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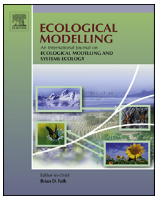

A frame-based modelling approach to understanding changes in the distribution and abundance of sardine and anchovy in the southern Benguela

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ABSTRACT

A number of ecologically and economically important species in the southern Benguela, including the forage fish sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, have undergone southward/eastward shifts in their distribution in the 1990s/early 2000s. In addition to the effects of changes in prey availability to top predators, the spatially-distinct nature of the system means the location of a stock has implications for its productivity. The spatial dynamics of small pelagic fish are of particular importance because they are thought to exert wasp-waisted trophic control on the system. An objective-driven frame-based model was constructed to investigate the ability of the approach to represent spatial and population dynamics of sardine and anchovy, and to explore the implications of possible management strategies. Climate variability and fishing pressure were assumed as drivers. Sensitivity analyses were performed and a number of scenarios tested. A frame-based approach appears to be useful within this context. Results suggest that the productivity of the sardine resource within the model is highly dependent on the spatial characteristics of fishing pressure. The role of anchovy within the model system has not yet been fully developed. Increasing our understanding of the relative suitability of environmental conditions of different regions is also important if we are to increase our capacity to predict trends in abundance and distribution. This study shows support for continued careful consideration of spatialized management approaches to the South African sardine fishery.

1. Introduction

The southern Benguela (Fig. 1) comprises two of the four subsystems of the Benguela Current Large Marine Ecosystem (BCLME) (Hutchings et al., 2009): the west coast, characterised by seasonal, wind-driven upwelling; and the south coast with characteristics of both a shelf system and an upwelling system (Hutchings et al., 2009; Shannon 1985).

1.1. *Biology*

As in most eastern boundary current systems, small pelagic fish in the southern Benguela play an important role in ecosystem function, acting as a trophic stepping stone between plankton and higher trophic level species such as predatory fish and seabirds. A system operating under this model of trophic function is described as 'wasp-waisted', with small pelagic fish exerting both top-down control on zooplankton populations as well as bottom-up influence on predatory groups. The southern Benguela is thought to operate in this manner (Cury et al., 2000), and the structure was generally supported when modelled data were fitted to observed data time-series (Shannon et al., 2008).

Sardine and anchovy have also formed the bulk of South Africa's commercially valuable purse-seine fishery since the 1940s (Crawford et al., 1987; Fairweather et al., 2006). Their ecological and commercial importance make the dynamics of sardine and anchovy populations of particular interest from an ecosystem research and fisheries management perspective. Historically both research and management have focused on a target resource–oriented, two species approach, but more recently with the increasing emphasis on the application of an ecosystem approach to fisheries management, more importance is being placed on better understanding the role of sardine and anchovy within the system as a whole.

Sardine and anchovy populations around the world have been observed as highly variable on an interannual and decadal scale,

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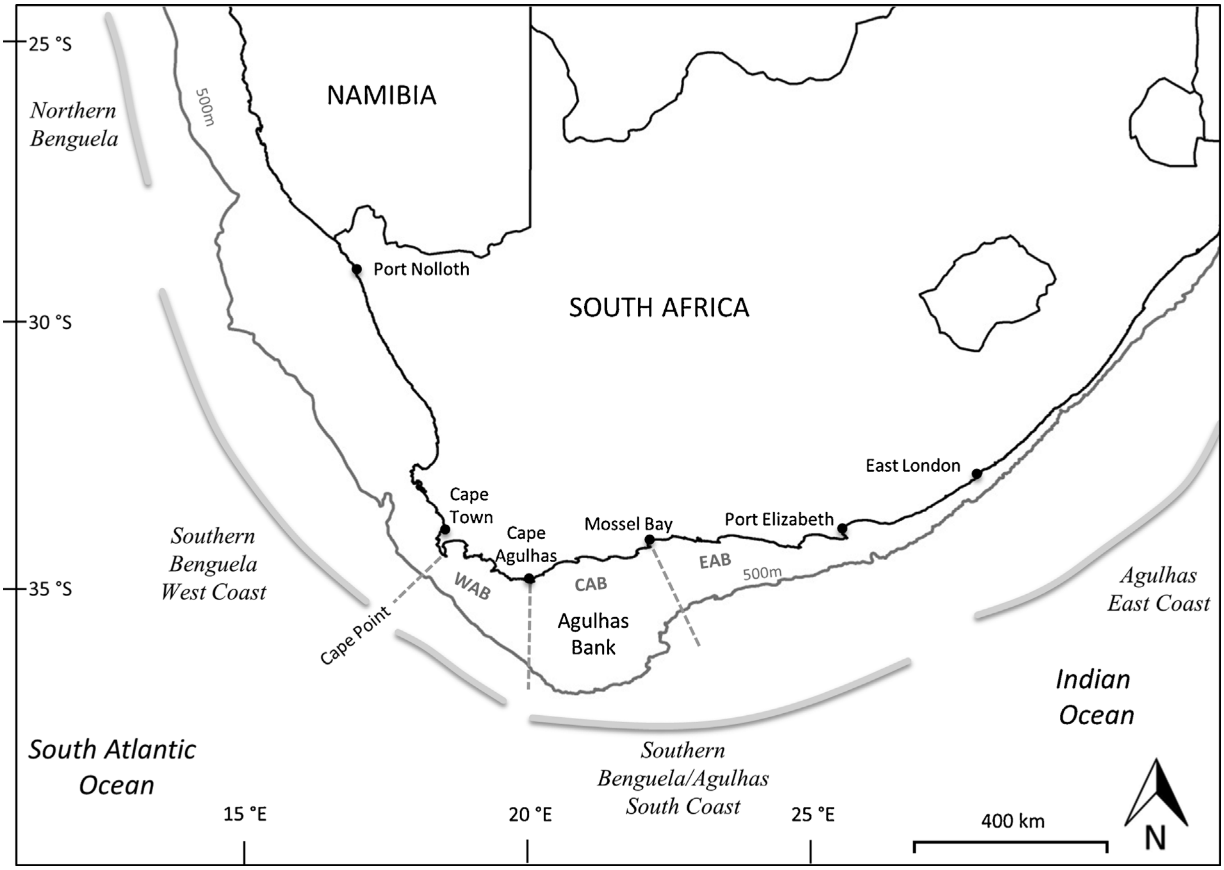


Fig. 1. The southern Benguela extending from 29°S around the west and south coasts of South Africa, divided at Cape Agulhas, to 28°E at East London. Adapted from Blamey et al. (2015).

with decadal-scale dominance shifts between the two species (Schwartzlose et al., 1999; Cury and Shannon 2004). This holds true for populations of sardine and anchovy in the southern Benguela, where one species has been dominant for a period (on a decadal scale), followed by a change in the community structure and dominance of the other species. The southern Benguela has also seen a period of high abundance of both species during the early 2000s, as a consequence of an ecosystem regime shift (Blamey et al., 2012; Howard et al., 2007).

Recent decades have seen the concept of regime shifts in marine systems become a more common approach to describing long-term changes at an ecosystem level (de Young et al., 2004). Here we are defining a regime shift as a sudden change from one quantifiable state to another, occurring at a large spatial scale (de Young et al., 2004; Jarre et al., 2006). Shifts in a number of physical and biological time series for the southern Benguela, have been detected in the late 1990s–early 2000s (Roy et al., 2007; Howard et al., 2007; Blamey et al., 2012; Atkinson et al., 2012), including in the distribution of sardine and anchovy: since the late 1990s the majority of small pelagic fish spawner biomass has been found east of Cape Agulhas (south coast, Fig. 1), whereas historically biomass was located largely on the west coast, illustrated in Fig. 2 (van der Lingen et al., 2005, 2002). This has had serious implications for both the management of the fishery, and the structure and function of the ecosystem itself (e.g. Coetzee et al., 2008; Crawford et al., 2008a; Jarre et al., 2013; Sherley et al., 2013; Watermeyer et al., 2016).

The physical and biological differences between the west and south coasts mean that the location of a stock has implications for its productivity: the west coast is characterised by high but episodic wind- induced productivity; the south coast has lower concentrations, but more continuous availability of nutrients and a higher biomass of consumers/predators. As a result, the population dynamics of small pelagic fish have been shown to be quite different on each coast, with sardine recruitment poorer on the south coast (van der Lingen 2011; de Moor and Butterworth 2012).

The mechanisms behind the distributional shifts in sardine and anchovy are not well understood. Fishing pressure and environmental shifts, in combination with possible natal homing of those sardine spawned further east are thought to be the main drivers behind the changes in distribution (Coetzee et al., 2008; Cury, 1994). Coetzee et al. (2008) outline the role that maintaining high fishing pressure on the west coast, while the stock had shifted south and east, may have played: the sardine fishery is managed using an Operational Management Procedure (OMP) that until now has assumed a single stock and with no spatial structure. Consequently, during the late 1990s and 2000s when the majority of biomass has been on the south coast, fishing effort remained largely where it had been focused for the previous 50 years and where the majority of processing infrastructure had been developed–on the west coast. The resulting high fishing pressure exerted on the diminished biomass of sardine on the west coast may have contributed to the continued lower abundance. As a result, spatial management of the sardine fishery is now under consideration (de Moor et al., 2014, 2013). In the case of anchovy, Roy et al. (2007) suggest links between changes in anchovy distribution and shifts in SST on the Agulhas Bank.

1.2. Modelling sardine and anchovy in the southern Benguela

Given the levels of complexity and interdisciplinarity inherent in any attempt to apply an ecosystem approach to fisheries (EAF), the use of models and indicators as means of increasing both our

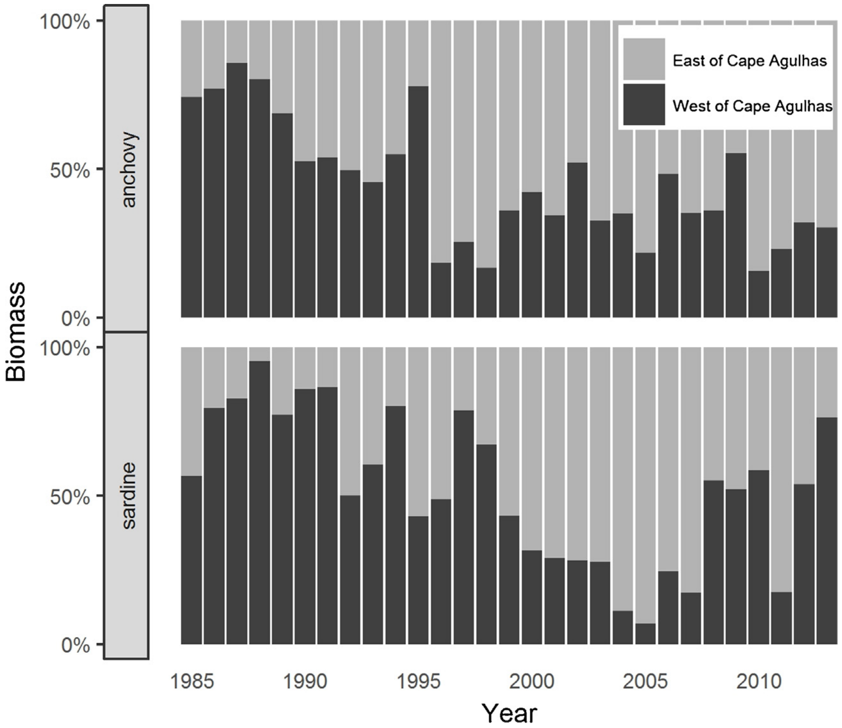


Fig. 2. Percentage of the adult anchovy and sardine biomass found west and east of Cape Agulhas, referred to in the text as the west and south coasts respectively, from 1985 to 2013.

Adapted from DAFF (2015).

understanding of and our ability to communicate system functioning and status has become a vital and accepted practice (Garcia and Staples 2000; Degnbol and Jarre 2004; Starfield and Jarre 2011). Indicators have been and continue to be developed and used to evaluate various aspects of the southern Benguela (e.g. Cury et al., 2005; Yemane et al., 2008; Shannon et al., 2009; Shin et al., 2010), and these in turn can be used as inputs for various modelling techniques that allow for the distillation and clearer communication of findings to stakeholders and management alike (McGregor, 2015; Paterson et al., 2007; Shin and Shannon, 2010).

Modelling in the context of an EAF includes the full spectrum of modelling approaches available, ranging in complexity from simple to very complex. Fulton et al. (2003) have shown a 'humped' relationship between the complexity and the effectiveness of ecosystem models, recommending an array of 'minimum-realistic' models as most effective. One approach that has been suggested as suitable for the modelling of long-term, ecosystem-level change is frame-based modelling (FBM), where possible stable system states and the shifts between them are modelled (Starfield et al., 1993). FBM applies a 'minimum-realistic' approach with a particular objective in mind (Starfield and Jarre, 2011). This is similar to the 'Models of Intermediate Complexity for Ecosystem assessments' (MICE) approach described by Plagányi et al. (2014), where a model somewhere between the complexity of a single-species model and an ecosystem model is developed to answer specific questions relating to management. Although without the complexity of some of the ecosystem models currently developed for the southern Benguela (Shannon et al., 2008, 2003; Shin et al., 2004), the minimum realistic and MICE modelling paradigms allow specific questions to be addressed with the minimum level of complexity, and thus investment of resources, necessary (Starfield et al., 1993).

A FBM approach (Starfield et al., 1993) is suitable when dynamic ecosystem functioning can be divided into distinct states or 'frames', as is the case for small pelagic fish globally and in the southern Benguela (Cury and Shannon, 2004; Howard et al., 2007; Schwartzlose et al., 1999), where frames would represent the stable periods between shifts. A simple model for each frame is constructed that represents only the processes relevant to the objective of the model. Only one frame is operational at any time, and rules must be developed for when the model should switch to a different frame. The approach lends itself to the technique of rapid prototyping, which allows for the simplest possible model to be developed quickly, at which point it can be tested, and adapted or complexity added in the next iteration if necessary (Starfield and Jarre, 2011). This has the advantage of allowing results of testing and feedback on the current generation model to inform developments in the next version, making the final version more useful than if it had been developed from scratch to a high level of complexity. Rapid prototyping also means that fully functional versions of the model are available at increasing levels of complexity, allowing hypotheses to be addressed before the final version of the model has been reached, which is of value for time-sensitive projects (Staples, 1997), as well as demonstrating effective use of limited funding.

Previously the frame-based approach has been used to model shifting vegetation patterns in terrestrial ecosystems (Rupp et al., 2000; Starfield et al., 1993), but more recently it has also been applied to the southern Benguela to explore regime shifts in the dominance patterns between sardine and anchovy (Smith and Jarre, 2011). In this model, single stocks of anchovy and sardine that migrate around the coastline were assumed, in line with current assessment practice, and frames represented high or low population levels. More recently however there has been investigation into whether sardine in the southern Benguela are in fact made up of two stocks, one on the west coast and one on the south coast east of Cape Agulhas, with some mixing between them (Coetzee et al., 2008). The possibility of a small third stock on the KZN south coast had also been hypothesised (van der Lingen et al., 2010). Differences in biological characteristics of sardine on the west and south coasts and a separation of distributions and spawning areas at medium to low biomass levels support the hypothesis of functionally, although not genetically, separate stocks (de Moor and Butterworth, 2011; van der Lingen, 2011). As a result a recommendation to explore the incorporation of a two-stock approach into the management of the sardine fishery in South Africa is currently being investigated (de Moor and Butterworth, 2013, 2012; van der Lingen, 2011). Unfortunately this approach is complicated by the need to model an unknown but high degree of mixing between the proposed stocks (although studies using parasites as a means of estimating possible mixing are currently underway (van der Lingen et al., 2013; van der Lingen and Hendricks, 2014). This situation is difficult to model, and current management retains the assumption of a single stock but a two stock with mixing component hypothesis is also being considered in ongoing development of a revised OMP (de Moor, 2017). An alternative approach, as explored here, could assume a single stock operating in different 'frames' or regimes, depending on location, i.e. a west coast frame or a south coast frame, where the majority of the biomass is located west or east of Cape Agulhas respectively.

The formulation of an additional regime shift between west and south coast modes should therefore allow for better representation of the system dynamics than the previous model version (Smith and Jarre, 2011), which simulated shifts between high and low population levels. Additionally, the simple sardine population model used by Smith and Jarre (2011) is updated in this model version to an age-structured population model based on that originally used in sardine population assessments in the OMP, as described by de Oliveira (2002). The model objective is thus to investigate whether our current understanding of the drivers of the west/south shifts in small pelagic fish can roughly reproduce the observed dynamics. If that is the case, further testing of possible strategic management options will then be performed and evaluated on performance in terms of catch, stability and a food base for the wider ecosystem. The robustness of model results under alternate management strategies, and sensitivity of outputs to uncertainties in our understanding of the relevant dynamics, will also be explored.

2. Materials and methods

2.1. Model structure

The model is a FBM designed according to the steps outlined by Starfield et al. (1993), incorporating sardine and anchovy population models for the southern Benguela parameterised according to the current frame. Frames represent biomass (high or low) and distribution (the majority of the population is based on the west or south coast) and are determine based on a frame-switching rules. Model design and structure has been described following the TRACE ("TRAnsparent and Comprehensive model Evaluation") for-

Table 1

Summary of model documentation in TRACE format (Grimm et al., 2014; Schmolke et al., 2010). See TRACE document, online supplement S1, for full detail.

TRACE element	Element summary
1. **Problem formulation** *Decision-making context, stakeholders, questions addressed, required outputs* S1 Section 1, pg. 3–5	Several ecologically and economically important species in the southern Benguela have undergone southward/eastward shifts in their distribution in recent decades, including the small pelagic fish sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the mid-1990s. Due to the spatially-distinct nature of the system, the location of a stock appears to have implications for its productivity. The model is intended to represent the important processes in these changes in sardine and anchovy as we understand them, and allow the exploration of scenarios involving drivers. Outputs assist in examining our current understanding of the mechanisms behind the shifts, and in gaining insight into possible outcomes of strategic decisions in the management of the sardine fishery regarding spatial direction of fishing pressure.
2. **Model description** *Detailed description of all model processes* S1 Section 2, pg. 6–31	The model is designed following the six steps outlined by Starfield et al. (1993) for constructing a frame-based model. Sardine and anchovy population models form the basis of the model, driven by fishing pressure and an environmental proxy (ESI). Current frame* is determined by frame-switching rules** on which daemons*** base frame-switching 'decisions'.
3. **Data evaluation** *Detailed description of model data and data sources* S1 Section 3, pg. 32–38	Where possible, model parameters are based on published data or those used in the OMP-02 sardine stock assessment model. Values for south coast-specific parameters were obtained from (de Moor and Butterworth, 2012) where applicable. Where data are unavailable, qualitative relationships or expert opinion are utilised.
4. **Conceptual model evaluation** *Conceptual design decisions and simplifying assumptions* S1 Section 4, pg. 39–43	The model is adapted from a previous frame-based model of sardine and anchovy abundance in the southern Benguela (Smith and Jarre 2011), expanded in this version to include an age-structured sardine population model and a spatial element via the addition of a south coast frame. Both spatial and frame-based modelling approaches were considered prior to model construction, and a frame-based model selected as more appropriate. Processes incorporating Stochasticity as well as general assumptions made in the design of the model are listed.
5. **Implementation evaluation** *Error testing and options for execution, manipulation, output presentation and model extension* S1 Section 5, pg. 44–55	Model processes were tested extensively during and after model construction, and general tests to verify basic model function are presented.
6. **Model output verification** *Fit to data and parameter calibration* S1 Section 6, pg. 56–57	The objective-driven approach, using rapid prototyping, taken in development of this system model means that the model is not suited for direct fitting to observational data. Model structure, parameterisation and behaviour was, however, dictated by and calibrated to observed values or ranges, as described in sections 2 and 3.
7. **Model analysis** *Sensitivity tests and interpretation of individual process outputs* S1 Section 7, pg. 58–103	Model sensitivity to inputs was thoroughly tested in two parts according to developmental steps: first, after the addition of an age-structured sardine population model to the simple model described by Smith and Jarre (2011), and then after the inclusion of a spatial element and the south coast frame. A number of alternate environmental effect and shifting rule scenarios were also tested.
8. **Model output corroboration** *Corroboration by data not used in the model.* S1 Section 8, pg. 104	Alternate datasets and their applicability within the model are currently limited. Developments in modelling and monitoring may allow for increased potential for corroboration in the future.

*Frame: a unique system state, containing a dynamic model of relevant processes; **Switching rule: rule governing switching between alternate frames; ***Daemon: software agent that may trigger a switch between frames according to switching rules.

mat (Grimm et al., 2014; Schmolke et al., 2010). Table 1 provides a summary of the TRACE document, however for details regarding model design, implementation and sensitivity analyses, refer to the TRACE documentation directly, available as an online supplement (S1).

Compared with the previous version (Smith and Jarre, 2011), this model incorporates an age-structured sardine population model, and a spatial element via the addition of west and south frames. As before, dynamics are driven by fishing pressure and an environmental proxy signal.

Model outcomes reflect implications for the functioning of the system as a whole. Additionally, in this version an indicator of system state has also been included in the model outputs: Cury et al. (2012) have shown over multiple systems that if forage fish biomass in a marine ecosystem falls below approximately 1/3 of their maximum long-term abundance, seabird breeding success is likely to be negatively affected, providing a useful link between patterns in small pelagic abundance to top level predators. This is particularly topical in the southern Benguela, where fluctuations, and in the case of the African penguin, serious declines, in seabird populations have been strongly linked to small pelagic fish abundance and distribution (Crawford, 2013; Crawford et al., 2008a,b; Ludynia et al., 2010; Sherley et al., 2013; Weller et al., 2014, 2016). Thus, in addition to monitoring current frames of sardine and anchovy (high/low and west/south), the model also records whether the system as a whole is in a) 'west coast mode', i.e. the majority of small pelagic biomass is located on that coast, b) 'south coast mode', or c) whether the conditions as a whole are unfavourable for predators (i.e. small pelagic biomass is < 1/3 of its long-term maximum). For example, if sardine and anchovy are on opposite coasts, the coast with the higher population is set as the current mode. If species are on opposite coasts and have equivalent population levels, the system mode is biased towards sardine, and thus system mode is set to that of sardine. This is based on the higher calorific value of sardine compared to anchovy (Balmelli and Wickens, 1994; Pichegru et al., 2010), and the seasonal transience of anchovy which makes them less accessible as prey. The system state is flagged as c), unfavourable for predators (or 'bad') when the combined biomass of both species falls below 1/3 of the long-term maximum within the model (based on the average maximum biomass of sardine and anchovy during a 100 year run, over 100 runs).

A model structure diagram is shown in Fig. 3, and the TRACE documentation Section 2.3 should be referred to for details of model construction and function. The basic model elements are, however, as follows:

2.1.1. Population models

Sardine and anchovy population models comprise the dynamic model that runs within each frame, each parameterised according to that frame. An age-structured sardine population model and a simple anchovy population model, stochastically variable around a midpoint, are used as the basis of the model. The possibility of the occurrence of extreme recruitment events in the sardine population was considered, and the model both incorporates this possibility as well as average functioning of the system as far as it I known (see S1: TRACE Section 3.2.2). With the inclusion of the spatial element of west and south frames, rather than modelling the populations on each coast separately the model assumes that the majority of the population is on one coast, while at least a small nucleus remains on the other (termed the 'other coast' population when referred to, see Section 2.3.1.1.3 of the TRACE document for details). Unless conditions on the 'other' coast are conducive, this nucleus won't grow (i.e. a shift from one coast frame to another will not occur). Sardine have more successful recruitment on whichever coast is currently more favourable in terms of environment and fishing pressure, and thus that population expands. The population on the current coast, i.e. the majority of the population, is modelled explicitly using a population model. The 'other coast' population is assumed to be anything from 0–40% of the modelled biomass, with interannual variability constrained to less than 20%. This value is then used by the sardine daemon, the software agent that may trigger a switch, to calculate whether fishing pressure on the 'other' coast is high or low to inform the shifting decision (see "*Daemons and switching rules*" below and TRACE document Section 2.3.4).

2.1.2. Environmental suitability index (ESI)

The ESI is one of the model drivers and used as a proxy for natural environmental variation. As such, the units are arbitrary and created purely for modelling purposes. Parameters defining the ESI were chosen based on those previously used in Smith and Jarre (2011) and updated where necessary. The ESI is modelled as variability around a sine function. Two ESI signals run simultaneously within the model, one representing conditions on each coast. Based on observed decadal-scale variability, the ESI signal for the west coast is set as slightly shorter (20 years) than that for the south coast (30 years). Note model outputs were only moderately sensitive to this assumption when tested, with some combinations of period length (west coast: south coast period equal to 20:20 and 40:20 years) resulting in a slight increase in time spent in a west frame (TRACE document Section 7.3.3). Conditions are then evaluated by the model as having either a positive or a negative influence on recruitment. On the west coast, as in the previous model version and based on different feeding preferences of the two species, what is good for one species is bad for the other and vice versa; on the south coast the same conditions are good for both, based on the relatively food-poor environment. (Model outputs only registered as moderately sensitive to alternate assumptions re. impact of ESI on recruitment, see TRACE Section 7.3.4).

2.1.3. Fishing

Sardine and anchovy-directed fishing, including bycatch of juvenile sardine, are also drivers within the model. Sardine-directed fishing can be applied via one of three possible routines:

1) Individual TACs: This strategy allows the user to set a fixed sardine TAC for the duration of the run for each species. Unlike the previous where model this was set in kilotons, in this current version it is a percentage of total biomass. With the addition of the spatial element, the user can also now specify a further spatial fishing strategy for sardine: focused on the west coast (MaxW); south coast (MaxS); or the TAC can be split between the coasts based on the proportion of total biomass on each coast each year (Dynamic). If either of the first two options is chosen, the model will catch the maximum TAC possible on the chosen coast, even if this means fishing sardine on that coast to zero, and redirect the remainder of the TAC to the other coast.
2) Active management: This strategy is the same as in Smith and Jarre (2011), allowing the user to reset the TAC every three years as a default, which enables the user to explore various reactive management options over the course of run.
3) AutoManager: In Smith and Jarre (2011), the AutoManager was set up as a sliding scale from conservative to severe. The population size was evaluated based on pre-set thresholds, and a sardine TAC in kilotons was assigned based on whether the population was identified as low, moderate or high. Although theoretically this approach could allow for a more nuanced evaluation of fishing effects, in reality the results tended to be fairly stable up to a 'tipping point' (e.g. results for 0 – 40% severity were quite similar, but differed from results for 50 – 80%), and when used for model testing generally only one of three settings was applied (0%, 50% or 100% severity). In the current model the sliding-scale was therefore replaced by a strategy like that used

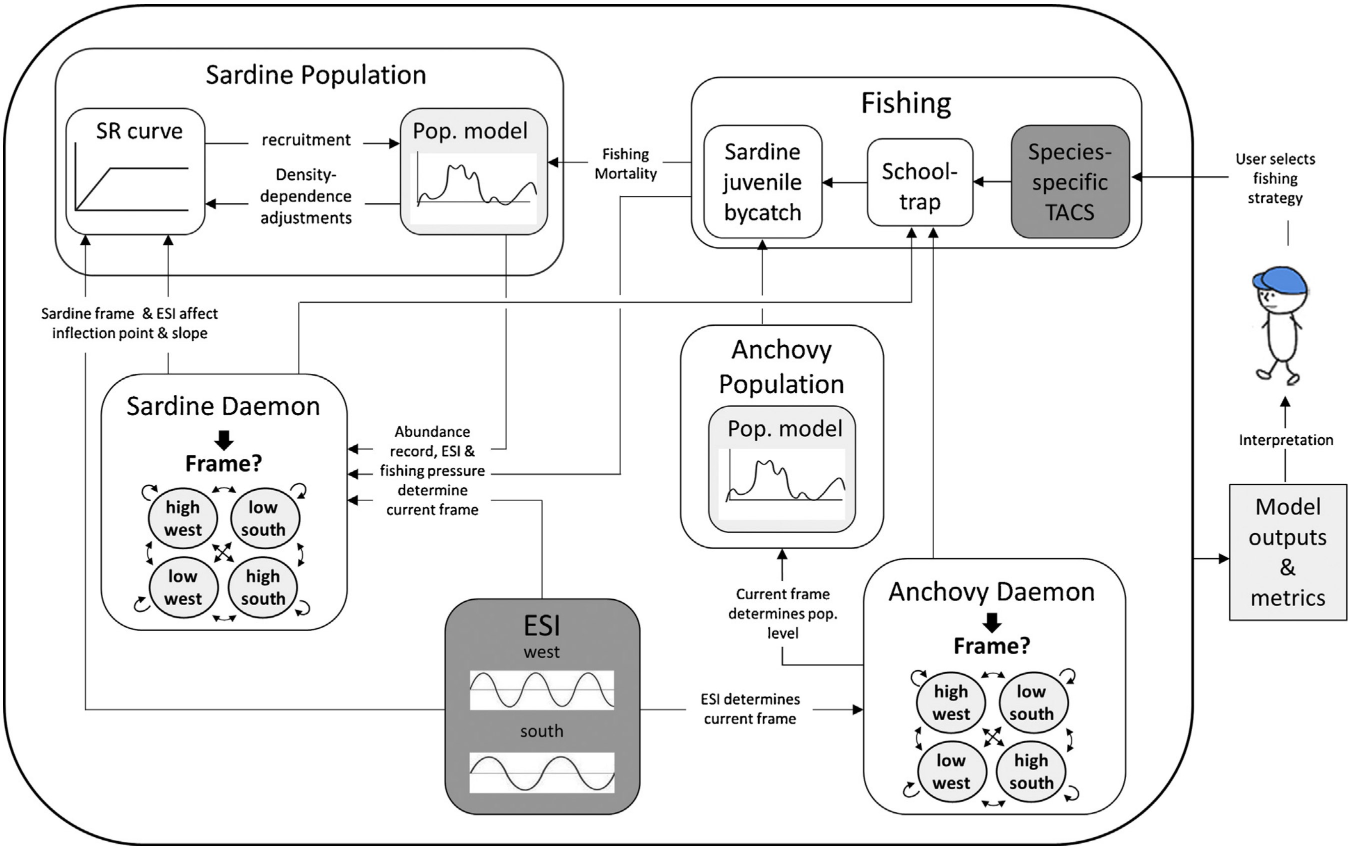


Fig. 3. Model structure diagram showing outputs, such as population time-series, in pale grey, and forcing components, such as Environmental Suitability Index (ESI) in dark grey.

in the OMP for sardine, with three discrete options that result in minimal loss of meaningful detail: conservative; moderate and severe. Like the individual fishing strategy, TAC is now also set proportional to biomass, rather than as a set value as before: below a lower population threshold the TAC is set to zero; between this and an upper threshold the TAC is constant and set to a minimum TAC specific to that level of fishing pressure; above the upper threshold the TAC is proportional to biomass with the slope again related to the chosen severity (TRACE document, Fig. 2.6). Minimum TAC and TAC slope increase with increasing severity and the lower threshold is reduced.

The focus of scientific effort and the small pelagic fishing industry has been on sardine during recent years (Hutchings et al., 2012; Shannon et al., 2006). Because of this, as well as the historically conservative management and highly variable recruitment of anchovy, in this model and the previous version (Smith and Jarre 2011) a very simple anchovy model is used, where only environment (and not fishing) affects the population. Anchovy are fished within the model, but only in order to account for calculation of the bycatch of juvenile sardine taken in the anchovy-directed catch when sardine are in a west frame. Anchovy landings do not influence the anchovy population.

2.1.4. Daemons and switching rules

The sardine and anchovy daemons monitor variables and 'decide' whether to stay in the current frame or whether to shift into a new frame. If a shift occurs, the daemons then determine which frame to shift into. The switching rules govern switching behaviour between high and low, and west and south frames. The sardine switching rules incorporate population levels, and ESI and fishing pressure per coast, while anchovy switching rules only rely on ESI.

2.2. Sensitivity analyses

Comprehensive sensitivity analyses were performed to test the degree to which model outputs are affected by the selected input parameters. Due to the iterative nature of the development process, sensitivity analyses for this model were performed in two stages. The initial development step involved updating Smith & Jarre's (2011) simple FBM of sardine and anchovy abundance, designed for a system operating in a west coast frame only, to incorporate an age-structured sardine population model. The second iterative step included the addition of the spatial element by way of the south and west frames. Sensitivity analyses were performed on each step, and analyses are thus presented in two parts: analyses of the non-spatial west-coast-based model after the addition of the age-structured sardine population model (Table 4, TRACE Section 7.2.1 for details), and after the addition of the spatial element (south frame) (Table 5, TRACE Section 7.2.2 for details). For parameters and

Table 2
Recruitment parameters in kt for anchovy used for each frame. Altered parameters used during Test 6 in the south frame are shown below in grey.

	Anchovy Frame	Midpoint	Variability
Baseline	West High	3000	± 1500
	West Low	1500	± 750
	South High	2000	± 1500
	South Low	1000	± 1500
Test6	South High	3000	± 2000
	South Low	1500	± 1500

Table 3
Thresholds for categorising sensitivity of outputs to inputs tested. The sensitivity index is a measure of proportional change in output relative to the change in input, where 1 represents equal change in both.

Category	Sensitivity Index
Negligible effect	< 0.001
Slightly sensitive	0.001 – 0.49
Moderately sensitive	0.5 – 0.99
Sensitive	1 – 1.49
Extremely sensitive	> 1.5

estimates used in the model see S1: TRACE document, Section 3.2. In all sensitivity analyses of quantitative variables, inputs were varied ± 50% from baseline in 10% increments. For details of all tests performed, see S1: TRACE document, Section 7.

2.3. Spatial fishing and south coast effect tests

In addition to model function and sensitivity analyses, the model was tested further for sensitivities to and effects on outputs of spatial fishing pressure and assumptions regarding the south coast:

2.3.1. Test 1: spatial fishing

Assuming, as suggested by Coetzee et al. (2008), that increased pressure on the west coast contributed to the relative increase in biomass on the south coast in the late 1990s and since, and given the design of the rules governing switching for sardine, the MaxW and MaxS fishing strategies (fishing pressure focused on the west or south coasts) should result in increased residency of sardine in south and west frames respectively, which would in turn affect model outputs such as total population based on the differences in productivity of sardine on each coast. The Dynamic strategy (fishing pressure proportionate to distribution) should have little to no effect on west and south frame residency which should be driven rather by ESI because high fishing pressure on either coast should be avoided under this scenario. All scenarios were run over 100 years, to avoid any potential influence of ESI fluctuations, and outputs averaged over 1000 runs. Using the individual fishing strategy, model outputs were compared over MaxW, MaxS, and Dynamic strategies, as well as over different levels of fishing pressure. TAC's of 10%, 20% and 30% of total biomass were applied to both sardine and anchovy in three separate tests.

2.3.2. Test 2: spatial fishing when sardine are in a south frame

The low sardine recruitment observed since the early 2000s and until recently, when biomass has been primarily located on the south coast, indicates that sardine are less productive on the south coast than on the west coast (de Moor and Butterworth, 2012; Shabangu et al., 2012). As a result, and given that fishing is thought to play a role in their distribution (Coetzee et al., 2008), there is reason to establish whether any particular fishing strategy would be more or less likely to result in an increased biomass on the more productive west coast. In this test the effects of the possible fishing strategies on model outputs were tested with sardine starting out in a south frame, and the strategies resulting in the most rapid return to a west frame identified. Given the design of the shifting rules, and the fact that high fishing pressure on the south coast is most likely to arise during the MaxS strategy, this strategy would be expected to result in the quickest or most frequent shifting of sardine back into a west frame. This scenario was tested using a model configuration in which sardine are forced into a south frame for the first 15 years of a 100 year run.

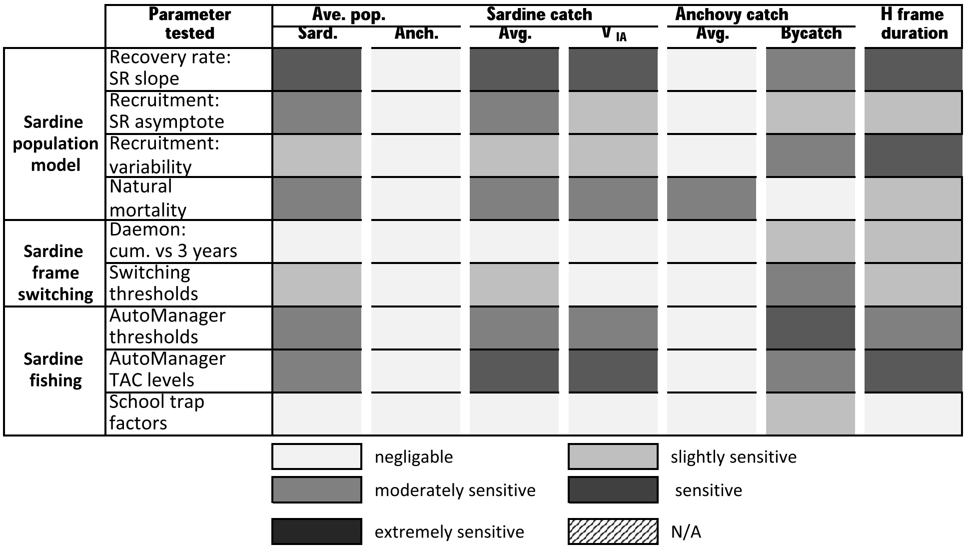
2.3.3. Test 3: alternate fixed proportions of biomass on the 'other' coast

In an expansion of test 7 in Section 7.2.2.6 of the TRACE document and to further interrogate assumptions made regarding the 'other coast' population, the baseline values for the maximum proportion of biomass on the 'other' coast and maximum interannual variability in the 'other coast' population were varied from −50% to +50% in 10% increments under the spatial fishing scenarios used in scenarios 1 and 2 here. Model outputs are expected to be sensitive to changes to 'other coast' population parameters under spatial fishing, as lower or higher biomasses on the 'other' coast will affect whether the sardine daemon evaluates fishing pressure on that coast as 'low' or 'high' and thus shifting is likely to be affected.

2.3.4. Test 4: alternate shifting rules

In an expansion of the test in Section 7.4.1 of the TRACE document, alternate shifting rules were further tested under the spatial

Table 4
Overview of sensitivity analyses on initial model update step, the addition of an age-structured sardine population model (without spatial element). Sensitivity of average population, catches and frame duration (proportion of model run spent in a high frame) to the following inputs was tested: 1) sardine population model parameters; 2) sardine frame switching strategy and thresholds; and 3) sardine fishing settings.



	Parameter tested	Ave. pop.		Sardine catch		Anchovy catch		H frame duration
		Sard.	Anch.	Avg.	V_{IA}	Avg.	Bycatch	
Sardine population model	Recovery rate: SR slope	▓	⬜	▓	▓	⬜	▒	▓
	Recruitment: SR asymptote	▒	⬜	▒	░	⬜	░	░
	Recruitment: variability	░	⬜	░	░	⬜	▒	▓
	Natural mortality	▒	⬜	▒	▒	▒	⬜	░
Sardine frame switching	Daemon: cum. vs 3 years	⬜	⬜	⬜	⬜	⬜	░	░
	Switching thresholds	░	⬜	░	⬜	⬜	▒	░
Sardine fishing	AutoManager thresholds	▒	⬜	▒	▒	⬜	▓	▒
	AutoManager TAC levels	▒	⬜	▓	▓	⬜	▒	▓
	School trap factors	⬜	⬜	⬜	⬜	⬜	░	⬜

⬜ negligable ░ slightly sensitive
▒ moderately sensitive ▓ sensitive
█ extremely sensitive ▨ N/A

Table 5
Overview of sensitivity analysis results after the addition of the south and west frames. Sensitivity to the following inputs was tested: 1) sardine SR curve parameters–high and low y-intercepts a_1 and a_2, the slope of the curve S_{max}, the inflection point B_{max}, and recruitment variability S_{cor} and s_r; 2) sardine juvenile and adult mortality (Juv. and Ad. Mort.); 3) AutoManager fishing settings including values used for conservative (C), moderate (M) and severe (S) levels of fishing pressure – lower threshold, upper threshold, min. TAC and TAC slope; 4) sardine daemon high-low frame shift thresholds (L-H and H-L); 5) sardine daemon fishing pressure threshold, tested at all fishing intensity levels (C, M and S); and 6) ESI period and variance for each frame (west/south). Sensitivity of the following outputs was calculated: average population (sardine and anchovy); sardine catch (west coast, south coast, and interannual variability V_{IA}); anchovy catch on the west coast and bycatch of juvenile sardine; time spent by sardine in a high or west frame. Model version refers to whether the model was forced to run in only a west or south frame, or whether the full model with shifting between the two was used. Note that bycatch represents juvenile sardine caught in the anchovy-directed catch.

	Parameter tested	Model version	Ave. population		Sardine catch			Anchovy catch		Frame duration	
			Sard.	Anch.	WC	SC	V_{IA}	WC	Bycatch	H	W
SR curve	**a_1**	SC	░	□	▨	▒	▒	□	▨	░	▨
	a_2	SC	░	□	▨	▒	▒	□	▨	░	▨
	B_{max}	SC	░	□	▨	░	░	░	▨	░	▨
	S_{max}	SC	░	□	▨	░	░	░	▨	░	▨
	S_{cor}	SC	░	□	▨	░	░	░	▨	░	▨
	σ_r	SC	░	□	▨	░	▒	□	▨	░	▨
Mortality	**Juv.**	SC	▒	□	▨	▒	▓	□	▨	░	▨
	Ad.	SC	▒	□	▨	░	▒	□	▨	▒	▨
Automanager thresholds	**Low C**	SC	█	█	▨	█	█	█	▨	█	▨
	Low M	SC	█	█	▨	█	█	█	▨	█	▨
	Low S	SC	█	█	▨	█	█	█	▨	█	▨
	Upper C	SC	░	□	▨	░	░	□	▨	░	▨
	Upper M	SC	░	□	▨	░	░	□	▨	░	▨
	Upper S	SC	░	□	▨	░	░	░	▨	░	▨
Automanager TAC	**MinTAC C**	SC	░	□	▨	▒	█	□	▨	░	▨
	MinTAC M	SC	█	█	▨	█	█	█	▨	█	▨
	MinTAC S	SC	█	█	▨	█	█	█	▨	█	▨
	TAC slope C	SC	░	□	▨	░	░	░	▨	░	▨
	TAC slope M	SC	░	□	▨	░	░	░	▨	░	▨
	TAC slope S	SC	░	□	▨	░	░	░	▨	▒	▨
Shifting threshold	**L-H**	SC	░	□	▨	░	░	□	▨	▒	▨
	H-L	SC	░	□	▨	░	░	░	▨	▒	▨
Fishing pressure threshold	**C**	FULL	░	□	░	░	░	□	░	░	░
	M	FULL	░	□	░	░	░	░	░	░	░
	S	FULL	░	□	░	░	░	□	▒	░	░
ESI	**Variance**	WC	□	□	□	▨	□	□	□	□	▨
	Period	WC	░	░	░	▨	░	░	▒	░	▨
	Variance	SC	░	░	▨	░	░	□	▨	░	▨
	Period	SC	░	░	▨	░	░	░	▨	▒	▨
'Other coast' pop.	**Max. prop**	FULL	░	░	░	░	░	░	░	░	░
	Var.	FULL	░	░	░	░	░	░	░	░	░

□ negligable
░ slightly sensitive
▒ moderately sensitive
▓ sensitive
█ extremely sensitive
▨ N/A

fishing scenarios used in the above scenarios. The alternate rules tested were as follows:

I Only fishing pressure is considered.
II Only ESI is considered In both of the above cases, the current coast was first evaluated. If it was found favourable, no shift occurred. If not, the other coast was evaluated and either a shift occurred if it was favourable, or there was a 50/50 probability of a shift occurring if not.
III Under conditions when a probability of a shift occurring is the outcome, the probability is high (80/20).
IV Under conditions when a probability of a shift occurring is the outcome, the probability is low (20/80).

2.3.5. Test 5: alternate minimum years between shifts

In an expansion of the test in Section 7.4.2 of the TRACE document addressing alternate minimum number of years between shifts, the min. years between shifts was set to 0, 5, 7 and 10 (baseline = 3), and model outputs under spatial fishing scenarios used above compared with those of the baseline model.

2.3.6. Test 6: positive impact of a south frame on anchovy

As discussed previously, based on observations of lower productivity in sardine on the south coast, and theory on the structure and functioning of the south coast/shelf-based system versus the west coast of the southern Benguela, it was assumed in the model that both sardine and anchovy would be less productive there than when on the west coast. This may not be the case, however, given that anchovy biomass has been on average higher from 2000 to 2015 than it was before the 1996 change in proportional abundance. This scenario tests the implications for model outputs of increased productivity of anchovy in a south frame, rather than lower productivity as previously assumed. Tests were run on a model version parameterised to allow increased recruitment success for anchovy in a south frame. Recruitment parameters used are shown in Table 2. The assumption that variability is higher in a south frame was retained and, as in the standard model, variability was set at half of the high frame mid-point. The spatial fishing strategies and range of TACs used in previous scenarios were applied and results compared with those from the standard model in Scenario 1.

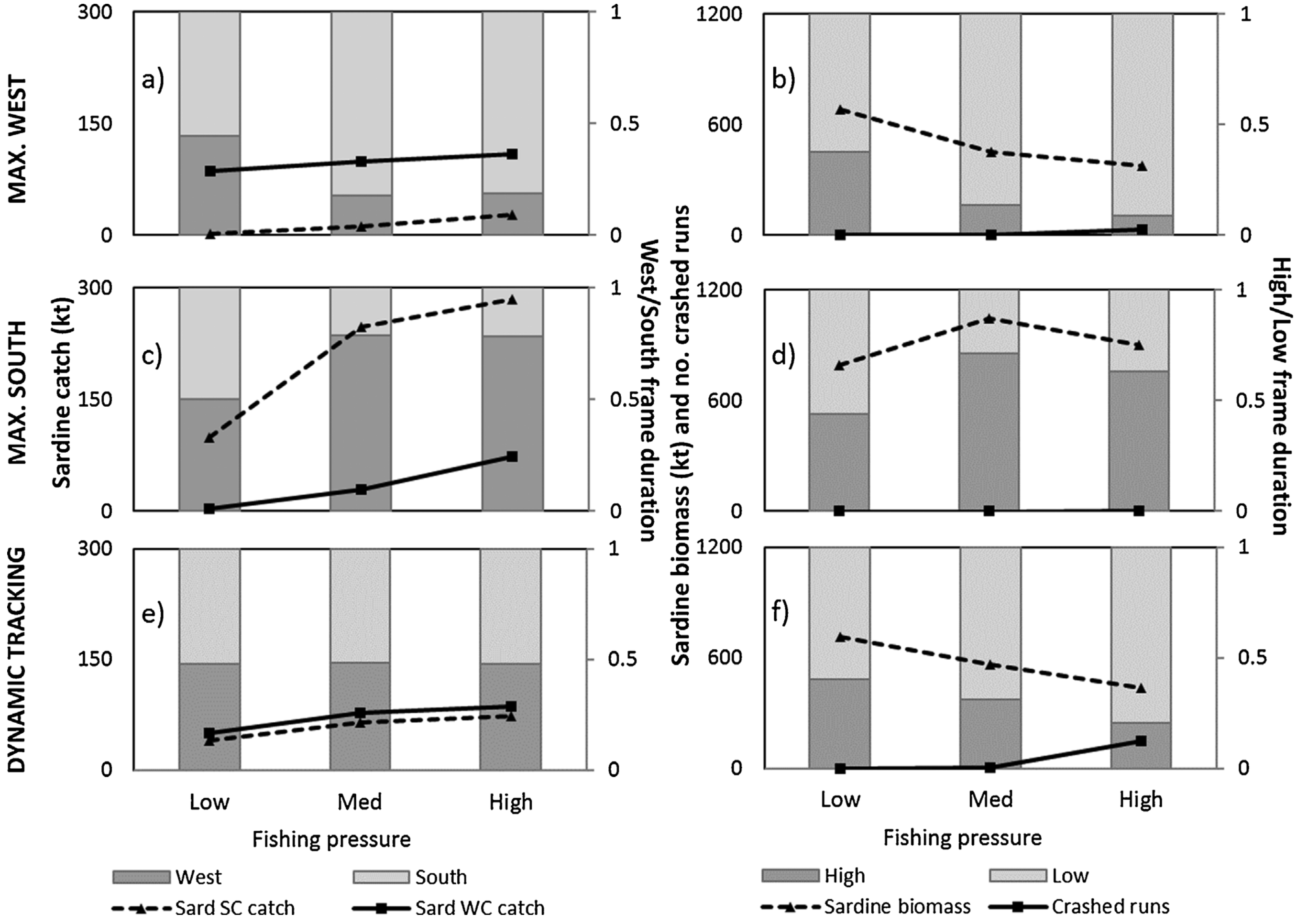


Fig. 4. a–f: Selected outputs for sardine in Test 1 over different spatial fishing strategies: maximum catch from the west coast (a and b); maximum catch from the south coast (c and d); and dynamic tracking (e and f). Low, medium and high TACs were applied. For each strategy, the first plot shows the proportion of the run spent in a West or South frame and the catch from each coast. The second plot shows the proportion in High or Low frame, the sardine biomass and number of runs crashed.

3. Results

3.1. Sensitivity analyses

The following provides an overview of results from the sensitivity analyses; comprehensive details of results from all tests performed are presented in the TRACE documentation Section 7. Output metrics in sensitivity analyses were ranked by degree of sensitivity to input parameters from negligible to extremely sensitive. Note that these were ranked based on a sensitivity index calculated as the relative change in output compared to that in the variable being tested–an output categorised as ‘negligible effect’ or ‘slightly sensitive’ is still responding to the change in input, but not outside the expected bounds. Details of categories are provided in Table 3. An overview of results from tests performed on the model updated to include an age-structured sardine population model is shown in Table 4, and from analyses of the further update and inclusion of the spatial element/south and west frame in Table 5. For tests run on a model forced to the south coast frame only in Table 5, west coast catch, sardine juvenile bycatch (taken in the anchovy fishery, which operates in the west frame only) and west frame duration are not applicable.

3.2. Spatial fishing and south coast effect tests

3.2.1. Test 1: effects of spatial fishing on model outputs

As expected, the spatial strategy chosen does affect model outputs, and sardine tend to shift away into the coastal frame that is experiencing lower fishing pressure. For example, under MaxW fishing, sardine spend the majority of the run in a south frame, which has implications for overall productivity. Change in selected outputs for each strategy over the different fishing pressures are shown in Fig. 4a–f. Somewhat counterintuitively from a historic fisheries management perspective, MaxS appears to be the strategy that resulted in increased residency time in west and high frames, maximising both the biomass and catch of sardine as a result. Note that under this strategy, although the majority of the catch is taken from the south coast, some is still taken from the west, and this proportion increases with increasing pressure (see WC catch, Fig. 4a). Crash rates also benefit under this strategy and remain close to zero even at high levels of fishing pressure. However, the interannual variability of the catch is the highest under this strategy (Fig. 5a). Surprisingly, the Dynamic strategy, where the TAC is split according to the division of biomass west and south, performed the worst both in terms of total yield and sustainability and resulted

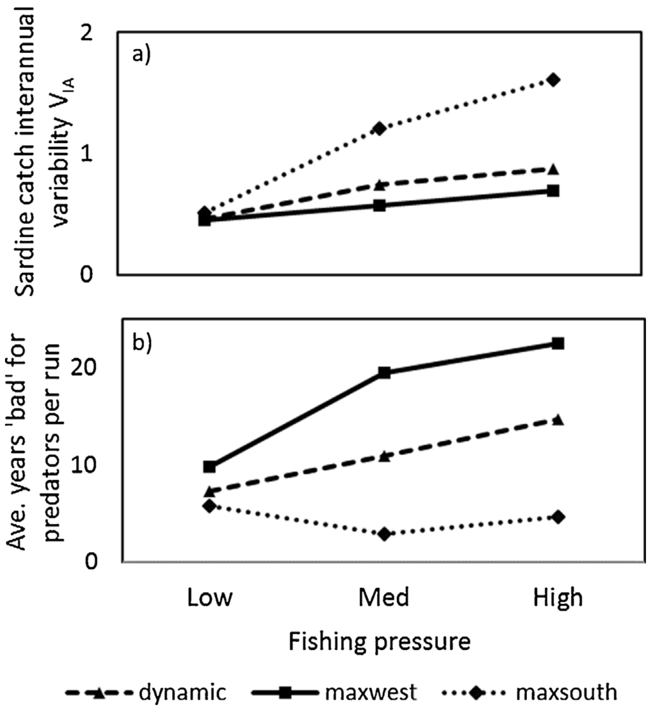


Fig. 5. a and b: Interannual variability of the sardine catch, and the numbers of years on which the system state is classified as 'bad' for each strategy (dynamic tracking, maximum catch from the west coast, and maximum catch from the south coast) at increasing fishing pressure.

in relatively high crash rates at heavy fishing pressure (151/1000). Predictably, this strategy did not affect west/south frame residency, however high frame duration did decline over time. Although the MaxW strategy appears more sustainable than the Dynamic tracking approach, with fewer crashes under high fishing pressure, it resulted in the lowest population levels and total catch due to low catch returns on the south coast resulting from increased time spent in a south frame (Fig. 4c and d). Catch variability was similar under Dynamic and MaxW strategies.

As an indicator of food availability to top predators, the system state indicator fell below the threshold of 1/3 of the long-term maximum fish biomass increasingly with increasing fishing pressure under all strategies (Fig. 5b). Under both MaxW and MaxS strategies, the difference in number of bad years per run was greatest between low to medium pressure, when compared with medium–high pressure. Under the MaxW strategy particularly, the number of 'bad' years per run almost doubled under medium pressure when compared with low. The number of 'bad' years for top predators was highest under the MaxW strategy and lowest under MaxS as a result of those strategies leading to increased time in the less productive south frame and more productive west frame respectively, as discussed above.

3.2.2. *Test 2: effects of spatial fishing on model outputs when sardine are in a south frame*

Note for this test sardine were forced to the south coast for the first 15 years of a run. When the model was run with no fishing, sardine remained on the south coast 15–25 years after shifting restrictions were lifted i.e. sardine first moved to a west frame no earlier than 30 years and no later than 40 years into the run over 50 runs of 100 years each (see Table 6.2). When MaxW fishing was applied, although the earliest shift remained at 30 years, when 10% TAC was applied the latest shift moved to 60 years into the run, and at 20 and 30% TACs in some runs sardine never shifted west. When a Dynamic fishing strategy was applied, there was no real difference under any level of fishing pressure between the timing of the earliest and latest shift when compared with runs performed under zero fishing. The MaxS strategy at 20% and 30% TAC were the only ones to change the timing of the earliest shift, which moved forward to 15 years. The latest shifts for those levels of fishing were also earlier than under other fishing strategies, at approximately 32 years into the run (compared with 40–60 years under other strategies).

Table 6
Timing in years of shifts to a west frame in a model where sardine were forced into a south frame the first 15 years of a 100 year run. Earliest and latest occurrences of a shift were recorded over 50 runs.

Fishing	%TAC	Earliest W shift	Latest W shift
None	0	30	40
MaxW	10	30	60
	20	30	never
	30	31	never
Dynamic	10	30	4
	20	30	40
	30	30	40
MaxS	10	30	40
	20	15	32
	30	15	32

3.2.3. *Test 3: alternate fixed proportions of biomass on the 'other' coast under spatial fishing scenarios and increasing fishing pressure*

While model outputs were only slightly sensitive to alternate proportions of biomass on the 'other' coast under the Dynamic tracking fishing strategy, as expected, multiple outputs ranged from sensitive to extremely sensitive under the MaxW and MaxS strategies. These were notably sardine catch, frame duration, the indicator bad years for predators and crash rate (Fig. 6). Effects were particularly strong where the 'other' coast population was set to 0 (i.e. if sardine are in a west frame, the model assumes all biomass is on the west coast; zero on the south coast). At 0% of biomass, the 'other' coast population is likely to experience what is evaluated as 'high' fishing pressure if any fishing at all is directed at it under low MaxW and MaxS fishing strategies (where F is not proportional to biomass), making the coast frame unlikely to shift to this 'other' coast. For example under MaxW fishing, as shown in test 1, the model is most likely to be in a south frame, making the west coast the 'other' coast. The compounding effect of forcing this population to equal zero is that fishing pressure on the west coast almost always registers as 'high'. The model is therefore even more unlikely to shift back into a west frame than in the baseline model. Residence in a south frame, and thus also south coast catch, are increased. Likewise, under MaxS fishing with 0% biomass on the 'other' coast, the model spends more time in a west frame, and west coast catch is increased. This effect on catch is less pronounced under higher fishing pressures (20% and 30%) due to the baseline model already experiencing this effect (the other coast often evaluates as experiencing 'high' pressure, which is not the case at low/10% fishing pressure unless the 'other' coast population is very low). This increased time spent in a less productive south frame under MaxW fishing at 0% 'other' coast biomass also resulted in the increased in number of crashed runs under higher fishing pressures.

At higher proportions of biomass on the 'other' coast (30% or 40%), catches were also affected, but due to the increased population available to be 'caught' rather than a change in frame residence time. Under MaxW fishing for example, as discussed under test 1 above, the majority of the run was spent in a south frame, making the west coast more likely to be the 'other' coast. Because the MaxW fishing strategy dictates that the TAC is directed first at the west coast and the remainder taken from the south regardless of current

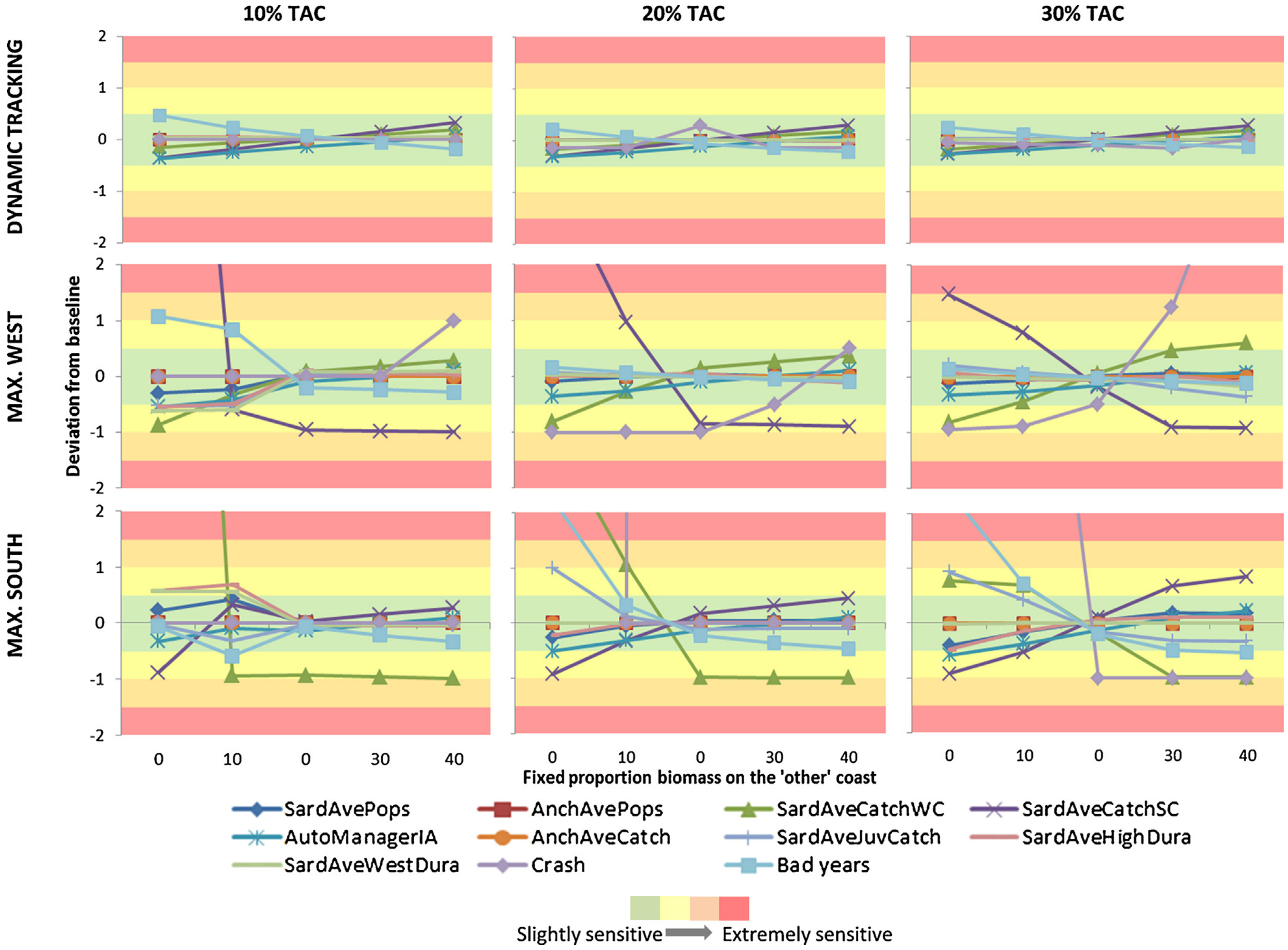


Fig. 6. Change in outputs from baseline values for alternate fixed proportions of biomass on the ‘other’ coast. Tests were performed under spatial fishing scenarios: ‘dynamic tracking’ allows effort to track fish location; ‘max. west’ and ‘max. south’ focus effort on the west and south coast respectively and for TACs of 10%. 20% and 30% of biomass. 1 reflects equal change in input and output. Outputs measured include: average population of sardine and anchovy (SardAvePops and AnchAvePops); average catch of sardine on west and south coasts, juvenile sardine, and anchovy (SardAveCatchWC, -CatchSC, -JuvCatch, AnchAveCatch); interannual variability in sardine catch (AutoManagerIA); years spent by sardine in high and west frames (SardAveHighDura and -WestDura); proportion crashed runs (Crash) and years per run classified as bad for predators (Bad years).

frame, when the west coast is the ‘other’ coast, and the ‘other’ coast population is relatively high, west coast catches increase. Likewise under a MaxS strategy, south coast catches increase (Fig. 6). Crash rates were also sensitive to higher ‘other’ coast populations under MaxW fishing, because the TAC is calculated as a percentage of total biomass including the ‘other’ coast population. A higher overall TAC is therefore set by the model, but fishing is still targeted at the now proportionally smaller modelled population on the west coast. Under MaxW fishing, juvenile sardine are also being caught as bycatch, which is not the case on the south coast (see TRACE document Section 2.3.3.1 *‘School trap effect’*) This adds to directed fishing pressure, and results in a higher crash rate. This effect was not evident under a MaxS strategy because overall population levels were higher due to the majority of the run being spent in the more productive west frame.

3.2.4. Test 4: alternate shifting rules under spatial fishing scenarios and increasing fishing pressure

At low levels of fishing pressure, outputs across all fishing strategies were only slightly sensitive to changes in switching rules (Fig. 7). Stronger effects were visible at 20% and 30% TACs, but overall only crash rate and years bad for predators were strongly affected. The moderate sensitivity of crash rate under MaxW fishing with 20% TAC, as well as extreme sensitivity under MaxS 30% TAC, reflect relatively small changes in real rather than relative terms: in the first instance, a change from a baseline rate of 2/1000 to 0/1000 in the ‘ESI’ and ‘80/20¢ tests was recorded, and in the second from a baseline rate of 1/1000 to 4/1000 in the ‘Fishing’ and 0/1000 in the ‘ESI’ and ‘80/20¢ tests. In this case and in test 6 as discussed below, the use of a relative measure as a sensitivity index produced an overstated result, when in reality the outputs were not particularly sensitive. The system state indicator of bad years for predators was however sensitive under the ‘fishing’ rule test for MaxS 20% and 30% TAC, and crash rate was moderately sensitive under the same test (‘fishing’) for MaxW 30% TAC.

Overall, the model behaves as one would expect and under spatial fishing was most sensitive to the switching rule scenario where only fishing pressure and not ESI influences shifts. Outputs were also slightly sensitive to the rules which resulted in increased probability of a shift (80/20), visible in the deviation from zero for this test under MaxW and MaxS fishing. These changes in output reflect the slight increase in the amount of time spent by sardine in a high frame under these rules, as one would expect if a shift is more likely under unfavourable conditions.

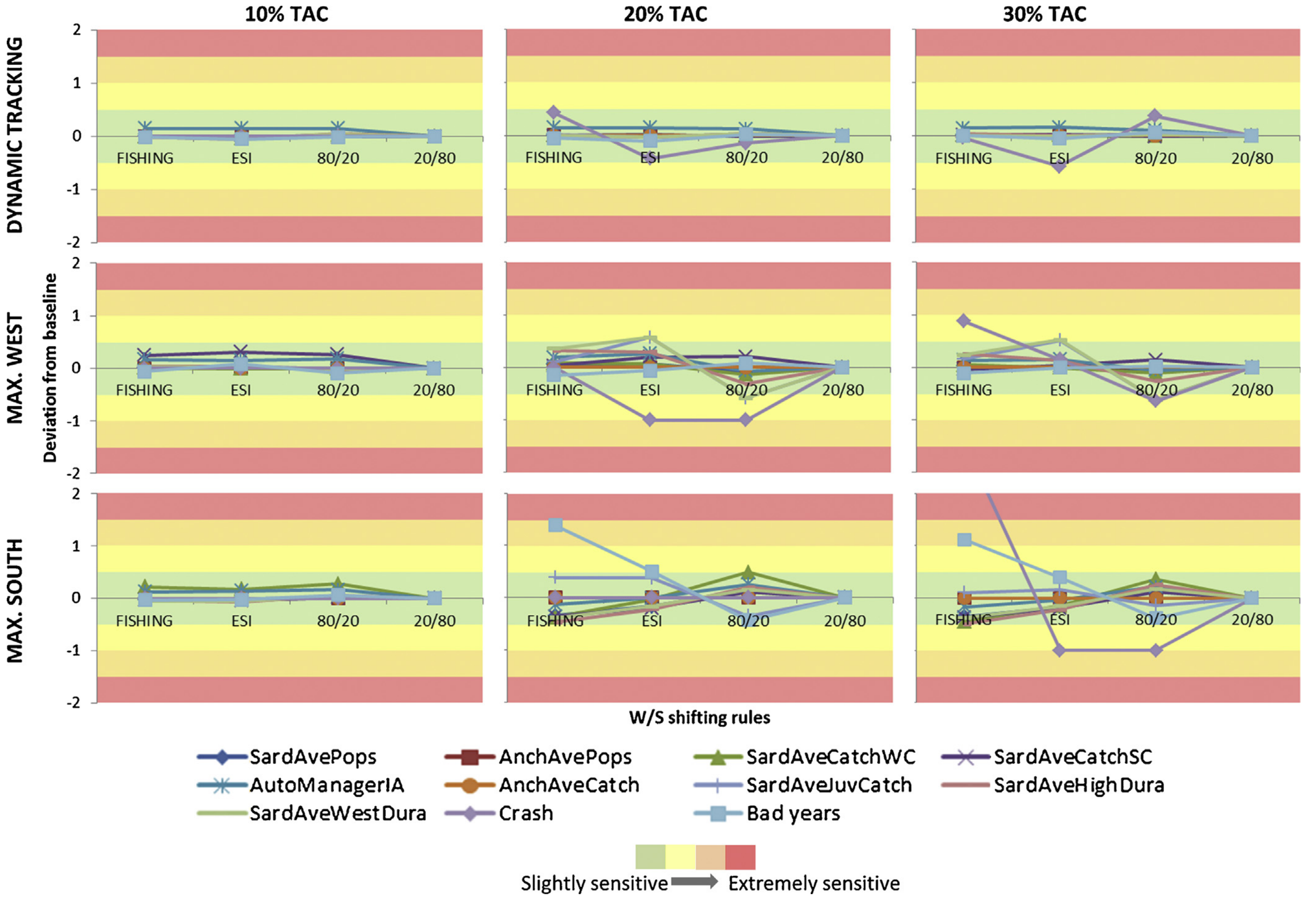


Fig. 7. Change in outputs from baseline values for the following alternate west/south frame shifting rules: only fishing pressure influences shifts (FISHING); only environmental signal (ESI) influences shifts; where a probability of a shift occurs, a shift is likely (80/20); and where a probability of a shift occurs, a shift is unlikely (20/80). Tests were run under three spatial fishing scenarios ('dynamic tracking' allows effort to track fish location, 'max. west' and 'max. south' focus effort on the west and south coast respectively) and at TACs of 10%. 20% and 30% of biomass. Outputs are as in Fig. 6.

3.2.5. Test 5: alternate minimum years between shifts under spatial fishing scenarios and increasing fishing pressure

Under spatial fishing pressure the effects on outputs of alternate minimum years between shifts (Fig. 8) were similar to those shown during sensitivity analyses using the Automanager to apply fishing pressure (Section 7.4.2 of TRACE document): the number of years flagged as 'bad' for predators increased, particularly at the lowest TAC (10%). This output was not as sensitive at higher TAC levels, with the effect of fishing pressure at 20% and 30% TAC outweighing that of the increased years between shifts. At these levels of fishing pressure, however, the number of crashed runs became extremely sensitive to the min. years between shifts, and was the only output variable that registered as anything more than 'slightly sensitive'. Again, this was a response to the increasingly negative effects of being forced to remain in an unfavourable frame at high fishing pressures. Note that while relative crash rate registers as extremely sensitive under the MaxS strategy at 30% TAC, showing a change from baseline of up to 200%, the absolute crash rate only varied between 1 and 3/1000.

In this test sardine were most vulnerable to crashing under the MaxW fishing. As shown above (Fig. 4) this strategy results in increased time spent by sardine in the less productive south frame, and high fishing pressure is more likely to lead to crashes. As in sensitivity analyses (Section 7 of TRACE document), outputs were on average no more than slightly sensitive to changes in the min. years between shifts, with the exception of crash rate and to a lesser degree the indicator 'bad years' for predators. Effects were minimal when there was no restriction on shifting (0 years), supporting the use of the baseline restriction of three years between shifts as means of increasing realism without greatly impacting outputs.

3.2.6. Test 6: positive effect of a south frame on anchovy

Only anchovy biomass and catch were sensitive to the assumption that the south coast is beneficial for anchovy rather than decreasing their productivity as is assumed in the baseline model (Table 7). The only other output that changed more than 3% from the standard model outputs was crash rate of the sardine population, although as above these are actually reflecting very minor absolute changes (e.g. the 28.6% change under 20% Dynamic fishing reflects a change from 7/1000–9/1000 crashes, and the 100% changes are from 1/1000 to 2/1000).

4. Summary and conclusions

4.1. Summary of model results

The model was constructed to reproduce our current understanding of system function and drivers; thus those drivers are required to be represented within the model. Model testing (see TRACE document Sections 5 and 7) serves to further illustrate the effects of assumptions made regarding structure, as well as to build confidence in the model so that it could be used to explore possible management scenarios. As expected, model results imply that the fishing strategy applied has a significant impact on whether or not

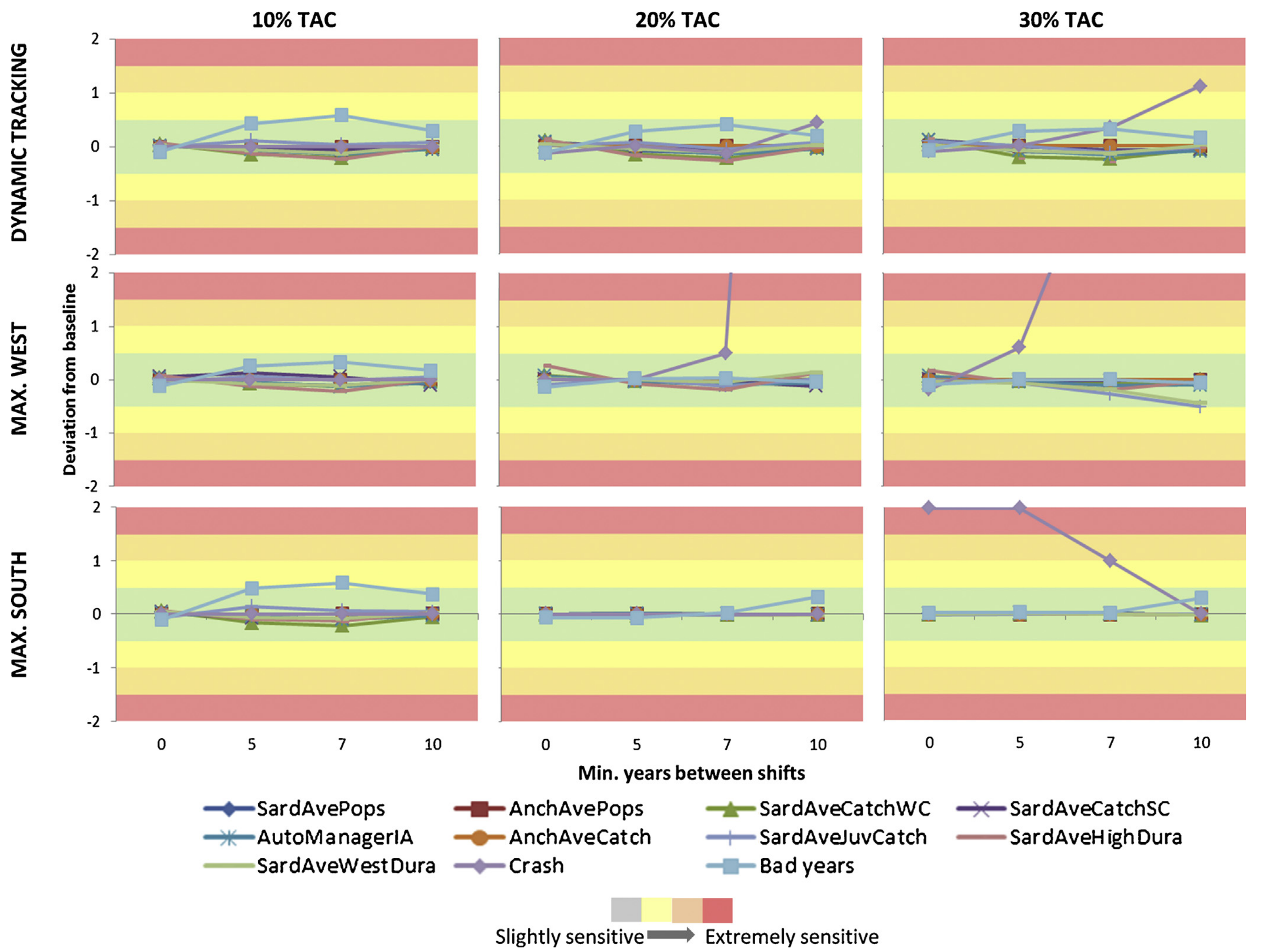


Fig. 8. Change in outputs from baseline values for alternate minimum years between shifts. Tests were run under three spatial fishing scenarios ('dynamic tracking' allows effort to track fish location, 'max. west' and 'max. south' focus effort on the west and south coast respectively) at TACs of 10%. 20% and 30% of biomass. Outputs are as in Fig. 6.

Table 7
Percentage change in model outputs when the south frame is assumed beneficial for anchovy rather than decreasing their productivity as in the baseline model.

Fishing		Biomass		Sardine catch				Anch. catch	Sard. frame dur.		Crash
Strategy	% TAC	Sardine	Anchovy	WC	SC	V IA	Bycatch	WC	High	West	rate
Dynamic	**10**	−0.9	34.6	−1.3	−0.9	−1.8	−0.7	34.8	−1.9	−0.5	0.0
	20	0.5	35.0	0.9	0.6	0.9	2.9	35.1	0.2	0.7	28.6
	30	0.6	34.7	0.7	1.0	−0.1	1.0	34.9	2.5	0.2	−1.3
MaxW	**10**	−0.5	34.6	−0.4	−2.2	0.3	−0.1	34.9	−0.6	−0.5	0.0
	20	0.4	34.4	0.2	1.0	0.3	−0.2	34.7	0.9	0.9	−100.0
	30	−0.3	34.0	−0.5	0.3	−0.2	−1.7	34.7	0.6	−2.0	−12.1
MaxS	**10**	0.5	34.7	−0.7	0.7	0.7	−0.1	34.8	1.1	0.7	0.0
	20	0.1	34.4	1.2	0.0	0.8	−0.5	34.7	−0.4	−0.1	0.0
	30	0.9	34.0	0.1	1.2	0.9	2.4	34.4	0.6	0.2	−100.0

sardine ever switch back into a west frame from a south frame. In the absence of fishing pressure, the environmental signal drives a shift to the west at some point, but given focused pressure on one coast or the other, the shift may be hastened or prevented entirely. This has implications for distributions and productivity, impacting both the fishery and dependent predators.

The main factor behind the differences in outputs under different spatial fishing strategies in test 1 relates to west or south frame switching and duration due to the lower productivity assumed on the south coast in the model. For example, the MaxS strategy results in more time spent by sardine in a west frame. This in turn results in higher, west coast based, sardine biomass under that strategy, increased high frame residency and total catch and resulting in fewer years below the threshold below which the system is classified as 'bad' for predators.

Counterintuitively, catches are highest on the south coast under MaxS fishing. This is because of the overall increase in biomass induced when sardine are in a west frame where, as discussed above, they are more likely to be under the MaxS strategy. As discussed, the current frame is assumed to be the location of only the *majority* of biomass. The proportion of that explicitly modelled biomass estimated to be on the 'other' coast population is therefore also higher when the current coast biomass is high. For example in this case because sardine are in a west frame and the modelled population is high, the estimated and proportional 'other' (or south coast) population from which the south coast catch is taken is also higher than it would be in a less productive south frame. A high south coast catch is then taken even though sardine are in a west frame. Conversely, when a MaxW strategy is applied, sardine are more likely to be in a south frame, resulting in lower productivity. Consequently, biomass and catches from both coasts during those runs are also relatively low, and the system is more likely to be limiting ('bad') for predators.

Interannual catch variability may be higher during MaxS runs due to the increased influence of the 'other' coast catches in those runs, which are in turn correlated with the fluctuating minority population on that 'other' coast.

The unexpected production of the highest crash rates under the Dynamic strategy can be explained by the fact that the TAC is set as a percentage of the total biomass, rather than just the biomass modelled on the dominant coast (i.e. explicitly modelled biomass and 'other coast' biomass combined). Because Dynamic tracking splits the TAC according to biomass distribution, this means that both coasts are always experiencing the specified fishing pressure. If this is not strictly conservative, it will lead to increasing crashes. This in contrast to the MaxW strategy for example, where fishing tends to drive sardine to the south frame but the fishing pressure remains directed at the west coast. As a result, the estimated proportion of the population on the 'other', in this case west, coast will generally be subjected to a substantial proportion of the TAC before any fishing pressure is placed on the sardine in the south frame, lowering the probability of crashing.

The system state indicator included in the model is useful in that it allows a quantitative interpretation of the implications of fishing strategies within the model for seabirds and other top predators. Although the indicator is generalised, it does allow for this link to be made and adds some depth to the discussion of the implications of spatial fishing strategies within the context of an EAF. Within the model, heavy fishing focusing on the west coast (and resulting in increased residence of sardine in the south frame) leads to more years in which forage fish are too low to sustain seabird populations. Again, this is due to lower productivity in the south frame. If this is the case, it lends further weight to the question of whether spatialised fishing pressure has a role to play in the real world in increasing the biomass of sardine on the west coast, where they are more accessible to both the fishery infrastructure and seabird predators. This is particularly relevant for birds such as African penguins (e.g. Weller et al., 2016, 2014), which are restricted in their breeding habitat and less able to adapt to change in prey distribution.

The sensitivity of the model to changes in the proportion of biomass found on the 'other' coast under spatial fishing places further emphasis on the need to investigate spatial management of the small pelagic fisheries. Decisions in this regard may strongly influence the shift or lack thereof of sardine from a west to a south frame or vice versa. This sensitivity reflects what is suspected to have occurred in the early 2000s on the west coast, where fishing remained directed at the west coast despite the majority of biomass shifting to the south (Coetzee et al., 2008), and which may have prevented a complete shift back to the west since.

Although the results under alternate switching rules tested (Fig. 7) do not suggest changes are required to the baseline model, they do highlight the need to better understand how the relative environmental suitability of each coast affects whether or not a shift occurs, confirming results from model function and sensitivity analyses tests in Section 7 of the TRACE document. Given that the biggest determinant of outputs is the current frame, this indicator–shift or no shift–ultimately determines the productivity of the stock. If shifts away from unfavourable condition are more or less likely either directly, due to probability settings in the model, or because of relative conditions on each coast, this can mean the difference between a crash and a stable, productive stock. Increased understanding of this interaction in the real world should be a priority.

Although whether or not the environment on the south coast is beneficial to anchovy definitely warrants further investigation, for reasons previously discussed the focus of the development of this model has focused on sardine. As a result the model is not particularly sensitive to changes in anchovy productivity (e.g. Test 6 above), and in its current iteration is not well suited to answering questions in that regard. The bycatch of juvenile sardine in anchovy catches does influence the model sardine population however, and sardine bycatch is related to the proportion of anchovy catch. Therefore, sardine bycatch is not affected by changes in anchovy population but only by an increase in the proportion of anchovy caught. In further development of this FBM, the anchovy population model should distinguish anchovy recruits from adults, and also refine the anchovy fishery.

The design of the ESI within the model is currently quite simplistic, although it is functional. It assumes that either completely disparate conditions are favourable for sardine and anchovy or that suitable conditions completely overlap. This excludes conditions that are unfavourable for both on the west coast, as well as the possibility of some overlap in the range of suitable environmental states. This area also warrants further attention in view of the expected climate change.

While the current approach of using coupled single-species stock assessment models to manage sardine and anchovy fisheries in the southern Benguela is successful in terms of short-term prediction and the output of specific and quantifiable assessments of risk, it is not well suited to addressing more long-term changes in conditions, or variability in productivity over time (e.g., Fréon et al., 2005; Jarre et al., 2006). Given that no approach at this time can be assumed to take into account all relevant variables, considering multiple modelling techniques when attempting to answer management problems is the only way to achieve a more well-rounded understanding of the issues at hand. The model described here could in no way be used in the capacity of a stock assessment model for tactical management recommendations, since it is not designed in this way. It can and does however provide insight unavailable from that approach in terms of the possible system-level implications of various management strategies. The assumptions made when designing the switching rules for this model should however be kept at the forefront when considering model outcomes, given that by determining frame (west or south) they heavily influence results. Nonetheless, a FBM does add to the general understanding in terms of overall system stability related to strategic management choices. The system state indicator is a useful addition to the toolkit of quantitative indicators.

When considering what modelling approach would best meet the objectives in addressing the spatial element in small pelagic distribution in this study, both spatial and frame-based models were considered. The advantages of using a FBM approach are that the model structure is well-suited to represent regime shifts such as those observed in the system; the model assumes the same stock structure as used in the current OMP–that of a single stocks, the main distribution of which shift around the coast; and it is readily modified further along with increased understanding of the processes in the real world. Although a FBM does require the proportion of biomass on the 'other' coast to be estimated within the model, this estimate can be based on observed proportions on each coast. Tests showed that the corresponding model assumptions (i.e. proportion of and variability in biomass on the 'other' coast–test 3 above and test 7 in Section 7.2.2 of the TRACE document) did not affect outputs greatly. Outputs were only affected notably when the model system was subjected to spatial fishing pressure, as thought to be the case in reality. On the other hand a spatial model would represent the hypothesised two-stock or single stock with two mixing components structure previously discussed, with no need to estimate biomass on the other coast. The two stock hypothesis however has so far not been supported by genetic data (Hampton, 2014) or in the stock assessment paradigm (Dunn et al., 2016). Additionally, in both the two-stock or single stock with two mixing components cases, an estimate would still need to be made; this time of the degree of mixing between the two stocks, and based on what is currently very limited knowledge.

Outputs of a FBM are by design highly dependent on the rules used to drive shifts. While the current rules are based on the best available information to date, our understanding of the relative importance of fishing pressure and environmental signal remains fairly crude. When this understanding improves, it will be straightforward to change the model in line with the improved understanding.

The spatial fishing scenarios tested here allow for useful exploration of potential outcomes based on various candidate strategies. Although a spatial model may produce similar results, the clearly defined breaks that are inherent in a FBM as shifts occur are particularly useful in the context of regime shifts. These breaks or shifts also make for clearer interpretation, allowing for the simplification of a complex situation in support of fisheries management.

5. Conclusions

Although a spatial model could certainly be a useful tool in enhancing our evaluation of likely consequences of fishing, there were no key sensitivities that came up in the FBM that would be directly resolved within a spatial model. Similar population models would be used as a basis for both approaches, retaining sensitivities to parameters such as mortality and the thresholds used in applying fishing pressure. As long as migration in the spatial model is not linked to an environmental signal, this FBM provides a unique perspective which is in line with our understanding of long-term, ecosystem-scale processes. Hence, the FBM is a useful and provides insights unavailable from current approaches. Despite the possibilities for further improvement, model results show that the productivity of the sardine resource within the model is highly dependent on the spatial characteristics of the fishing pressure it experiences, as is the ability of the system to sustain top predators. This paper attempts to lay out model results in such a way that they are informative and useful for future considerations, but does not recommend any specific strategy, as the most appropriate one may vary based on trade-offs between social, economic and ecological objectives governing management decisions at a specific time. Results suggest that future research should focus on understanding the implications of the relative environmental conditions on each coast for the sardine stock, and how these affect the probability of a shift occurring. This emphasises the need for sustained and comprehensive long-term monitoring of environmental variables throughout the southern Benguela. The role of anchovy within with model system has not yet been fully developed, and further effort in this area may allow for more robust results. In conclusion, this study shows support for continued careful consideration of spatialized management approaches to the South African sardine fishery.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2017.12.017.

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