The Quantitative Use of Parasite Data in Multi-Stock Modelling of South African Sardine (*Sardinops sagax*)

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Abstract: Differences in parasite infection have previously been used to distinguish between fish stocks. We demonstrate a novel use of parasite prevalence-by-length data to inform quantitatively on stock mixing. An initial two mixing stock hypothesis proved consistent with biological and survey data suggesting that there are different stocks of sardine off the west and south coasts of South Africa. That hypothesis assumed that only recruits moved from the west to the south stock. However, new "tetracotyle"-type metacercarian parasite bio-tag data indicate a need to allow older fish to move between the stocks as well. We demonstrate extension of bio-tagging to inform on the plausibility of population structure hypotheses by including parasite prevalence-by-length data in the model's likelihood. Our method enables the estimation of the magnitude of mixing between semi-discrete stocks, providing more precise estimates of annual movement. Such improved precision may be important in better informing future movement hypotheses and thereby management. Our research provides a framework to use to inform quantitatively on stock structure and movement hypotheses for other fish species with bio-tagging data.

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Introduction

The use of parasites as biological tags – or parasite "bio-tagging" as it is commonly known – to discriminate between marine fish stocks has become widespread in fisheries science (e.g. MacKenzie 1990; MacKenzie and Abaunza 2014). Large differences in the composition of selected parasite species, or in the infection levels of a single parasite, in fish from different areas may indicate a lack of mixing between those areas and hence the possibility of separate stocks. An overall probability of the correct classification of fish to their group of origin based on parasite data was estimated from a meta-analysis to be about 70%, almost double that expected by chance alone (Poulin and Kamiya 2015).

Sardine (*Sardinops sagax*) is a short-lived, rapidly-growing and highly productive small pelagic fish species found distributed off the entire coastline of South Africa (Beckley and van der Lingen 1999). A commercial fishery that targeted this and other pelagic fish using purse-seine vessels was established in the late 1940s. Historically this harvested sardine almost exclusively off the west coast, but the fishery expanded onto the south coast in more recent decades (Fig. 1). Commercial catches have shown large fluctuations with periods of high (>200 000t) annual catches in the early 1960s and early 2000s preceded and followed by lower catches. The abundance, distribution and size structure of the sardine population has been monitored via bi-annual hydro-acoustic surveys conducted since the mid-1980s (de Moor et al. 2008). Historically, these sardine have been assessed and managed as a homogeneous fishery management unit ("stock") under the assumption that the resource consists of a single biological population (de Moor et al. 2011, 2015; de Moor and Butterworth 2016). Sardine found sporadically off the east coast are postulated to be a separate stock (Fréon et al. 2010), are harvested by a beach-seine fishery with catches typically <1% of those from the west and south coasts, and are excluded from this analysis.

A boom in abundance and an almost simultaneous eastward shift in distribution at the turn of the 21st century prompted renewed research into sardine population structure. The hypothesis of separate west and south coast "stocks" was originally proposed after noting a separation between west and south coast spawning aggregations – particularly at low to medium biomass levels (van der Lingen et al. 2005; Coetzee et al. 2008a; van der Lingen et al. 2009; see Fig. 1). Studies of phenotypic differences between sardine sampled from the west and south coasts also showed differences in some morphometric characteristics (van der Lingen et al. 2009; van der Lingen 2011), demonstrating the possible existence of two functionally discrete “stocks” of sardine, perhaps with some mixing.

Parasite bio-tagging was employed to complement these stock structure studies following an initial investigation that documented sardine parasites and identified a Strigeid digenean “tetracotyle”-type metacercarian parasite (TTMP) of the genus *Cardiocephaloides* as a suitable bio-tag (Reed et al. 2012). Analysis of commercial catch samples from 2011 and 2012 showed strong differences in the prevalence, mean infection intensity and mean abundance of this parasite between sardine from the South African west and the south coasts (Weston 2013; Weston et al. 2015). Fish from the west had higher values for all three infection indices than those from the south coast, strengthening support for the hypothesis of some structure in the South African sardine population.

de Moor and Butterworth (2015) investigated these developing hypotheses about alternative sardine stock structure further, and showed that a hypothesis of two mixing stocks was compatible with the fishery dependent and fishery independent data typically used for assessments of this resource. That hypothesis assumed west and south stocks of sardine, separated at Cape Agulhas (Fig. 1). There was clear evidence in hydro-acoustic survey length frequencies of recruits having moved from the west to the south coasts between May/June and November in some years, as well as initial indications from TTMP prevalence data that the extent of any movement of sardine of age 2+ would likely be low (Smith et al. 2011). Mixing between the stocks was therefore modelled by assuming a year-varying proportion of west stock recruits only to move permanently to the south stock at the time that they become 1-year-olds.

Data on sardine infection by the TTMP has continued to be collected from both commercial and research survey samples. These data now indicate that a refinement of earlier versions of the hypothesis of two mixing stocks should be considered, in order to allow older individuals to move permanently from the west to the south stocks as well. In this paper we revise the hypothesis used by de Moor and Butterworth (2015) and fit a sardine model directly to parasite prevalence-by-length data. In doing so, we demonstrate the value of the information contained in the six continuous years of TTMP prevalence data sampled from hydro-acoustic surveys. Our research provides a framework which could be used to inform quantitatively on stock structure hypotheses and movement between stocks for other fish species for which bio-tagging data are available.

Data and methods

Of seven parasites documented for South African sardine, the TTMP found in sardine eyes showed the greatest bio-tag potential for the following reasons (Reed et al. 2012). It is endoparasitic and has a discontinuous distribution with substantial spatial variability in infection within the sardine's distributional range. It also likely has a long lifespan in its sardine host and is site specific, which facilitates ease of detection and identification.

The TTMP belongs to the family Strigeidae, which have life-cycles involving gastropod as first intermediate hosts, fish as second intermediate hosts, and piscivorous bird as final (or definitive) hosts (Niewiadomska 2002). Importantly for stock identification purposes, there is no fish-to-fish transmission of these Strigeid parasites (Niewiadomska 2002). While sardine and the African penguin (*Spheniscus demersus*) have been identified as the second intermediate and definitive TTMP hosts, respectively, the first intermediate host has yet to be identified. However, this host is hypothesised to be *Burnapaena papyracea* (Weston 2013; van der Lingen et al. 2015), an abundant subtidal gastropod distributed off the southern African west coast from Cape Agulhas to Lüdertiz (Branch et al. 1994; Fig. 1). If *B. papyracea* is indeed the first intermediate host, this means that the parasite endemic area (that geographic region within which conditions are suitable for parasite transmission, MacKenzie and Abaunza 2014) occurs off the west coast only. Hence infected sardine found outside the hypothesised west coast endemic area must have spent some time on the west coast. That sardine off the west coast show TTMP infection at a smaller size than those off the south coast (van der Lingen et al. 2015) supports the hypothesis of a west coast endemic area. The observed pattern of increasing infection with fish length and hence age (Weston 2013; Weston et al. 2015) indicates that infection is cumulative, and that sardine continue to be re-infected the longer they remain in the endemic area.

Sardine samples for parasite analysis have been collected between 2010 and 2015 during annual hydro-acoustic surveys to estimate pelagic fish biomass conducted off the South African west and south coasts in austral spring/early summer (e.g. Coetzee et al. 2008b). Fish were processed for the TTMP as described by Weston et al. (2015). Sardine samples collected between 20 and 22˚E were not included in this analysis so that any age-1 individuals in this hypothesized mixing zone that may include west stock fish would be excluded (Dunn et al. 2015). This resulted in 3 130 sardine from 103 trawls having been processed for TTMPs, and being used in this analysis (Fig. 2). Annual prevalence-by-length values – i.e. the percentage of sardine infected with the TTMP by length – were derived for each 0.5 cm CL class for each stock.

The sardine assessment model is detailed in the online supplementary material (Section B[1]). This sex-aggregated model with Bayesian estimation uses an age-structured production model framework, but due to the lack of reliable ageing data for sardine, the model is fit directly to length- rather than to age-structured survey and commercial catch data. This is achieved through the estimation of von Bertalanffy growth curves within the model, and accounting for variability in length about these growth curves at each point in time (de Moor et al. 2015). One important new aspect of this model is the allowance for early/late recruitment each year by modelling annual variability in these growth curves (online supplementary material, Equation S8[2]). The model is area- and stock-disaggregated with west and south stocks modelled to be west and south-east of Cape Agulhas (de Moor and Butterworth 2015, Fig. 1), with allowance for one-way movement from the west to the south stock. Recruitment to each stock is modelled assuming a hockey-stick stock-recruitment relationship dependent on the spawner biomass of that stock only. Maturity is assumed to change over time, possibly due to density dependence (van der Lingen et al. 2006), but as there is no current information indicating differences in maturity between the stocks, the same maturity ogives are used for both stocks. Natural mortality is similarly assumed to be the same for both stocks, with juveniles having a higher natural mortality rate than 1+ sardine. In line with the assumption that the TTMP has no appreciable negative impacts on sardine, no difference in growth, maturity, natural or fishing mortality or movement is assumed between infected and uninfected sardine.

This revised two mixing stock hypothesis now models the additional movement of older fish by assuming the annual proportion of age 2+ sardine which move permanently from the west to the south

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[1] Supplementary data are available with the article through the journal Web site at XXXX.

[2] Supplementary data are available with the article through the journal Web site at XXXX.

stock to be a time-invariant proportion of the 1-year olds that move each year (online supplementary material, Table S1[3]). This revision was based on the increasing prevalence of TTMP infection with length on both coasts (Fig. 2). This increase is to be expected for the west stock given that all ages are found in the endemic area and are therefore subject to possible infection each year. However, this increase would not be anticipated for south stock fish under an “only 1-year-old movement” hypothesis, as prevalence would be anticipated to plateau at a level dependent on the prevalence of infection of incoming 1-year-olds. Hence this information suggests that west stock fish older than age-1 move to the south stock. It is further assumed that there is no permanent movement of south stock sardine to the west stock.

Since the endemic area is hypothesized to be on the west coast, only west stock sardine are modelled to become infected by the parasite, and this is assumed to occur in an annually-varying pulse from 2008[4] onwards. Prior to 2008, a time-invariant proportion of west stock sardine not already infected is assumed to become infected each year, though this assumption is inconsequential to results as parasite prevalence-by-length data are available only between 2010 and 2015. For the purposes of simplicity, both infection and subsequent movement to the south stock are assumed to occur immediately after sardine are modelled to increase their age on 1st November each year.

In addition to the new time series of parasite prevalence-by-length data, the model was conditioned on more than three decades of hydro-acoustic surveys of November biomass and May/June recruitment (de Moor et al. 2008 and unpublished extended data), as well as on length frequency data collected from the November surveys and quarterly commercial catches. A binomial distribution was chosen to model the prevalence-by-length data so that the varying sample sizes by length and year would be explicitly considered in weighting the prevalence observations (online supplementary material[5], equation S36).

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[3] Supplementary data are available with the article through the journal Web site at XXXX.

[4] Some information on 2008-2009 prevalence can be obtained from available data on TTMP prevalence at larger lengths in 2010-2011.

[5] Supplementary data are available with the article through the journal Web site at XXXX.

Two models were run in order to test the effect of including the new time series of parasite prevalence-by-length data in the model. The first model, S_{with}, included these data in the likelihood (online supplementary material, Equation S36[6]), while the second model, $S_{without}$, ignored these data and consequently also the estimation of the annual proportion of west stock sardine infected from 2008 onwards. Numerical integration was performed using Markov Chain Monte Carlo (Gelman et al. 1995) in AD Model Builder (Fournier et al. 2012). Chains of length 13.5 million (S_{with}) and 14.5 million ($S_{without}$) samples were run and the posterior distributions were estimated after discarding 6 million samples for burn in and subsequently thinning by 2 000.

Results

Both S_{with} and $S_{without}$ models produced near identical fits to the hydro-acoustic survey data, with predictions being mostly within the 95% CIs of the survey means (Fig. 3). Although there was some evidence of temporal trend in the standardised residuals in model fits to the south stock November survey biomass, there was little evidence of temporal trend in the residuals for the other three abundance series (online supplementary material, Fig. S1[7]). The general patterns in the length frequency data were also well represented by both models, despite there being some pattern in the standardised residuals (online supplementary material Figs. S2 and S3[8]).

The variability about the von Bertalanffy growth curves is larger for lower ages (online supplementary material, Fig. S4). Fig. 4 shows that a reasonably large range is estimated for the annual age at which length is expected to be zero, thereby facilitating some improvement in the model fit to the length frequency data through the associated assumption that this allows representation of annual changes in the peak spawning time. The estimated hockey-stick stock recruitment relationships are similar for the two models for the west stock, while the maximum recruitment to the south stock is estimated to be some 30% higher at the joint posterior mode under S_{with} than under $S_{without}$ (Fig. 5). Consistent with the finding by de Moor and Butterworth (2015), the west stock is estimated to be substantially more productive than the south stock, with the maximum recruitment to the former being estimated to be an order of magnitude higher than that for the latter.

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[6] Supplementary data are available with the article through the journal Web site at XXXX.
[7] Supplementary data are available with the article through the journal Web site at XXXX.
[8] Supplementary data are available with the article through the journal Web site at XXXX.

The model is able to fit the observed prevalence-by-length of sardine infected with the TTMP reasonably well (Fig. 6). Account needs to be taken of the differences in sample sizes between length and also years in drawing this conclusion (see above). The allowance now made for the movement of 2+ fish enables the model to explain the feature evident in the data of an increase in prevalence at larger lengths on the south coast. The differences between annual observed prevalence-by-length inform the estimates of the proportions infected each year (Fig. 7).

Estimates of the proportion of sardine moving from the west to the south each year are important because their magnitude is the primary determinant of the extent to which harvest rates on the west coast may need to be reduced, as discussed below. The annual proportion of 1-year olds that move from the west to the south stock differs between the models, with a much greater inter-annual variability estimated for recent years for S_{with} (Fig. 8; online supplementary material, Fig. S5[9]). Movement is estimated to be substantial in some years, particularly after the mid-1990s, with over 50% of the 1-year olds estimated to have moved from the west to the south stock in 12 out of 32 years. The further information provided by the TTMP prevalence data on past stock mixing is such that the proportions moving are estimated far more precisely for S_{with} than for $S_{without}$, and particularly so between 2012 and 2015 (Fig. 8). The average standard deviation of the 2008 to 2015 proportions of age-1 sardine moving is decreased substantially from 0.20 for $S_{without}$ to 0.11 for S_{with}. The 95% posterior probability intervals of the $S_{without}$ proportions of age-1 are large in many years, reflecting only slight updating of the prior distributions' 95% probability interval of [0.03,0.97] (online supplementary material, Table S1) from the information indirectly available from (primarily) the hydro-acoustic survey data. In contrast, the additional information contained in the TTMP prevalence-by-length data update these prior distributions substantially more for S_{with}, particularly in recent years. These more precise estimates display a variable pattern of higher and lower median proportions of 1-year-olds moving in recent years under S_{with} (Fig. 8). The large probability intervals for the proportion of 1-year olds estimated to move in November 2014 under $S_{without}$ (Fig. 8) are indicative of the lack of information about movement from the abundance (Fig. 3) or length frequency data. No sardine less than 19cm were found to be infected with the TTMP on the South Coast in November 2014 (Fig 6). These prevalence data are therefore highly informative

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[9] Supplementary data are available with the article through the journal Web site at XXXX.

through being able to indicate that a very low proportion of 1-year-old sardine only could have moved from the west to the south stock that year. The >10% model estimated prevalence for the south stock for sardine more than 15cm results from individuals of ages 2+ (online supplementary material Fig. S4a), which would have moved from the west to the south stock in former years.

Furthermore, S_{with} estimates a greater proportion of age 2+ sardine to have moved than that estimated by $S_{without}$ (online supplementary material, Fig. S6[10]). The median time invariant proportion of the 1-year-olds that inform the proportion of 2+ sardine that move is estimated to be 0.31 [95% probability interval 0.04-0.68] under S_{with} compared to 0.23 [95% probability interval 0.01-0.70] under $S_{without}$. This results in a greater overall biomass of sardine being estimated to have moved from the west to the south stocks under S_{with} compared to $S_{without}$.

Discussion

This revised stock structure hypothesis for the South African sardine of two mixing stocks has been fit to an extended time series of hydro-acoustic survey abundance estimates together with commercial and survey proportion-by-length data, and the new time series of TTMP prevalence-by-length data. This analysis draws similar overarching conclusions to those which de Moor and Butterworth (2015) reached using the initial hypothesis. These are that the west stock is estimated to be substantially more productive than the south stock, and that movement of individuals from the west to the south stock has had a much greater impact on south stock biomass than have any years of above average south stock recruitment (Figs. 3, 5 and 8). In particular, the peak in south stock biomass at the beginning of the 21st century (Fig. 3) is estimated to have resulted primarily from west stock fish having moved permanently to the south stock.

Parasite data have previously been used to investigate inter-stock dynamics in sockeye salmon *Oncorhynchus nerka*. Bailey et al. (1987) simulated mixtures of juvenile sockeye salmon stocks originating from different lakes in British Columbia using data on the infection of these salmon by twelve parasites and demonstrated that bio-tagging could be used to quantitatively estimate stock compositions during periods of mixing. Bio-tagging using two parasites (the brain parasite *Myxobolus*

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[10] Supplementary data are available with the article through the journal Web site at XXXX.

arcticus and muscle parasite *Henneguya salminicola*) was utilised to provide time-invariant estimates of the composition of a mixture of three sockeye salmon stocks in British Columbia, and thereby inform management such that overexploitation of individual stocks was avoided (Margolis 1998). Moles and Jensen (2000) also reported that the brain parasite *M. arcticus* could serve as an effective biological marker to distinguish between the origins of sockeye salmon in Alaska, given the apparent low inter-annual variability in parasite prevalence. However, Margolis (1998) added that continuous baseline sampling of the stocks over time was required to consider inter-annual changes in parasite prevalence and intensity among the stocks in order that such stock-discrimination remained possible.

In contrast, this study has quantitatively evaluated the inter-annual variability in the (permanent) mixing of sardine on the south coast which originated from both the west (endemic area) and south stock recruitment. The continuous collection of prevalence-by-length data is required to inform these changing levels of infection and age-dependent movement – information that is important for the sustainable management of such short lived species.

The high inter-annual variability in the proportion of west stock sardine infected with TTMP (Fig. 7) is consistent with the highly dynamic oceanography off the west coast, which shows strong seasonal and inter-annual variability (Hutchings et al. 2009). It is also consistent with information that the release of Strigeid cercariae from their gastropod first intermediate host may be driven by environmental changes such as an increase in temperature (e.g. Harrod and Griffiths 2005).

These results have important management implications. The conclusion that the west stock is the key "feeder" stock for both coasts raises concerns for the future of the resource, given that the west stock has experienced poor to low recruitment for the majority of the past 12 years. In addition, with the historical distribution of the resource having been primarily along the west coast, and the subsequent development of processing plants for the small pelagic fishery along this coast, the fishing effort on the west coast has been appreciably higher than that on the south coast (online supplementary material, Fig. S7[11]). Under this hypothesis of two mixing stocks of sardine, the resource should be carefully

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[11] Supplementary data are available with the article through the journal Web site at XXXX.

managed, with reduced harvest rates in the traditional western fishing area, so that over-exploitation of the west stock - with potential serious consequences for the resource as a whole - does not occur.

The confirmation of the assumption that the endemic area for infection by TTMP is west of Cape Agulhas only is important, particularly in the light of the potential management implications of the hypothesis of two mixing stocks. Future research into the definitive identification of this first intermediate host therefore remains a high priority (van der Lingen et al. 2015). Even so, the absence of infection in the small sardine east of Agulhas is difficult to reconcile with an endemic area that extends further east than is currently hypothesised.

In line with this concern of possible over-exploitation of the west stock, the Small Pelagic Scientific Working Group of the Fisheries Branch of the South African Department of Agriculture, Forestry and Fisheries, which is responsible for providing scientific advice for the management of the sardine resource is now additionally considering alternative hypotheses which may also be consistent with these parasite prevalence-by-length data. These include the possibility that recruitment to the west stock depends on a combination of the west stock spawning biomass and some relatively small proportion of the south stock spawning biomass (Miller et al. 2006; Coetzee 2014), or that part of the south stock is distributed west of Cape Agulhas for a relatively short period each year (de Moor et al. 2014). Operating Models for the development of future Management Procedures (de Moor and Butterworth 2016) for the sardine resource will need to be based on variants of these hypotheses for two mixing stocks.

In this light, the inclusion of the TTMP prevalence data directly in the likelihood of the model is noteworthy. The movement proportions were not precisely estimated in the de Moor and Butterworth (2015) analysis; this is a concern when alternative assumptions for future movement can lead to substantially different projections for the population as a whole. This research has demonstrated the precision with which these movement proportions can be estimated is substantially improved by the inclusion of the TTMP prevalence-by-length data, with the posterior standard deviations for these proportions being almost halved from $S_{without}$ to $S_{with.}$ The marked inter-annual differences in proportions moving in recent years have been informed by the inter-annual differences in the observed prevalence-by-length, indicating the importance of sampling these data on an annual basis to inform the mixing dynamics of this short lived species. This highlights the value of the further information provided through this bio-tagging study. While the movement parameters are more precisely estimated mainly for recent years, those may nevertheless be important in better informing the choice of hypotheses for future movement.

Conclusions

Whereas previous studies restricted the use of bio-tagging to the identification of and discrimination between stocks, or to the identification of assumed time-invariant mixing between stocks, we have shown that bio-tagging can be extended to inform the inter-annual extent of mixing between stocks as well. Our results have therefore demonstrated that parasite bio-tagging can be used not only qualitatively, but also quantitatively to inform on stock structure hypotheses.

The reasonably large sample size of TTMP prevalence-by-length data collected continuously over six years for the western and southern sardine stocks enabled the estimation of annual proportions of west stock infected and a more precise estimation of proportions moving, particularly in recent years. These improvements in the precision of the estimates of movement – almost halving the posterior standard deviation of the proportion of age-1 fish moving in recent years - indicate that the TTMP prevalence-by-length data contribute substantial quantitative value towards informing stock structure hypotheses. While conventional tagging data have previously been used to inform on stock mixing (e.g. Sibert et al. 1999; Kurota et al. 2009), this is the first case of which we are aware where a stock assessment model has been fit directly to parasite bio-tagging data in order to inform on the extent of inter-annual stock mixing. This analysis shows that these inter-annual differences can be substantial for this sardine resource.

In addition, this research provides a good example of how the incorporation of spatial structure in a stock assessment model can lead to more informed management. The method developed for this study could readily be extended for use for other resources.

In addition to the prevalence data used in this analysis, TTMP infection intensity-by-length data have also been collected. Given that TTMP infection in sardine is cumulative, this index may be able to provide an index of residence time on the west coast, and future studies may additionally use these data if the cumulative number of parasites within a sardine can be modelled adequately, rather than only the first stage of infection compared to no infection as used here. These data have the potential to further inform differences in annual movement by length (age).

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Figure Legends

Fig. 1. Map of the southern African coastline showing places mentioned in the text and the 200m depth contour (dashed line). The composite egg density (eggs per square metre; circles with diameter proportional to abundance and the maximum size = 9 193 eggs per m^2) is shown, derived from CalVET net samples collected during annual hydro-acoustic surveys of small pelagic biomass, conducted between Hondeklip Bay and Port Alfred from 1986–2010; updated from van der Lingen (2011). The insert shows the annual total sardine landings taken by the small pelagic fishery to the west and east of Cape Agulhas over the period 1950-2015.

Fig. 2. The locations of sardine sampled from November hydro-acoustic surveys that have been processed for the “tetracotyle”-type metacercarian parasite (TTMP), excluding samples between 20° and 22°E. The insert shows the average 2010-2015 prevalence-by-length in sardine sampled west of 20°E and east of 22°E.

Fig. 3. The hydro-acoustic survey estimated (▲) and associated model-predicted sardine abundance (— S_{with} and ······ $S_{without}$) at the joint posterior mode for a) November total biomass for the west stock, b) November total biomass for the south stock, c) May recruitment for the west stock, and d) May recruitment for the south stock. Observations are shown together with their 95% confidence intervals.

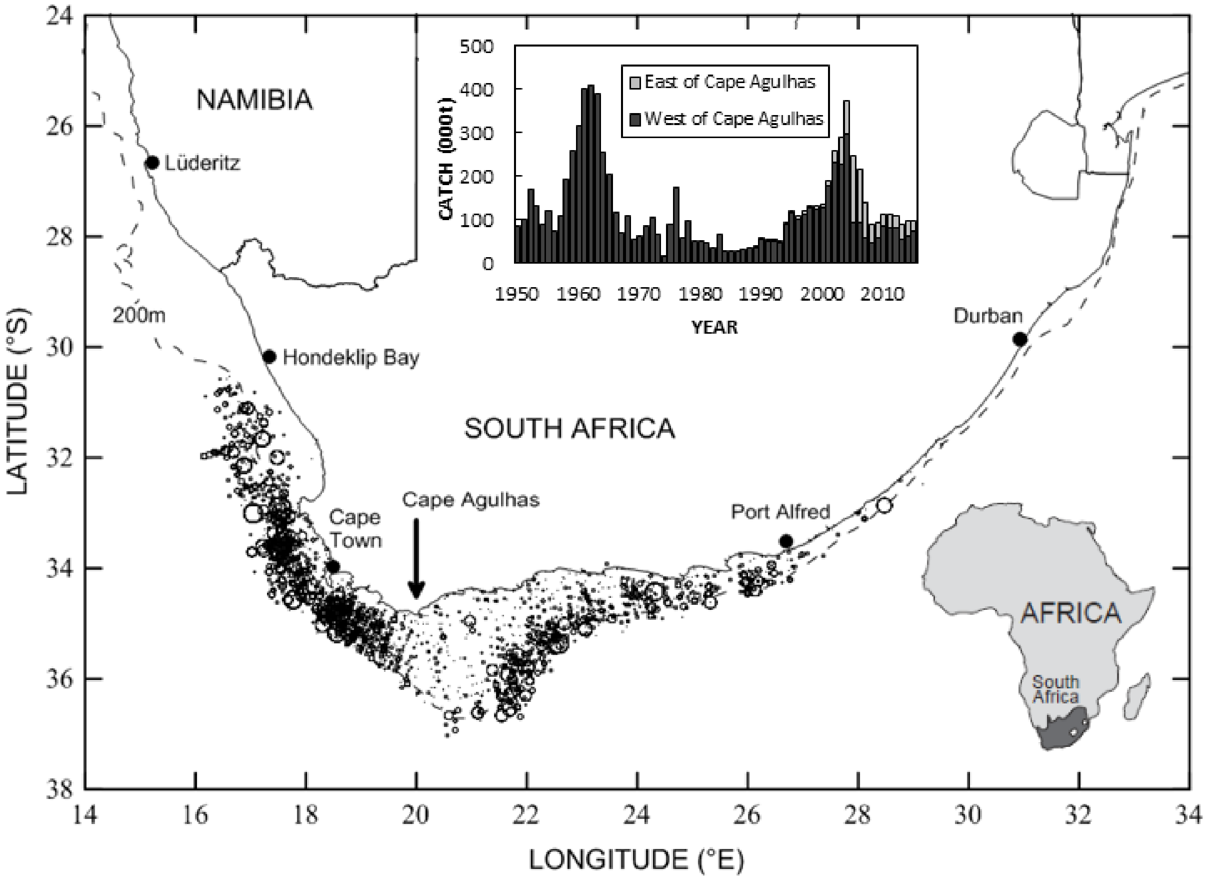
Fig. 4. The annual von Bertalanffy growth curves estimated for the west stock for S_{with} by allowing for auto-correlated residuals for variation about the age at which length is zero.

Fig. 5. Model-predicted November sardine recruitment plotted against spawner biomass from 1984 to 2014, with the estimated hockey stick stock-recruitment relationships at the joint posterior mode, for a) the west stock and b) the south stock. Results for S_{with} (♦, —) and $S_{without}$ (◊, —) are overlaid for ease of comparison. The dotted lines indicate the replacement lines. Note the scale of the axes differ between the plots.

Fig. 6. The prevalence-by-length of sardine infected with the TTMP, as sampled from the November hydro-acoustic surveys between 2010 and 2015 (♦), and predicted by S_{with} (—). The light grey bars indicate the sample size-at-length.

Fig. 7. The posterior median (♦) and 95% probability intervals of proportions of west stock sardine not already infected with the parasite that become infected between 2008 and 2015, from S_{with}.

Fig. 8. The posterior median and 95% probability intervals of proportions of 1-year olds estimated to move from the west to the south stock each November from 2008 to 2015, for S_{with} (♦) and $S_{without}$ (●). Results for all years are shown in the online supplementary material (Fig S6[12]).



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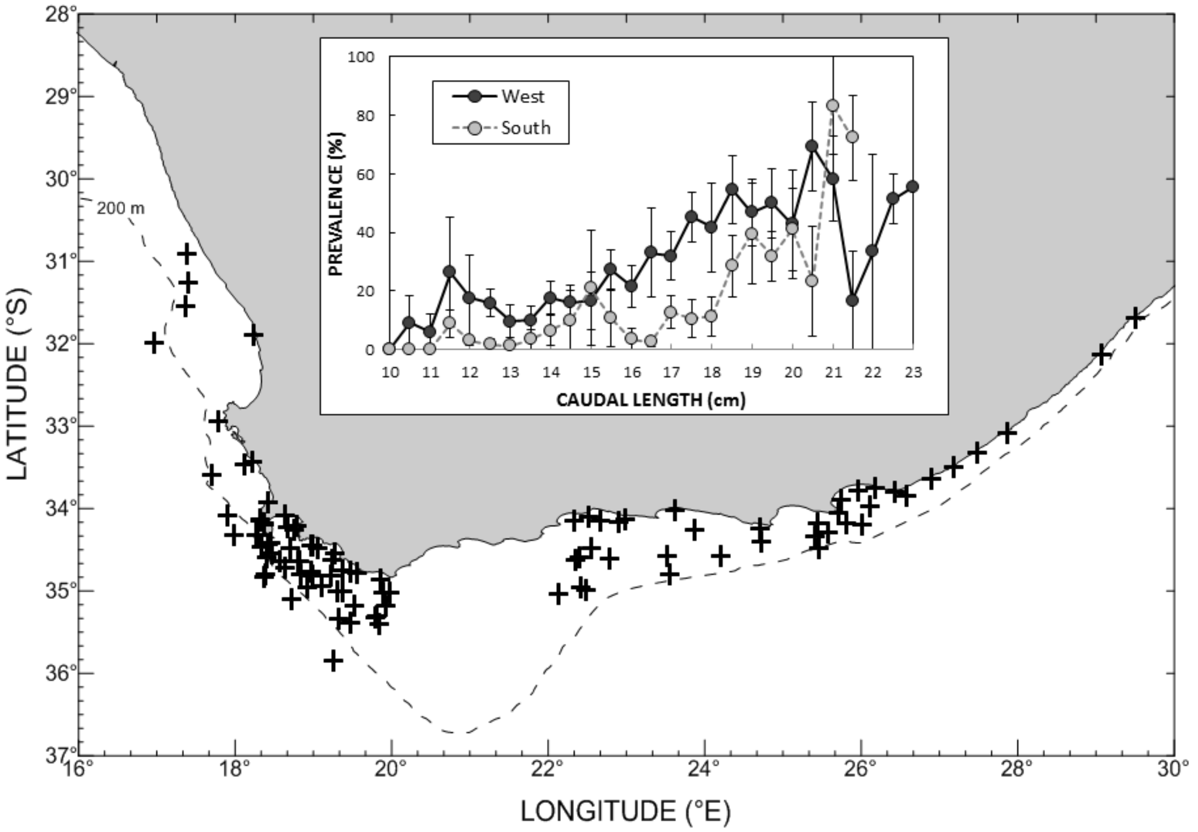
[12] Supplementary data are available with the article through the journal Web site at XXXX.



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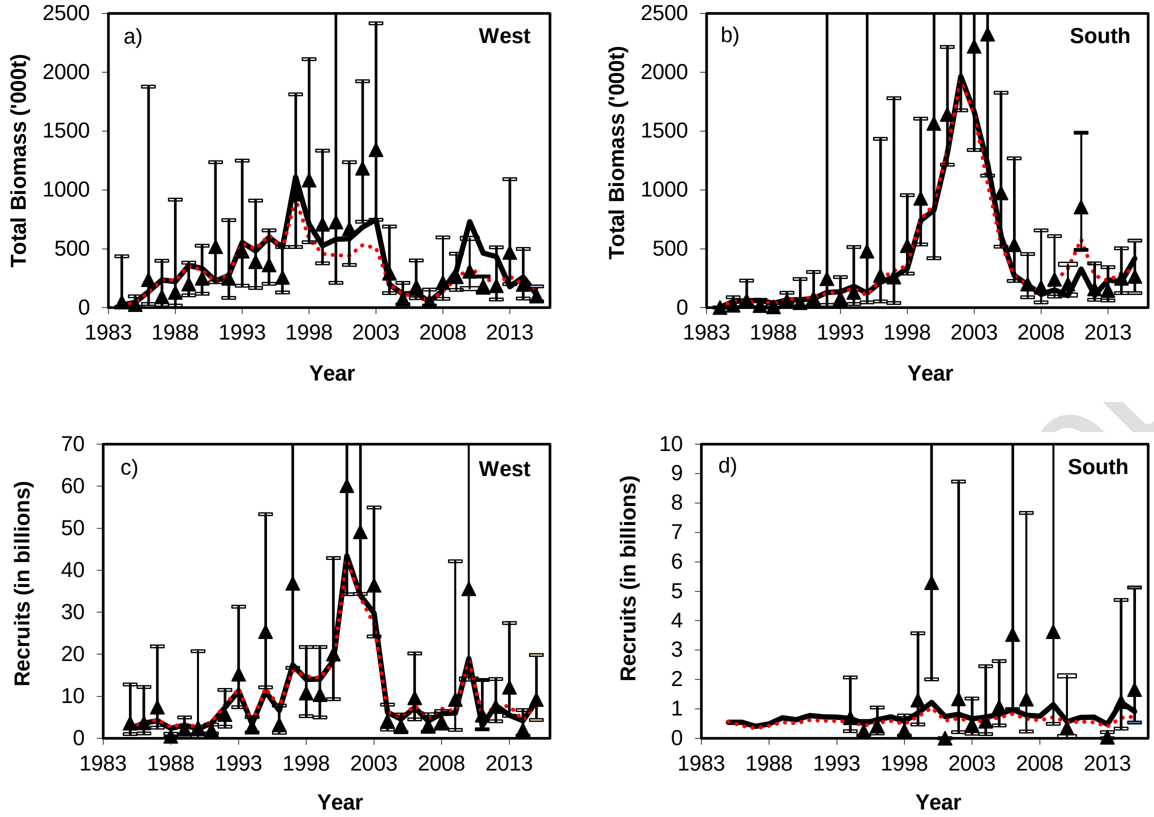

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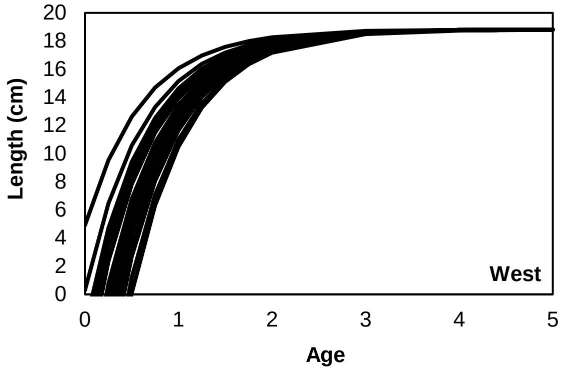

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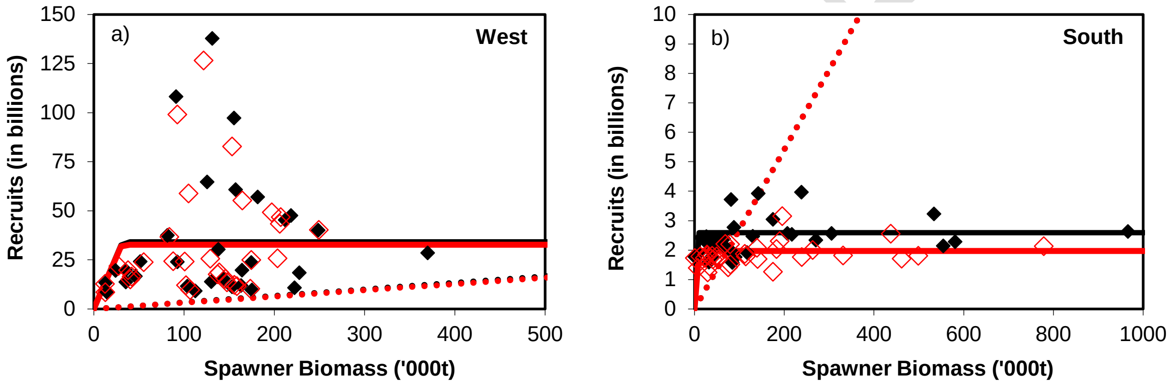

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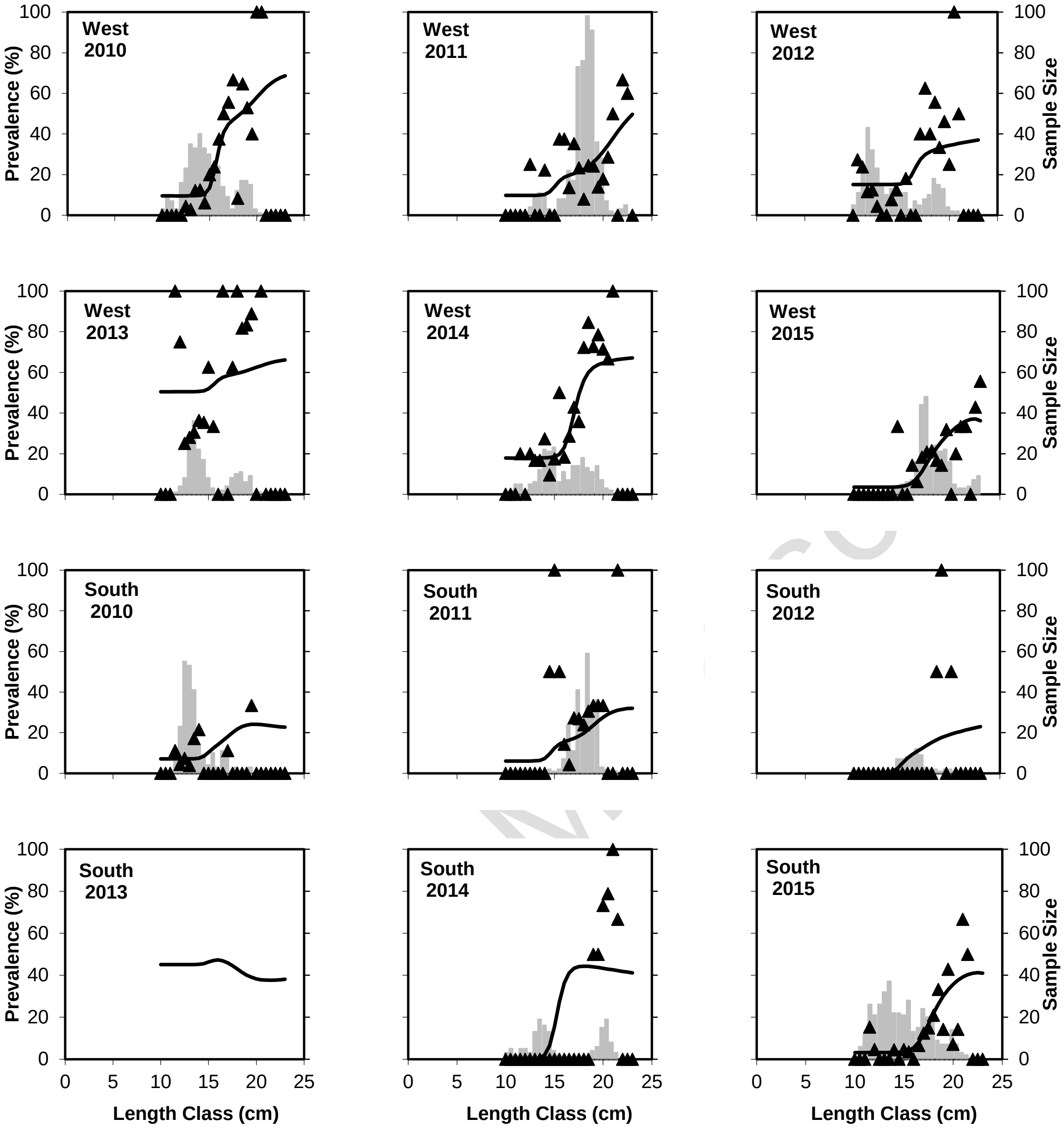

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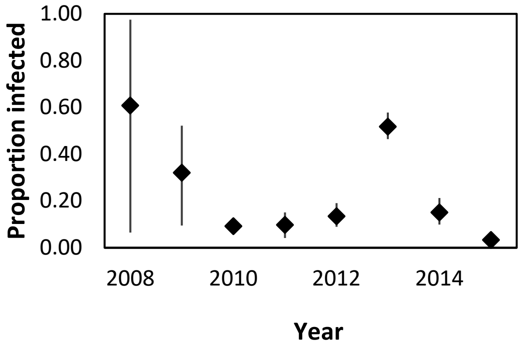

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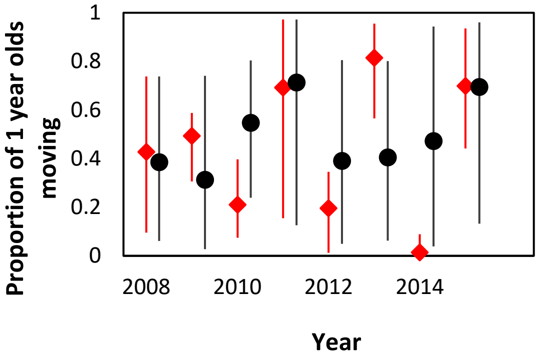

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The Quantitative Use of Parasite Data in Multi-Stock Modelling of South African Sardine (*Sardinops sagax*)

Carryn L. de Moor, Douglas S. Butterworth, Carl D. van der Lingen

This supplementary material consists of three sections: Section A shows further results not given in the main text; Section B details the Bayesian assessment model for the South African sardine resource; and Section C details the derivation of the method used to inform the prior distribution for hydro-acoustic survey bias.

Section A: Additional results

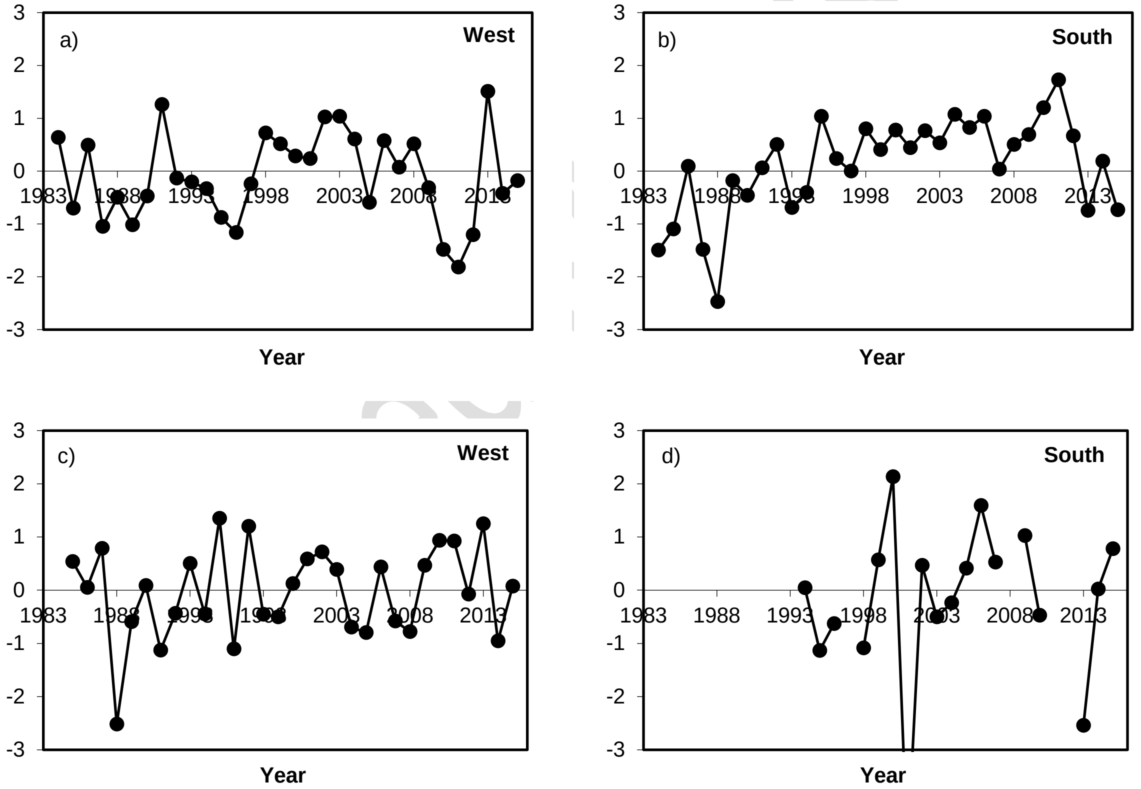

Fig. S1. Standardised residuals from the fit of S_{with} to a) November total biomass for the west stock, b) November total biomass for the south stock, c) May recruitment for the west stock, and d) May recruitment for the south stock. The corresponding plots for $S_{without}$ are similar.

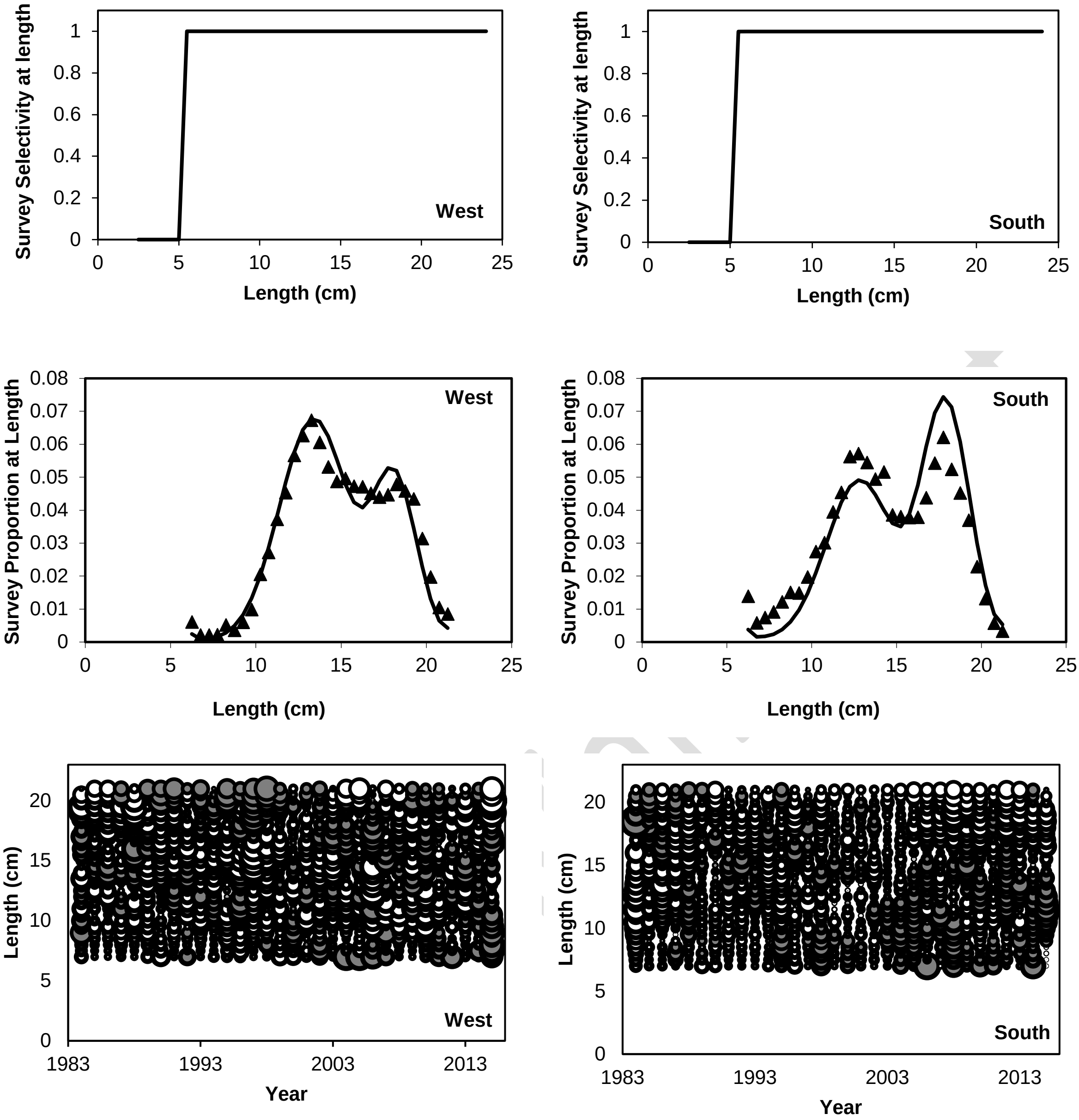

Fig. S2. The model estimated survey selectivity curves for S_{with} (top row), the average (over all years) observed (▲) and model predicted (▬) proportions-at-length in the hydro-acoustic surveys (middle row), and the standardized residuals from these fits (lower row). The radius of the bubbles in the lower plots corresponds with the absolute residual size, while the clear/opaque bubbles denote negative/positive residuals. The corresponding plots for $S_{without}$ are similar, with some improvement in the fit for the South stock.

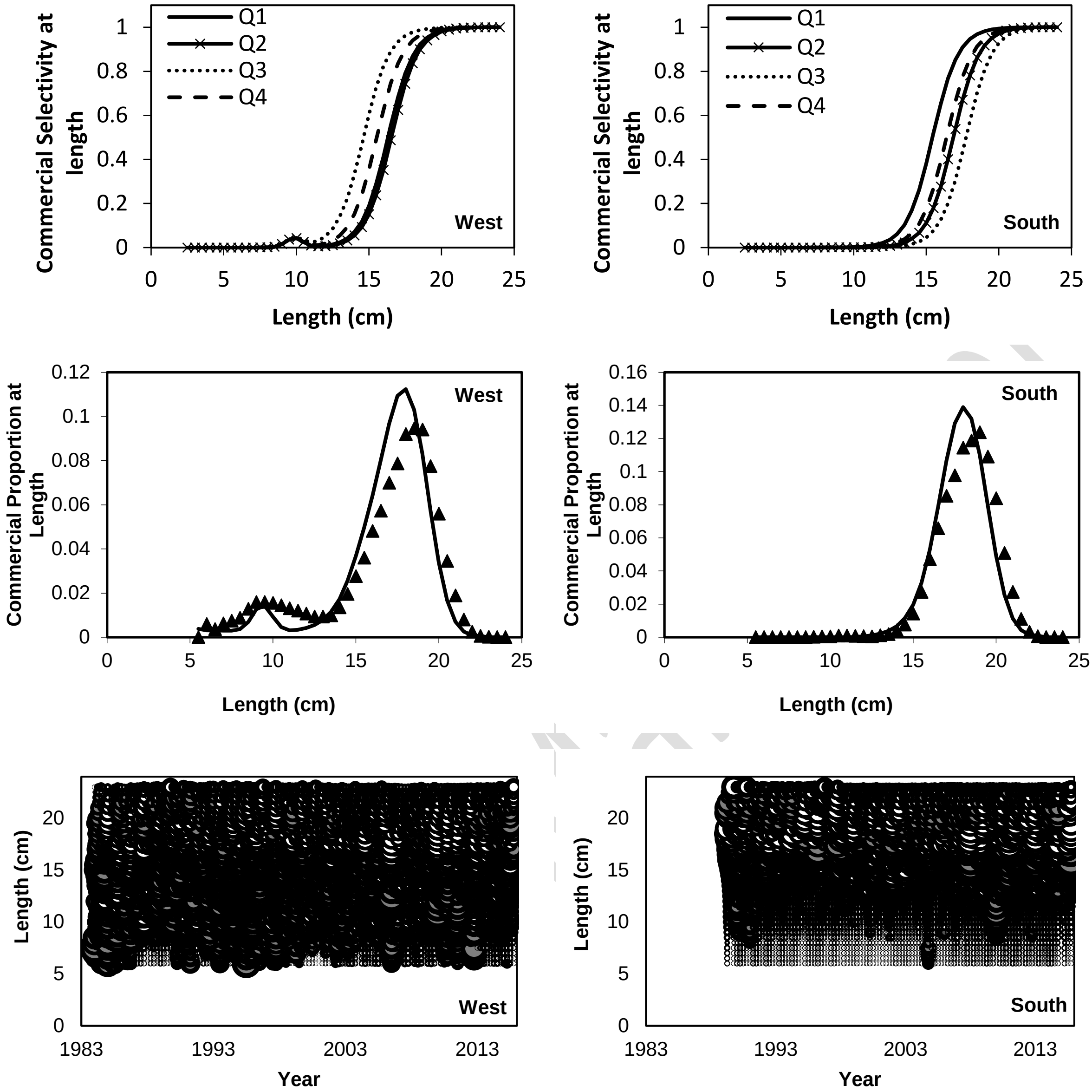

Fig. S3. The model estimated commercial selectivity curves for S_{with} for 2002-2015[1] (top row), the average (over all quarters and years) observed (▲) and model predicted (▬) proportions-at-length in the commercial catches (middle row), and the standardized residuals from these fits (lower row). The radius of the bubbles in the lower plots corresponds with the absolute residual size, while the clear/opaque bubbles denote negative/positive residuals. The corresponding plots for $S_{without}$ are similar.

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[1] Four pre-determined time periods are used (Table S1).

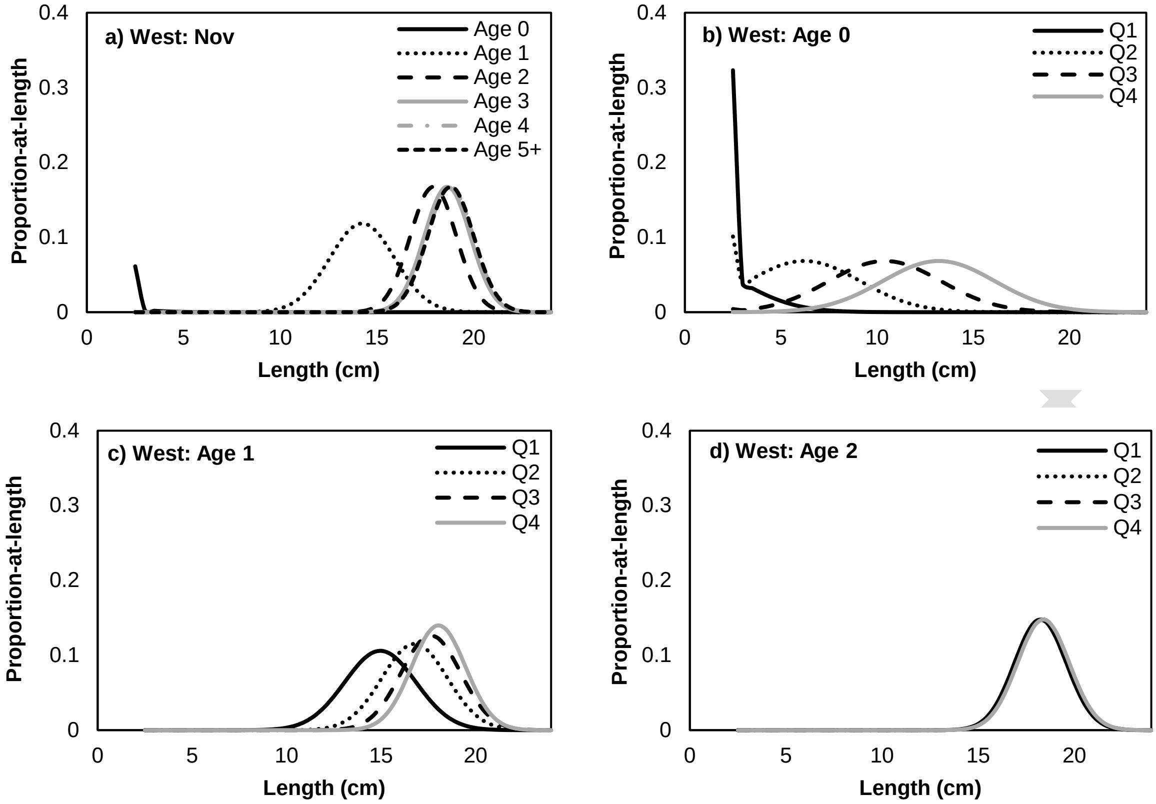

Fig. S4. The model estimated distribution of length-at-age for S_{with} in 2014. The distributions vary between years, with greater variability for the smaller age groups (Equation S8). The plots show a) the difference in length distributions at all ages at the time of the November hydro-acoustic survey, the difference in length distributions mid-way through each quarter for b) age 0, c) age 1 and d) age 2. The sudden increase in the proportion of the 2^- cm length class is due to this being a minus group. The distribution at age 0 excludes any individuals not yet recruited to the population, and hence may not sum to 1 at the time of the survey. The distributions for the south stock and for $S_{without}$ are similar.

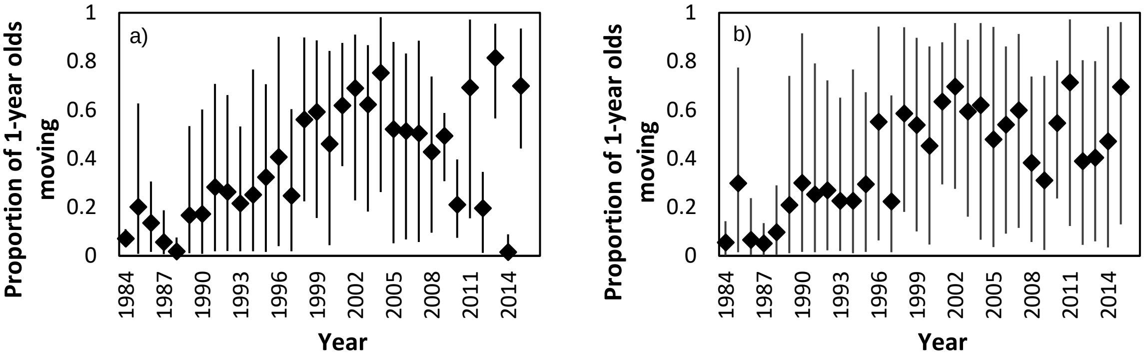

Fig. S5. The posterior median and 95% probability intervals of proportions of 1-year olds estimated to move from the west to the south stock each November, for a) S_{with} and b) $S_{without}$.

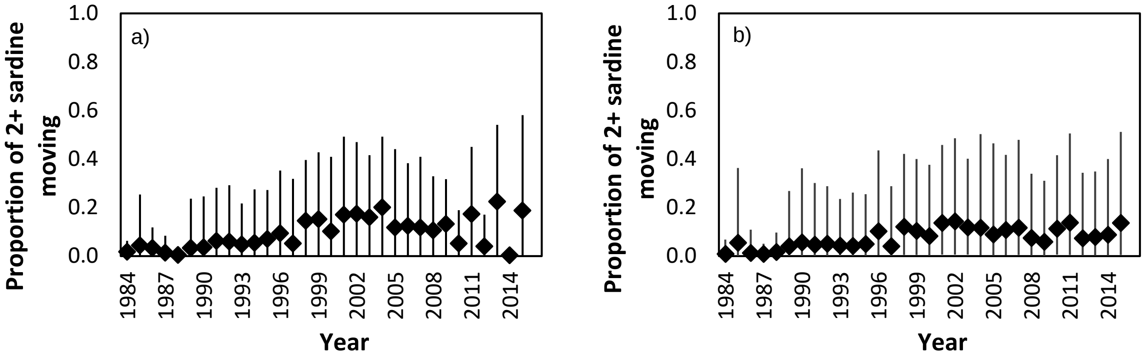

Fig. S6. The posterior median and 95% probability intervals of proportions of 2+ sardine estimated to move from the west to the south stock each November, for a) S_{with} and b) $S_{without}$.

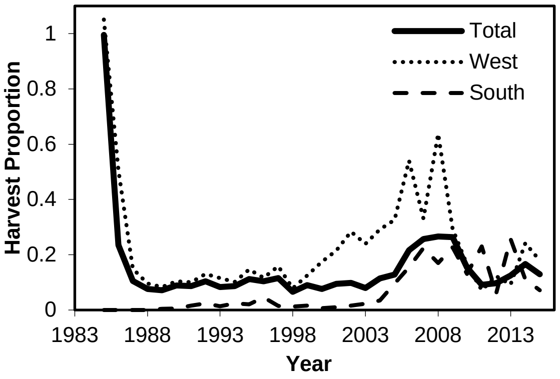

Fig S7. The harvest rate (annual catch in tons divided by the total model predicted biomass from the previous November in tons) from S_{with}. The corresponding plot for $S_{without}$ is similar.

Section B: Bayesian assessment model for the South African sardine resource

The assessment is run from November $y_1 = 1984$ to November $y_n = 2014$, with the following subscript notation:

- quarters $q = 1$ denoting November $y-1$ to January y, $q = 2$ denoting February to April y, $q = 3$ denoting May to July y and $q = 4$ denoting August to October y;
- ages $a = 0$ to a plus group of $a = 5^+$;
- lengths from a minus group of $l = 2.5^- cm$ to a plus group of $l = 24^+ cm$;
- stocks $j = W$ or $j = S$ denote the west and south stocks, respectively;
- infection $p = NI$ or $p = I$ denote the sardine uninfected and infected with the digenean 'tetracotyle-type' metacercarian parasite (TTMP), respectively.

All parameters are defined in Tables S1 and S2.

Population Dynamics

Numbers-at-age at 1 November before movement or infection

$$N^{S*}_{j,p,y,a} = \Bigg(\Bigg(\Bigg(\Bigg((N^{S}_{j,p,y-1,a-1} e^{-M^{S}_{y,a-1}/8} - C^{S}_{j,p,y,1,a-1}) e^{-M^{S}_{y,a-1}/4}\Bigg) - C^{S}_{j,p,y,2,a-1}\Bigg) e^{-M^{S}_{y,a-1}/4} - C^{S}_{j,p,y,3,a-1}\Bigg) e^{-M^{S}_{y,a-1}/4} - C^{S}_{j,p,y,4,a-1}\Bigg) e^{-M^{S}_{y,a-1}/8}$$

$$p = I, NI\ ,\ y_1 \le y \le y_n, 1 \le a \le 4$$

$$\begin{aligned} N^{S*}_{j,p,y,a=5+} = &\Bigg(\Bigg(\Bigg(\Bigg((N^{S}_{j,p,y-1,4} e^{-M^{S}_{y,4}/8} - C^{S}_{j,p,y,1,4}) e^{-M^{S}_{y,4}/4}\Bigg) - C^{S}_{j,p,y,2,4}\Bigg) e^{-M^{S}_{y,4}/4} - C^{S}_{j,p,y,3,4}\Bigg) e^{-M^{S}_{y,4}/4} - C^{S}_{j,p,y,4,4}\Bigg) e^{-M^{S}_{y,4}/8} \\ &+ \Bigg(\Bigg(\Bigg(\Bigg((N^{S}_{j,p,y-1,5+} e^{-M^{S}_{5+}/8} - C^{S}_{j,p,y,1,5+}) e^{-M^{S}_{y,5+}/4}\Bigg) - C^{S}_{j,p,y,2,5+}\Bigg) e^{-M^{S}_{y,5+}/4} - C^{S}_{j,p,y,3,5+}\Bigg) e^{-M^{S}_{y,5+}/4} - C^{S}_{j,p,y,4,5+}\Bigg) e^{-M^{S}_{y,5+}/8} \end{aligned}$$

$$p = I, NI\ ,\ y_1 \le y \le y_n \qquad \text{(S1)}$$

Infection of west stock sardine

$$N^{S**}_{W,NI,y,a} = (1 - I_y) N^{S*}_{W,NI,y,a} \qquad y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+$$

$$N^{S**}_{W,I,y,a} = N^{S*}_{W,I,y,a} + I_y N^{S*}_{W,NI,y,a} \qquad y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+$$

$$N^{S**}_{S,p,y,a} = N^{S*}_{S,p,y,a} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+ \qquad \text{(S2)}$$

Movement of west stock ($j = W$) sardine to the south stock ($j = S$)

$$N^{S}_{W,p,y,a} = (1 - move_{y,a}) N^{S+*}_{W,p,y,a} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+$$

$$N^{S}_{S,p,y,a} = N^{S*}_{S,p,y,a} + move_{y,a} N^{S*}_{W,p,y,a} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+ \qquad \text{(S3)}$$

Numbers-at-age mid-way through each quarter (for use in catch equations)

$$N^S_{j,p,y,1,a} = N^S_{j,p,y-1,a} e^{-M^S_{y,a}/8} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 1 \le a \le 5^+$$

$$N^S_{j,p,y,q,a} = (N^S_{j,p,y,q-1,a} - C^S_{j,p,y,q-1,a}) e^{-M^S_{y,a}/4} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 2 \le q \le 4\ ,\ 1 \le a \le 5^+ \qquad \text{(S4)}$$

Numbers-at-length at 1 November (after infection and movement)

$$N^S_{j,p,y,l} = \sum_{a=0}^{5+} A^{sur}_{j,y,a,l} N^S_{j,p,y,a} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 2.5^- cm \le l \le 24^+ cm \qquad \text{(S5)}$$

The model predicted numbers-at-length of ages 1+ only are given by:

$$N^{S,1+}_{j,p,y,l} = \sum_{a=1}^{5+} A^{sur}_{j,y,a,l} N^S_{j,p,y,a} \qquad p = I, NI\ ,\ y_1 \le y \le y_n\ ,\ 2.5^- cm \le l \le 24^+ cm \qquad \text{(S6)}$$

The proportion of sardine of age a in stock j that fall in length group l at 1 November, $A^{sur}_{j,y,a,l}$, is calculated under the assumption that length-at-age is normally distributed about a von Bertalanffy growth curve:

$$A^{sur}_{j,y,a,l} \sim N\left(L_{j,\infty}\left(1 - e^{-\kappa_j\left(a - t_{0,j,y}\right)}\right), \vartheta^2_{j,a}\right) \qquad y_1 \le y \le y_n\ ,\ 0 \le a \le 5^+\ ,\ 2.5^- cm \le l \le 24^+ cm \qquad \text{(S7)}$$ [2]

with

$$t_{0,j,y} = \begin{cases} t_{0,j} + \varepsilon^t_y & y = y_1 \\ t_{0,j} + \rho^t \varepsilon^t_{y-1} + \sqrt{1 - \left(\rho^t\right)^2}\, \varepsilon^t_y & y_1 < y \le y_n \end{cases} \qquad \text{(S8)}$$ [3]

Spawning biomass and biomass associated with the November survey

$$SSB^S_{j,y} = \sum_p \sum_{l=2.5^-}^{24^+} f^S_{j,y,l} N^{S,1+}_{j,p,y,l} w^S_{j,y,l} \qquad y_1 \le y \le y_n \qquad \text{(S9)}$$

$$B^S_{j,y} = k^S_{j,N} \sum_p \sum_{l=2.5^-}^{24^+} N^S_{j,p,y,l} w^S_{j,y,l} \qquad y_1 \le y \le y_n \qquad \text{(S10)}$$ [4]

where $w^S_{j,y,l} = w^S_{j,l} \times \dfrac{\tilde{w}_{j,y}}{\left(\sum\limits_p \sum\limits_{l=2.5^-}^{24^+} N^S_{j,p,y,l} w^S_{j,l}\right) \Big/ \left(\sum\limits_p \sum\limits_{l=2.5^-}^{24^+} N^S_{j,p,y,l}\right)} \qquad y_1 \le y \le y_n\ ,\ 2.5^- cm \le l \le 24^+ cm \qquad \text{(S11)}$

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[2] Given the allowance for early/late recruitment in varying $t_{0,y}$ estimates annually, there may be some proportion of this distribution below a length of zero (due to late recruitment). In these cases, this proportion is removed from the proportion-at-length of the minus length class.

[3] Additive error allows for early or late recruitment. While the timing of recruitment may vary between stocks due to differing environmental conditions on the west and south coasts, the same autocorrelation parameters are assumed here for simplicity.

[4] The biomass in $y_n = 2015$ excludes age 0 fish, although the contribution of age 0 fish to the total biomass should be minor.

Commercial selectivity

$$S_{j,y,q,l}=\begin{cases} 0 & l\le 5.5cm \\ \chi_j\exp\left\{-\dfrac{\left(l+0.25-\bar{l}_{1,j}\right)^2}{\left(\sigma_1^{sel}\right)^2}\right\}+\dfrac{1}{1+\exp\left\{-\left(l-\bar{l}_{2,j,y,q}\right)/\sigma_{2,y}^{sel}\right\}} & 6cm\le l\le l_{\max}=23cm \\ S_{j,y,l\max} & l>l_{\max} \end{cases}$$

$$y_1\le y\le y_n\,,1\le q\le 4 \qquad \text{(S12)}$$

$$S_{j,y,q,a}=\sum_{l=2.5^-}^{23.5^+}A_{j,y,q,a,l}^{com}S_{j,y,q,l} \qquad y_1\le y\le y_n\,,\ 1\le q\le 4\,,\ 0\le a\le 5^+ \qquad \text{(S13)}$$

where $A_{j,y,q,a,l}^{com}\sim N\left(L_{j,\infty}\left(1-e^{-\kappa_j\left(a+(2q-1)/8-t_{0,y}\right)}\right),\vartheta_{j,a}^2\right)$

$$y_1\le y\le y_n\,,1\le q\le 4\,,0\le a\le 5^+,\ 2.5^- cm\le l\le 24^+ cm \qquad \text{(S14)}$$

Bycatch in the anchovy directed fishery

$$C_{j,p,y,q,a}^{bycatch}=\begin{cases} N_{j,p,y,q,a}^S F_{j,y,q,a}^{By} & 0\le a\le 1 \\ 0 & 2\le a\le 5^+ \end{cases} \qquad p=I,NI\,,\ y_1\le y\le y_n\,,1\le q\le 4 \qquad \text{(S15)}^{5}$$

Catch in the directed sardine and round herring bycatch fisheries

$$C_{j,p,y,q,a}^{dir}=\left(N_{j,p,y,q,a}^S-C_{j,p,y,q,a}^{bycatch}\right)S_{j,y,q,a}F_{j,y,q} \qquad p=I,NI\,,\ y_1\le y\le y_n\,,1\le q\le 4\,,0\le a\le 5^+ \qquad \text{(S16)}$$

Total catch

$$C_{j,p,y,q,a}^S=C_{j,p,y,q,a}^{bycatch}+C_{j,p,y,q,a}^{dir} \qquad p=I,NI\,,\ y_1\le y\le y_n\,,1\le q\le 4\,,0\le a\le 5^+ \qquad \text{(S17)}$$

Fished proportion of the available biomass from the bycatch in the anchovy directed fishery

$$F_{j,y,q=1,a=0}^{By}=\frac{\sum\limits_{m=11}^{12}\sum\limits_{l<lcut_{y,m}}C_{j,y-1,m,l}^{RLF,\,fleet=3}+\sum\limits_{l<lcut_{y,m}}C_{j,y,1,l}^{RLF,\,fleet=3}}{\sum\limits_{p}N_{j,p,y,q=1,a=0}^S} \qquad F_{j,y,q=1,a=1}^{By}=\frac{\sum\limits_{m=11}^{12}\sum\limits_{l>=lcut_{y,m}}C_{j,y-1,m,l}^{RLF,\,fleet=3}+\sum\limits_{l>=lcut_{y,m}}C_{j,y,1,l}^{RLF,\,fleet=3}}{\sum\limits_{p}N_{j,p,y,q=1,a=1}^S}$$

$$F_{j,y,q=2,a=0}^{By}=\frac{\sum\limits_{m=2}^{4}\sum\limits_{l<lcut_{y,m}}C_{j,y,m,l}^{RLF,\,fleet=3}}{\sum\limits_{p}N_{j,p,y,q=2,a=0}^S} \qquad F_{j,y,q=2,a=1}^{By}=\frac{\sum\limits_{m=2}^{4}\sum\limits_{l>=lcut_{y,m}}C_{j,y,m,l}^{RLF,\,fleet=3}}{\sum\limits_{p}N_{j,p,y,q=2,a=1}^S}$$

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[5] "Selectivity" is incorporated in $F_{j,y,q,a}^{By}$, as the sardine bycatch is typically independent of sardine abundance, but rather correlated with anchovy recruitment which varies from year to year.

$$F^{By}_{j,y,q=3,a=0} = \frac{\sum_{m=5}^{7} \sum_{l<lcut_{y,m}} C^{RLF,\,fleet=3}_{j,y,m,l}}{\sum_{p} N^{S}_{j,p,y,q=3,a=0}} \qquad F^{By}_{j,y,q=3,a=1} = \frac{\sum_{m=5}^{7} \sum_{l>=lcut_{y,m}} C^{RLF,\,fleet=3}_{j,y,m,l}}{\sum_{p} N^{S}_{j,p,y,q=3,a=1}}$$

$$F^{By}_{j,y,q=4,a=0} = \frac{\sum_{m=8}^{10} \sum_{l<lcut_{y,m}} C^{RLF,\,fleet=3}_{j,y,m,l}}{\sum_{p} N^{S}_{j,p,y,4,0}} \qquad F^{By}_{j,y,q=4,a=1} = \frac{\sum_{m=8}^{10} \sum_{l>=lcut_{y,m}} C^{RLF,\,fleet=3}_{j,y,m,l}}{\sum_{p} N^{S}_{j,p,y,4,1}} \qquad \text{(S18)}$$

A penalty is imposed within the model to ensure that $F^{By}_{j,y,q,a} < 0.95$.

Fished proportion of the available biomass from the directed catch and round herring bycatch fisheries

$$F_{j,y,q=1} = \frac{\sum_{fleet=1}^{2} \sum_{m=11}^{12} \sum_{l\geq 6cm} C^{RFL,\,fleet}_{j,y-1,m,l} + \sum_{fleet=1}^{2} \sum_{l\geq 6cm} C^{RFL,\,fleet}_{j,y,1,l}}{\sum_{p} \sum_{a=0}^{5+} \left(N^{S}_{j,p,y,1,a} - C^{bycatch}_{j,p,y,1,a}\right) S_{j,y,1,a}}$$

$$F_{j,y,q=2} = \frac{\sum_{fleet=1}^{2} \sum_{m=2}^{4} \sum_{l\geq 6cm} C^{RFL,\,fleet}_{j,y,m,l}}{\sum_{p} \sum_{a=0}^{5+} \left(N^{S}_{j,p,y,2,a} - C^{bycatch}_{j,y,2,a}\right) S_{j,y,2,a}}$$

$$F_{j,y,q=3} = \frac{\sum_{fleet=1}^{2} \sum_{m=5}^{7} \sum_{l\geq 6cm} C^{RFL,\,fleet}_{j,y,m,l}}{\sum_{p} \sum_{a=0}^{5+} \left(N^{S}_{j,p,y,3,a} - C^{bycatch}_{j,y,3,a}\right) S_{j,y,3,a}}$$

$$F_{j,y,q=4} = \frac{\sum_{fleet=1}^{2} \sum_{m=8}^{10} \sum_{l\geq 6cm} C^{RFL,\,fleet}_{j,y,m,l}}{\sum_{p} \sum_{a=0}^{5+} \left(N^{S}_{j,p,y,4,a} - C^{bycatch}_{j,y,4,a}\right) S_{j,y,4,a}} \qquad \text{(S19)}$$

A penalty is imposed within the model to ensure that $S_{j,y,q,l} F_{j,y,q} < 0.95$. Fish <6cm were seldom[6] caught and were thus not used in fitting this model. Commercial selectivity-at-length is fixed to zero for length classes <6cm (equation S12).

Recruitment

$$N^{S}_{j,p,y,a=0} = \begin{cases} a^{S}_{j} e^{\varepsilon^{S}_{j,y} - 0.5\left(\sigma^{S}_{j,r}\right)^{2}} & \text{if } p = I \text{ and } SSB^{S}_{j,y} \geq b^{S}_{j} \\ \dfrac{a^{S}_{j}}{b^{S}_{j}} SSB^{S}_{j,y} e^{\varepsilon^{S}_{j,y} - 0.5\left(\sigma^{S}_{j,r}\right)^{2}} & \text{if } p = I \text{ and } SSB^{S}_{j,y} < b^{S}_{j} \\ 0 & \text{if } p = NI \end{cases} \qquad y_1 \leq y \leq y_n \qquad \text{(S20)}$$

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[6] Less than 6% of the quarters west of Cape Agulhas, less than 2% of the quarters south-east of Cape Agulhas and less than 4% of the quarters for the whole coast.

Carrying Capacity

$$K_j^S = a_j^S e^{-0.5\left(\sigma_{j,r}^S\right)^2} \left(\sum_{a=1}^{4} \overline{w}_{j,a}^S e^{-M_j^S-(a-1)\overline{M}_{ad}^S} + \overline{w}_{j,5+} e^{-M_j^S-4\overline{M}_{ad}^S} \frac{1}{1-e^{-\overline{M}_{ad}^S}} \right) \tag{S21}$$

Number of recruits associated with the recruit survey

$$N_{j,y,r}^S = k_{j,r}^S \left(\left(N_{j,NI,y,2,0}^S - C_{j,NI,y,2,0}^S \right) e^{-\left(1/8+0.5t_y^S/12\right) M_{y,0}^S} - \tilde{C}_{j,y,0bs}^S \right) e^{-0.5t_y^S \times M_{y,0}^S/12} \qquad y_1 \le y \le y_n \tag{S22}$$

Multiplicative survey bias

$$k_{j,N}^S = k_{ac}^S \tag{S23}$$

$$k_{j=W,r}^S = k_{\mathrm{cov}}^S \times k_{ac}^S \tag{S24}$$

$$k_{j=S,r}^S = k_{\mathrm{cov}\,S}^S \times k_{\mathrm{cov}}^S \times k_{ac}^S \tag{S25}$$

Survey trawl selectivity

$$S_{j,l}^{survey} = \begin{cases} 0 & l = 2.5^- cm \\ \left[1+\exp\left\{-\left(l+0.25-S_{50}\right)/\delta\right\}\right]^{-1} & 3cm \le l \le 24^+ cm \end{cases} \qquad y_1 \le y \le y_n \tag{S26}$$

Proportion-at-length associated with the November survey

$$p_{j,y,l}^S = \begin{cases} \dfrac{\sum_p \sum_{l \le 6cm} N_{j,p,y,l}^S S_{j,l}^{survey}}{\sum_p \sum_{l=2.5^-}^{24^+} N_{j,p,y,l}^S S_{j,l}^{survey}} & l = 6^- cm \\ \dfrac{\sum_p N_{j,p,y,l}^S S_{j,l}^{survey}}{\sum_p \sum_{l=2.5^-}^{24^+} N_{j,p,y,l}^S S_{j,l}^{survey}} & 6.5cm \le l \le 20.5cm \\ \dfrac{\sum_p \sum_{l=21}^{23.5} N_{j,p,y,l}^S S_{j,l}^{survey}}{\sum_p \sum_{l=2.5^-}^{24^+} N_{j,p,y,l}^S S_{j,l}^{survey}} & l = 21-23.5cm \\ \dfrac{\sum_p N_{j,p,y,24^+}^S S_{j,24^+}^{survey}}{\sum_p \sum_{l=2.5^-}^{24^+} N_{j,p,y,l}^S S_{j,l}^{survey}} & l = 24^+ cm \end{cases} \qquad y_1 \le y \le y_n \tag{S27}$$ [7]

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[7] The inclusion of model predicted proportion-at-length 24$^+$cm is deliberate to take into account the zero samples of 24$^+$cm sardine in the survey.

Proportion-at-length of fish infected with the parasite in November

$$P^S_{j,y,l} = \frac{N^S_{j,I,y,l}}{\sum_p N^S_{j,p,y,l}} \qquad y_1 \le y \le y_n \,, 10cm \le l \le 23cm \tag{S28}$$

Catch-at-length from the directed and round herring bycatch fisheries

$$C^{dir}_{j,p,y,q,l} = \sum_{a=0}^{5+} \left(N^S_{j,p,y,q,a} - C^{bycatch}_{j,p,y,q,a} \right) A^{com}_{j,q,a,l} S_{j,y,q,l} F_{j,y,q} \quad p = I, NI \,,\ y_1 \le y \le y_n \,, 1 \le q \le 4 \,,\ 2.5^- cm \le l \le 24^+ cm \tag{S29}$$

Proportion-at-length associated with the directed catch and round herring bycatch

$$p^{coml,S}_{j,y,q,l} = \begin{cases} \dfrac{\sum_p C^{dir}_{j,p,y,q,l}}{\sum_p \sum_{l=6}^{24^+} C^{dir}_{j,p,y,q,l}} & 6cm \le l \le 22.5cm \\[2ex] \dfrac{\sum_p \sum_{l=23}^{24^+} C^{dir}_{j,p,y,q,l}}{\sum_p \sum_{l=6}^{24^+} C^{dir}_{j,p,y,q,l}} & l = 23^+ cm \end{cases} \qquad y_1 \le y \le y_n \,,\ 1 \le q \le 4 \tag{S30}$$

Fitting the Model to Observed Data (Likelihood)

$$-\ln L = -\ln L^{Nov} - \ln L^{rec} - \ln L^{sur\ propl} - \ln L^{com\ propl} - \ln L^{prev} \tag{S31}$$

where

$$-\ln L^{Nov} = \tfrac{1}{2} \sum_j \sum_{y=y1}^{yn} \left\{ \left\{ \frac{5^5 \left(\dfrac{\left| \ln\left(\hat{B}^S_{j,y}\right) - \ln(B^S_{j,y}) \right|}{\sqrt{(\sigma^S_{j,y,Nov})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,N})^2}} \right)^5}{5^5 + \left(\dfrac{\left| \ln\left(\hat{B}^S_{j,y}\right) - \ln(B^S_{j,y}) \right|}{\sqrt{(\sigma^S_{j,y,Nov})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,N})^2}} \right)^5} \right\}^{2/5} + \ln\left[2\pi \left((\sigma^S_{j,y,Nov})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,N})^2 \right) \right] \right\} \tag{S32}$$

$$-\ln L^{rec} = \tfrac{1}{2} \sum_j \sum_{y=y1+1}^{yn} \left\{ \left\{ \frac{5^5 \left(\dfrac{\left| \ln\left(\hat{N}^S_{j,y,r}\right) - \ln(N^S_{j,y,r}) \right|}{\sqrt{(\sigma^S_{j,y,rec})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,r})^2}} \right)^5}{5^5 + \left(\dfrac{\left| \ln\left(\hat{N}^S_{j,y,r}\right) - \ln(N^S_{j,y,r}) \right|}{\sqrt{(\sigma^S_{j,y,rec})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,r})^2}} \right)^5} \right\}^{2/5} + \ln\left[2\pi \left((\sigma^S_{j,y,rec})^2 + \left(\phi^S_{ac}\right)^2 + (\lambda^S_{j,r})^2 \right) \right] \right\} \tag{S33}$$

$$-\ln L^{sur\ propl} = w^{sur}_{propl} \sum_{j} \sum_{y=y1}^{yn} \left\{ \sum_{l=6^-}^{21^+} \left\{ \frac{\left(\sqrt{\hat{p}^{S}_{j,y,l}} - \sqrt{p^{S}_{j,y,l}} \right)^2}{2\left(\sigma^{S}_{j,ur}\right)^2} + \ln\left(\sigma^{S}_{j,sur}\right) \right\} + \frac{\left(0 - \sqrt{p^{S}_{j,y,24^+}} \right)^2}{2\left(\sigma^{S}_{j,ur}\right)^2} + \ln\left(\sigma^{S}_{j,sur}\right) \right\} \qquad \text{(S34)}^{8}$$

$$-\ln L^{com\ propl} = w^{com}_{propl} \sum_{j} \sum_{y=y1}^{yn} \sum_{q=1}^{4} \sum_{l=6}^{23^+} \left\{ \frac{\left(\sqrt{\hat{p}^{S,coml}_{j,y,q,l}} - \sqrt{p^{S,coml}_{j,y,q,l}} \right)^2}{2\left(\sigma^{S}_{j,com}\right)^2} + \ln\left(\sigma^{S}_{j,com}\right) \right\} \qquad \text{(S35)}$$

$$-\ln L^{prev} = \sum_{j} \sum_{y=2010}^{2014} \sum_{l=5cm}^{23cm} \left\{ -n^{prev}_{j,y,l} \ln\left(P^{S}_{j,y,l}\right) - \left(N^{prev}_{j,y,l} - n^{prev}_{j,y,l}\right) \ln\left(1 - P^{S}_{j,y,l}\right) \right\} \qquad \text{(S36)}$$

A “robustified likelihood” is used for the contributions from the hydro-acoustic surveys to ensure no undue influence from any extreme (outlying) values for residuals. The functional form chosen to robustify makes negligible difference for standardised residuals of magnitude three or less, but essentially treats large standardised residuals as if they do not exceed five in magnitude.

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[8] The 21^+ group in this equation consists of the length classes 21cm, 21.5cm, 22cm, 22.5cm, 23cm and 23.5cm.

Table S1. Assessment model parameters and variables with associated fixed values or prior distributions and, for derived variables, associated equation numbers. As the majority of prior distributions are uninformative, notes are provided only for informative priors and/or bounds.

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Annual numbers and biomass	$N^S_{j,p,y,a}$	Model predicted numbers-at-age a at the beginning of November in year y of stock j that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S1 - S3, S20	
	$N^S_{j,p,y,q,a}$	Model predicted numbers-at-age a mid-way through quarter q of year y of stock j that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S4	
	$M^S_{y,a}$	Rate of natural mortality of age a in year y	Year^{-1}		$M^S_{y,0} = 1.0$ $M^S_{y,1+} = 0.8$	de Moor and Butterworth (2015)
	I_y	Proportion of uninfected west stock sardine that are infected with the endoparasite in year y		$I_y = I \sim U(0,1)$ $2008 \le y \le y_n$ $=0,\ y_1 \le y \le 2007$		
	$move_{y,a}$	Proportion of west stock sardine of age a which move to the south stock at the beginning of November of year y	-	$move_{y,1} \sim Beta(1.05,1.05)$, $move_{y,2+} = \phi \times move_{y,1}$, $\phi \sim U(0,1)$		
	$SSB^S_{j,y}$	Model predicted spawning biomass of stock j at the beginning of November in year y	Thousand tons		S9	
	$B^S_{j,y}$	Model predicted total biomass of stock j at the beginning of November in year y, associated with the November survey	Thousand tons		S10	

Table S1 (Continued).

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Annual numbers and biomass	$f^{S}_{j,y,l}$	Proportion of stock j sardine that are mature in length class l in year y	-		$\left[1+\exp\left\{-\left(l-17.2\right)/1.17\right\}\right]^{-1}$ $1984 \le y \le 1987$ $\left[1+\exp\left\{-\left(l-18.6\right)/1.26\right\}\right]^{-1}$ $1988 \le y \le 1995$ $\left[1+\exp\left\{-\left(l-19.4\right)/1.40\right\}\right]^{-1}$ $1996 \le y \le 2003$ $\left[1+\exp\left\{-\left(l-17.4\right)/0.95\right\}\right]^{-1}$ $2004 \le y \le 2014$	Refit from data used by van der Lingen et al. (2006) using midpoints of length classes. Assuming maturity post-2003 reflects that of 1965-1975 as maturity is hypothesized to be density dependent (van der Lingen et al. 2006) and both these periods correspond to low biomass following a peak in abundance
	$w^{S}_{j,l}$	Mean mass of sardine of stock j in length class l	Grams		$1.1639\times10^{-5}\times l^{3.03155}$	van der Lingen et al. (2006)
	$w^{S}_{j,y,l}$	Mean mass of sardine of stock j in length class l at the beginning of November in year y	Grams		S11	
	$\tilde{w}_{j,y}$	Mean mass of sardine sampled from stock j during the November survey of year y	Grams		$\dfrac{\sum_{p}\sum_{l=3}^{23.5} N^{S}_{j,p,y,l}\, w^{S}_{j,l}}{\sum_{p}\sum_{l=3}^{23.5} N^{S}_{j,p,y,l}}$	
	$\overline{w}^{S}_{j,a}$	Mean mass of age a from stock j sampled during each November survey, averaged over all years	Grams		$\sum_{l=2.5^{-}}^{24^{+}} A^{sur}_{j,a,l}\, w^{S}_{j,l}$	

Table S1 (Continued).

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Proportions-at-length and growth curve	$N^{S}_{j,p,y,l}$	Model predicted numbers-at-length l at the beginning of November in year y of stock j that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S5	
	$p^{S}_{j,y,l}$	Model predicted proportion-at-length l of stock j associated with the November survey in year y	-		S27	
	$A^{sur}_{j,y,a,l}$	Proportion of age a of stock j sardine that falls in the length group l in November of year y	-		S7	
	κ_j	Somatic growth rate parameter for stock j	Year^{-1}	$U(0,3)$		
	$L_{j,\infty}$	Maximum length (in expectation) of stock j	Cm	$L_{j,a=1} \sim U(5,25)$ $L_{j,a=3} \sim U(5,25)$		$L_{j,\infty}$ and $t_{0,j}$ derived from estimated length at ages 1 and 3
	$t_{0,j,y}$	Age at which the length (in expectation) is zero in year y	Year		S8	
	$t_{0,j}$	Average age at which the length (in expectation) is zero		$\frac{1}{\kappa_j}\ln\left\{\frac{e^{\kappa_j}\left(L_{j,a=1}-L_{j,a=3}\right)}{L_{j,a=1}e^{-2\kappa_j}-L_{j,a=3}}\right\}$		
	ε^{t}_{y}	Annual residuals about the age at which the length is zero		$N(0,2)$		
	ρ^{t}	Autocorrelation coefficient in these residuals		$U(-1,1)$		
	$\vartheta_{j,a}$	Standard deviation of the distribution about the mean length for age a of stock j	-	$U(0.01,3)$, $a = 0,1,2+$		Upper bound chosen to preclude unrealistically large lengths for very young fish
	$p^{coml,S}_{j,y,q,l}$	Model predicted proportion-at-length l of stock j in the directed catch and round herring bycatch during quarter q of year y	-		S30	
	$A^{com}_{j,y,q,a,l}$	Proportion of age a of stock j sardine that falls in the length group l mid-way through quarter q of year y	-		S14	
	$P^{S}_{j,y,l}$	Model predicted proportion-at-length l of stock j that are infected with the endoparasite, at the time of the November survey in year y			S28	

Table S1 (Continued).

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Selectivity	$S_{j,l}^{survey}$	Survey selectivity-at-length l in the November survey for stock j	-		S26	Some smaller fish escape through the trawl net
	S_{50}	Length at which survey selectivity is 50%	Cm	$U(2.5,7)$		
	δ	Inverse of slope of survey selectivity-at-length ogive when selectivity is 50%	-	$U(0.05,5)$		
	$S_{j,y,q,l}$	Commercial selectivity-at-length l during quarter q of year y of stock j	-		S12	
	$S_{j,y,q,a}$	Commercial selectivity-at-age a during quarter q of year y of stock j	-		S13	
	χ_j	Height of the Gaussian component for stock j relative to the height of the logistic component	-	$U(0,1)$		
	$\bar{l}_{1,j}$	Mean of the Gaussian distribution for stock j	Cm	$U(5,15)$		
	$\bar{l}_{2,j,y,q}$	Length at 50% selectivity in the logistic component for stock j in quarter q of year y	Cm	$U(0,25)$		Estimated for four time periods 84-86, 87-97, 98-01, 02-15
	$\left(\sigma_1^{sel}\right)^2$	Variance parameter of the Gaussian distribution	Cm	$U(2,7)$		
	$\left(\sigma_{2,y}^{sel}\right)^2$	Variance parameter of the logistic distribution	Cm	$U(0,10)$		
Multiplicative bias	$k_{j,N}^S$	Multiplicative bias associated with the November survey of stock j	-		S23	
	$k_{j,r}^S$	Multiplicative bias associated with the recruit survey of stock j	-		S24 – S25	
	k_{ac}^S	Multiplicative bias associated with the hydro-acoustic survey	-	$\ln\left(k_{ac}^S\right) \sim N\left(-0.310, 0.094^2\right)$		Section C
	k_{cov}^S	Multiplicative bias associated with the coverage of the recruits by the recruit survey in comparison to the 1+ biomass by the November survey	-	$\sim U(0.3,1)$		Lower bound selected in discussions with scientists on these surveys and their field experience
	$k_{\text{cov}S}^S$	Multiplicative bias associated with the coverage of the south stock recruits by the recruit survey in comparison to the west stock recruits during the same survey		$\sim U(0,1)$		

Table S1 (Continued).

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Catch	$C^{S}_{j,p,y,q,a}$	Model predicted number of age a fish of stock j caught during quarter q of year y that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S17	
	$lcut_{y,m}$	Cut off length for recruits in month m of year y	Cm	de Moor et al. 2016		Differ by month and year as informed by the recruit surveys
	$C^{bycatch}_{j,p,y,q,a}$	Number of age a fish of stock j bycaught in the anchovy-directed fishery in quarter q of year y that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S15	
	$C^{dir}_{j,p,y,q,a}$	Number of age a fish of stock j caught in the sardine-directed and round herring bycatch fisheries in quarter q of year y that are uninfected ($p = NI$) or infected ($p = I$) with the endoparasite	Billions		S16	
	$C^{dir}_{j,p,y,q,l}$	Number of length l fish of stock j caught in the sardine-directed and round herring bycatch fisheries in quarter q of year y	Billions		S29	
	$F^{By}_{j,y,q,a}$	Fished proportion in quarter q of year y for age class a of stock j, of bycatch in the anchovy-directed fishery	-		S18	
	$F_{j,y,q}$	Fished proportion in quarter q of year y for a fully selected age class a of stock j, by the directed and round herring bycatch fisheries	-		S19	
Initial Values	$N^{S}_{j,p,1983,a}$	Initial numbers-at-age a in stock j	Billions	$N^{S}_{j,NI,1983,a=1} \sim U(0,50)$ $N^{S}_{j,NI,1983,a} = 0$, $a \geq 2$ $N^{S}_{j,I,1983,a} = 0$, $0 \leq a \leq 5^{+}$		Estimating N>0 for older ages resulted in no noticeable differences in predicted numbers-at-age in former years

Table S1 (Continued).

	Parameter/ Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Recruitment	a_j^S	Maximum recruitment of stock j in the hockey stick model	Billions	$\ln\left(a_j^S\right) \sim U(0,5.5)$		Uninformative on log-scale as scale is not known *a priori*, with the maximum corresponding to about 10 million tons for K_j^S
	b_j^S	Spawner biomass below which the expectation for recruitment is reduced below the maximum for stock j	Thousand tons	$b_{j=W}^S / K_{j=W}^S \sim U(0,1)$ $b_{j=S}^S / K_{j=S}^S = 0.001$		Insufficient information in the data to estimate the inflection point for the south stock
	K_j^S	Carrying capacity for stock j	Thousand tons		S21	
	$\varepsilon_{j,y}^S$	Lognormal deviation of recruitment of stock j in year y	-	$\varepsilon_{j,y}^S \sim N\left(0,\left(\sigma_{j,r}^S\right)^2\right)$		
	$\left(\sigma_{j,r}^S\right)^2$	Variance in the residuals (lognormal deviation) about the stock recruitment curve of stock j	-	$\sim U(0.16,10)$		Lower bound chosen to restrict the influence of the stock recruitment curve on the assessment results
	$N_{j,y,r}^S$	Model predicted number of juveniles of stock j at the time of the recruit survey in year y	Billions		S22	

Table S1 (Continued).

	Parameter / Variable	Description	Units / Scale	Fixed Value / Prior Distribution	Equation	Notes
Likelihood	$-\ln L^{Nov}$	Contribution to the negative log likelihood from the model fit to the November 1+ survey biomass data	-		S32	
	$-\ln L^{rec}$	Contribution to the negative log likelihood from the model fit to the recruit survey data	-		S33	
	$-\ln L^{sur\ propl}$	Contribution to the negative log likelihood from the model fit to the November survey proportion-at-length data	-		S34	
	$-\ln L^{com\ propl}$	Contribution to the negative log likelihood from the model fit to the quarterly commercial proportion-at-length data	-		S35	
	$-\ln L^{sur\ prev}$	Contribution to the negative log likelihood from the model fit to the November parasite prevalence-by-length data	-		S36	
	ϕ_{ac}^{S}	CV associated with factors which cause bias in the acoustic survey estimates and which vary inter-annually rather than remain fixed over time	-	$=0.227$		Section C
	$\left(\lambda_{j,N/r}^{S}\right)^2$	Additional variance (over and above $\left(\sigma_{j,y,Nov/rec}^{S}\right)^2$ and $\left(\phi_{ac}^{S}\right)^2$) associated with the November/recruit surveys of stock j	-	$\sim U(0{,}10)$		
	w_{propl}^{sur}	Weighting applied to the survey proportion-at-length data	-	$=0.167$		To allow for autocorrelation[9]
	$\sigma_{j,sur}^{S}$	Standard deviation associated with the survey proportion-at-length data of stock j	-	$\sqrt{\sum_{y=y1}^{yn}\sum_{l=6^-}^{21^+}\left(\sqrt{\hat{p}_{j,y,l}^{S}}-\sqrt{p_{j,y,l}^{S}}\right)^2 \Big/ \sum_{y=y1}^{yn}\sum_{l=6^-}^{21}1}$ [10]		Closed form solution
	w_{propl}^{com}	Weighting applied to the commercial proportion-at-length data		$=0.04$		To allow for autocorrelation[11]

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[9] Based upon data being available ~6 times more frequently than annual age data which contain maximum information content on this.

[10] The 21^+ group in this equation consists of the length classes 21cm, 21.5cm, 22cm, 22.5cm, 23cm and 23.5cm.

[11] Based upon data being available ~4x6 times more frequently than annual age data which contain maximum information content on this.

$\sigma^{S}_{j,com}$	Standard deviation associated with the commercial proportion-at-length data of stock j	-	$\sqrt{\sum_{y=y1}^{yn}\sum_{q=1}^{4}\sum_{l=6}^{23^+}\left(\sqrt{\hat{p}^{comlS}_{1,y,q,l}}-\sqrt{p^{comlS}_{1,y,q,l}}\right)^2 \Big/ \sum_{y=y1}^{yn}\sum_{q=1}^{4}\sum_{l=6}^{23^+}1}$ $\sqrt{\sum_{y=y1}^{yn}\sum_{q=1}^{4}\sum_{l=13}^{23^+}\left(\sqrt{\hat{p}^{comlS}_{2,y,q,l}}-\sqrt{p^{comlS}_{2,y,q,l}}\right)^2 \Big/ \sum_{y=y1}^{yn}\sum_{q=1}^{4}\sum_{l=13}^{23^+}1}$	Closed form solution[12]

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[12] A shorter range of lengths is used given the near absence of data outside this range, resulting in small/zero residuals, which would negatively bias this estimate.

Table S2. Assessment model data, detailed in de Moor et al. (2016).

Quantity	Description	Units / Scale	Shown in Figure
t_y^S	Time lapsed between 1 May and the start of the recruit survey in year y	Months	
$\tilde{C}^S_{j,y,0bs}$	Number of juveniles of stock j caught between 1 May and the day before the start of the recruit survey in year y	Billions	
$C^{RFL,fleet}_{j,y,m,l}$	Number of fish in length class l landed by $fleet$ in month m of year y of stock j. $fleet=1$ denotes the sardine directed fishery, $fleet=2$ denotes the sardine bycatch with round herring (1984-2011) or ≥14cm sardine bycatch (2012-14) and $fleet=3$ denotes the juvenile sardine bycatch with anchovy (1984-2011) or <14cm sardine bycatch (2012-15)	Billions	
$\hat{B}^S_{j,y}$	Acoustic survey estimate of biomass of stock j from the November survey in year y	Thousand tons	Fig. 2
$\sigma^S_{j,y,Nov}$	Survey sampling CV associated with $\hat{B}^S_{j,y}$ that reflects survey inter-transect variance	-	Fig. 2
$\hat{N}^S_{j,y,r}$	Acoustic survey estimate of recruitment of stock j from the recruit survey in year y	Billions	Fig. 2
$\sigma^S_{j,y,rec}$	Survey sampling CV associated with $\hat{N}^S_{j,y,r}$ that reflects survey inter-transect variance	-	Fig. 2
$\hat{p}^S_{j,y,l}$	Observed proportion (by number) of stock j in length group l in the November survey of year y	-	Fig. S3
$\hat{p}^{S,coml}_{j,y,q,l}$	Observed proportion (by number) of the directed catch and round herring bycatch of fish of stock j and length group l during quarter q of year y	-	Fig. S4
$n^{prev}_{j,y,l}$	Number of sardine of stock j in length class l sampled from the November survey in year y that were tested and found to be infected with the parasite	Numbers	Fig. 5
$N^{prev}_{j,y,l}$	Number of sardine of stock j in length class l sampled from the November survey in year y that were tested for infection with the parasite	Numbers	Fig. 5

Section C. Calculating the bias in estimates of sardine from the May and November hydro-acoustic surveys

The probability density functions (pdfs) for the bias in the May and November acoustic survey that relate directly to the acoustic survey (rather than, for example the coverage of the stock), k_{ac}^{S}, and the CV associated with variable error factors which cause bias in the acoustic survey estimates, ϕ_{ac}^{S}, have been updated from that calculated by de Moor and Butterworth (2015).

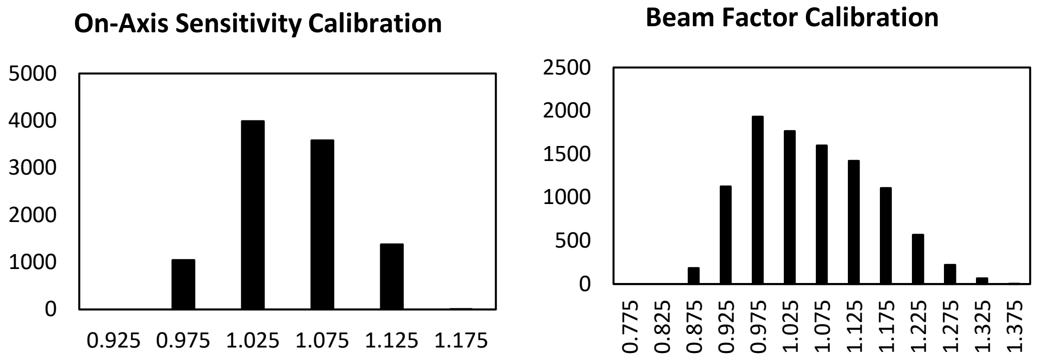
Anon. (2000) distinguished two different types of acoustic error factors (Table S3). Constant error relates to a factor whose value is not known exactly, but whatever it is, it is the same for each year. In contrast variable errors relate to a factor whose true value will change from one year to the next.

Ten thousand samples were drawn from the individual pdfs for each source of error. These sampled numbers were then all inverted so as to correspond directly to k_{ac}^{S} which applies to the model biomass rather than observed biomass. The inverted sample of constant errors is denoted as C_j, $j=1,\ldots,10000$ for the only constant error factor (calibration – beam factor), and the inverted sample of variable errors – or errors that vary inter-annually – is denoted as V_j^k, $j=1,\ldots,10000$ for error factor *k*. Histograms of the samples are given in Figure S9.

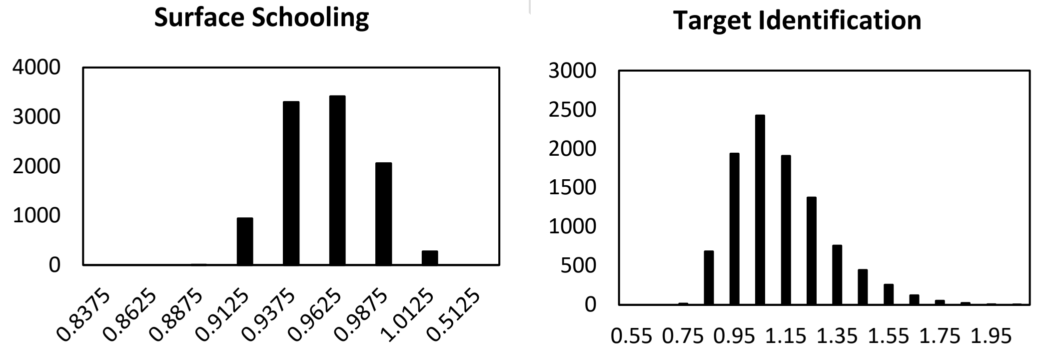
As the survey biomass estimates are considered in log-space in the likelihood (equations S32-S33), the distributions of k_{ac}^{S} and ϕ_{ac}^{S} are similarly considered in log-space. Histograms of the $\ln(C_j)$ and $\ln(V_j^k)$ samples are given in Figure S10. The median of $\ln(k_{ac}^{S})$ is subsequently calculated as the median of the sample: $\ln(C_j)+\sum_k \ln(V_j^k)$, $j=1,\ldots,10000$, which is -0.310. The standard deviation of $\ln(k_{ac}^{S})$ is based only on the log of the constant factor, and thus it is calculated as the standard deviation of the sample: $\ln(C_j)$, $j=1,\ldots,10000$, which is 0.094. The prior distribution for $\ln(k_{ac}^{S})$ is taken to be normally distributed, i.e. $\ln(k_{ac}^{S})\sim N(-0.310,0.094^2)$ (Fig. S11). The standard deviation of the log of the variable factors is considered similar to additional variance in the likelihood calculation, and is calculated as the standard deviation of the sample: $\sum_k \ln(V_j^k)$, $j=1,\ldots,10000$, giving $\phi_{ac}^{S}=0.227$. There may, however, still be systematic errors relating to the target strength that have not been taken into account in these pdfs. These could be taken into account through sensitivity tests by using alternative priors for k_{ac}^{S}.

Table S3. Individual error factors for hydro-acoustic surveys of sardine biomass, where the values define trapezium form pdfs (Anon. 2000). Note that these error factors apply to the observed biomass, i.e. they reflect the inverse of the multiplicative bias factor k_{ac}^{S} in the model.

Error	Minimum	Likely (lower)	Likely (midpoint)	Likely (upper)	Maximum	Nature
Calibration						
(On-axis sensitivity)	0.90	0.95	1.00	1.05	1.10	Variable[14]
(Beam factor)	0.75[13]	0.90	1.00	1.10	1.25	Constant
Surface Schooling	1.00	1.05	1.075	1.10	1.15	Variable
Target Identification	0.50	0.90	1.00	1.10	1.50	Variable[6]
Weather Effects	1.01	1.05	1.15	1.25	2.00	Variable


On-Axis Sensitivity Calibration

Beam Factor Calibration


Surface Schooling

Target Identification

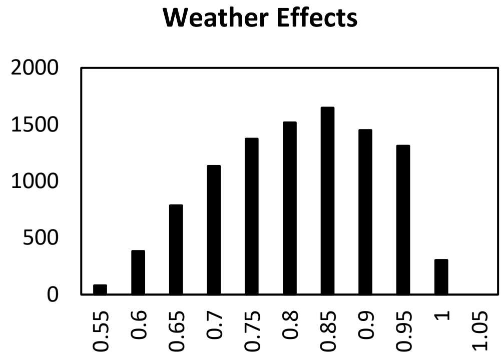

Weather Effects

Fig. S9. The histograms of 10 000 samples of the individual error factors C_j and V_j^k .

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[13] This was originally reported as 0.8 in Anon 2000, but subsequently corrected (I. Hampton pers. Comm.).

[14] This was recorded in Anon. (2000) as random error denoting that it would be positive or negative rather than purely positive or negative.

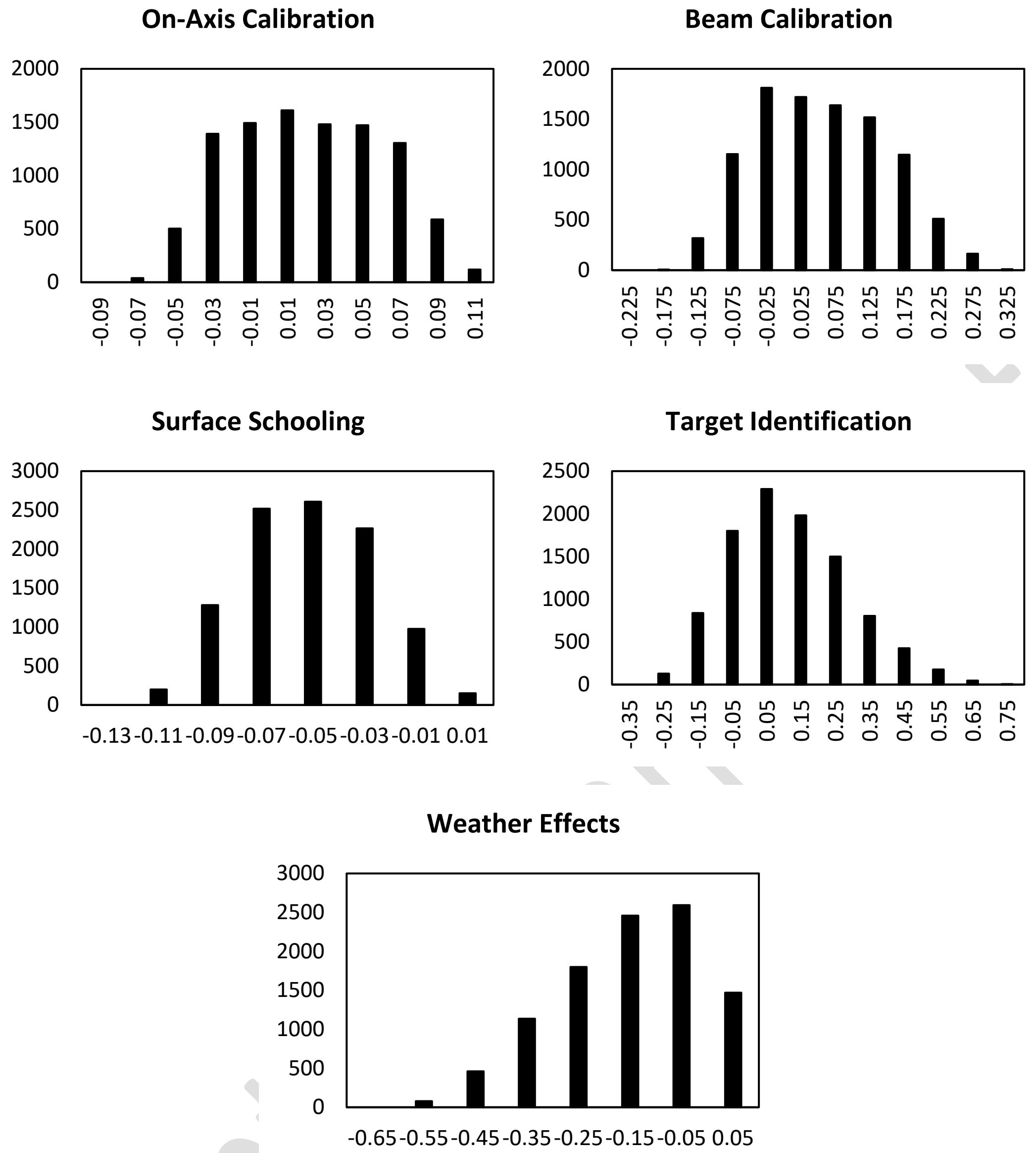

Fig. S10. The histograms of 10 000 samples of the individual error factors $\ln(C_j)$ and $\ln(V_j^k)$.

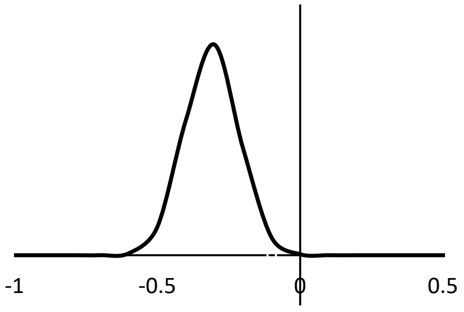

Fig. S11. The resultant assumed prior distribution for $\ln(k_{ac}^{S})$.

Supplementary Material References

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