Demographic effects on sardine reproduction

C.D. van der Lingen

Offshore Resources Research, Department of Agriculture, Forestry and Fisheries, South Africa; and
Marine Research Institute, University of Cape Town, South Africa; CarlVDL@daff.gov.za

Introduction

Stock/recruit relationships used for fisheries management have typically assumed that spawning stock biomass is proportional to reproductive potential (total egg production; Marshall 2009). However, several recent studies have questioned this assumption and suggested that the reproductive potential of a population (or sub-population) may not necessarily be proportional to its spawning biomass for both demersal (e.g. Marshall *et al*., 2003) and pelagic (e.g. Ganias *et al*., 2014) fish species, with spatial and temporal variability in population age, size and sex structure, and in female fish condition, maturity and fecundity being suggested as the major factors affecting proportionality or lack thereof (Scott *et al*., 2006). Many studies have reported that older and/or larger female fish make a larger *per capita* contribution to annual egg production than do smaller and/or younger fish. This is due to increases in relative fecundity (eggs.g^{-1}) with increasing female length for some species (e.g. Marshall *et al*., 2003 for Atlantic cod *Gadus morhua*), and a longer spawning season duration and higher frequency of spawning of larger fish compared to smaller fish for several batch-spawning species (Fitzhugh *et al*., 2012). This latter point applies to sardines (a batch-spawning species), since an increase in duration of the spawning season and in the spawning frequency of larger fish has been documented for *Sardinops sagax* off California (Clark, 1934), Namibia (Le Clus, 1989) and Chile (Claramunt and Herrera, 1994; Claramunt *et al*., 2007), for *Sardina pilchardus* off Portugal (Zwolinski *et al*., 2001; Ganias *et al*., 2003; Nunes *et al*., 2011), and for common sardine *Strangomera bentincki* off Chile (Cubillos and Claramunt, 2009). This indicates that the reproductive potential of larger female sardine will be more than that of smaller females, with le Clus (1989) reporting that the annual number of annual spawning events of Namibian sardine increased by 50-70% for each 1 cm increase in fish length.

Gonad maturation in clupeoids appears to be dependent to a large extent on stored energy, with Hunter and Leong (1981) estimating that approximately two-thirds of the energy required by northern anchovy *Engraulis mordax* for repeated spawning during the reproductive season was derived from lipid reserves. Hence the body condition of female fish before and during spawning will likely impact egg production; female Japanese sardine *Sardinops sagax* in good condition (higher muscle lipid levels) produced more eggs with higher yolk content than fish in poor condition (Morimoto, 1996). Similarly, the survival and hatching success of eggs of Baltic herring *Clupea harengus membras* were positively linked with female condition (Laine and Rajasilta, 1999). Therefore, lipid reserves in clupeoids impact on reproductive output and can be considered an important determinant of spawning success. This appears to also apply to demersal fish species too, with recruitment of Atlantic cod being partly dependent on parental condition as indexed by total lipid energy (Marshall *et al*., 1999).

Stock-specific assessment models presently used for the South African sardine population use 2+ biomass as an index of reproductive potential (SSB), but because of potential differences in demographic (length frequency) structure and fish condition between the two stocks, and interannual variability in these, a unit of 2+ biomass of western (or southern) fish may not produce the same number of eggs each year, and a unit of 2+ biomass of western fish may not produce the same number of eggs as a unit of 2+ biomass of southern fish. This document provides results from a preliminary analysis that uses Le Clus' (1989) observation of the effect of fish size on the number of spawning events for Namibian sardine, and a significant positive relationship between relative fecundity and length of South African sardine (van der Lingen et al., 2009), to assesses how inter-stock and interannual differences in length frequency distributions may impact estimated annual egg production (AEP) for the western and southern stocks. Stock-specific time-series of estimated AEP are then compared with survey-derived 1+ biomass estimates and stock-specific assessment model-estimated spawner biomasses (de Moor and Butterworth 2013). Possible age/size effects on sexual maturation and sex ratio, and effects of fish condition on egg production, will be examined subsequently.

Materials and Methods

The annual egg production (AEP) for each stock was estimated following the steps described in Table 1.

Table 1: Steps followed in estimating AEP for each sardine stock.

Step	Data, calculations and assumptions
1. Estimate number of mature females per CL class per year.	1. Annual, stock-specific, acoustically-weighted length frequency distributions (in numbers per 1-cm CL class) from spawner biomass surveys, 1994-2013. 2. Assume 1:1 sex ratio so divide numbers per length class by 2 to get number of females. 3. Assume all female sardine in the 16 cm CL class and above only are sexually mature.
2. Calculate annual egg production of an individual mature female per CL class.	1. Use $WBM = 0.011639*CL^{3.03155}$ (van der Lingen *et al.*, 2006) to estimate the average WBW of an individual in each CL class. 2. Calculate # eggs produced per spawn for each 1-cm CL class (16 cm and larger) using RF (# $eggs.g^{-1}$) = 33.38*CL – 257.16 (n=22, r2=0.2481, p<0.005; van der Lingen *et al.*, 2009) multiplied by the average WBM of an individual in each CL class. 3. Estimate the number of spawning events per year for each 1-cm size class assuming that female sardine in the 16 cm CL class spawn 5 times per year and that the number of spawns increases by 50% per 1 cm increase (Le Clus, 1989; applying this means that a 22cm sardine will spawn 57 times per year). 4. Calculate the AEP of an individual female in each CL class by multiplying the # eggs produced per spawn by # spawning events.
3. Estimate stock-specific AEP	5. Multiply the number of mature females per CL class by estimated annual individual AEP to determine AEP per CL class. 6. Sum AEP for all mature females.

Results

Examples of three annual, stock-specific mature (16 cm CL or larger) female length frequency distributions and estimated AEP per CL class of those mature females are shown in Figure 1. These plots emphasize the increased reproductive output of larger fish relative to smaller ones when size-based effects are used to estimate AEP.

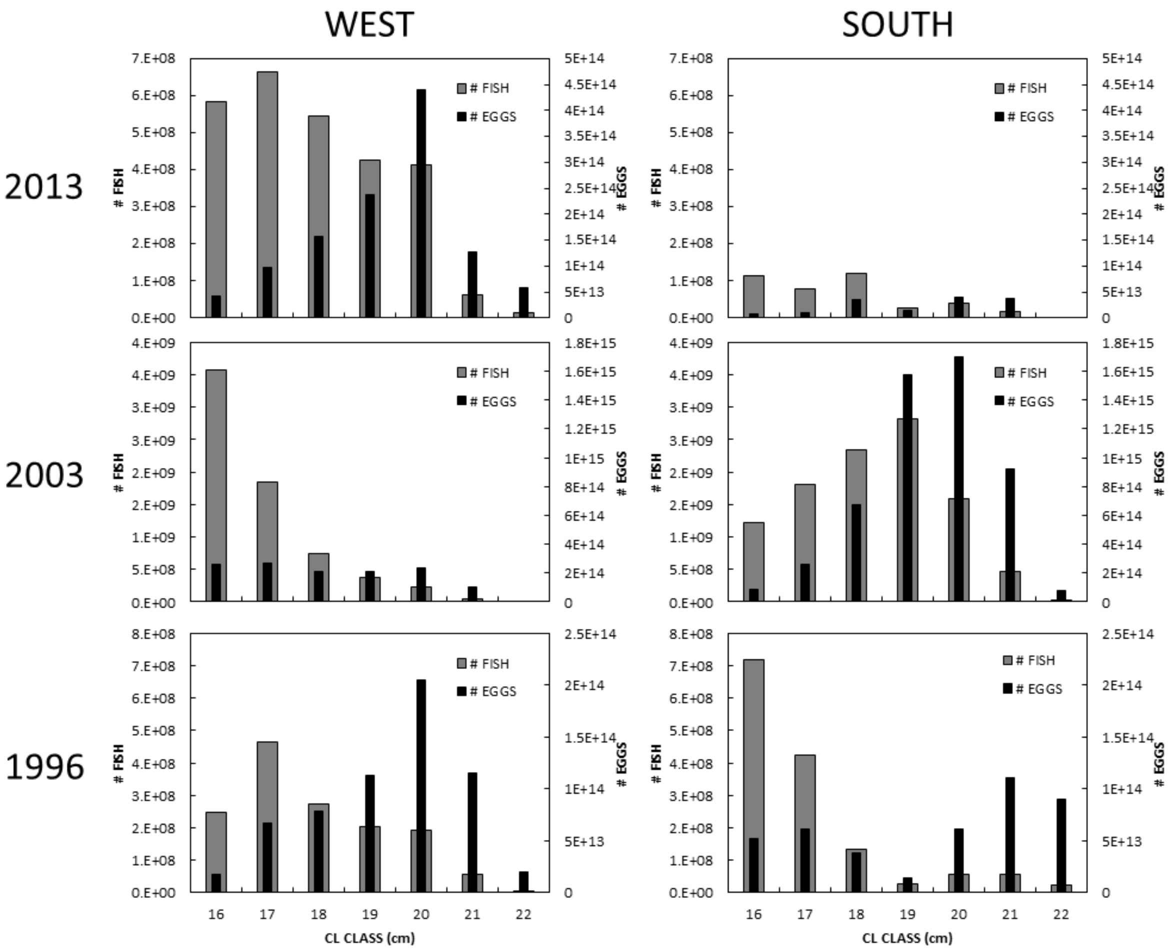

Figure 1: Number of female fish (wide grey histograms) and estimated AEP (narrow black histograms; # of eggs produced) per length class of mature fish for western (left) and southern (right) stock sardine in 2013, 2003 and 1996.

Figure 2 shows a time-series of estimated total AEP for the western and southern sardine stocks over the period 1994-2013 and compared to survey-estimated 1+ biomass (courtesy J. Coetzee) and assessment-model estimated 2+ (spawner) biomass (courtesy C. de Moor) time-series. Overall there is reasonably good correspondence between the estimated total AEP and the both biomass time-series for both stocks; for the western stock all three indices were high over the period 1987-2003 and subsequently low (except for 2013), and for the southern stock all three indices were high over the period 1999-2005 and again in 2011, but low in other years..

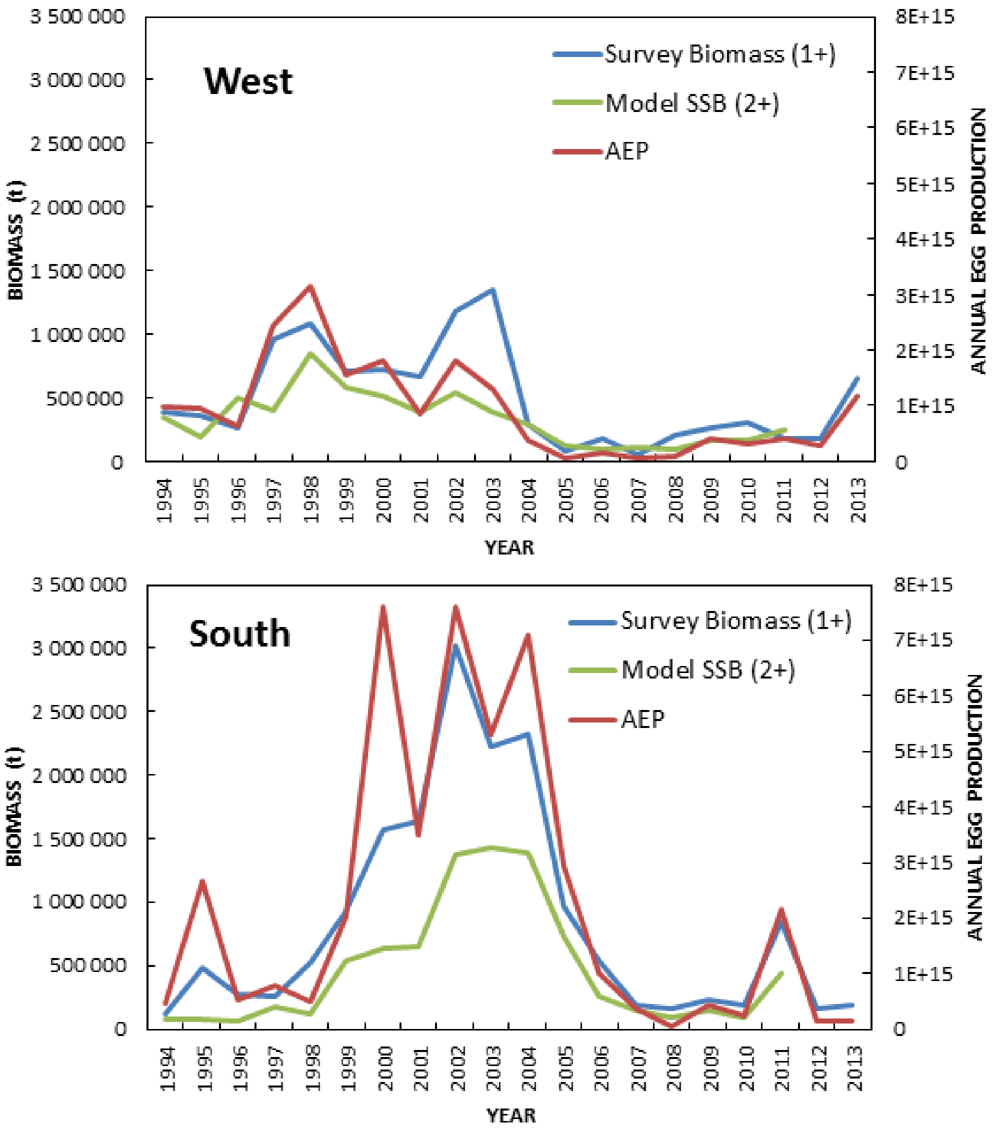

Figure 2: Time-series of survey-estimated 1+ biomass (blue lines), model-estimated 2+ (SSB) biomass (green lines) and estimated annual egg production (red lines) for sardine from the putative western (upper plot) and southern (lower plot) stocks.

Scatterplots of estimated total AEP and model-estimated 2+ (SSB) biomass for sardine from the putative western and southern stocks are shown in Fig. 3a. Significant ($p<0.001$) positive linear regressions between estimated total AEP and 2+ biomass are apparent for both stocks and goodness of fit (r^2) values for the fitted linear regressions are similar (0.75) for both stocks. Annual egg production per unit SSB appears to be higher for sardine from the southern stock than those from the western stock. AEP residuals (calculated as observed-predicted) are shown in Fig 3b. For western sardine, estimated AEP was markedly higher than predicted (using the regression equations given in Fig. 3a) in 1995 and in 2000-2002, and lower than predicted in 2003. For southern sardine estimated AEP showed less absolute variation from predicted levels, with the highest positive residual being for 1997 and the lowest negative residual for 1996. Residuals for both stocks were small from 2006-2011.

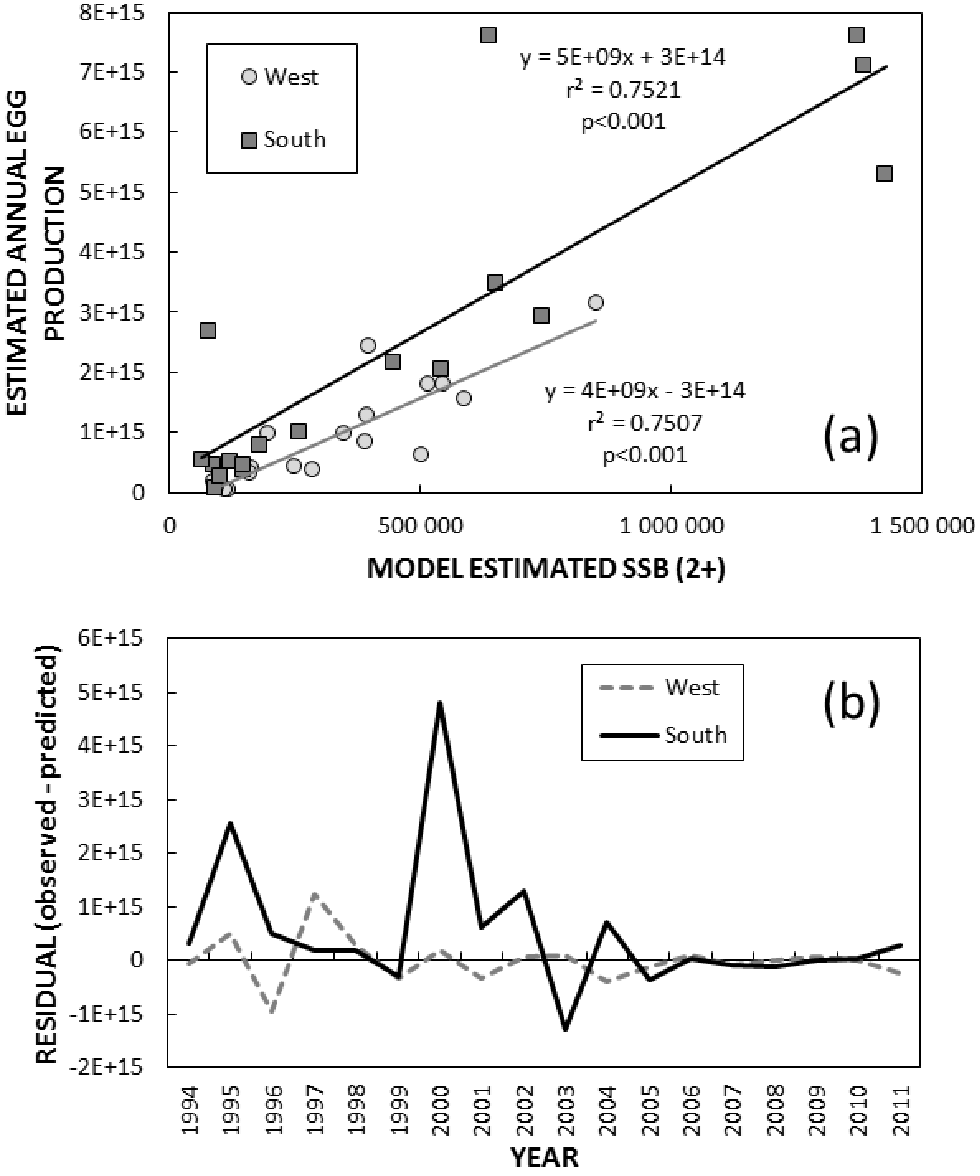

Figure 3: (a) Scatterplot of estimated annual egg production (AEP) and model-estimated 2+ (SSB) biomass for sardine from the putative western (dark grey squares) and southern (light grey circles) for the period 1994-2011 with fitted linear regressions, and their equations, r^2 values and significance levels shown; and (b) residuals (observed-predicted) AEP time-series for western and southern sardine.

Discussion

Total AEP of western and southern sardine stocks was estimated over the time period 1994-2013 using a simple approach that assumed a knife-edged sexual maturity (at 16 cm) and combined survey-derived length frequency data with an increasing annual number of spawning events with fish size and a length-varied relative fecundity value for mature fish. As expected this approach resulted in estimated AEP being disproportionately higher for larger fish than smaller fish, as indicated in Fig. 1. Time-series of estimated total AEP and survey estimated 1+ biomass and assessment model-estimated 2+ (SSB) biomass were broadly similar. Estimated total AEP was significantly ($p<0.001$) correlated with model-estimated 2+ biomass for both western and southern sardine stocks, with the goodness of fit values for the fitted linear regressions being 0.75 for both stocks. Despite these similar r^2 values there appears to be more variability in the residuals for the southern sardine stock than for the western stock. Total AEP per unit 2+ biomass appears to be higher for fish off the south than the west coast, possibly as a result of larger fish being more abundant in the south than the west in most years, but also possibly arising from other biological differences between fish from the two stocks.

Total EAP estimated in this analysis was significantly correlated with 2+ biomass estimated by stock-specific assessment models, but there were some large differences between the two time-series in some years, particularly for sardine from the southern stock in the early-2000s. These differences may indicate that "….the size structure of the spawning biomass can influence recruitment in ways that are not properly accounted for using SSB as the sole measure of reproductive potential." (Nunes *et al*., 2011), since "…the same weight of young fish (smaller) and old fish (bigger) do not have the same reproductive contribution, consequently the spawning stock biomass is not an accurate measure of reproductive potential" (Claramunt *et al*., 2007). Hence incorporating the effects of fish size on sardine reproductive biology could lead to improved stock-specific stock-recruit relationships developed for South African sardine, as has been found in other studies. Fitzhugh *et al*., (2011) reported that "for fishes with indeterminate or uncertain fecundity type, age (size) dependence in the annual number of batches is more common than age invariance and that this dependence merits consideration in population models." Similarly, Morgan *et al*., (2011) reported that stock-recruit models paired with complex indices of reproductive potential gave a better estimate of recruitment in more than half of the tests conducted on several demersal fish species.

Additional points to consider for incorporation should this approach be taken further include:

1. Adding more realistic estimations of the size at sexual maturity of sardine (e.g. using annual maturity ogives from observations on commercial catch and research survey samples (see van der Lingen *et al.,* 2009), and how this may vary with biomass (see van der Lingen *et al*., 2006);
2. Incorporating an index of fish condition (e.g. relative weight) which shows significant interannual variation (Ndjaula *et al.* 2014) from observations on commercial catch and research survey samples; and
3. Determining sex ratios per size class from observed data to assess whether this changes significantly with length and if so incorporate into analysis.

References

Claramunt, G. and G. Herrera. 1994. A new method to estimate the fraction of daily spawning females and the numbers of spawnings in *Sardinops sagax* in northern Chile. *Sci. Mar. Espafia* **58(3)**: 169-177.

Claramunt, G., Serra, R., Castro, L.R. and L. Cubillos. 2007. Is the spawning frequency dependent on female size? Empirical evidence in *Sardinops sagax* and *Engraulis ringens* off northern Chile. *Fish. Res*. **85**: 248-257.

Clark, F.N. 1934. Maturity of the California sardine (*Sardina caerulea*) determined by ova diameter measurements. *Calif. Fish Game* **42**: 49 p.

Cubillos, L.A. and G. Claramunt. 2009. Length-structured analysis analysis of the reproductive season of anchovy and common sardine off central southern Chile. *Mar. Biol.* **156**: 1673-1680.

de Moor C.L. and D.S. Butterworth. 2013. Assessment of the South African sardine resource using data from 1984-2011: results for a two stock hypothesis at the posterior mode. FISHERIES/2013/AUG/SWG-PEL/20, 45pp.

Fitzhugh, G.R., Shertzer, K.W., Kellison, G.T. and D.M. Wyanski. 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fish. Bull*. **110**: 413-425.

Ganias, K., Somarakis, S., Machias, A. and A.J. Theodorou. 2003. Evaluation of spawning frequency in a Mediterranean sardine population *Sardina pilchardus sardina*. *Mar. Biol*. **142**: 1169-1179.

Ganias, K., Somarakis, S. and C. Nunes. 2014. Reproductive Potential. In: Ganias, K. (Ed.). *Biology and Ecology of Sardines and Anchovies*. CRC Press, pp. 79-121.

Hunter, J.R. and R.J.H. Leong. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. *Fish. Bull.* **79(2)**: 215–230.

Laine, P. and M. Rajasilta. 1999. The hatching success of Baltic herring eggs and its relation to female condition. *J. Expl. Mar. Biol. Ecol*. **237**: 61–73.

Le Clus, F. 1989. Size-specific seasonal trends in spawning of pilchard *Sardinops ocellatus* in the northern Benguela system, 19073/74. S*. Afr. J. Mar. Sci.* **8**: 21-31.

Marshall, C.T. 2009. Implementing information on stock reproductive potential in fisheries management: The motivation, challenges and opportunities. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A. and E. Moksness (Eds). *Fish Reproductive Biology: Implications for Assessment and Management*. Wiley Blackwell, pp. 395-420.

Marshall, C.T., O'Brien, L., Tomkiewicz, J., Koster, F.W., Kraus, G., Marteinsdottir, G., Morgan, M.J., Saborido-Rey, F., Blanchard, J.L., Secor, D.H., Wright, P.J., Mukhina, N.V. and H. Bjornsson. 2003.

Developing alternate indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *J. Northw. Atl. Fish. Sci.* **33**: 161-190.

Marshall, C.T., Yaragina, N.A., Lambert, Y. and O.S. Kjesbu. 1999. Total lipid energy as a proxy for total egg production by fish stocks. *Nature* **42**: 288–290.

Morgan, M.J., Perez-Rodriguez, A and F. Saborido-Rey. 2011. Does increased information about reproductive potential result in better prediction of recruitment? *Can. J. Fish. Sci.* 68(8): 1361-1368.

Morimoto, H. 1996. Effects of maternal nutritional conditions on number, size and lipid content of hydrated eggs in the Japanese sardine from Tosa Bay, southwestern Japan. In: Watanabe, Y., Yamashita, Y. and Y. Oozeki (Eds.). *Survival Strategies in Early Life Stages of Marine Resources*. Rotterdam, A. A. Balkema, pp 3–12.

Ndjaula, H.O.N., Gerow, K.G., van der Lingen, C.D., Moloney, C.L., and A. Jarre. 2013. Establishing a baseline for evaluating changes in body condition and population dynamics of sardine (*Sardinops sagax*) in the southern Benguela ecosystem. *Fish. Res*. 147: 253-263.

Nunes, C., Silva, A. Marques, V. and K. Ganias. 2011. Integrating fish size, condition, and population demography in the estimation of Atlantic sardine annual fecundity. *Cienc. Mar.* **37(4B)**: 565-584.

Scott, B.E., Marteinsdottir, G.,Begg, G.A., Wright, P.J. and O. Kjesbu. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecol. Model*. **191**: 383-415.

van der Lingen, C.D., Freon, P., Fairweather, T.P. and J.J. van der Westhuizen. 2006. Density-dependent changes in reproductive parameters and condition of southern Benguela sardine *Sardinops sagax*. Afr. J. Mar. Sci. **28(3&4)**: 625–636.

van der Lingen, C.D., Durholtz, M.D., Fairweather, T.P. and Y. Melo. 2009. Spatial variability in biological characteristics of southern Benguela sardine and the possible existence of two stocks. MCM/2009/SWG-PEL/39, 21pp.

Zwolinski, J., Stratoudakis, Y. and E. Soares. 2001. Intra-annual variation in the batch fecundity of sardine off Portugal. *J. Fish Biol.* **58**: 1633-1645.