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Assessing the South African sardine resource: two stocks rather than one?

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Sardine *Sardinops sagax* distributed off the west and south coasts of South Africa have traditionally been assumed to comprise a single well-mixed stock for assessment and management purposes. New research, however, lends weight to the possibility of two stocks in this region. A precautionary management approach thus needs to consider the impact of management decisions on the hypothesised two individual stocks as well as on the resource as a whole. As a first step in this process, Bayesian assessments of South African sardine are presented, which compare results for the traditional single-stock hypothesis with those that follow from a new two-mixing-stock hypothesis. Recruits from the west stock are assumed to move to and remain part of the south stock in annual pulses of varying size. This movement is estimated to be appreciable, and to take place from a substantially more productive west stock to the south stock. This immigration makes a greater contribution to the south-stock biomass than do years of above-average south-stock recruitment. Importantly, this two-mixing-stock hypothesis is shown to be consistent with the data available. Further alternative sardine stock-structure hypotheses suggested by the most recent data are discussed.

Keywords: assessment, multiple stocks, *Sardinops sagax*, stock structure, two-mixing-stock hypothesis

Online supplementary material: Supplementary material containing further results and discussion can be found online at http://dx.doi.org/10.2989/1814232X.2015.1009166.

Introduction

A major commercial fishery for sardine *Sardinops sagax* off South Africa commenced in 1943 during World War II in response to a demand for canned fish. Such short-lived species with highly variable recruitment typically experience large fluctuations in abundance and catch landings (e.g. Soutar and Isaacs 1969; Baumgartner et al. 1992; Schwartzlose et al. 1999). This fishery has exhibited these features with two 'booms': the first in the early 1960s when annual landings peaked at over 400 000 t in 1961–1962 (Butterworth 1983), and the second at the turn of the 21st century when landings were permitted to peak at over 250 000 t in 2002–2004 as surveys had indicated the presence of some particularly strong year classes (de Moor and Butterworth 2009). In both cases catches dropped sharply after these peaks – in the second instance this was a regulatory response to surveys showing successive years of poor recruitment.

Sardine are caught by purse-seiners, which over recent decades have also targeted anchovy *Engraulis encrasicolus* and round herring *Etrumeus whiteheadi*, in a fishery that is the second most valuable in monetary terms in South Africa. Both anchovy and round herring have an associated sardine bycatch (Louw et al. 2014). The juvenile sardine bycatch with anchovy is non-negligible, increasing with the size of anchovy catch allowed, and consequently impacts the size of the directed adult sardine catches that can be permitted in subsequent years. The industry's preference is for adult sardine catches because they can be canned for direct human consumption; this provides a much higher profit margin than can be achieved for the rest of the catch, most of which is used to produce fishmeal. Because of the relationship between the allowable anchovy and adult sardine catches, the two species are managed jointly (De Oliveira and Butterworth 2004; de Moor et al. 2011).

Multiple biological populations of sardine are already known to exist in many regions worldwide, including the Benguela region where sardine are separated into northern (off southern Angola and Namibia) and southern (off South Africa) populations (Barange et al. 2009). As further advances in understanding sardine stock structure are made, assessment models for sardine resources are frequently adapted to test new findings. The northern subpopulation of Pacific sardine *Sardinops sagax*, for example, has recently been assessed with landings data by subpopulation apportioned using an environmental- rather than a port-based approach (Demer and Zwolinski 2014; Hill et al. 2014). Cunningham and Roel (2006) tested alternative hypotheses of stock structure and immigration/emigration to/from the assessment area following advances in understanding of *Sardina pilchardus* stock structure in the North-East Atlantic during the 'Sardine dynamics and stock structure in the North-eastern Atlantic (SARDYN)' project (Anon. 2006 and e.g. Silva 2003; Laurent et al. 2006).

Historically, the South African sardine resource has been assessed and managed as a single homogeneous fishery management unit, under the perception that the resource consists of a single biological population (e.g. de Moor and Butterworth 2009; de Moor et al. 2011). However, a boom in abundance at the turn of the 21st century and the almost-simultaneous eastward shift in the population prompted renewed research into the stock structure of sardine off the South African coast. In considering these changes in spawning distribution patterns, van der Lingen et al. (2005a, p 19) cautioned against the consequences of the depletion of a 'west coast sub-stock', if such existed. Coetzee et al. (2008a) observed that the sardine distribution was concentrated in two widely separated areas at low and medium (but not high) biomass levels, raising the possibility of the existence of two separate adult spawning aggregations. Furthermore van der Lingen et al. (2009) drew attention to the presence of distinct and separated western and southern spawning grounds. Van der Lingen (2011) subsequently reported differences in some morphometric and meristic data for sardine caught off the West and South coasts, demonstrating the possible existence of two functionally discrete subpopulations of sardine distributed off this region of South Africa. The overlap in other morphometric and meristic data is consistent with some limited mixing between these populations. Initial results showing differences in the prevalence, mean infection intensity and mean abundance of a parasite (considered to be of the genus *Cardiocephaloides*) have further strengthened the support for this multiple-stock hypothesis (van der Lingen 2011; Weston 2013; van der Lingen et al. 2015), which according to ICES (2011) would reflect a metapopulation.

Noting the difference in the catch-to-biomass ratio off the West and the South coasts, Coetzee et al. (2008a) raised a question of whether spatial management was required to make allowance for the possible existence of two separate biological populations. There have also been calls for spatial management of South African sardine in the interests of some natural predators of the species, such as the African penguin *Spheniscus demersus*, though these have tended to focus more on suggesting restricting purse-seine fishing in the near-vicinity of islands where these predators breed (as argued, for example, in Hamann et al. 2012 and Pichegru et al. 2012). However, as far as the status of the sardine resource is concerned, spatial management restrictions would make no difference if sardine comprise only one fully mixed biological population. Furthermore, predator foraging on a somewhat wider scale than the near-vicinity of islands would not be impacted unless the population mixes very slowly. However, if more than one biological population is present, but management proceeds under the assumption of a single fishery management unit, the potential for overexploitation of one or more of the populations if catches are not spread appropriately in space or time is well known (e.g. Kirkwood 1992, 1997; Kell et al. 2009; Kerr et al. 2014). There are already models of resources and their fisheries, some of which are quite complex, which take account of alternative hypotheses of population structure (e.g. Cunningham et al. 2007; Kell et al. 2009; Allison et al. 2014; Kerr et al. 2014).

Given the mounting evidence of the existence of more than one biological population of South African sardine, an alternative assessment of the sardine resource, treating it as two interacting biological populations rather than only one, is thus urgently required. As the fishery management unit(s) assessed are designed to match the biological population(s), they are referred to as 'stocks' for the remainder of this paper, in line with South African usage. This alternative assessment is necessary first to determine if a two-mixing-stock hypothesis is consistent with the data available. If so, operating models for both these stock-structure hypotheses will be needed when developing the operational management procedures (OMPs), which provide the basis for management recommendations for this fishery (de Moor et al. 2011). This process would need to address the impact of future management possibilities for the sardine resource, including spatial management options (e.g. some form of areal allocation in addition to the current global total allowable catch [TAC] to achieve more balanced levels of exploitation on the West and South coasts), which may prove necessary given these circumstances of a plausible two-stock hypothesis. Only in this way is it possible to assess whether and to what extent it might be necessary to amend the current single-stock management approach to ensure robust resource management performance whatever the true underlying stock structure.

This paper is the first attempt to assess the sardine resource under the assumption that it comprises two stocks (which also mix), using Bayesian analysis. The two-stock hypothesis considered in this paper assumes a 'west' and a 'south' stock distributed to the west and south-east of South Africa, respectively, and separated at Cape Agulhas (Figure 1) (Coetzee et al. 2008a; van der Lingen 2011). Clear evidence of recruits moving from the West to the South coasts at some time between May/June and November, as evidenced by survey length frequencies in some years (JC Coetzee, Department of Agriculture, Forestry and Fisheries, pers. comm.), excludes the hypothesis of two discrete stocks. Smith et al. (2011) considered information on differences in parasite loads, together with the presence of large differences in the length-at-50%-maturity between the West and the South coasts, to suggest that the extent of any movement of sardine of age 2+ would be likely to be low. Mixing between these stocks is thus assumed to occur by way of recruits moving to, and subsequently remaining as part of, the south stock. Assessment results are also presented here for treating the resource as a single homogeneous stock, to allow comparisons between the current status and productivity estimates for these alternative stock-structure hypotheses. Finally, we briefly discuss the potential of further data that are expected to become available in the near future to refine the stock-structure hypotheses that the paper considers.

Methods

Data

There are three primary types of data used in the assessment: (i) survey estimates of abundance; (ii) catches; and (iii) the length distribution information available from both these sources.

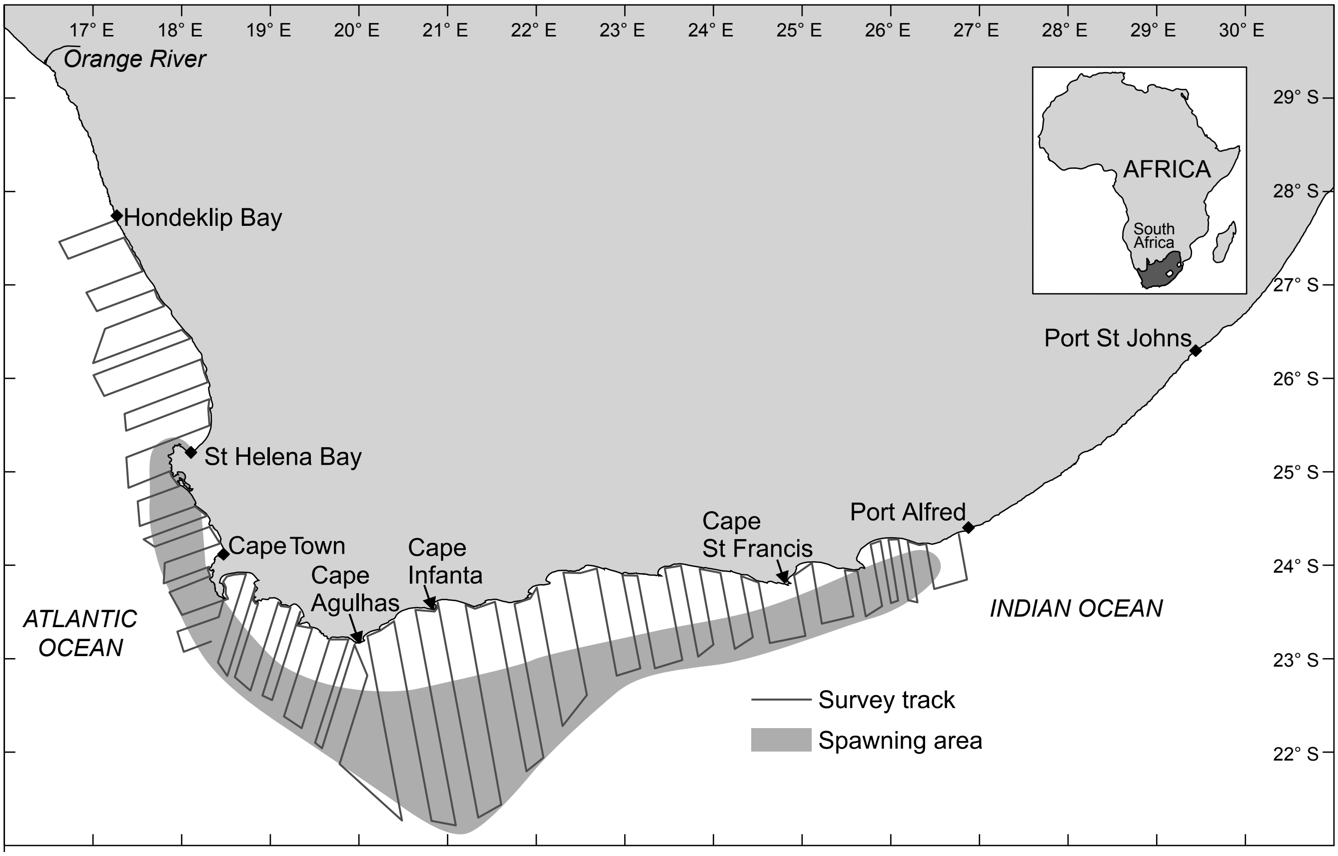

Figure 1: Map of South Africa showing the November 2011 survey track line

Two hydro-acoustic surveys have been undertaken each year since November 1984. The first takes place in November and surveys the adult biomass, whereas the second – known as the recruit survey – is in May/June and surveys juvenile (0-year-old) sardine (Coetzee et al. 2008b; de Moor et al. 2008). The standard November survey area extends from Hondeklip Bay on the West Coast to Port Alfred on the South Coast (Figure 1). The standard recruit survey extends from the Orange River on the West Coast to Cape Infanta on the South Coast, with surveys since 1999 frequently extending as far as Port Alfred or Port St Johns (Figure 1). These surveys are assumed to provide relative indices of abundance with a bias the size of which is unknown and which is assumed not to change over time, i.e. is time-invariant (see Supplementary Material, Section S3).

Sardine are landed by three major components of the fishery: the sardine-directed fishery that targets adults for canning, but also takes a bycatch of smaller sardine; the round herring-directed fishery that takes a bycatch of mainly adult sardine; and the anchovy-directed fishery that takes a bycatch of primarily juvenile sardine. For reasons explained in the methods section below, the assumption is made that all sardine caught by this anchovy-directed fishery that are smaller than a predetermined cut-off length, which varies by month and year, are 0-year-olds, and the larger sardine that constitute the remaining bycatch from this fishery are assumed to be 1-year-olds (de Moor et al. 2012).

Length frequencies from the November surveys and for the directed sardine catch and bycatch with round herring are available. Although some ageing has been undertaken, there are still numerous surveys and years with commercial catch otoliths available for which age-length keys have yet to be developed. Furthermore, concerns have been raised about the reliability of the available proportion-at-age estimates, because they fail to reflect traceability over time of cohorts that are known from the surveys to have been strong, suggesting problems with either ageing or the construction of survey length frequency data, or both (Smith et al. 2011). For this reason, age-structure data are not appropriate for use in the assessment. Whereas it could then be argued that one should not use the length-structure data either, it seemed desirable to make some use of size-composition data that might nevertheless be reliable at broad levels of information.

Assessment methods

The Bayesian assessment of South African sardine has developed from an age-structured production method framework, but also incorporates key elements of statistical catch-at-age and Integrated Analysis methods (ICES 2012; de Moor et al. in press).

The model is age-structured, and based on Pope's approximation (Pope 1972) with catch assumed to be taken in a pulse every quarter (Equation S1 of the Supplementary

Material). Natural mortality is time-invariant, but is accorded a higher value for 0-year-olds than for older fish (Table S2). A hockey stick stock-recruitment relationship is estimated for each stock (Equation S6). For the single-stock hypothesis, the extent of variation about this relationship is estimated to differ during the 'peak' recruitment years of 2000–2004 compared to the remaining years (Table S2).

Movement of west-stock juveniles to the South Coast likely occurs throughout the latter half of the year. However, for convenience of implementation, the model assumes that these recruits move in an annually varying pulse as they age in November each year (Equation S2). In order to avoid possibly biasing estimation of the annual proportions moving, the assessment estimates these proportions using independent uninformative prior distributions (Table S2), rather than assuming some relationship between movement and abundance or environmental factors.

Given the lack of proportion-at-age data, the assessment is fit directly to length frequency data. Numbers-at-age in the model are converted to numbers-at-length under the assumption of time-invariant length-at-age distributions (Equations S12 and S23). The associated matrix is calculated assuming that length-at-age is Normally distributed about a von Bertalanffy growth curve (Equations S13 and S24), with the standard deviation of this distribution estimated separately for ages 0, 1 and 2+ (Table S2). An additional advantage of this approach of fitting to length- rather than to age-structured data is that it is more realistic to assume that commercial selectivity is length- rather than age-specific, particularly in circumstances where the combination of the distribution of length-at-age coupled with age-specific selectivity inevitably predicts catches of fish at younger length than are observed. A bimodal selectivity-at-length relationship was selected for the combined directed sardine and round herring fisheries (Equation S17). This relationship was informed by an initial overparameterised assessment for which selectivity for each length class was estimated as a free parameter. The bimodality arises from the juvenile sardine bycaught with the targeted large sardine and round herring; the juveniles are readily available, though for a limited period only, on the West Coast. The selectivity is domed at larger lengths.

Because the November survey is designed to provide unbiased sampling from the whole population, trawl sampling selectivities during the survey are permitted to differ from 1 for only the smallest sardine (the minus length class) that are still recruiting to the resource at the time of the survey, and for the largest sardine (the plus length class) to allow for possible avoidance of trawls or emigration from the area surveyed by the oldest age groups. Uniform selectivity is assumed to apply to the biomass estimated from the acoustic signals detected during the survey (Equation S4).

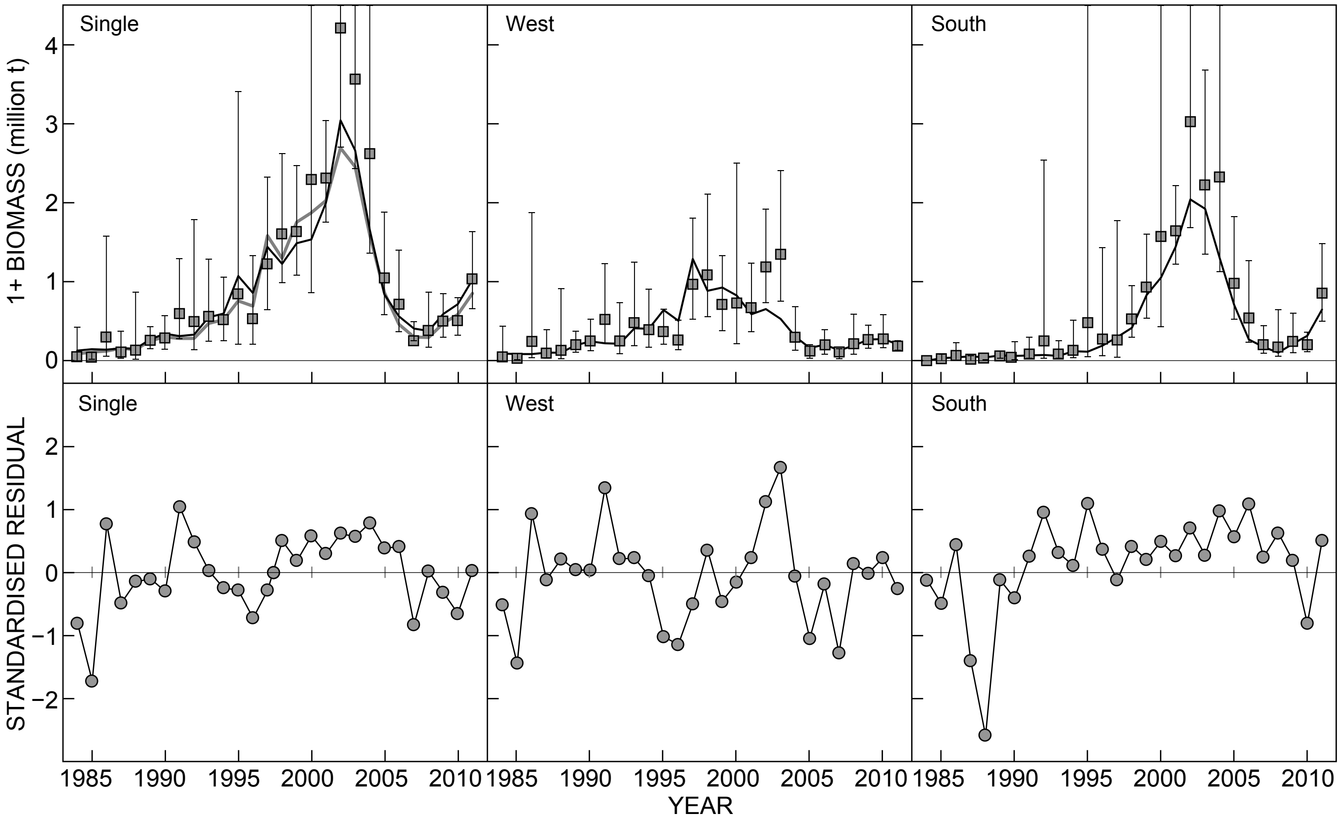

Figure 2: Acoustic survey estimated and associated model-predicted sardine 1+ biomass at the joint posterior mode from November 1984 to 2011 under both the single- and two-stock hypotheses. The observations are shown together with their 95% confidence intervals. The standardised residuals are given in the lower plots. The combined west- and south-stock biomass is shown by the grey line together with the biomass estimated under the single-stock hypothesis

The primarily juvenile bycatch from anchovy-directed fishing is considered separately from the directed sardine catch and the primarily adult bycatch with round herring. This bycatch depends on the amount of anchovy caught as well as on the fraction of juvenile sardine in anchovy shoals, rather than directly on (juvenile) sardine abundance alone. It would therefore not be appropriate to assume a time-invariant selectivity for this bycatch. Instead, this bycatch is separated into ages 0 and 1, as described in the data section, and is assumed to be known without error (Equation S19).

In formulating the likelihood function for the data for use in the Bayesian integration, the survey estimates of abundance and the survey and commercial catch estimated proportions-at-length are assumed to be lognormally distributed, with the variance of these proportions taken to be inversely proportional to the proportion observed (Punt and Kennedy 1997; Maunder 2011). The November survey estimates of abundance west/south-east of Cape Agulhas are taken to correspond to the west/south stocks. The recruit survey estimates of numbers of recruits west of Cape Infanta (Figure 1) are taken to reflect recruitment for the single-stock assessment, whereas values for west/south-east of Cape Infanta are assumed to correspond to the west/south stocks for the two-stock assessment. The November survey is assumed to cover the whole sardine distribution. However, since not all recruits are available by the start of the recruit survey, this is assumed to correspond to a proportion only of the recruit abundance (Equations S9 and S10). In addition, for the two-stock assessment, an estimate of the proportion of the south-stock recruit abundance covered by the recruit survey compared to that for the west stock is also required (Equation S11). This proportion is taken to be bounded above by 1 (Table S2) because winter spawning has been observed on the South Coast, but not on the West Coast. In addition, as the recruit survey is limited in its eastward coverage, it likely covers a smaller fraction of the south compared to the west recruits. Thus, the recruit survey likely underestimates the recruitment to the south stock to an even greater extent.

The Bayesian integration was implemented numerically using Markov Chain Monte Carlo (Gelman et al. 1995) in AD Model Builder (Fournier et al. 2012). Further details are provided in the Supplementary Material.

Results and discussion

The assessment model fits to the survey abundance data shown in Figures 2 and 3 are reasonably good. The underprediction by the model of the peak survey 1+ biomass and recruitment in the early 2000s is driven primarily by the need to fit the sharp decrease in abundance in subsequent years given time-invariant natural mortality. Similarly, the

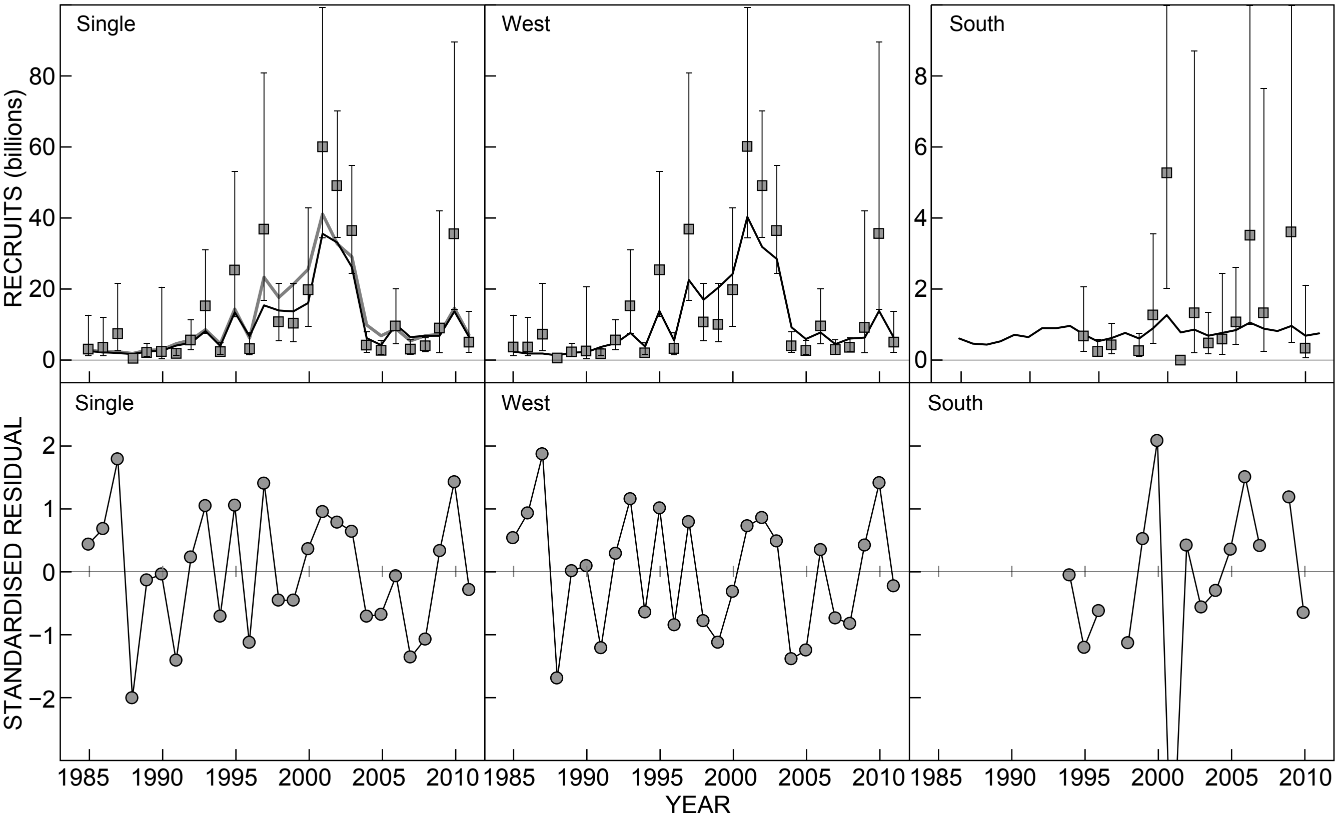

Figure 3: Acoustic survey estimated and associated model-predicted sardine recruitment at the joint posterior mode from May 1985 to 2011 under both the single- and two-stock hypotheses. The observations are shown together with their 95% confidence intervals. Note the scale of the vertical axis for the south stock is different from the others. The standardised residuals are given in the lower plots. The combined west- and south-stock recruitment is shown by the grey line together with the recruitment estimated under the single-stock hypothesis

model underpredicts the survey estimate of west/single-stock recruitment in 2010 as it is unable to reconcile the conflicting data of above-average recruitment in May 2010 with almost no increase in the November survey estimate of abundance from 2009 to 2010. Visually, the fit to the South Coast survey estimates of recruitment appears worse than the fits for the West Coast or the single stock. However, such a comparison fails to take account of the different CVs of these estimates. The standardised residuals do so, and show that all three fits are similar in quality. The one exception is for the South Coast in 2001, a feature discussed further in the Supplementary Material.

The bias associated with the November hydro-acoustic survey is estimated to be very similar for both stock-structure hypotheses, whereas the coverage of the recruit survey in comparison to that of the November survey is estimated to be higher under the two-stock hypothesis, i.e. the model estimates that the survey reflects a greater proportion of the true numbers of recruits under the two-stock compared to the single-stock hypothesis (see further discussion and Figure S3 of the Supplementary Material).

Expected recruitment to the west stock at high spawning biomass is an order of magnitude greater than that estimated for the south stock (Figure 4 and Figures S4 and S5). Importantly, however, average recruitment for the west stock declines for spawning biomasses below about 800 000 t, whereas, in contrast, the smaller average maximum recruitment to the south stock is impaired only if spawning biomass falls to extremely low levels. The stock-recruitment function for the single-stock hypothesis is similar to that for the west stock, but reflects a lower maximum expected recruitment. The variability about this single-stock relationship during the peak years of 2000–2004 is more than three times greater than that estimated for all other years (Table S1).

The assessment is configured to estimate recruit movement only for years for which the recruit surveys first extended sufficiently far eastwards to be able to provide survey estimates of recruitment for the south stock. As there is little information to estimate the movement of recruits precisely prior to 1994, movement is set at zero for those years (Table S2). Movement between the stocks from 1994 onwards is estimated to be substantial, and an average of over 50% of the west-stock recruits are estimated to move to the south stock in eight out of 18 years (Figure 5). The greatest proportions of west-stock recruits moving to the south stock are estimated to have occurred from the late 1990s to the early 2000s (contributing substantially to the peak in the South Coast biomass

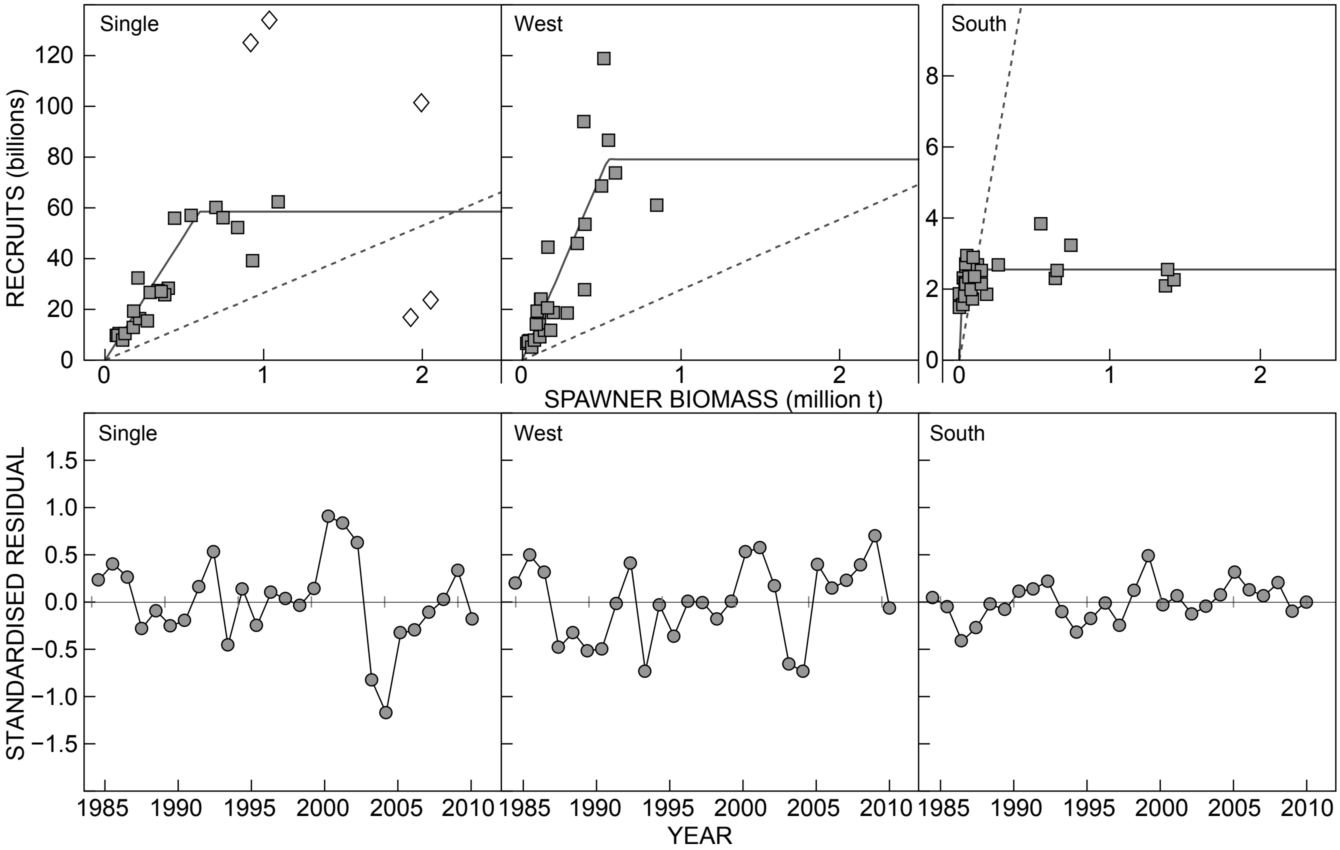

Figure 4: Model-predicted November sardine recruitment under both stock-structure hypotheses plotted against spawner biomass from 1984 to 2011 with the estimated hockey stick stock-recruitment relationships at the joint posterior mode. The open diamonds denote the peak years' (2000–2004) recruitments. The dotted line indicates the replacement line. Note the scale of the vertical axis for the south stock is different from the others. The standardised residuals from the fit are given in the lower plots

at that time), and then again at the end of the time-series.

These results indicate that under the two-stock hypothesis used in this analysis, the west stock is substantially more productive than the south stock, with the movement of west-stock recruits to the south stock having a greater impact on the south-stock biomass than years of above-average south-stock recruitment.

Given the restriction that survey selectivities were permitted to differ from 1 for the minus and plus length classes only, and only by a limited amount (Figure 6, see Table S2), the difference between the model-predicted and survey-estimated average November survey proportions-at-length are to be expected and are not extreme (Figure 7). The lower bound on the survey selectivity in the minus length class constrains the ability of the model to fit to the west-stock minus-length-class proportion.

A higher commercial selectivity is estimated for smaller lengths of the west and single stocks compared to the south stock (Figure 8). On average, the model-predicted commercial proportions-at-length match the general pattern observed, although the peak at the larger lengths is underpredicted (Figure 9). This mismatch appears to result from a conflict between data and model assumptions of time-invariant commercial selectivity. Under this assumption, this mismatch can be rectified only at the expense of a poorer fit to the more reliable survey indices of abundance. Allowing commercial selectivity to change over time proved a plausible alternative, reducing some non-random patterns in the residuals, but risked overparameterisation of the model (de Moor and Butterworth 2013).

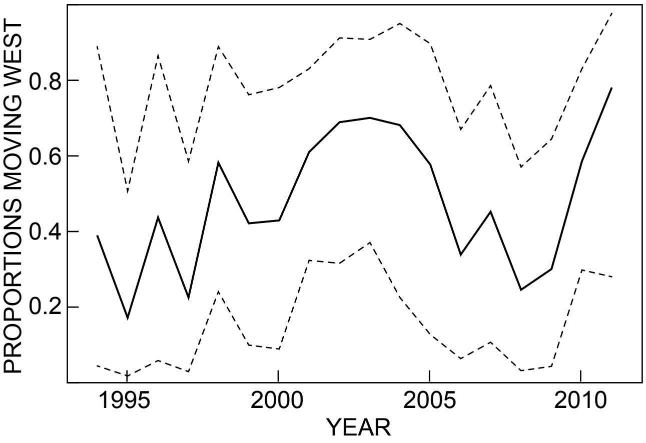

Figure 5: Posterior median and 95% probability intervals of annual proportions of recruits that move from the west to the south stock in November (prior to 1994, this movement is taken to be zero, given the lack of data to allow its estimation)

Concluding remarks

The posterior mean total South African sardine 1+ biomass in November 2011 is estimated to be 1.2–1.5 million tonnes, depending respectively on whether a two-mixing-stock or single-stock hypothesis is assumed. However, although this total biomass is indicated to be near its 1984–2011 average under both hypotheses, the posterior mean of the west-stock 1+ biomass is estimated to be about 400 000 t only under the two-stock hypothesis, about two-thirds of its 1984–2011 average. The west stock is estimated to be considerably more productive than the south stock, and much of the peak in the south-stock biomass at the turn of the 21st century is attributed by the two-stock assessment to recruits originating from the west stock. The current below-average west-stock abundance is thus of concern, given that this assessment estimates this stock's spawner biomass and recruitment to be the key 'feeder' to sardine on the South as well as the West coasts. The proportion of the west stock estimated to have been harvested increased during the late 1990s to early 2000s, reaching a maximum of 40% (compared to a maximum of 25% if the resource is considered as a whole). This occurred during the years when the population as a whole boomed, with high TACs being set in response. The resource has since suffered below-average recruitment in seven out of the last eight years of the time-series considered here. Although the south stock has experienced above-average recruitment in nine out of the last 13 years, with a posterior mean 1+ biomass of about 840 000 t in 2011, this recruitment is small compared to that possible from the west stock.

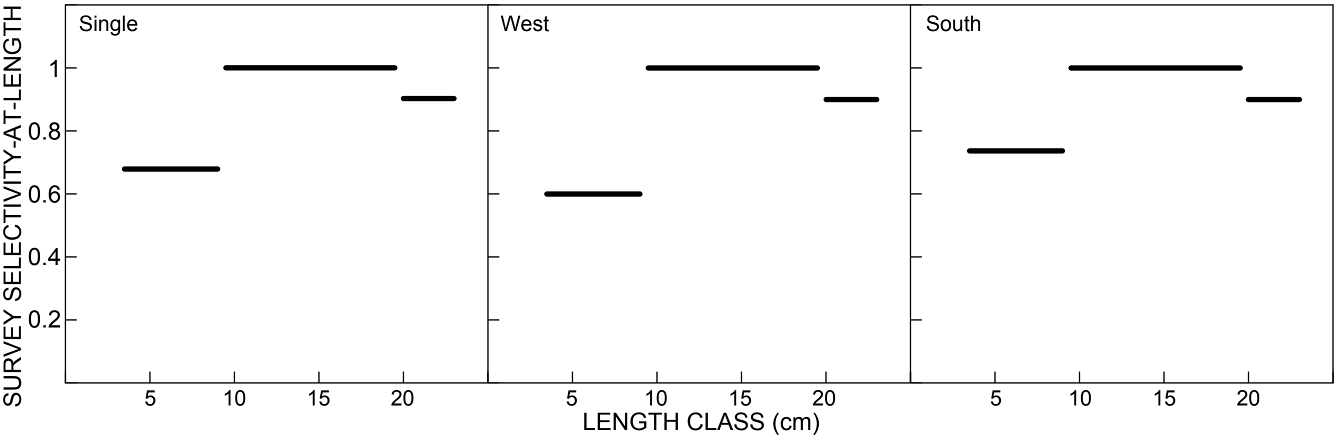

Figure 6: Model-estimated November survey selectivity-at-length at the joint posterior mode

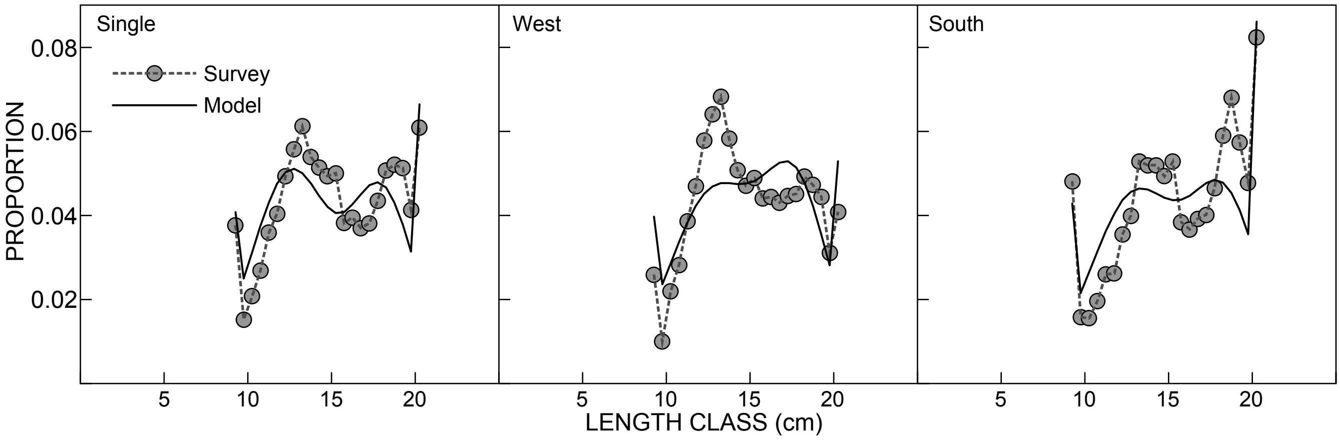

Figure 7: Average (over all years) proportions-at-length in November as predicted by the models at the joint posterior mode and as observed in the surveys

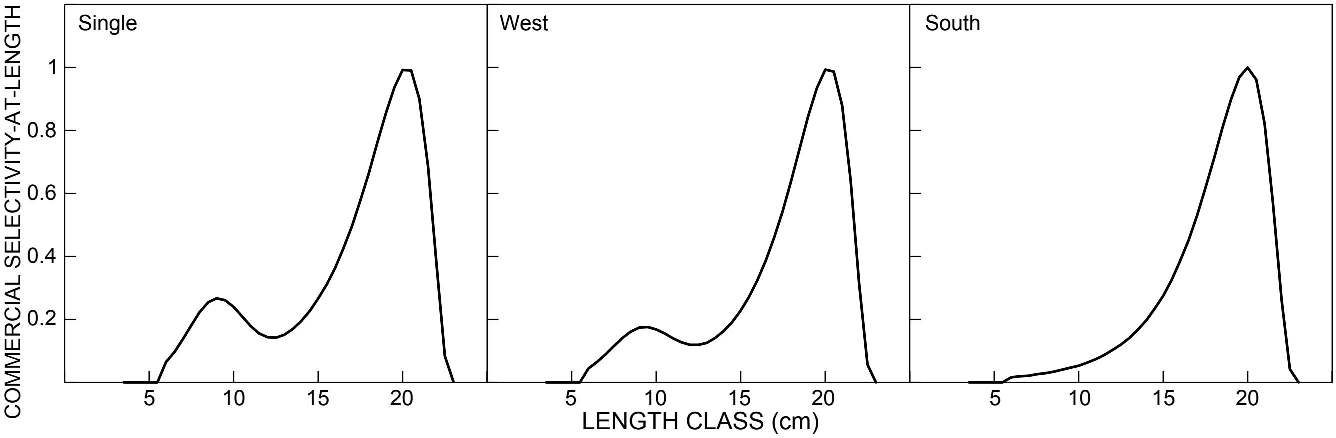

Figure 8: Model estimated selectivity-at-length at the joint posterior mode for the directed sardine fishery and bycatch in the round herring fishery

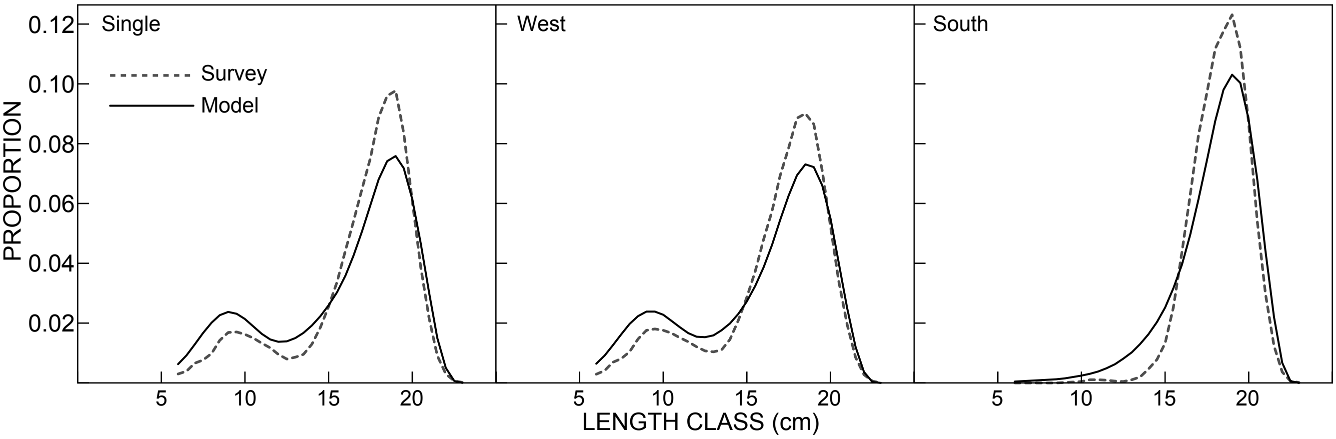

Figure 9: Average (over all years and quarters) proportions-at-length in the directed sardine fishery and bycatch in the round herring fishery, as predicted by the model at the joint posterior mode and as observed

Kerr et al. (2014) similarly showed that alternative stock-structure hypotheses can result in different perceptions of a resource's productivity. Their model of North-West Atlantic cod in USA waters as consisting of three biological units compared to the two management units considered for decades, resulted in a less-productive resource overall. Cunningham and Roel (2006) also estimated the geometric mean of annual recruitment to be lower under a two-stock hypothesis of sardine in the North-East Atlantic and under a single-stock hypothesis allowing immigration/emigration to/from the assessed population, compared to that estimated assuming a single-closed-stock hypothesis.

The development of the two-mixing-stock hypothesis for South African sardine has been an iterative process. Initial data analysis and assessment results prompted reanalysis to ensure that hypotheses and model assumptions were consistent with the data available. These initial assessments also facilitated the exclusion of unrealistic hypotheses such as that of two discrete stocks. The assessments have also helped to highlight the key areas of uncertainty regarding stock structure on which further research needs to be focused. Recently, results showing the impact of the alternative stock-structure hypotheses on future management of sardine (e.g. de Moor 2013; de Moor and Butterworth 2014) have prompted further evaluation of exactly how the two stocks mix. At the same time, new research is emerging that indicates that alternative two-mixing-stock hypotheses may be plausible. In addition to the west-to-south recruit movement assumed in this paper, further analyses of parasite data have, without contradicting earlier conclusions of multiple sardine stocks (Weston 2013; van der Lingen et al. 2015), led to the hypothesis that older west-stock fish may migrate to and remain in the south stock or that south-stock individuals may move to the West Coast (but not form part of the west stock) for some part of the year (this latter hypothesis would also impact the catch assumptions) (van der Lingen and Hendricks 2014). The conclusions drawn by Smith et al. (2011) thus require re-examination. It is hoped that in future assessments of this resource, this movement might be estimated more accurately by conditioning the assessment on proportions of sardine by length infected with a digenean 'tetracotyle-type' metacercarian endoparasite, which is hypothesised to be endemic to the West Coast only (van der Lingen and Hendricks 2014).

The ability to assess a resource taking into account more than one biological population is critically dependent on the availability of data for the individual biological populations. Separating catch data by biological unit when mixed-population fishing occurs is frequently dependent on information about mixing rates (e.g. Allison et al. 2014), although incorrect assumptions of mixing rates can be highly influential (Powers and Porch 2004). Fortunately, the commercial-catch and November survey data for South African sardine have been split at Cape Agulhas (with yet further disaggregation) for decades, easing the modelling of a two-mixing-stock hypothesis. The recruit survey, however, was extended east of Cape Infanta for the latter part of the time-series only, and has not always progressed sufficiently far eastwards to provide a reliable estimate of the recruits of the year.

The annual winter survey estimates of sardine recruitment east of Cape Infanta are low in comparison to those west of Cape Infanta and to the numbers of recruits needed to give rise to the observed boom in 1+ biomass on the South Coast. The two-stock assessment consequently estimates the majority of the south-stock biomass to originate from west-stock recruits, at least across the turn of the 21st century. Although sardine are known to spawn throughout the year, the winter recruit survey is timed to measure the recruits emanating from the postulated spawning peak between September and March (van der Lingen and Huggett 2003). However, in contrast to observations on the west coast of South Africa, high sardine egg concentrations have also been observed in winter on the South Coast (van der Lingen et al. 2005b). This could potentially give rise to local South Coast recruitment, which would not be detected during the winter recruit surveys, but would contribute to biomass surveyed in November. It may be possible in the longer term to obtain information on this hypothesised South Coast winter recruitment by acquiring separate estimates of recruit and adult abundance from the November survey (de Moor et al. 2014).

This paper is the first to document the differences in assessing the South African sardine resource under two alternative stock-structure hypotheses. The resource is considered either as consisting of a single homogeneous stock – the hypothesis that traditionally has been assumed – or as consisting of two mixing stocks. The latter hypothesis has thus far assumed the only mixing between the stocks to be that of recruits moving from the west to the south stock. Importantly, and in answer to a key question posed in the Introduction, this two-stock hypothesis has proven to be consistent with the data available.

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