be a single distribution of I+ fish during several surveys. When the results from this splitting were used to estimate growth parameters, they agreed closely with previous estimates (Agnalt 1995). Through frequent surveys and sampling of commercial catches, the different cohorts can be followed closely (Boyer *et al.* 2001).

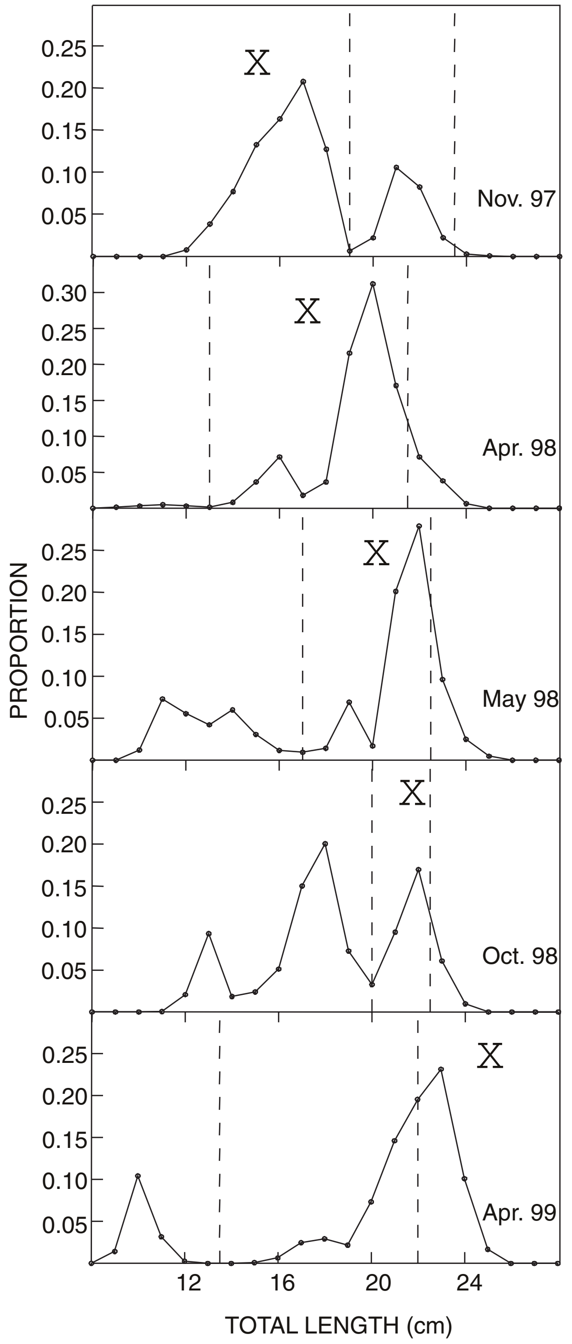

Fig. 2: Length frequencies for five surveys of sardine biomass between November 1997 and April 1999. Vertical dashed lines indicate the sizes used to differentiate the year-classes (0, I and II+), and X indicates the same year-class

Possible changes in the rate of growth are therefore not believed to have influenced the dividing of cohorts. It was assumed that all fish spawned during the same spawning season were hatched on 1 January and therefore were treated as a 0-group until the following 1 January.

Although dividing cohorts from length frequencies is not the best method for determining age structure of a stock, it is believed to give an indication adequate for the purpose of the present study. Splitting 0-group fish from older cohorts was carried out in an easy and precise manner. Failing to divide the I- from the II+ group accurately will, when used in mortality estimation, be averaged, so this potential error is believed to be of little importance in the analysis.

The use of the proportion of 0-group fish as an indication of longevity makes it possible to use the same method for the complete time-series. The method is independent of previous age determination, but it may be sensitive to changes in the rate of natural mortality used in the assessment before 1990; it will also reflect variability in annual recruitment. The proportion of 0-group fish in the stock is likely to increase if longevity is reduced, so that proportion was used to give an indication of changes in age composition and longevity.

Thomas (1986) described changes in mean age for the northern Benguela sardine stock. For the 1990s mean age was calculated to the beginning of each year, based on splitting survey data as detailed above. As there were few fish older than two years in the catches, it was assumed that the existence of older fish would have little influence on the average age. Mean age was calculated from the equation

$$\text{Mean age} = [(N_{0\text{gr}} * 0) + (N_{\text{Igr}} * 1) + (N_{\text{II+gr}} * 2)] \;/\; \text{total } N \text{ in the stock} \quad .$$

Numbers of fish in each year-class on 1 January were obtained by back-calculation of I- and II+ group fish from the March survey and 0-group fish back from the November survey. The calculations were adjusted for catches between 1 January and the individual survey, and the rate of natural mortality (*M*) was assumed to be 0.8 year^{-1} (MacCall 1986, Boyer *et al.* 2001). To gain an indication of how sensitive this calculation was regarding *M,* recalculations were made using *M* values of both 0.5 and 1.2. On average, the estimated mean age for the 1990s changed by -5.2 and 6.7% respectively. An indication of sensitivity in the calculation of mean age towards the possibility of having several age-classes in the II+ group was given by assuming that 50% of the II+ group was 3 years old. Recalculation of mean age using this assumption increased the estimated mean age by less than 10% on average.

Table I: Theoretical calculations of natural mortality for the northern Benguela sardine stock based on two sets of stock parameters (see text for different methods of estimating *M*)

Technique	Estimated M (length-based) $K = 1$, $L_{inf} = 27.1$ cm, $t_m = 1.8$ years, $t_{max} = 6$ years, $T = 15$°C	Estimated M (age-based) $K = 1.49$, $L_{inf} = 22.7$ cm, $t_m = 1.8$ years, $t_{max} = 5$ years, $T = 15$°C
Pauly (1980)	1.37	1.87
Beverton and Holt invariant (Jensen 1997)	1.60	2.38
1% rule (Alagaraja 1984)	0.77	0.92
Rikhter and Efanov (1977)	0.84	0.84

Mortality

Mark-recapture studies were carried out in the early 1960s and natural mortality then was estimated to be less than 0.59 (Newman 1970). On that basis, Butterworth (1983) used 0.5 year^{-1} as input in a virtual population analysis. By the end of the 1980s and at the beginning of the 1990s, scientists decided that this level of natural mortality was seemingly too low. As a result, the estimated *M* of sardine stocks in the southern Benguela (the South African stock; Glazer and Roel 1996) was adopted for northern Benguela sardine. Since 1990, a value of *M* of 0.8 year^{-1} has been assumed for Namibian sardine (Boyer *et al.* 1997).

The surveys had coefficients of variation (*CV*s) on the order of 25%, so imprecise estimates of biomass were expected (Boyer *et al.* 2001). However, because the calculation of *M* was made repeatedly over long periods during the decade, the changes in the estimated value of *M* were unlikely to be caused by survey variance alone. Size-selectivity in the surveys, such that older fish were potentially not surveyed, could result in a higher *M*. However, this possibility seems unlikely because the length structure in commercial purse-seine catches was similar to that on the surveys (trawl catches), suggesting that fish were not being missed consistently by the surveys (Boyer *et al.* 2001). The steady improvements through larger nets and vessels used by the commercial fleet further suggest that the catchability of large fish had not decreased. Splitting of cohorts allowed age-classes to be treated separately, so possible biases between them in the survey estimates could not explain the indications of a higher *M* in all age-classes.

M was calculated between surveys and between years using the formula of Sparre and Venema (1992):

$$M = -\ell n\ ((N_{t,c} + C)\ /N_{0,c})\quad ,$$

where $N_{t,c}$ is the number of fish at time *t* in cohort *c*, *C* the number of fish from cohort *c* caught between N_0 and N_t, and $N_{0,c}$ is the previous estimate of number of fish in cohort *c*. The equation ignores the effect of natural mortality on the fish caught and assumes that all fish caught would have stayed alive. This would lead to *M* being underestimated. The extent of this bias depends on the proportion between *C* and *N*.

Calculations between years were made from the number of I-group fish during one year and the number of II+ group the year after, and similarly between 0- and I-group fish. The use of a plus group will, of course, result in a slight underestimate of *M*.

Given the potential sources of error in the estimates of *M* from the direct calculations, the impact of different values of total mortality on biomass over time was examined for comparison. A spreadsheet model was used to simulate the trajectory of total biomass over time of the sardine stock in November each year of the 1990s. These values were compared with survey estimates. The model input was the estimated number of 0-group fish in November each year from recruitment surveys (Boyer *et al.* 2001) and an assumed rate of total mortality (*Z*). The model included four age-classes and the average weight of each age-class in November was used in estimating total stock biomass (35, 86, 100 and 125 g for 0-, I-, II- and III+ group fish respectively). The number of fish of age *i* at time *t* was estimated from

$$N_{it} = N_{i-1,t-1} {*} e^{-Z}\quad ,$$

where $N_{i-1,t-1}$ is the number of fish of age *i*-1 during the preceding year.

The number of recruits was taken directly from the estimated numbers on surveys each year, namely:

$$N_{recruits} = \text{Estimated } N_{recruits}\quad .$$

At the starting point, i.e. 1991, the numbers of 0-, I- and II+ group fish estimated during the November survey of that year were used. Simulated biomasses were not sensitive to changes in these values. For example, when the values were increased or decreased by 50%, the simulated biomass changed by 12% after two years and by <5% after four years. The model was run several times using different values of

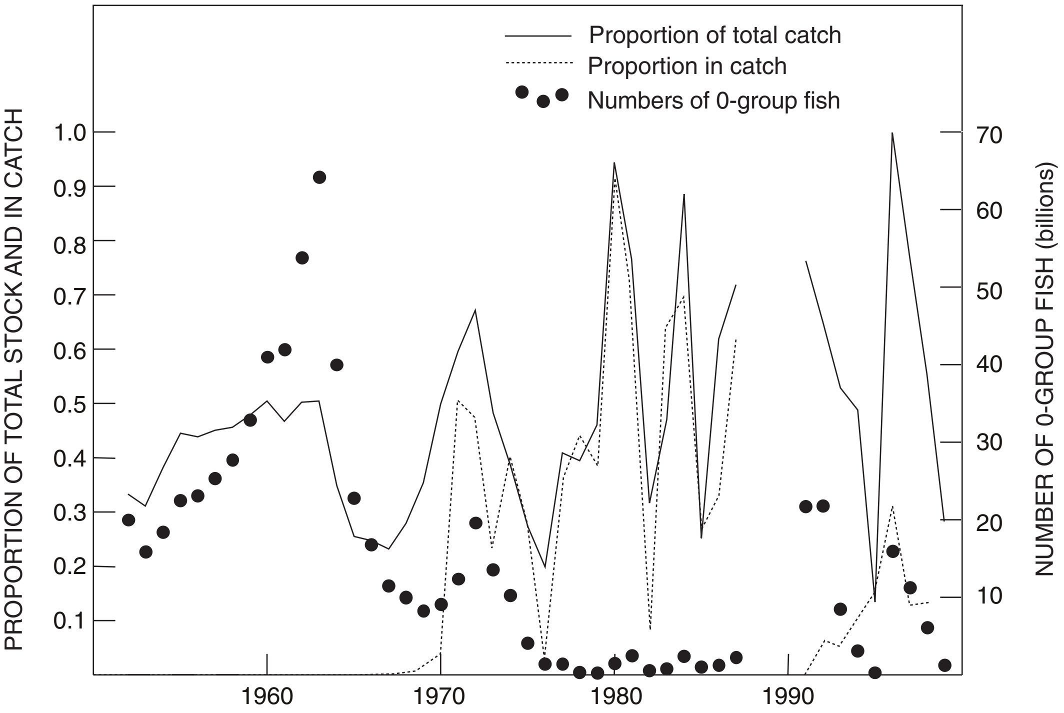

Fig. 3: Estimated proportion of 0-group sardine in the total stock, the observed proportion in commercial catches, and the estimated number of 0-group fish at 1 January each year, 1952–1999

Z and the outcome compared to the estimated biomass from the surveys. The value of *Z* that best fitted the yearly biomass estimates in November was estimated using a fitting criterion that minimized the sum of the squared differences between observed and fitted biomasses.

A third method used to obtain an indication of *M* was through empirical calculations (Rikhter and Efanov 1977, Pauly 1980, Alagaraja 1984, Jensen 1997). These methods are based on the relationships between population parameters, environmental temperatures (used by one technique) and mortality for a number of fish stocks worldwide. Theoretical rates of natural mortality were calculated using four different techniques and with two sets of input data (Table I). Average environmental temperature was assumed to be 15°C, but failing to assume the correct temperature by up to ±5°C had little influence on the estimation of *M* by such a method.

The first set of stock parameters used in the calculation was derived from a length-based calculation of the von Bertalanffy growth parameters from length frequencies for the years 1990–1995 (Sparre and Venema 1992). A new set of parameters was estimated using the cohort-slicing method for the 0-II+ year-classes. This allowed calculation of the growth parameters based on length-at-age data from six year-classes (Von Bertanlanffy 1934).

These empirical methods of estimating *M* are all subject to considerable error, resulting from the impact on *M* of other variables not included in the model, and the results are therefore imprecise. However, they frequently provide the only available estimates of *M* for a stock and, in this study, are considered sufficiently informative to complement the estimates from the other methods.

RESULTS

Age distribution

Age determination of fish showed fish up to 10 years of age during the 1950s and 1960s (Le Clus *et al.* 1988). This was reduced to 5 or 6 age-classes by the

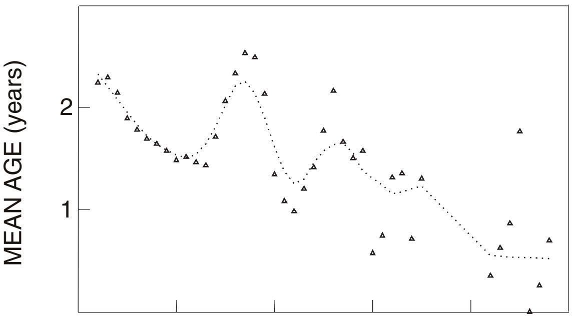

Fig. 4: Estimates of the mean age of the population each year, 1952–1999 (smoothing based on raw data – Clevland 1979). Data prior to 1985 after Thomas (1986)

mid 1970s (Le Clus *et al.* 1988) and, by the end of the 1980s, only a small proportion of the population was aged three years or older (Hewitson and Gilles unpublished, cited in Boyer *et al.* 1997). Splitting the length frequencies indicates few sardine two years of age or older during the 1990s.

On average, the proportion of 0-group fish in the population was higher during the last two decades than in earlier decades (t = -3.49, df = 43, p = 0.001), indicating a reduction in longevity (Fig. 3). The mean proportion of 0-group in the stock before 1980 was 0.406 (SE = 0.021, CV = 0.279), and after 1980, 0.596 (SE = 0.061, CV = 0.422), indicating an increase in the proportion of 0-group fish in the stock by 50%. Although the proportion of 0-group fish in the stock was stable during the early years of the fishery, it started to fluctuate widely after the stock collapsed in the mid 1970s, largely because of the small stock size and the fluctuations in recruitment after the collapse (Fig. 3). The estimated proportion of 0-group fish in the stock matched the proportion of 0-group fish observed in landings between 1970 and 1988. During the 1990s, restrictions on catching 0-group fish were introduced (Boyer *et al.* 2001).

The estimated mean age of the sardine stock has been highly variable from year to year (particularly post-1970), again as a result of low abundance and recruitment variability. If the decrease in mean age reflects actual changes in stock dynamics, it may indicate reduced lifespan (Fig. 4). It should be noted that, by calculating mean age for the period before 1990, using the same formula as used post-1990, the differences between the two series are less pronounced.

Mortality

When M was calculated for different age-classes between surveys, the estimates varied between -0.6 and 4.72 year^{-1} (mean = 1.74, SD = 1.24, n = 35), suggesting a high average M. The variability around this mean may be a result of the survey variance, or a reflection of a varying M, or perhaps both.

The estimated total biomass from the simulation model followed the trend of total biomass estimated by the surveys (Fig. 5). The simulation predicts that, with a Z of 0.5 year^{-1}, the biomass of the stock would have fluctuated around a million tons during the 1990s and, even with a total Z of 0.8 year^{-1}, the model predicts a biomass about twice the size of the acoustic estimates. Using a value of Z of 1.2 year^{-1} resulted in the predicted biomass being still above but much closer to the observed values. A Z of 1.44 year^{-1} gave the best fit to the survey estimates. Assuming that F was kept at 0.2 (Boyer *et al.* 2001), the simulation model consequently indicates an average M of some 1.2 year^{-1}.

The theoretical calculations of M are in line with the other indications and suggest an M between 0.77 and 2.38 year^{-1}, with an average of 1.15 and 1.51 year^{-1} for the two sets of input data (Table I).

DISCUSSION

Age distribution

Knowledge of the age structure of a fish stock is crucial to producing the best possible advice on management. However, age determination is often difficult, and knowledge of its accuracy and precision is lacking for most species (Beamish and McFarlane 1983). The northern Benguela sardine is no exception. With the current few age-classes in the stock, it seems reasonable to assume that splitting length frequencies would provide an accurate indication of the overall age structure of the stock (Thomas 1985, Kerstan 1997, Boyer *et al.* 2001).

From age determination exercises on otoliths prior to 1985 and splitting of length frequencies in the 1990s, there is a clear but steady decrease in the number of age-classes in the stock. Although age determination is expected to be inaccurate especially among older age-classes, this steady and marked decrease is believed, at least to some extent, to reflect actual changes in the age composition of the population.

The observed changes in the number of age-classes present in the stock, the proportions of 0-group fish

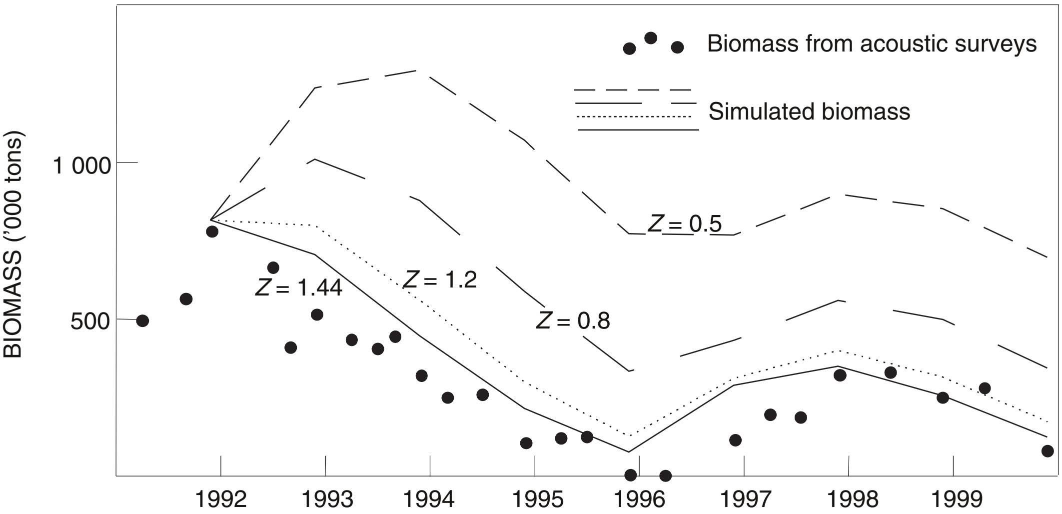

Fig. 5: Total sardine biomass estimated from acoustic surveys, and levels of biomass simulated using annual recruitment and values of total mortality (*Z*) of 0.5, 0.8, 1.2 and 1.44, 1991–1999

and the calculated mean annual ages together indicate a marked decline in longevity over the past four decades (Thomas 1986, Le Clus *et al.* 1987). The result is in line with the observation of strong year-classes only resulting in greater biomass for short periods of 1–2 years during the 1990s (Boyer *et al.* 2001).

Mortality

In most situations, precise estimation of total mortality is difficult (Pitcher and Hart 1982). Owing to the importance of this parameter in fish stock assessment, estimates often have to be made with inadequate information. Methods used to estimate natural mortality are, in particular, sensitive to the accuracy of abundance estimates or other biological parameters used in the calculation. A high level of survey precision is therefore critical if mortality estimates are to be based on survey data. Barange *et al.* (1996) indicated that the target strength used during acoustic surveys of southern African sardine might be 1.5 dB too low. If those authors are correct, this would mean that the survey results used for analysis of northern Benguela sardine would overestimate stock size by at least 30%. Although this would not affect the estimation of total mortality, it would increase the proportion of the total mortality attributable to fishing compared to that attributable to natural causes. However, most other biases in the survey estimates, notably signal attenuation in dense schools, vessel avoidance and fish lying outside the survey area, are negative and hence would (at least partially) compensate for any overestimate caused by an incorrect target strength.

The between-survey estimates of mortality suggest a higher *M* in the 1990s than in previous decades. This was supported both by simulating stock biomass and by theoretically calculating *M*. Some variation between the methods was observed, but all suggested an $M > 1.0$ year^{-1}. The observed change in age distribution agrees well with these findings. A natural mortality rate >1.0 year^{-1} is, however, high compared to other sardine stocks (Pauly 1980, 1983, Glazer and Roel 1996). Such a mortality rate would reduce the number of fish in an age-class by about 70% from one year to the next and would act as a strong force in determining the structure of the population (Stearns 1976, Cardinale and Modin 1999).

A number of other biological parameters are often linked to long-term changes in population abundance (Wootton 1990). Describing changes in different biological parameters might therefore help explain what caused the changes in abundance as well as showing how other stock parameters were influenced.

The relationship between spawner stock biomass (*SSB*) and the resultant recruitment can indicate the success of a given adult biomass in producing recruits (ICES 1997). *SSB*-recruitment data for the sardine

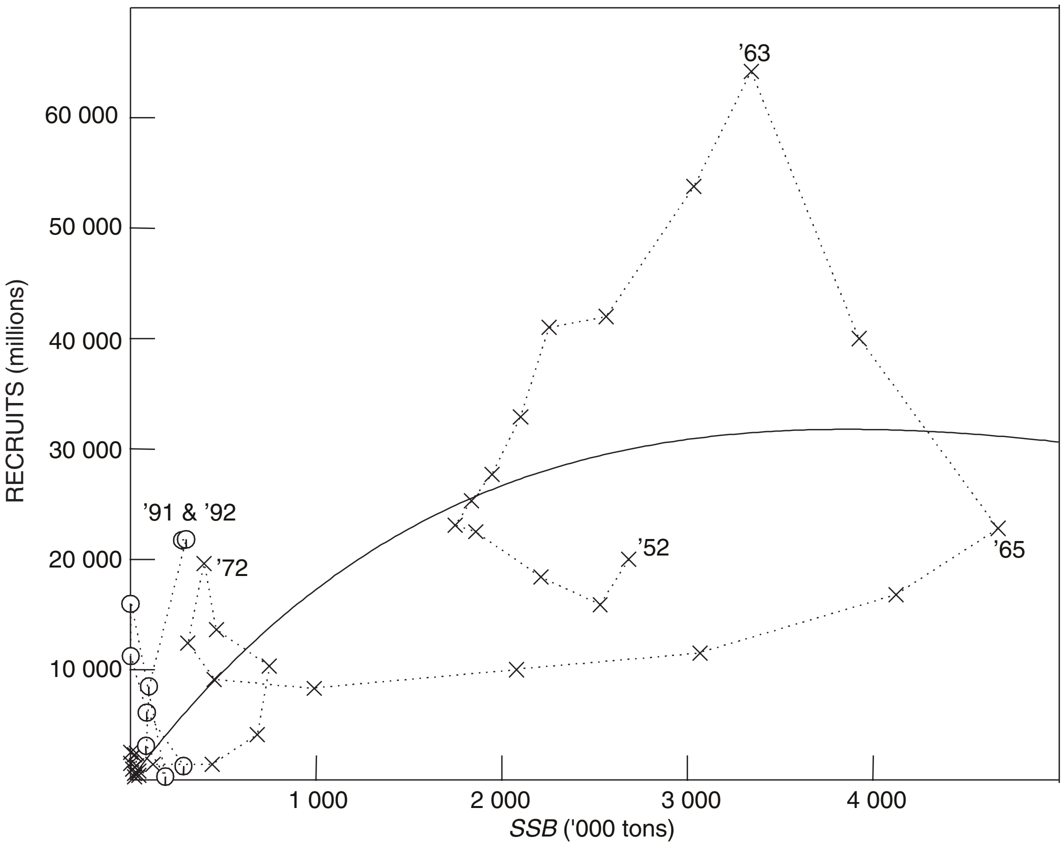

Fig. 6: Spawner stock biomass (II+ group) and resultant estimates of recruitment of northern Benguela sardine, 1952–1999. Data from the 1990s are shown as circles, and Ricker's spawner stock-recruitment relationship (Sparre and Venema 1992) is fitted to the data

stock in the northern Benguela are documented by Thomas (1986) for the period 1950–1985 and by Boyer *et al.* (2001) for the period 1990–2000. They are combined here to illustrate long-term changes in the relationship (Fig. 6). There seems to have been an overall reduction in recruitment since the 1960s, and particularly since 1975, when both recruitment and *SSB* were low. During several years of the 1990s, however, recruitment seems to have been relatively high compared to the estimated *SSB*.

In sardine, different sex ratios can be explained by females having the potential to grow older than males (Baird 1970, Thomas 1986). Thomas (1986) documented a change in the sex ratio of sardine catches from 1:1.8 in the 1950s to 1:1.2 during the 1970s. During the 1980s and 1990s the sex ratio was stable at between 1:1 and 1:1.2 in both surveys and catch (Thomas 1986, NatMIRC unpublished data). However, it is not possible to test the significance of these changes or to exclude the possibility of bias having been introduced by changes in the fishing pattern. Nevertheless, if this change in sex ratio reflects a real change in stock structure, it suggests a reduction in the longevity of the longer-lived female portion of the population. This further supports the contention of an increased rate of mortality over the past four decades.

Together with Pacific sardine *Sardinops sagax*, the northern Benguela sardine stock is among the few clupeiform populations that have failed to reach pre-exploitation biomass levels following a fisheries-induced collapse to a state where a few young age-classes now dominate the population. For Pacific sardine, Butler *et al.* (1996) suggested that the situation had been influenced by increase in natural mortality. In addition, age at maturity of the Pacific sardine dropped significantly after the population crashed (Butler *et al.* 1996), similar to the observation by Thomas (1986) for the northern Benguela sardine. Understanding how these changes are induced and how they affect production and abundance might bring management advisors closer to understanding the dynamics of both populations.

CONCLUSIONS

The estimates of biomass show marked reduction in sardine abundance since the start of the fishery (Fig. 1). A combination of excessive fishing and recruitment failure seems to have been the reason for the stock collapse in the 1960s and 1970s (Cram 1981). Since the mid 1970s, however, fishing mortality increased and was an important cause of mortality until 1990 (Thomas 1986). During that period, relatively large numbers of juvenile sardine were caught in the expanding anchovy *Engraulis capensis* fishery, and the total catches of sardine probably resulted in both growth- and recruitment-overfishing (Thomas 1986, Le Clus *et al.* 1987, 1988).

The changes in abundance, mean age and natural mortality have taken place gradually since exploitation started. Reduced recruitment success would also lead to lesser abundance, but it cannot explain changes in mean age, number of age-classes, increased natural mortality, or possible change in sex ratio. The most likely explanation for the reduced abundance seems to have been, at least partially, an increase in total mortality.

Except for a few years, there was a marked reduction in fishing mortality of northern Benguela sardine after 1990. However, by the end of the decade, the stock had shown no sign of real recovery (Boyer *et al.* 2001), so it can be concluded that other processes have prevented recovery of the stock. A possible change in growth rate would give an indication of whether or not the availability of food might control biomass. There are several indications of a density-dependent response, where the rate of growth seems to have increased after the stock collapsed, as shown by changes in length-at-age, weight-at-age, condition, age and size at maturity and changes in ovary weight over time (Thomas 1986, Le Clus 1990). Although there are several methodological problems in all of these comparisons (Thomas 1986), there are no indications that the present depleted state of the sardine stock was caused by scarcity of prey and hence reduced rate of growth. From 1970 until the end of the 1980s, the total biomass of sardine and anchovy was probably reduced by more than 90% (Le Clus *et al.* 1987, 1988, Boyer *et al.* 1997, 2001). Seeing the key role small pelagic species play in most marine systems, this reduction must have influenced the functioning of the ecosystem (Bakun 1996, Cury *et al.* 2000).

For many piscivores, small pelagic species often act as important sources of food (Crawford 1987, Young and Cockcroft 1994, Nilssen *et al.* 1995, Pillar and Wilkinson 1995, Cury *et al.* 2000). Owing to reduced abundance during the past three decades, less food has been available to the predators of small pelagic fish species in the northern Benguela. The shortage resulted in mass starvation of Cape fur seals *Arctocephalus pusillus pusillus* and bank cormorants *Phalacrocorax neglectus* during 1994 and 1995 (Roux 1998, Cury *et al.* 2000). However, a reduction of available prey will also increase predation pressure on the remaining individuals (Wootton 1990).

Normally, it can be assumed that, if predation were to bring a stock down, it would be followed quickly by a reduction in the number of predators, allowing the prey species to recover as a consequence of their shorter life cycle. In the northern Benguela, the Cape fur seal is one of the major top predators of pelagic fish (Wickens *et al.* 1992). The seal population was close to extinction in the early 1900s (David 1989), but it increased to about a million individuals by the mid 1990s (David 1997). Together with indications of species replacement (e.g. by horse mackerel *Trachurus trachurus capensis*) after the sardine stock crashed (Boyer *et al.* 2001), such a growth rate in a predator population may provide some explanation of why the rate of mortality of sardine has escalated over a longer time period.

Different explanations for the failure of the sardine stock to recover have been proposed (Beckley and van der Lingen 1999, Schwartzlose *et al.* 1999, Boyer *et al.* 2001). The orders of magnitude in the fluctuations in population size of northern Benguela sardine indicate that the system may have gone through a regime shift, as described for other sardine populations (Jacobson and MacCall 1995, Wada and Jacobson 1998). Originally it might well have been a "wasp-waist" or "bottom-up" system, in which sardine acted as controller of both predator and prey or where sardine abundance was controlled by lower trophic levels respectively (Bakun 1996, Cury *et al.* 2000). Indications of increased natural mortality at the present low level of biomass, however, indicate that sardine are now more heavily controlled by predation, i.e. subject to top-down regulation.

Both literature and the results in this study suggest that changes in biological parameters have been driven by the reduction in sardine abundance caused by overall increase in total mortality. The fishing pressure during the past four decades has been at least one of the reasons for the increased total mortality. Whereas high fishing pressure contributed to the stock collapse and low abundance during the 1970s and 1980s, mortality rates at present seem to be controlled mainly by other factors. The low biomass of sardine compared to previous levels is believed to make the population more vulnerable to predators. This may explain why the rate of natural mortality has increased and remained above historic levels.

Effort should be made to describe the controlling factors of natural mortality so that an understanding of the underlying mechanisms can be obtained (Hollowed *et al.* 2000, Boyer *et al.* 2001). If the indications of this study prove correct, the present level of mortality is likely to reduce permanently the available yield from the stock, and also reduce the likelihood of recovery even in a fishery moratorium situation.

The implications for management might therefore be to evaluate other possibilities for inducing recovery of the sardine. An option could be to introduce tighter controls, perhaps through multispecies management options, until the mechanisms controlling the rate of mortality are better understood, and the population, with or without human interference, is able to stabilize at a higher biomass.

ACKNOWLEDGEMENTS

We thank Dr A. Kreiner and Ms H. J. Boyer of the National Marine Information and Research Centre (NatMIRC) for their input into this work. Numerous discussions helped to clarify the issues presented, although any errors in the results and conclusions remain those of the authors. Drs I. Huse (DG Fisheries, European Union, Brussels) and K. L. Cochrane (F.A.O., Rome) plus two anonymous reviewers are also thanked for their useful comments on the draft manuscript.

LITERATURE CITED

AGNALT, A-L. 1995 — An attempt to validate the ageing of southern African pilchard (*Sardinops ocellatus*) caught off Namibia using back-calculation. Unpublished report, Ministry of Fisheries and Marine Resources, Namibia: 24 pp. (mimeo).

ALAGARAJA, K. 1984 — Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J. Fish.* **31**: 177–208.

ARMSTRONG, M. J., ROEL, B. A. and R. M. PROSCH 1989 — Long-term trends in patterns of maturity in the southern Benguela pilchard population: evidence for density-dependence? *S. Afr. J. mar. Sci.* **8**: 91–101.

BAIRD, D. 1970 — Age and growth of the South African pilchard, *Sardinops ocellata*. *Investl Rep. Div. Sea Fish. S. Afr.* **91**: 16 pp.

BAKUN, A. 1996 — *Patterns in the Ocean*: *Ocean Processes and Marine Population Dynamics*. University of California Sea Grant Program, San Diego, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Mexico: 323 pp.

BARANGE, M., HAMPTON, I. and M. SOULE 1996 — Empirical determination of *in situ* target strengths of three loosely aggregated pelagic fish species. *ICES J. mar. Sci.* **53**: 225–232.

BEAMISH, R. J. and G. A. McFARLANE 1983 — The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**(6): 735–743.

BECKLEY, L. E. and C. D. VAN DER LINGEN 1999 — Biology, fishery and management of sardines (*Sardinops sagax*) in southern African waters. *Mar. Freshwat. Res.* **50**: 955–978.

BLAXTER, J. H. S. and J. R. HUNTER 1982 — The biology of the clupeoid fishes. *Adv. mar. Biol.* **20**: 1–223.

BOYER, D. C., BOYER, H. J., FOSSEN, I. and A. KREINER 2001 — Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment? In *A Decade of Namibian Fisheries Science.* Payne, A. I. L., Pillar, S. C. and R. J. M. Crawford (Eds). *S. Afr. J. mar. Sci.* **23**: 67–84.

BOYER, D. C., CLOETE, R., BOYER, H. and G. D'ALMEIDA 1997 — The recent collapse of the northern Benguela pilchard stock. In *Proceedings of an International Workshop on the Research and Management of Pilchard in Namibia, Swakopmund, Namibia, February 1997*. Swakopmund; Ministry of Fisheries and Marine Resources: 118–130.

BUTLER, J. L., GRANADOS G., M. L., BARNES, J. T., YAREMKO, M. and B. J. MACEWICZ 1996 — Age composition, growth, and maturation of the Pacific sardine (*Sardinops sagax*) during 1994. *Rep. Calif. coop. oceanic Fish. Invest.* **37**: 152–159.

BUTTERWORTH, D. S. 1983 — Assessment and management of pelagic stocks in the southern Benguela region. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 329–405.

CARDINALE, M. and J. MODIN 1999 — Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a period of large variations in stock size and environmental conditions. *Fish. Res.* **41**: 285–295.

CLEVLAND, W. S. 1979 — Robust locally weighted regression and smoothing scatterplots. *J. Am. stat. Assoc.* **74**: 829–836.

CRAM, D. L. 1981 — Hidden elements in the development and implementation of marine resource conservation policy: the case of the South West African/Namibian fisheries. In *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*. Glantz, M. H. and J. D. Thompson (Eds). New York; Wiley: 137–155.

CRAWFORD, R. J. M. 1987 — Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 735–757.

CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353–505.

CURY, P., BAKUN, A., CRAWFORD, R. J. M., JARRE, A., QUIÑONES, R. A., SHANNON, L. J. and H. M. VERHEYE 2000 — Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. mar. Sci.* **57**(3): 603–618.

DAVID, J. H. M. 1989 — Seals. In *Oceans of Life off Southern*

Africa. Payne A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 288–302.

DAVID, J. H. M. 1997 — Foraging behaviour of Cape fur seals: interactions with commercial trawlers. *Proceedings of an International Workshop on Research and Management of Cape Fur Seals in Namibia, Swakopmund, June 1997*. Unpublished report, Ministry of Fisheries and Marine Resources, Namibia: 54–55.

GLAZER, J. P. and B. A. ROEL 1996 — Estimation of basic population parameters for sardine. In *WOSAS – Workshop on Southern African Sardine.* Barange, M. and C. D. van der Lingen (Eds). *Rep. Benguela Ecol. Progm.* **29**: 81–82.

HOLLOWED, A. B., IANELLI, J. N. and P. A. LIVINGSTON 2000 — Including predation mortality in stock assessments: a case study of Gulf of Alaska walleye pollock. *ICES J. mar. Sci.* **57**(2): 279–293.

ICES 1997 — Report of the study group on the precautionary approach to fisheries management. *ICES Doc.* **CM 1997/Assess 7**: 41 pp. (mimeo).

JACOBSON, L. D. and A. D. MacCALL 1995 — Stock-recruitment models for the Pacific sardine (*Sardinops sagax*). *Can. J. Fish. aquat. Sci.* **52**: 566–577.

JENSEN, A. L. 1997 — Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters. *Can. J. Fish. aquat. Sci.* **54**(5): 987–989.

KERSTAN, M. 1997 — Annulus completion periods in sardine (*Sardinops sagax*) otoliths vary with age and year-class. *ICES Doc.* **CM 1997/BB:14**: 13 pp. (mimeo).

KERSTAN, M. 2000 — Estimation of precise ages from the marginal increment widths of differently growing sardine (*Sardinops sagax*) otoliths. *Fish. Res.* **46**: 207–225.

LE CLUS, F. 1990 — Spatial variability in the seasonal trends of ovary weight in the Namibian pilchard population, 1965 –1979. *S. Afr. J. mar. Sci.* **9**: 69–83.

LE CLUS, F., HEWITSON, J. D., MELO, Y. C., COOPER, R. M. and P. E. MALAN 1987 — The multispecies pelagic fishery off Namibia 1982–1986 and stock assessments for pilchard and anchovy. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **14**(2): 7–25.

LE CLUS, F., MELO, Y. C. and R. M. COOPER 1988 — Impact of environmental perturbations during 1986 on the availability and abundance of pilchard and anchovy in the northern Benguela system. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **15**(2): 49–70.

MacCALL, A. D. 1986 — Virtual Population Analysis (VPA) equations for nonhomogeneous populations, and family of approximations including improvements on Pope's cohort analysis. *Can. J. Fish. aquat. Sci.* **43**: 2406–2409.

MURPHY, G. I. 1977 — Clupeoids. In *Fish Population Dynamics.* Gulland, J. A. (Ed.). London; Wiley-Interscience: 283–308.

NEWMAN, G. G. 1970 — Migration of the pilchard *Sardinops ocellata* in southern Africa. *Investl Rep. Div. Sea Fish. S. Afr.* **86**: 6 pp.

NILSSEN, K., HAUG, T., POTELOV, V., STASENKOV, V. A. and Y. K. TIMOSHENKO 1995 — Food habits of harp seals (*Phoca groenlandica*) during lactation and moult in March–May in the southern Barents Sea and White Sea. *ICES J. mar. Sci.* **52**: 33–41.

PAULY, D. 1980 — On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. int. Explor. Mer* **39**(2): 175–192.

PAULY, D. 1983 — Some simple methods for the assessment of tropical fish stocks. *F.A.O. Fish. tech. Pap.* **234**: 54 pp.

PILLAR, S. C. and I. S. WILKINSON 1995 — The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. *S. Afr. J. mar. Sci.* **15**: 225–239.

PITCHER, T. J. and P. J. B. HART 1982 — *Fisheries Ecology*. London; Croom Helm: 414 pp.

RIKHTER, V. A. and V. N. EFANOV 1977 — On one of the approaches to estimating natural mortality of fish populations. *Trudy̅ AtlantNIRO* **73**: 77–85 (in Russian).

ROCHET, M. J. 1998 — Short-term effects of fishing on life history traits of fishes. *ICES J. mar. Sci*. **55**(3): 371–391.

ROUX, J-P. 1998 — The impact of environmental variability on the seal population. *Namibia Brief* **20**: 138–140.

SCHWARTZLOSE, R. A., ALHEIT, J., BAKUN, A., BAUMGARTNER, T. R., CLOETE, R., CRAWFORD, R. J. M., FLETCHER, W. J., GREEN-RUIZ, Y., HAGEN, E., KAWASAKI, T., LLUCH-BELDA, D., LLUCH-COTA, S. E., MacCALL, A. D., MATSUURA, Y., NEVÁREZ-MARTÍNEZ, M. O., PARRISH, R. H., ROY, C., SERRA, R., SHUST, K. V., WARD, M. N. and J. Z. ZUZUNAGA 1999 — Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. mar Sci*. **21**: 289–347.

SPARRE, P. and S. C. VENEMA 1992 — Introduction to tropical fish stock assessment. 1. Manual. *F.A.O. Fish. tech. Pap.* **306/1**(Rev. 1): 376 pp.

STEARNS, S. C. 1976 — Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**(1): 3–47.

THOMAS, R. M. 1985 — Growth rate of the pilchard off South West Africa, 1971–1983. *Investl Rep. Sea Fish. Res. Inst. S. Afr*. **128**: 41 pp.

THOMAS, R. M. 1986 — The Namibian pilchard: the 1985 season, assessment for 1952–1985 and recommendations for 1986. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **13**(2): 243–269.

VON BERTALANFFY, L. 1934 — Untersuchungen über die Gesetzlichkeiten des Wachstums. 1. Allgemine Grundlagen der Theorie. Roux'Arch. *Entwicklungsmech. Org*. **131**: 613–653.

WADA, T. and L. D. JACOBSON 1998 — Regimes and stock-recruitment relationships in Japanese sardine (*Sardinops melanostictus*), 1951–1995. *Can. J. Fish. aquat. Sci.* **55**: 2455–2463.

WALDRON, M. 1998 — Annual ring validation of the South African sardine *Sardinops sagax* using daily growth increments. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources.* Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* **19**: 425–430.

WICKENS, P. A., JAPP, D. W., SHELTON, P. A., KRIEL, F., GOOSEN, P. C., ROSE, B., AUGUSTYN, C. J., BROSS, C. A. R., PENNEY, A. J. and R. G. KROHN 1992 — Seals and fisheries in South Africa – competition and conflict. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 773–789.

WOOTTON, R. J. 1990 — *Ecology of Teleost Fishes*. London; Chapman & Hall: 404 pp.

YOUNG, D. D. and V. G. COCKCROFT 1994 — Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialization? *J. Zool., Lond.* **234**: 41–53.