

## Simulating anchovy–sardine regime shifts in the southern Benguela ecosystem

Lynne J. Shannon<sup>a,b,\*</sup>, John G. Field<sup>b</sup>, Coleen L. Moloney<sup>a,b</sup>

<sup>a</sup> Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa

<sup>b</sup> Department of Zoology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa

### Abstract

Trophic models of the southern Benguela ecosystem have been developed to represent average ecosystem structures for two periods: 1980–1989 and 1990–1997. Ecopath with Ecosim software is used to simulate changes from the 1980s to the 1990s ecosystem structure. Two hypotheses are tested of mechanisms that could cause the changes. First, using the model of the 1980s, four scenarios are considered in which different combinations of fishing mortality rates of sardine, anchovy and horse mackerel are changed to mimic the situation in the 1990s model. Results show that it is unlikely that observed changes in pelagic fish catches between the 1980s and 1990s played a large role in driving the changes in abundance of anchovy and sardine. Second, changes in the susceptibility of phytoplankton and zooplankton prey to feeding by anchovy and sardine are simulated for the two decades. Results show that shifts between anchovy and sardine regimes in the southern Benguela ecosystem may be caused by changes in the availability of mesozooplankton prey to anchovy and sardine, mediated through changes in environmental conditions. The magnitudes and duration of environmental changes are important in understanding changes in the ecosystem.

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**Keywords:** Southern Benguela; Regime shifts; Ecosystem models; Ecopath; Ecosim; Anchovy; Sardine

### 1. Introduction

The Benguela upwelling ecosystem, one of the four major eastern boundary current systems of the world, is situated off the south west coast of Africa, and can be sub-divided into southern and northern sub-systems, separated by the Lüderitz upwelling cell (Fig. 1). In this study we concentrate on the southern Benguela ecosystem, where there has been alternation between anchovy-dominated and sardine-dominated ecosystem states (Fig. 2). This situation is similar to that found in most upwelling regions where anchovy and sardine co-exist (Lluch-Belda et al., 1992). The

changes in ecosystem state have been termed “regime fluctuations” (Lluch-Belda et al., 1992), and are frequently referred to as “regime shifts”. Regimes are defined as large ecosystems that are climate-ocean linked, undergo shifts in states over 10- to 30-year periods and to which fish and other marine biota respond by changing their dynamics (Beamish and Mahnken, 1999). The factors most likely to account for changes in states of upwelling ecosystems are changes in fishing pressure and environmental changes (Larkin, 1996). This study explores aspects of both factors in the southern Benguela ecosystem.

The South African pelagic fishery developed as a major commercial fishery from the 1940s, and initial catches were dominated by sardine (*Sardinops sagax*) and horse mackerel (*Trachurus trachurus capensis*). Prior to that in the 1920s, guano records suggest that

\* Corresponding author. Tel.: +27-21-402-3171;

fax: +27-21-4217-406.

E-mail address: [Lshannon@mcm.wcape.gov.za](mailto:Lshannon@mcm.wcape.gov.za) (L.J. Shannon).

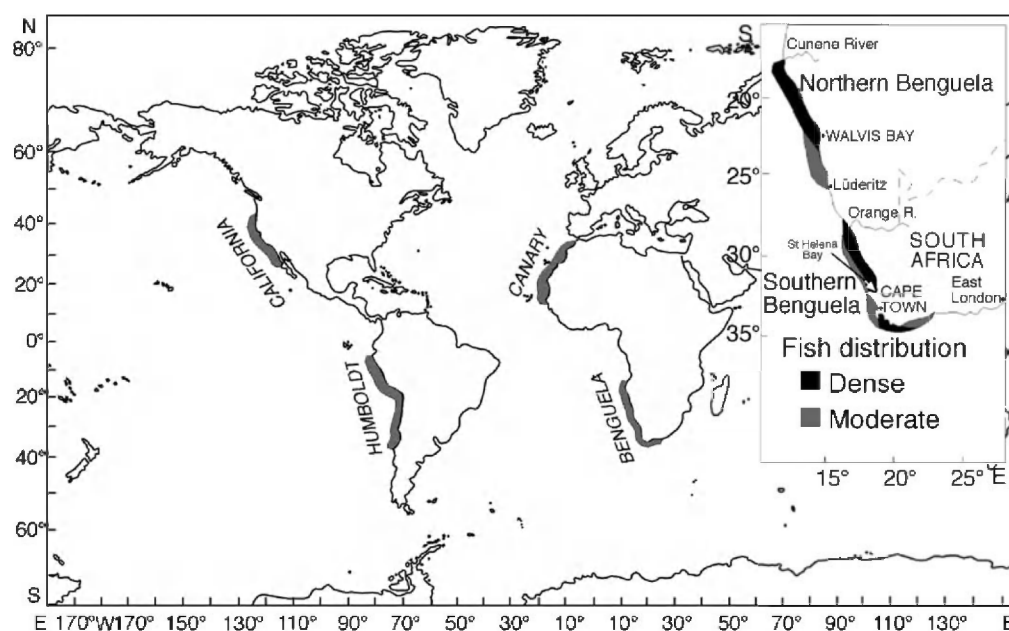


Fig. 1. The four major coastal upwelling areas of the world. Inset gives details of the Benguela upwelling ecosystem (after Jarre-Teichmann et al., 1998).

anchovy *Engraulis capensis* was the dominant pelagic species (Crawford and Jahncke, 1999). The catches of horse mackerel decreased by the late 1950s, and those of sardine from 1966 onwards (Fig. 2). In response

to the collapse of the sardine fishery, the minimum mesh size of the purse-seine nets was reduced from 38 to 13 mm, to allow catching of anchovy (Cochrane et al., 1997). In the late 1960s, chub mackerel *Scomber*

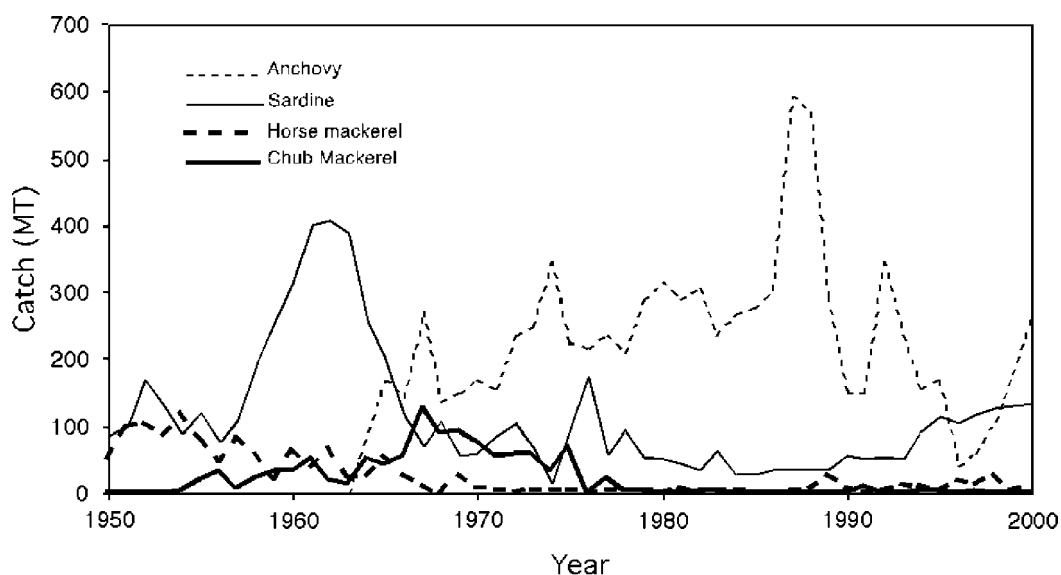


Fig. 2. Catches of anchovy, sardine, horse mackerel and chub mackerel in the southern Benguela ecosystem from 1950 to 2000. Catches are expressed in millions of tons (MT).

*japonicus* were important in the pelagic catches, but anchovy formed the bulk of the catches from the 1970s to the early 1990s (Crawford et al., 1987; Crawford, 1998), when a decrease in biomass caused a decrease in total allowable catch (Fig. 2). At the same time that anchovy were decreasing in the 1990s, hydroacoustic surveys indicated that the abundance of sardines was increasing (Barange et al., 1999).

The causes of the changes in relative abundance of sardines and anchovies in the southern Benguela have been the subject of a number of hypotheses. The decrease of sardine abundance in the 1960s has been interpreted to be the result of overexploitation (Butterworth, 1983), and Moloney and Wickens (1985) used a model of sardine–anchovy interactions from the 1950s to the 1980s to show that overfishing could cause replacement of one fish population by its competitor. Similarly, modelling by Korrübel (1992) showed that harvesting can play an important role in species replacement. In contrast to the overfishing hypotheses for the 1960s period, the ecosystem changes in the 1990s are hypothesised to be the result of large-scale environmental changes. Shannon et al. (1992) showed that there was a warm period during the 1980s, which could have impacted many species simultaneously. Verheye et al. (1998) found that there were substantial increases in biomass and shifts in the species composition and size structure of the crustacean zooplankton community in the St. Helena Bay region (Fig. 1) between 1951 and 1996. Current zooplankton communities show increased representation of small species compared with the 1950s, and two possible mechanisms have been proposed to explain this shift in community composition. The first is a bottom–up effect that results from long-term changes in the intensification of coastal upwelling, which affects the size structure of the phytoplankton community and hence the zooplankton (Verheye et al., 1998). The second is a top–down effect that occurs through differential feeding of sardines and anchovies on phytoplankton and small and large zooplankton (Van der Lingen, 1999). A combination of both these effects is assumed in this study, with environmentally mediated changes in the prey of small pelagic fish affecting ecosystem structure, but with top–down control affecting ecosystem functioning.

In general, upwelling ecosystems are characterised by a large number of species at low trophic levels (phy-

toplankton and zooplankton) and high trophic levels (predatory fish, such as, snoek, *Thyrssites atun*, marine mammals and birds, sharks, etc.), but few species at intermediate trophic levels, and these are mainly small pelagic fish. Such an ecosystem has been termed a “wasp-waist” ecosystem (Rice, 1995; Bakun, 1996). It has been hypothesised that changes in population sizes of small pelagic fish will have major effects on both their predators and their prey (Rice, 1995), so that control is neither top–down nor bottom–up, but rather from the “waist”, up and down (Bakun, 1996). The “wasp-waist” hypothesis is assumed to describe the dominant role of small pelagic fish in upwelling ecosystems (Cury et al., 2000), and this hypothesis has been adopted for this study. This study explores the possible causes of ecosystem changes in the southern Benguela ecosystem. We focus on two recent periods, and use Ecopath with Ecosim models (Walters et al., 1997; Walters et al., 2000; Christensen and Walters, 2004) to test hypotheses about causes of change from a 1980s ecosystem, when anchovy were abundant and sardine scarce, to a 1990s (1990–1997) ecosystem when sardine were increasing and anchovy decreasing in abundance. We test two hypotheses: (i) that fishing caused changes in ecosystem structure between the 1980s and the 1990s, and (ii) that large-scale changes in the environment (a ‘regime shift’) caused the observed changes in small pelagic fish.

## 2. Methods

Ecopath with Ecosim 4.0 (Walters et al., 1997) is a dynamic simulation tool developed for modeling trophic flows through ecosystems. It is an extension of the static mass-balanced Ecopath modeling approach (Christensen and Pauly, 1992), based on the original model of Polovina (1984). Using Ecopath with Ecosim 4.0 (Christensen and Walters, 2004), two separate, balanced Ecopath models of the southern Benguela ecosystem to represent the periods 1980–1989 and 1990–1997 have been constructed (Shannon and Jarre-Teichmann, 1999; Shannon, 2001; Shannon et al., 2003). Here, these are used as a basis for Ecosim simulations to explore the role of fishing and environmental factors in driving the regime shift in pelagic fish dominance in the southern Benguela ecosystem.

Table 1

Scenarios of altered fishing examined using Ecosim models of the southern Benguela ecosystem

Scenario	Species	Simulated changes in $F$	Explanation
1	Sardine	0.31 $\rightarrow$ 0.16	$F$ s of sardine and horse mackerel are altered from 1980s to 1990s estimates. Anchovy $F$ is unaltered
	Juvenile horse mackerel	0.11 $\rightarrow$ 0.07	
	Adult horse mackerel	0.09 $\rightarrow$ 0.06	
2	Anchovy	0.30 $\rightarrow$ 0.39	Anchovy $F$ is increased to simulate the observed reduction in anchovy biomass in the 1990s (to 69% of $B$ in the 1980s)
3	Sardine	0.31 $\rightarrow$ 0.16	$F$ s of sardine and horse mackerel are altered from the 1980s to the 1990s estimates. Anchovy $F$ is increased to simulate the observed reduction in anchovy biomass in the 1990s (to 69% of $B$ in the 1980s)
	Juvenile horse mackerel	0.11 $\rightarrow$ 0.07	
	Adult horse mackerel	0.09 $\rightarrow$ 0.06	
	Anchovy	0.30 $\rightarrow$ 0.39	
4	Sardine	0.31 $\rightarrow$ 0.16	$F$ s of sardine and horse mackerel are altered from the 1980s to the 1990s estimates. Anchovy $F$ is substantially increased to simulate a hypothetically large reduction in anchovy biomass in the 1990s (to 14% of $B$ in the 1980s)
	Juvenile horse mackerel	0.11 $\rightarrow$ 0.07	
	Adult horse mackerel	0.09 $\rightarrow$ 0.06	
	Anchovy	0.30 $\rightarrow$ 0.60	

To test the fishing hypothesis, the balanced 1980s Ecopath model is used to investigate four scenarios of altered fishing (Table 1). The model is forced by changes in fishing mortality ( $F$ ) using the dynamic Ecosim routines, and the resulting changes in biomass are assessed. In all Ecosim simulations, years 1–9 mimic the “equilibrium” ecosystem in the 1980s, and  $F$  values are changed from years 10 to 20. Thereafter,  $F$ s are returned to the original 1980s values.

To test the environment hypothesis (Fig. 3), the balanced Ecopath models for both the 1980s and the 1990s are used. Ecosim simulations are used in which forcing functions are applied to the links between anchovy and sardine and their prey, in an attempt to simulate the observed biomass changes between the 1980s and the 1990s (Table 2), and to predict possible changes from the 1990s back to a 1980s-type ecosystem structure. In Ecosim, a forcing function is

Table 2

Scenarios of altered environmental forcing examined using Ecosim models of the southern Benguela ecosystem

Scenario	Model	Trophic link examined	Forcing function	Effect
1	1980s	Anchovy $\leftarrow$ phyto- and zooplankton	–0.45	Fewer prey for anchovy
		Sardine $\leftarrow$ phyto- and zooplankton	0.40	More prey for sardine
2	1990s	Anchovy $\leftarrow$ phyto- and zooplankton	0.14	More prey for anchovy
		Sardine $\leftarrow$ phyto- and zooplankton	–0.38	Fewer prey for sardine
3	1980s	Anchovy $\leftarrow$ phyto- and zooplankton	0.00	No direct effect
		Sardine $\leftarrow$ phyto- and zooplankton	0.40	More prey for sardine
4	1990s	Anchovy $\leftarrow$ phyto- and zooplankton	0.14	More prey for anchovy
		Sardine $\leftarrow$ phyto- and zooplankton	0.00	No direct effect
5	1980s	Anchovy $\leftarrow$ macro- and mesozooplankton	–0.45	Fewer prey for anchovy
		Sardine $\leftarrow$ macro- and mesozooplankton	0.40	More prey for sardine
6	1990s	Anchovy $\leftarrow$ macro- and mesozooplankton	0.14	More prey for anchovy
		Sardine $\leftarrow$ macro- and mesozooplankton	–0.38	Fewer prey for sardine
7	1980s	Anchovy $\leftarrow$ mesozooplankton	–0.45	Fewer prey for anchovy
		Sardine $\leftarrow$ mesozooplankton	0.40	More prey for sardine
8	1990s	Anchovy $\leftarrow$ mesozooplankton	0.14	More prey for anchovy
		Sardine $\leftarrow$ mesozooplankton	–0.38	Fewer prey for sardine

Forcing functions are expressed as proportions of the maximum.

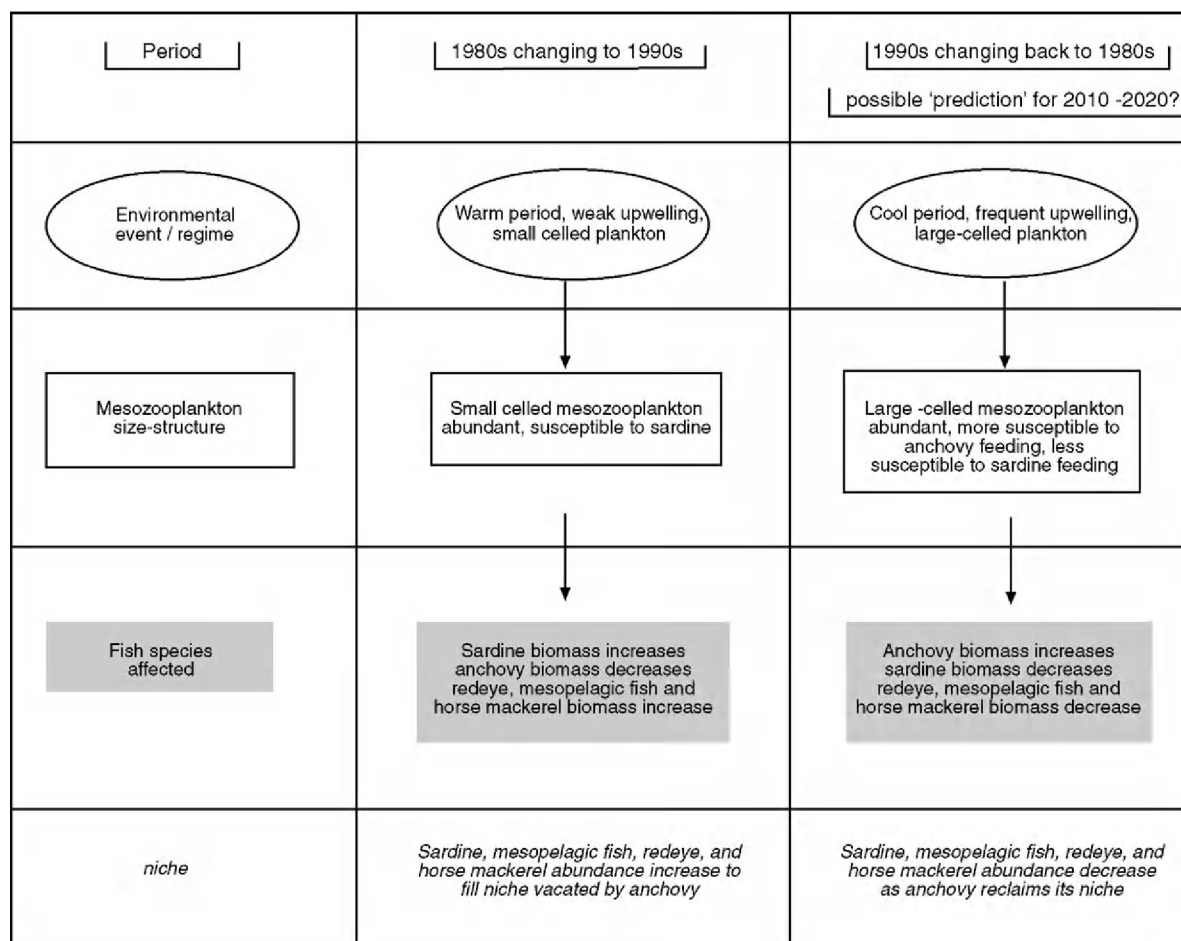


Fig. 3. Diagrammatic representation of the hypothesized environmental mechanisms causing alternating periods of anchovy and sardine dominance in the southern Benguela ecosystem.

a factor changing the susceptibility of a prey group to a predator, and these can be altered to reflect what may occur under different environmental conditions. The underlying hypotheses for these simulations are that in periods of intermittent mixing (i.e. cool periods with frequent upwelling events), a large phytoplankton biomass is supported, dominated by large, chain-forming diatoms (Fig. 3). Zooplankton are consequently larger in size (dominated by large copepods such as *Calanus* and *Calanoides*) and the environment is favourable to the biting feeding behaviour of anchovy (Van der Lingen, 1999). In warm periods the water column is stable, upwelling events are weak and less frequent, and the phytoplankton is dominated by

small cells (Fig. 3). As a consequence, small copepods dominate the zooplankton, favouring filter-feeding sardine (Van der Lingen, 1999).

All Ecosim simulations are run for 50 years using default Ecosim parameter settings apart from the “flow control” settings, which describe the respective vulnerabilities in each predator–prey interaction, i.e. whether there is top–down or bottom–up control of predators or their prey. Cury et al. (2000) present zooplankton and pelagic fish data that support the wasp-waist concept in upwelling systems, rather than simple bottom–up control of pelagic fish by zooplankton. In all simulations here, wasp-waist flow control was also assumed, i.e. there is bottom–up control of

predators of small pelagic fish and top-down control of zooplankton prey. Wasp-waist control was simulated by setting vulnerabilities in Ecosim to 0.9 for interactions between micro-, meso- and macrozooplankton and their predators (i.e. top-down control of zooplankton) and by setting vulnerabilities to 0.1 for interactions between small pelagic fish and their predators (i.e. bottom-up control of pelagic predators). Remaining interactions were assumed to be of mixed control type, with vulnerabilities set to 0.5. It was found that the effects of altered fishing are pronounced when wasp-waist control is assumed (Cury et al., 2000; Shannon et al., 2000), so that the effects of fishing and environmental forcing are unlikely to be hidden by a flattening of perturbations. By comparison, effects of altered fishing were found to be heavily dampened when straight bottom-up control of pelagic fish by their zooplankton prey was assumed, whereas assuming mixed control for all interactions gave effects intermediate between the wasp-waist and bottom-up control scenarios (Shannon et al., 2000).

### 3. Results

Comparisons between the balanced Ecopath models for the 1980s and the 1990s show that biomasses of sardine, juvenile horse mackerel and adult horse mackerel increase and that of anchovy decreases from the 1980s to the 1990s (Table 3). In contrast, the fishing mortality rates decrease for all four groups

Table 3

Mean annual estimates of fishing mortality rates ( $F$ ) and biomasses ( $B$ ) of some small pelagic fish in the southern Benguela ecosystem, from balanced *Ecopath* models of the 1980s and 1990s (Shannon, 2001; Shannon et al., 2003)

	1980–1989		1990–1997	
	$B$ (t km <sup>-2</sup> )	$F$ (per year)	$B$ (t km <sup>-2</sup> )	$F$ (per year)
Anchovy	5.216	0.30	3.573	0.23
Sardine	0.586	0.31	2.091	0.16
Juvenile horse mackerel	0.200	0.11	0.484	0.07
Adult horse mackerel	1.618	0.09	1.937	0.06

$F$  values are calculated according to input catches and biomasses in the models;  $B$  values are estimated from survey data to provide model input.

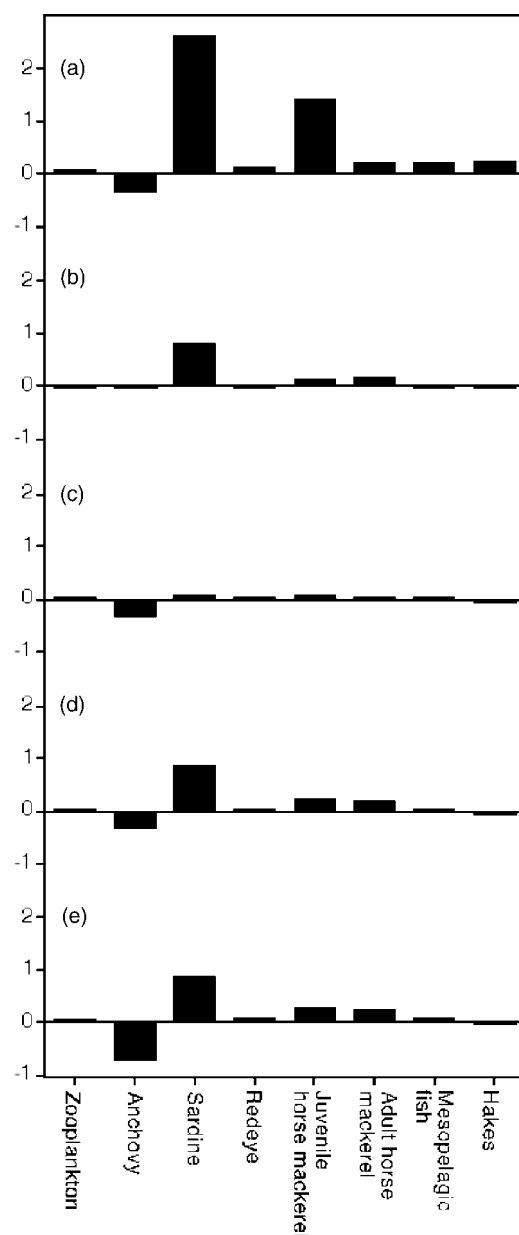


Fig. 4. Results of the models for testing the fishing hypothesis, showing changes in biomasses between two periods, expressed as the change at the end of the period relative to the biomass at the start. (a) The original 1980s and 1990s Ecopath models, (b–e) Ecosim fishing scenarios 1–4 (Table 1), results from Ecosim simulations are for year 15.



in the 1990s, based on estimates from catches, stock sizes and natural predation estimates in the models (Table 3).

When fishing mortality rates of sardine, juvenile horse mackerel and adult horse mackerel are altered over a 10-year simulation period to reflect those estimated for the 1990s, resulting biomasses of many groups (Fig. 4b) do not change by the same magnitudes or in the same directions as changes observed in the system between the 1980s and 1990s (Fig. 4a). Modelled changes in biomasses of the major groups are more realistic when anchovy biomass is reduced through heavier fishing and  $F_s$  of sardine and horse mackerel are altered simultaneously to reflect the 1990s situation (Fig. 4d). However, reduced anchovy biomass is accomplished by increasing model  $F$  for anchovy by a factor of 1.3, which is in contrast to the real situation in which anchovy  $F$  declined as biomass declined in the 1990s (Table 3). Simulated changes are not as large when only anchovy biomass is reduced and  $F_s$  of sardine and horse mackerel are

unaltered (Fig. 4c). When heavy fishing on anchovy reduces their biomass below the level estimated in the 1990s, changes occur in the major groups, irrespective of changes in fishing intensities on sardine and horse mackerel, as can be seen in the small differences between Fig. 4d and e.

When forcing functions are applied to both anchovy and sardine feeding in models of the 1980s and 1990s, model ecosystems describing the “opposite” regime are obtained, with changes in biomasses of many groups in the same direction and of a similar order of magnitude to changes from the 1980s to the 1990s estimated in the original models (Fig. 5a–l). Ecosystem changes similar to those observed can be simulated using forcing functions applied only to sardine feeding in the 1980s model (Fig. 5f), and only to anchovy feeding in the 1990s model (Fig. 5j). In these two simulations, feeding on phytoplankton, meso- and macrozooplankton is manipulated, but only for sardine in the 1980s model and only for anchovy in the 1990s model. In these scenarios, the magnitudes of

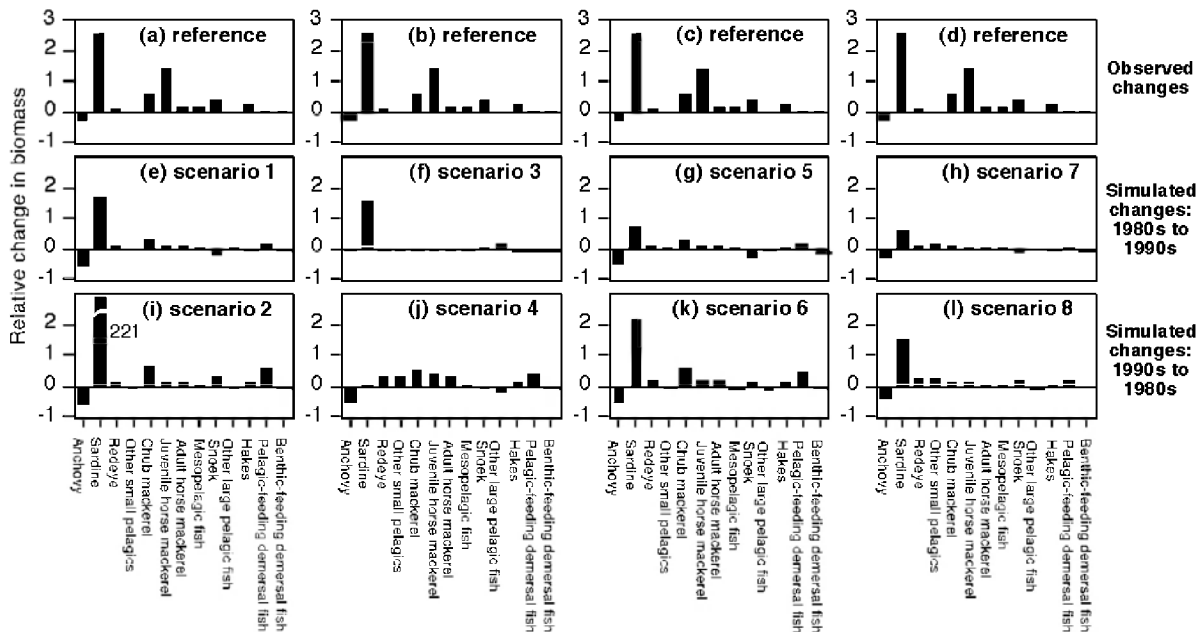


Fig. 5. Results of the Ecosim exercises for testing the environment hypothesis, showing relative changes in biomass between two periods, expressed as the change at the end of the period relative to the biomass at the start. (a–d) Identical reference cases, using the data from the original model structures. (e–h) Results of simulations for scenarios 1, 3, 5 and 7 (Table 2) when the original model of the 1980s is used to simulate the 1990s ecosystem structure. (i–l) Results of simulations for scenarios 2, 4, 6 and 8 (Table 3) when the original model of the 1990s is used to simulate the 1980s ecosystem structure.

the simulated biomass changes are smaller than those observed. When both anchovy and sardine feeding on all their prey are affected in both periods, the results are closer to the original estimates (Fig. 5e and i).

Tests in which the trophic paths from meso- and macrozooplankton to anchovy and sardine are manipulated (Fig. 5g and k) have similar effects (although of larger magnitude) to those in which only mesozooplankton links to anchovy and sardine are affected (Fig. 5h and l). These show that the susceptibility of mesozooplankton to anchovy and sardine in the 1980s and 1990s could be the key to simulating regime changes in the southern Benguela ecosystem. Using the 1980s model, a negative forcing

function is applied to the mesozooplankton–anchovy relationship, and a positive forcing function to the mesozooplankton–sardine link (Fig. 6). In a reverse process with the 1990s model, mesozooplankton are made less susceptible to sardine and more susceptible to anchovy (Fig. 7). The modelled changes in biomasses are in the observed directions and mostly of similar magnitudes to those in the two original models (Fig. 5h and l, compared to Fig. 5d). Two important exceptions are simulated changes in the biomasses of sardine and juvenile horse mackerel, which are smaller than the interdecadal changes observed. When the forcing functions are removed during the simulation of the forward progression from the 1980s to the

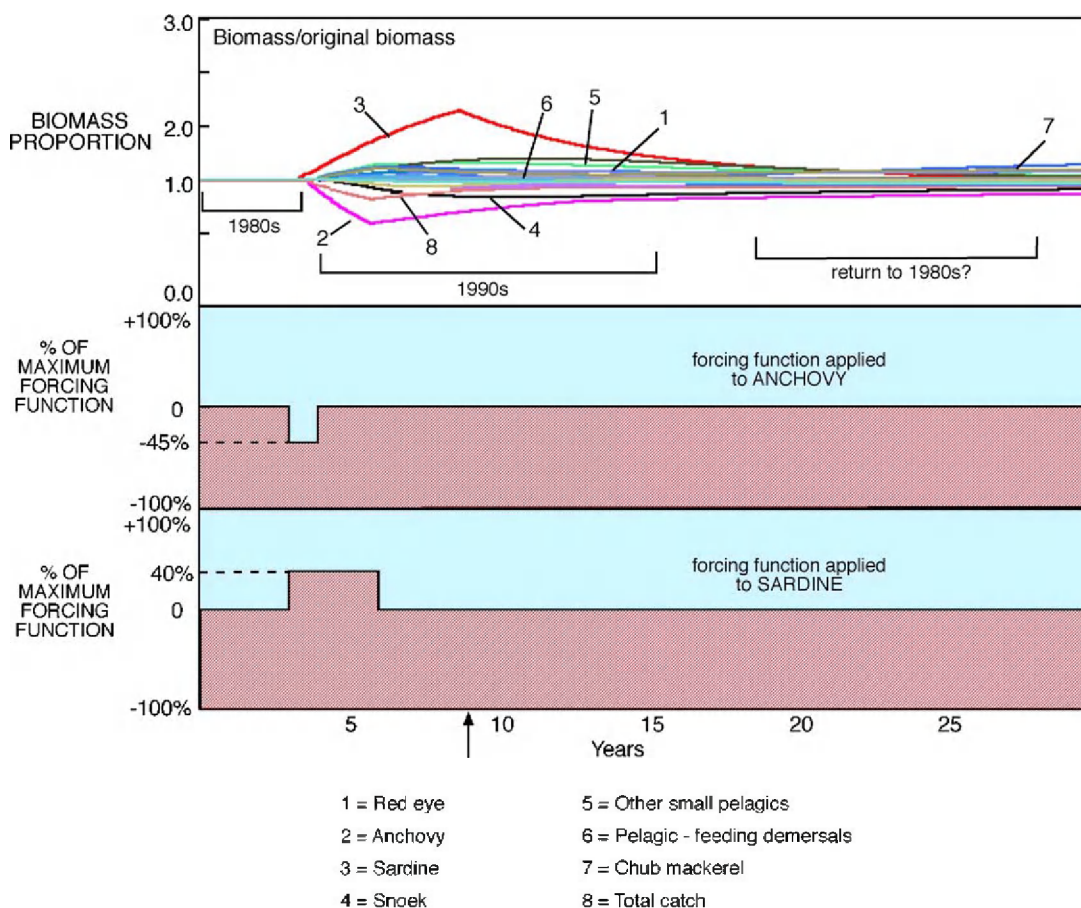


Fig. 6. Results of an Ecosim simulation of the forward progression from the 1980s to the 1990s, showing biomass as a proportion of the original biomass in the 1980s. A forcing function is applied so that mesozooplankton are less susceptible to anchovy feeding from years 3 to 4 and more susceptible to sardine feeding from years 3 to 6, causing changes in the system over a 10-year period (years 5–15). The middle panel depicts the forcing function applied over time to the mesozooplankton–anchovy link and the bottom panel depicts the forcing function applied over time to the mesozooplankton–sardine link. The arrow indicates the year used to estimate biomasses in Fig. 4.



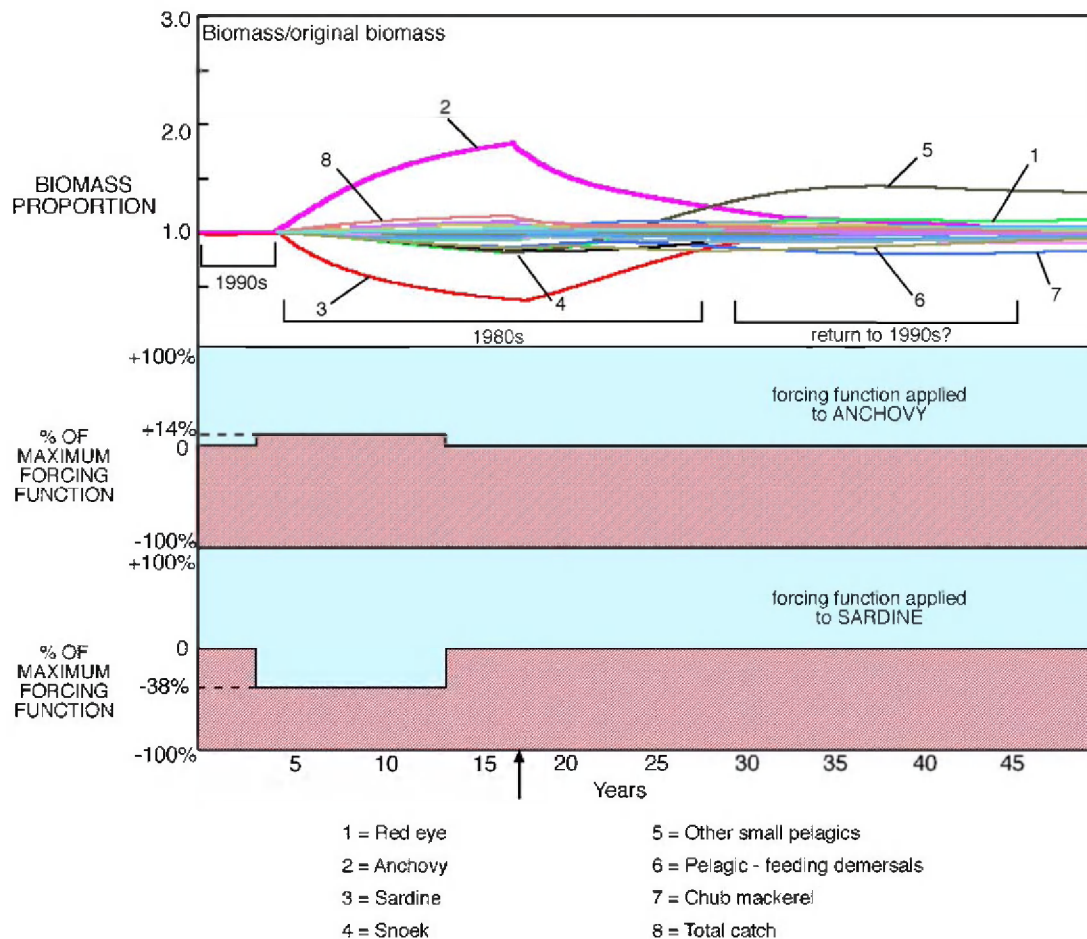


Fig. 7. Results of an Ecosim simulation of the reverse progression from the 1990s to the 1980s, showing biomass as a proportion of the original biomass in the 1990s. A forcing function is applied so that mesozooplankton are less susceptible to sardine feeding and more susceptible to anchovy feeding from years 3 to 13, causing changes in the system over a 20-year period (years 5–25). The middle panel depicts the forcing function applied over time to the mesozooplankton–anchovy link and the bottom panel depicts the forcing function applied over time to the mesozooplankton–sardine link. The arrow indicates the year used to estimate biomasses in Fig. 5.

1990s, the modelled ecosystem returns to its 1980s state (Fig. 6). However, in the reverse simulation from the 1990s to the 1980s, some groups (anchovy, other small pelagic fish, chub mackerel and pelagic-feeding demersal fish) do not “return” to 1990s states (Fig. 7).

#### 4. Discussion

Simulations of regime shifts in the southern Benguela ecosystem show that the observed changes

in pelagic fisheries (i.e. catches) between the 1980s and 1990s are unlikely to have played a large role in driving the changes in abundance of anchovy and sardine. This is not surprising, because the South African pelagic fishery was carefully and conservatively managed during these periods (Butterworth et al., 1992; De Oliveira et al., 1998), although there are uncertainties about the magnitudes and impacts of illegal discards. By contrast, the impacts of fishing are known to be important in other ecosystems. By manipulating fishing rates in a model of the Gulf of

Thailand ecosystem for 1980; Christensen (1998) was able to back-simulate changes in the ecosystem to obtain an ecosystem state close to that before intensive fishing began there in 1963. Hypotheses about fishing-induced changes do not necessarily lead to viable management options. The Namibian pelagic fishery in the 1970s was managed in such a way as to force an ecosystem change. The fishery targeted heavily on anchovy in order to benefit sardine by reducing interspecific competition (Butterworth, 1983). This attempt to enhance sardine abundance in Namibia failed, and both anchovy and sardine populations in the northern Benguela sub-system had suffered major decreases in abundance in the late 1970s.

Model shifts between an anchovy “regime” (1980s) and the possible move towards a sardine “regime” (1990s) in the southern Benguela ecosystem are likely to have been caused by changes in the availability of mesozooplankton to anchovy and sardine (Fig. 3). These changes are in opposite directions for anchovy and sardine, and are assumed to be mediated through changes in environmental conditions. This supports the hypothesis of Van der Lingen (1999), that alternating periods of anchovy and sardine dominance are related to complementary feeding strategies of the two species. Sardines derive most of their ingested carbon by non-selective filter feeding of small calanoid copepods less than 1200  $\mu\text{m}$ , crustacean eggs and nauplii, and anchovy eggs (Van der Lingen, 1999, 2002). These groups fall into the small end of the size range of the mesozooplankton group. By comparison, anchovy feed predominantly by biting at prey larger than 700  $\mu\text{m}$  (James and Findlay, 1989), which is in the upper range of modelled mesozooplankton (200–2000  $\mu\text{m}$ ) and within the macrozooplankton size range (2–20 mm). Although sardine eat greater amounts of phytoplankton than anchovy, they are better able to utilize zooplankton than phytoplankton, suggesting that sardine derive more energy from carnivory than herbivory (Van der Lingen, 2002). The differences in diet and feeding behaviour of anchovy and sardine in the southern Benguela enable zooplanktivorous anchovy to take advantage of periods during which large copepods dominate the zooplankton, and sardine, a plankton generalist, to maintain its populations under a range of zooplankton community structures.

Although in this study the fishery is shown not to play a primary role in “regime” shifts in the 1980s and 1990s, it should be remembered that only total fishing mortalities are considered here. The evolutionary effects of fishing and the spatial distribution and effects of fishing (e.g. Stokes and Law, 2000; Conover, 2000) have not been explored. Should they be examined in detail, it may be found that fishing played a role, in conjunction with environmental forcing, in driving abundance changes of pelagic fish in this region.

Based on analyses of the two Ecopath models used here, Shannon (2001) and Shannon et al. (2003) showed that predator and prey niche overlaps of anchovy, sardine, redeye *Etrumeus whiteheadii* and juvenile horse mackerel were larger in the 1990s than in the 1980s. This suggests that in the 1990s the pelagic niche previously occupied by anchovy was filled by a suite of other species of small pelagic fish. This has been discussed by Crawford (1987); it is frequently the case that generalised feeding allows more than one species to be able to take advantage of the energy made available by the collapse of a single stock. Whether a species becomes the dominant replacing species will depend on the extent of fishing on the species both during and after the collapse of the stock being replaced (Crawford, 1987). It cannot be expected that reduction of a stock through fishing will result in another single species being fully able to take its ecological place. It is unlikely that the different geographic distribution and behaviour of the replacing species are as well adapted to using the part of the resource vacated by the collapsed stock (Jones and Henderson, 1987).

In the eastern Bering Sea, Trites et al. (1999) found that fishing and trophic interactions alone did not account for the ecosystem changes that have been observed; there was an increase of 400% in the abundance of pollock between the 1950s and the 1980s. Their models suggest that environmental changes must have played a large part in changing the eastern Bering Sea ecosystem. These results support the conclusions of many, such as Schwartzlose et al. (1999) and Jennings and Kaiser (1998): collapses of pelagic fish stocks and subsequent replacement of dominant species are primarily environmentally linked, with fisheries usually serving to hasten and intensify the collapse rather than driving the regime shift.

Changes in the environment can have large impacts on the life history parameters of fish stocks. Such parameters form the basis of fisheries stock assessment models, and changes in these parameters can alter the underlying premises on which the models are based. Improved fisheries management requires that these factors are taken into account, and that historical and potential future ecosystem changes are incorporated into model executions and interpretations. To do this, it is necessary to understand the ways in which ecosystems respond to both past and potential future natural changes.

There are two main hypotheses regarding the environmental causes of regime shifts. The first involves changes induced by continuous environmental change, such as a prolonged period of warming, which could permit expanded spawning ranges and increased egg production of certain species. The second explanation is based on episodic environmental events, which could result in the formation of powerful year-classes of some species (Schwartzlose et al., 1999). In the southern Benguela ecosystem, there is good evidence that there has been a long-term, continuous environmental change, manifested through changes in the zooplankton communities (Verheye et al., 1998). However, there is also good evidence of episodic events that are primarily manifested through recruitment of pelagic species (Roy et al., 2001). The extent to which the short-term and long-term environmental factors interact is not clear, but is a question that needs to be addressed.

Related to this question about the interaction between short-term and long-term environmental changes, is the need to understand the duration and strength that is required of an environmental perturbation to cause interdecadal versus interannual changes in sardine and anchovy stocks. We used periods of 2–10 years over which forcing functions were applied in the Ecosim simulations, depending on the magnitude of the perturbation. Our choices were not guided by rigorous analyses, and we believe it is important to try and quantify the relationship between the magnitude and duration of environmental events, and their effects on the ecosystem. In this way, it might be possible to better understand the likelihood of short-term versus long-term changes in the pelagic ecosystem. This understanding is necessary to provide prognoses that are useful to management of pelagic fisheries.

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