



## Regime shifts in the Northern Benguela ecosystem: Challenges for management



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### ABSTRACT

An existing Ecopath with Ecosim model of the Northern Benguela ecosystem for 1956, previously fitted to time series for 50 years, was used to describe the impact that the different pressures (fishing and climate drivers) had on the structure of the ecosystem. Ecological network analysis indices and Integrated Trend Assessment of the input data and model outputs were used to describe the changes in this ecosystem over time. We test the hypothesis that the system has been reorganised over the course of the past 50 years, probably due to the cumulative effects of overfishing and environmental drivers such as the Benguela Niño, showing two large changes, with a transition period between the early 1970s and the early 1980s. The ecosystem has moved into a new stable state and this reorganised system will need a large shift to change with the consequential change not necessarily being back towards the pre-existing system.

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### 1. Introduction

Regime shifts are defined as low frequency, high-amplitude and sometimes abrupt changes in species abundance, community composition and trophic organisation that occur concurrently with physical changes in the system and propagate through several trophic levels (McKinnell et al., 2001; Collie et al., 2004). They have been described in several marine ecosystems including the Southern Benguela (Cury and Shannon, 2004), Southeast Alaska and Aleutian Islands (Heymans et al., 2007), the Baltic Sea (Tomczak et al., 2013) and in the demersal assemblages of the Northern Benguela ecosystem (Kirkman et al., 2015), although not in the full Northern Benguela ecosystem. Regime shifts are characterised by changes of the internal structure, organisation and size of an ecosystem (Cury and Shannon, 2004). Such food-web re-organisations are well described by Ecological Network Analysis (ENA) *sensu* Ulanowicz (1986), which represents the pattern of interactions among species and highlights their interdependence. In addition, knowledge of the network topology (e.g., connectance, number of species and interaction rates) provides insights to ecosystem functioning and stability (Dunne, 2006; Bascompte, 2009).

Managing marine ecosystems are encumbered by lack of information, the inability to sample at all trophic levels, the lack of understanding of the ecosystem structure (Travis et al., 2014) and how it changes due to pressures on the system. Thus it is very difficult to understand where the “tipping points” are in any system with imperfect information, when a system is moving towards a regime shift, and very difficult to know how to manage a system that have switched into a new regime. They cause disruptive changes in ecosystem structure and significant changes in the possible harvest of fish stocks, and are to a large extent driven by human actions (Folke et al., 2004).

In well-studied systems such as the North Sea (Kenny et al., 2009; Mackinson et al., 2009) and the Baltic Sea (Tomczak et al., 2013) these problems of lack of understanding have been overcome and the changes in the ecosystem structure are relatively well understood. However in a system which has been significantly less well studied, such as the Northern Benguela ecosystem (Fig. 1), our understanding of how the ecosystem has changed and how this system is best managed, is limited. The system has shown changes in the spatial extent and population structure of many of the important species (Jarre et al., 2015). Although no strong relationships were found between long-term bottom temperature and distributional changes alone, other environmental variables and the effects of fishing have been highlighted for consideration (Jarre et al., 2015). According to Jarre et al. (2015), there are complex interactions between jellyfish, gobies, horse mackerel and zooplankton which might mask direct oceanographic effects and the

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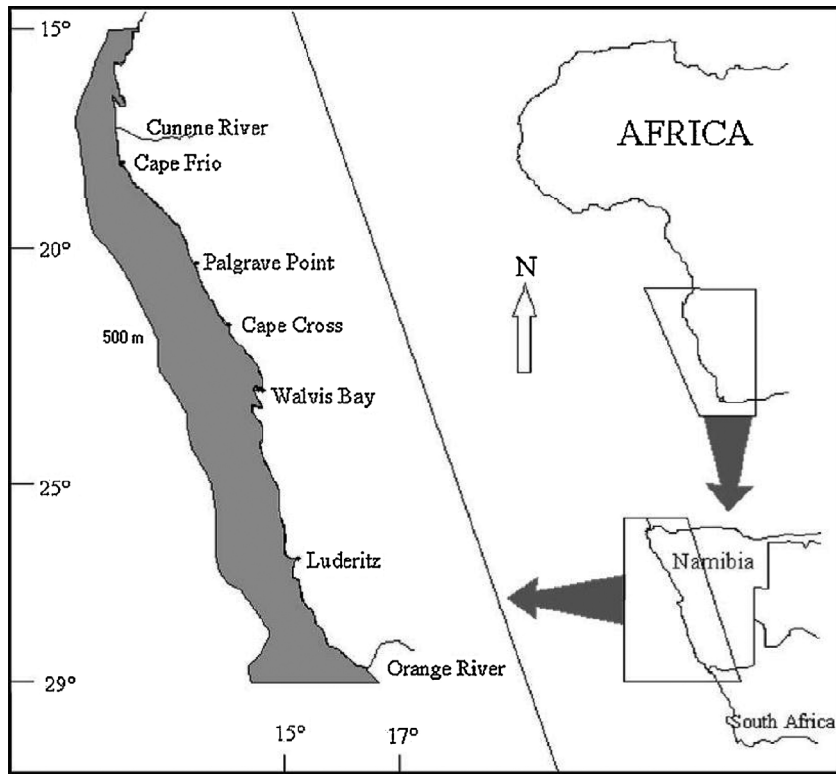


Fig. 1. The area covered by the northern Benguela model, from the coast to the 500 m depth contour between 15 and  $-29^{\circ}$ S (redrawn from Heymans and Baird, 2000).

absence of clear links between oceanography and more demersal fish species points to the combined effects of climate and fishing as drivers of dynamics in the northern Benguela. Jarre et al. (2015) suggest that the adoption of appropriate regime-specific management strategies need greater understanding of the impacts of long-term climate variability and change and further understanding of the roles of gobies and jellyfish (among others) in the system.

Over the past 50 years, overexploitation and environmental variation has caused the Northern Benguela to be much less productive in terms of fish yield (Hampton and Willemse, 2012). The environmental variation includes events such as the Benguela Niño's (Hutchings et al., 2009) which are generated by specific wind stress events in the west-central equatorial Atlantic, and eventually propagate to the south-west African coast (Florenchie et al., 2003). During the past 50 years the main planktivorous fish in the system changed from sardines, *Sardinops ocellatus*, to horse mackerel, *Trachurus capensis*, bearded gobies, *Suffoglobius bibarbus* and jellyfish (Cury and Shannon, 2004; Utne-Palm et al., 2010; Kirkman et al., 2015). The Northern Benguela has been subjected to similar environmental variation as the Southern Benguela, but the management of the two systems differed. Prior to Namibian Independence in 1990 the Namibian fish stocks were not as well managed (Armstrong and Sumaila, 2004; Bergh and Davies, 2004) as those off South Africa, and therefore the stocks are now not as robust as similar species in the south (Cury and Shannon, 2004; Hutchings et al., 2009; Jarre et al., 2015).

In this paper an existing ecosystem model of the Northern Benguela for 1956 (Fig. 2), fitted to time series for 50 years (Heymans et al., 2009), was used to describe the impact that the different pressures (fishing and climate drivers) had on the structure of the ecosystem, and the consequential regime shifts that occurred during that time. We used ecological network analysis indices (calculated in Ecopath with Ecosim, [www.ecopath.org](http://www.ecopath.org)) and Integrated Trend Assessment of the input data and model outputs to describe the changes over time. An understanding of the cumulative impact

that different drivers had on this ecosystem and how these cumulative impacts affected this ecosystem will help to address the issues of how to manage a changed ecosystem into the future. We test the hypothesis that the system has been reorganised over the course of the past 50 years, probably due to the cumulative effects of over-fishing and environmental drivers such as the Benguela Niño, and that the reorganised system will need a large shift to change with the consequential change not necessarily being back towards the pre-existing system.

## 2. Materials and methods

The Ecopath with Ecosim model of the northern Benguela ecosystems previously calibrated and described by Heymans et al.

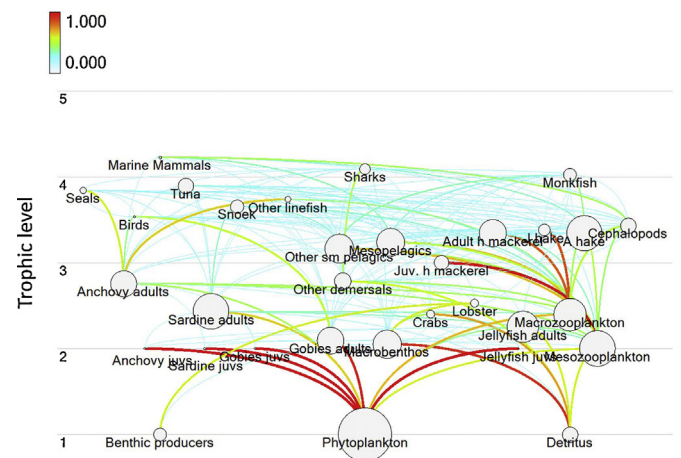


Fig. 2. Food web representation of the northern Benguela ecosystem with size of groups related to the size of the nodes and flow scaled by weight between blue and red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(2009) was subjected to the Ecological Network Analysis (ENA) algorithms in Ecosim to obtain emergent indices of ecosystem change. These indices as well as the environmental drivers used to fit the models and estimates of total biomass and catch were then subjected to the Integrated Trend Assessment (ITA) methods adopted by Tomczak et al. (2013) to describe the regime shift phenomenon in the Baltic Sea.

### 2.1. Ecopath methodology

Ecopath with Ecosim (EwE, [www.ecopath.org](http://www.ecopath.org)) is a suite of algorithms used to describe static food webs of ecosystems (Ecopath) and dynamic interactions in these ecosystems (Ecosim). The algorithms and the theories behind the software was described in detail by Walters et al. (1997, 2000), Walters and Kitchell (2001), Christensen and Walters (2004) and Christensen (2009) among others. It was comprehensively compared to other ecosystem modelling techniques and tools by Plagányi (2007).

### 2.2. The northern Benguela model

The EwE model of the northern Benguela constructed for 1956 and fitted from 1956 to 2003 by Heymans et al. (2009) used for this study covers the area (Fig. 1) from the shore to the 500 m depth contour and ranges from the Angola–Benguela front (around 15°S) to approximately the Orange River (29°S)—an area of approximately 179,000 km<sup>2</sup> (Brown and Cochrane, 1991). The model consists of 32 compartments: 18 of which are fish, 2 marine mammals, 1 sea bird, 8 invertebrates, 2 primary producers and 1 detritus (Fig. 2). Six groups were split into adult and juvenile stanzas: anchovy, sardine, gobies, horse mackerel, hake and jellyfish. See Heymans et al. (2009) and Heymans and Sumaila (2007) for more details on the model construction, data, model balancing and fitting. The model was driven by the forcing parameters in including forced catches (CF), fishing mortalities (F) and fishing effort (E) and compared to the biomass (B) and catch (C) time series. The model was calibrated to time series data of catch (C) and biomass (B), by changing the “vulnerability” parameters of all prey to their predator (Heymans et al., 2009). These parameters describe the interactions between each predator and prey combination. As no estimates of these parameters are available, they were estimated by reducing the log likelihood sum of squares between the predicted and observed estimates of catch and biomass. When the best vulnerability settings were achieved, the residuals were still substantial, and a nonlinear optimisation algorithm was then used to estimate a primary production anomaly. The anomaly is estimated by using a different primary production value in each time step, and the anomaly that reduces the sum of squares between the predicted and observed biomass the most was then correlated to the known environmental drivers such as wind stress and sea surface temperature. The anomaly showed a significant positive correlation with the wind stress anomaly used in Klingelhoeffer (2006) and a significant negative correlation with the sea surface temperature anomaly (SST\_anom, Fig. S1) given by Sherman et al. (2007). The best statistically fitted model was achieved by including sea surface temperature as a driver of primary production rate.

The impact of these forces on the ecosystem is depicted by the changes in the biomass. However, as a complete biomass time series for all species do not exist from 1956 onwards, modelled biomass time series were used in the subsequent ITA analysis (see below). The model was fitted to the known biomass time series, thus we assume that the modelled biomass was sufficiently validated. Due to the high trophic cascades and strong interactions between some predator and prey species, correlated biomasses were not excluded. This best fitted model was then used to calculate the ecological network analysis indices over the time period of the model,

1956–2003. The changes in the internal structure of the ecosystem were described using the ecological network analysis indices that were not strongly cross-correlated and we subsequently did and integrated trend assessment (ITA) on these ENA results.

### 2.3. Integrated trend assessment (ITA)

Integrated Trend Assessment (ITA) (Diekmann and Möllmann, 2010) includes the following sub-analyses:

The Sequential Regime Shift Analysis (STARS) following Rodionov (2004) used for each single time series, after correcting for autocorrelation, using probabilities of 0.05, cut-off length of 10 years and a Huber parameter of 4. Principal Component Analysis (PCA) based on the correlation matrix of chosen variables (drivers of the model, modelled biomass and network analysis indices) was carried out on the transformed values ( $\ln + 1$ ) of the given data set. The PC-scores of the first and second axis have been used to visualise and analyse the time trajectory of the system. To detect sudden changes on the integrated modelled, system level STARS were performed on the first two PC scores time-series. The same settings were used as for single time series. Finally, Chronological Clustering (Legendre et al., 1985) was used on the normalised data to detect changes represent as chronological data clusters. The significance level ( $\alpha$ ), which can be considered as a clustering-intensity parameter, was set to 0.01. The connectedness level was set to 50%. In accordance with the use of the correlation coefficient in the PCA, the data were first normalised, and then the Euclidean distance was calculated to determine similarity between years.

### 2.4. Ecological network analysis indices

Various descriptive indices, ecological network analysis and exploitation indices were extracted from the Ecosim model. A full description of ENA indices available from Ecopath with Ecosim are described in Heymans et al. (2007). We tested for cross-correlation between indices, and only used those that did not or very little correlate, such as the (1) estimated primary production (PP), (2) proportion of all flows (TST) that cycles through detritus (PFD), (3) proportion of primary production required for the catch (PPRc), (4) Trophic level of the catch (TLc), (5) ecosystem Redundancy and (6) Average Mutual Information. The redundancy (R) and average mutual information (AMI) are both related to the resilience of the ecosystem, with the AMI indicating the distribution of links in the ecosystem, and the R indicating how energy flows among these links (Ulanowicz, 2004). These indices (defined in Table 1) were calculated from the modelled ecosystem from 1956 to 2003. An ITA was performed to describe the emergent properties of the ecosystem, and to test for regime shifts.

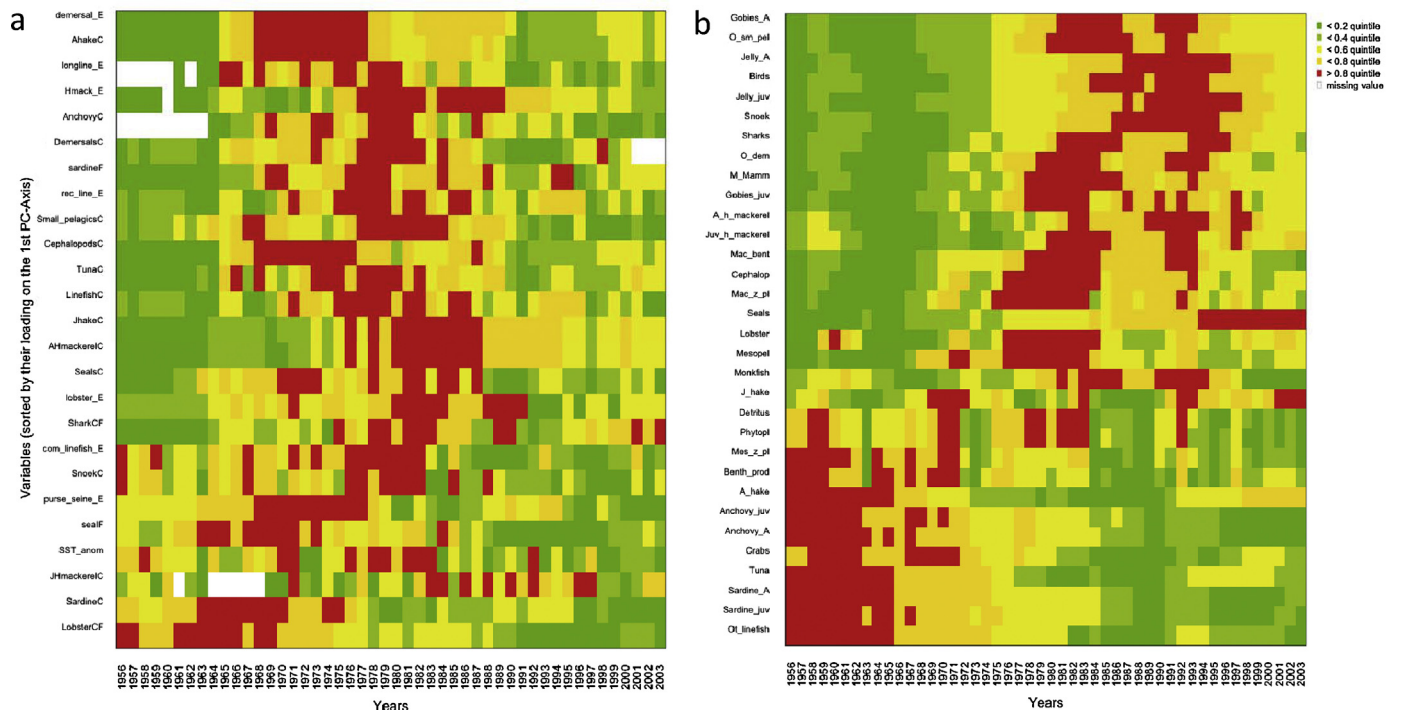
## 3. Results

The PCA of pressures on the system (i.e., catch, effort, SST, Fig. S1) shows (Fig. S3a) that the PC1 (which explains 38% of variation) is mainly related to the effort of the demersal fleet and the catch of hake. The PC2 explains 20% of the variation and is mostly related to sardine catch and purse seine effort as well as horse mackerel catch. Fig. S3a indicate that SST does not impact PC1 or PC2, as is shown by the traffic light plot (Fig. 3a) which sorts the variables based on their impacts on PC1, and show high values of pressure variables in the middle of the analysed time period. STARS analyses on PC1 and PC2 indicates that these ecosystem drivers (or pressures) showed abrupt changes approximately around 1964–66, 1972–76 and 1984–88 (Fig. 4a). These shifts are broadly confirmed by chronological cluster analyses (Table 2).

The impacts of ecosystem drivers are seen in the modelled biomasses of the ecosystem. The PCA biplots (Fig. S3b) and

**Table 1**  
Indices, formulas and definitions of indices used to describe the emergent properties of the northern Benguela ecosystem.

Index	Formula and descriptor
Estimated primary production (PP)	Primary production estimated for each time step
Proportion of flow to detritus (PFD)	PFD is proportion of TST that flows through detritus. TST is the sum of all flows in the model (Finn, 1976) and is calculated as $TST = \sum_{i=1}^n \sum_{j=1}^n T_{ij}$ where, $T_{ij}$ is flow of energy from compartment $i$ to $j$ . The PFD shows the distribution of energy through primary producers vs detritus food chain, thus indicates pelagic–benthic distribution of flows
Primary production required for the catch (PPRc)	PPRc indicates the amount of primary production that is required to maintain the catches and are usually higher when higher trophic level species are prevalent in the catch. It is calculated as: $PPRc = \sum_{Paths} \left[ Y \cdot \prod_{Pred, Prey} \frac{Q_{pred}}{P_{pred}} \cdot DC_{Pred, prey} \right]$ where, $P$ is production, $Q$ consumption, and $DC$ is the diet composition for each predator–prey interaction in each path, with cycles removed from the diet compositions (Christensen et al., 2005). PPRc is expressed in percentage when normalised with the primary production ( $PPRc/PP = PPRc\%$ )
Trophic level of the catch (TLC)	(TLC) is calculated as the weighted average of the trophic levels of all caught species: $TLC = \frac{\sum_i TL_i \cdot Y_i}{\sum_i Y_i}$ , where, $Y_i$ is the yield of compartment $i$ , and $TL_i$ is the trophic level of that compartment, calculated as: $TL_j = 1 + \sum_i DC_{ij} \cdot TL_i$ where, $TL_i$ is the trophic level of prey $i$ and $DC_{ij}$ is the proportion of prey $i$ in the diet of predator $j$ .
Ecosystem redundancy (R)	$R$ is an indicator of the change in degrees of freedom of the system, or the distribution of energy flow among the pathways in the ecosystem (Ulanowicz, 2004), and is calculated as: $R = - \sum_{i=1}^n \sum_{j=1}^n (T_{ij}) \cdot \log \left( \frac{\frac{T_{ij}^2}{n}}{\sum_{j=1}^n T_{ij} \sum_{i=1}^n T_{ij}} \right)$
Average Mutual Information (AMI)	where, $T_{ij}$ is flow of energy from compartment $i$ to $j$ The AMI measures the organisation of the exchanges among components. It shows how orderly and coherently the flows are connected. The AMI is calculated as: $AMI = \sum_{i,j} \frac{T_{ij}}{TST} \cdot \log \left( \frac{T_{ij} \cdot TST}{T_j \cdot T_i} \right)$ where, $T_i$ is the sum of all material leaving the $i$ th component and $T_j$ is the sum of all flows entering the $j$ th component (Ulanowicz, 2004).



**Fig. 3.** Traffic light plots of (a) drivers (left) and (b) modelled biomass estimates (right) for the northern Benguela ecosystem sorted by loading on the 1st PCA axis.

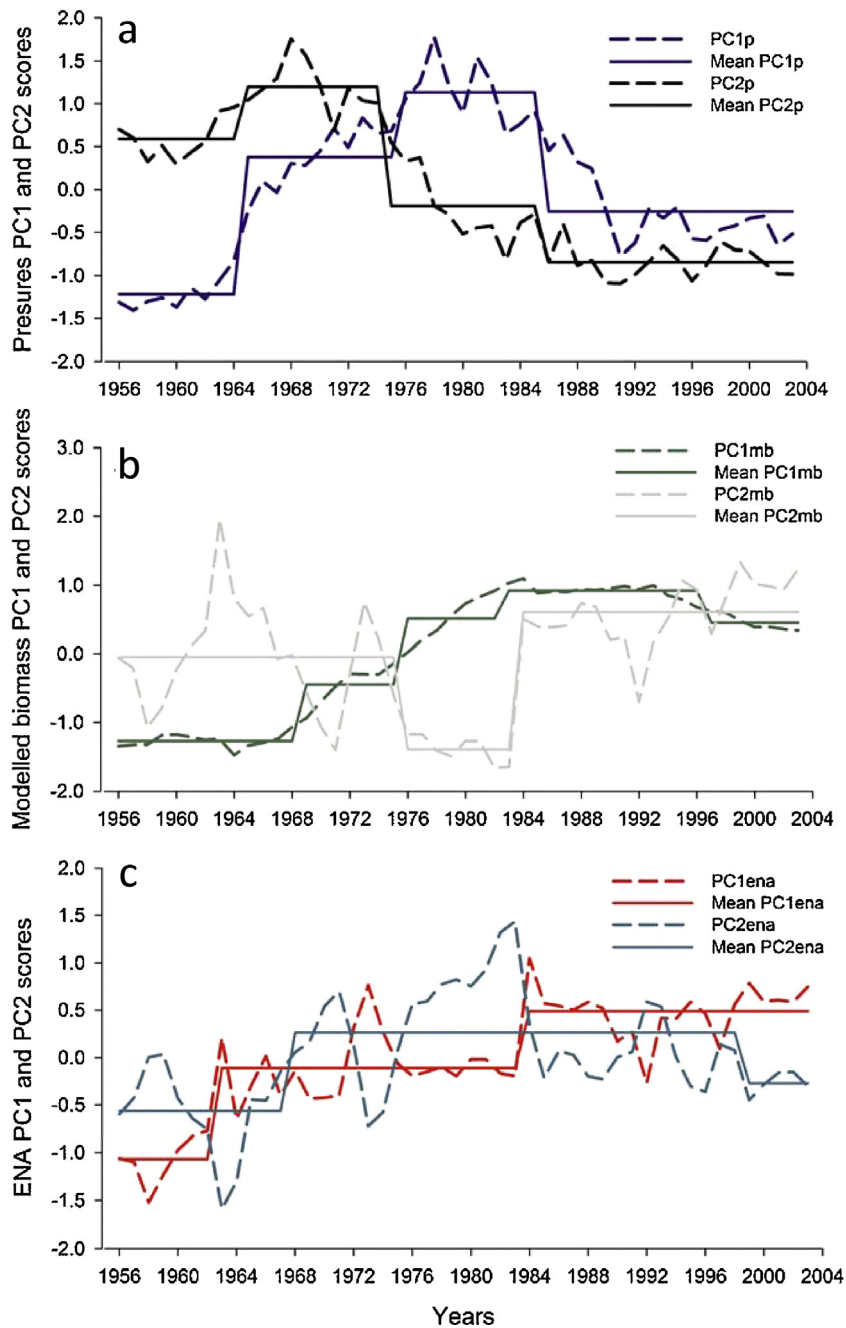


Fig. 4. STARS analyses on PC1 and PC2 for (a) ecosystem drivers, (b) modelled biomasses and (c) ecological network analysis indices.

traffic light plot (Fig. 3b) shows the dichotomy between the biomass of linefish, sardine, tuna and anchovy which had higher biomasses in the 1950/60s and the gobies, small pelagics and jellyfish that had higher biomasses in the 1980/90s. The PC1, which explains 66% of the variation, represents the trend in biomass for adult gobies, small pelagics and jellyfish, while being negatively driven by sardine, linefish and tuna. The PC2 (which explains 15% of the variation) best represents the variation in phytoplankton, mesopelagics, seals and hake (Fig. S3b). The shifts in the PC1 scores of biomasses were detected in 1968, 1976, 1982 and 1996, while shifts in PC2 were detected in 1975 and 1984 (Fig. 4b). These shifts are also broadly confirmed by chronological cluster analyses (Table 2).

Thus, from the input data and the modelled biomasses, three main time periods are apparent: (1) 1956–early 1970s, were the fish catches were increasing (the break in the early 1960s was mainly

due to the growth of the fishing fleet, although there was also a Benguela Niño in 1963, although the combination did not cause a large scale shift, and thus disregarded here), (2) early 1970s to mid-1980s, when the catches are high and the biomasses still stable and (3) post mid-1980s when the catches are reduced and the biomass of many commercially important species have declined. The impact it has on the demersal and pelagic parts of the ecosystem are shown in Fig. 5. Energy flow through hake (Fig. 5a, demersal) are averaged based on the shifts predicted by PC1. This shows that prior to the early-1970s the biomass of hake was high and fishing pressure (red arrow) about 3 times predation pressure. Post mid-1970s the biomass of hake is reduced, and fishing pressure is four times that of predation pressure and subsequent to the mid-1980s hake biomass has increased again, with fishing pressure being only double that of predation pressure. By contrast the energy flow through the

**Table 2**

Results of STARS analysis and chronological cluster analysis done on ecosystem pressures, pressures post 1984, ecosystem biomass estimates and ecological network analysis indices (ENA).

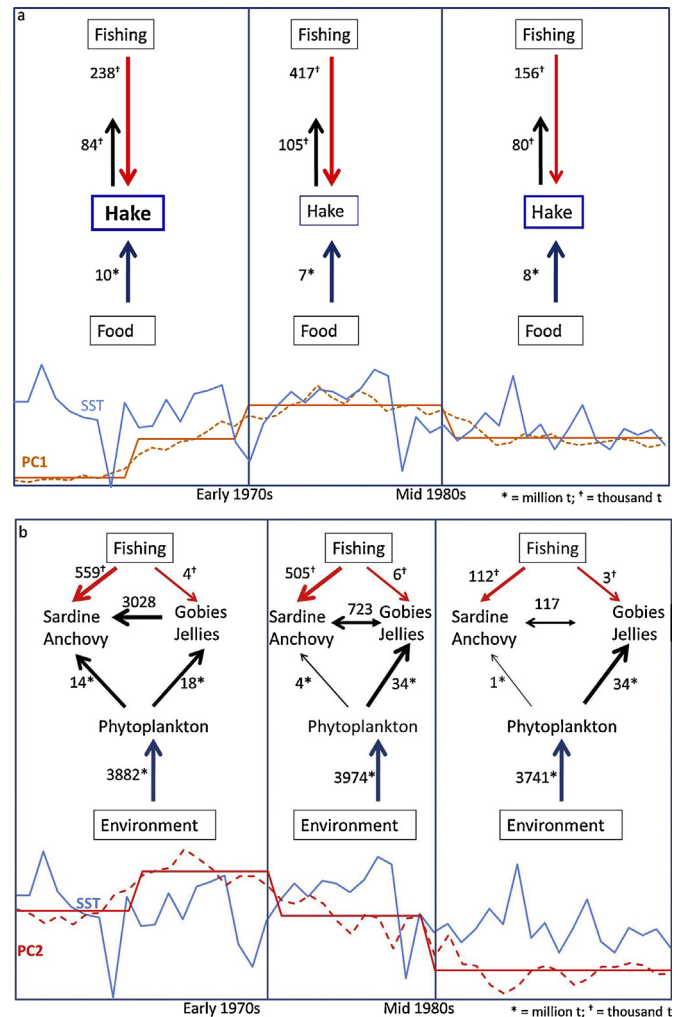
Method/data set	Pressures	Pressures post 84	Ecosystem biomass	ENA
<b>STARS</b>				
PC1	1965	1990	1969	1963
	1976		1976	1984
	1986		1983	
PC2	1965	1996	1997	
	1975		1976	1968
	1986		1984	
<b>Chronological cluster</b>				
alfa = 0.01	1964	1990	1970	1965
	1978		1979	
	1985		1984	1984
alfa = 0.05	1963	1996	1993	
	1967		1963	1964
	1975		1970	
	1988	1979	1984	1984
	1992	1990	1990	
	1998	1996	2000	

pelagic food web was described best by PC2, and is more complex (Fig. 5b). The main energy flow prior to the early 1970s is mainly through sardine and anchovy, with equal energy flow going to both anchovy/sardine, and gobies/jellies. The main fishing pressure and predation pressure is on sardine/anchovy. In the mid-1970s–mid-1980s period sardine/anchovy are much less prevalent, although there is still a significant fishing pressure while the predation pressure is reduced from gobies/jellies, and main energy flow from the primary producers now go through the gobies/jellies pathway. Post the mid-1980s the energy pathways are significantly changed, with most primary production being redirected to the gobies/jellies, and these groups are still consuming sardine/anchovy, although the fishing pressure has reduced due to lack of production in these groups. Thus it is clear that the ecosystem has been reorganised post 1984.

The PCA on ENA indices describes these emergent changes of the internal structure of the food web are given in Fig. 5. ENA indices (Fig. 6) showed the dichotomy between redundancy and TLc in the ecosystem with high redundancy during the 1950–70s, when the trophic level of the catch was low, and vice versa in the 1990s. The PCA (Fig. S3c) shows opposite relationship between R and TLc and CPPR in PC1 (explaining 60% of the variation), and between AMI and PFD in PC2 (explaining 25% of the variation). The shifts in PCA scores (Fig. 4c) showed abrupt changes in the emergent properties of this system in 1963, 1968 and 1984, which broadly agrees with the chronological clustering analysis (Table 2).

A comparison of two emergent ecosystem descriptors, the redundancy and the average mutual information, indicators of ecosystem resilience (distribution of energy flows among pathways) and of the internal organisation of flows respectively (Fig. 7) are given. The AMI and R followed similar trends until approximately the early 1970s, although the redundancy of the system was constantly decreasing over that time. After 1974, the AMI increases until 1984 after which both the AMI and R decrease.

Finally, to understand why the system did not recover in resilience, even though it had high internal structure (AMI) post 1984, we re-analysed the ITA on ecosystem pressures for the 1984–2003 time period (Fig. S3d). It shows that PC1 (which explains 34% of the variation), is most positively correlated with SST, and negatively correlated with hake and horse mackerel catches. PC2 (explaining 17% of the variation) is correlated with the demersal

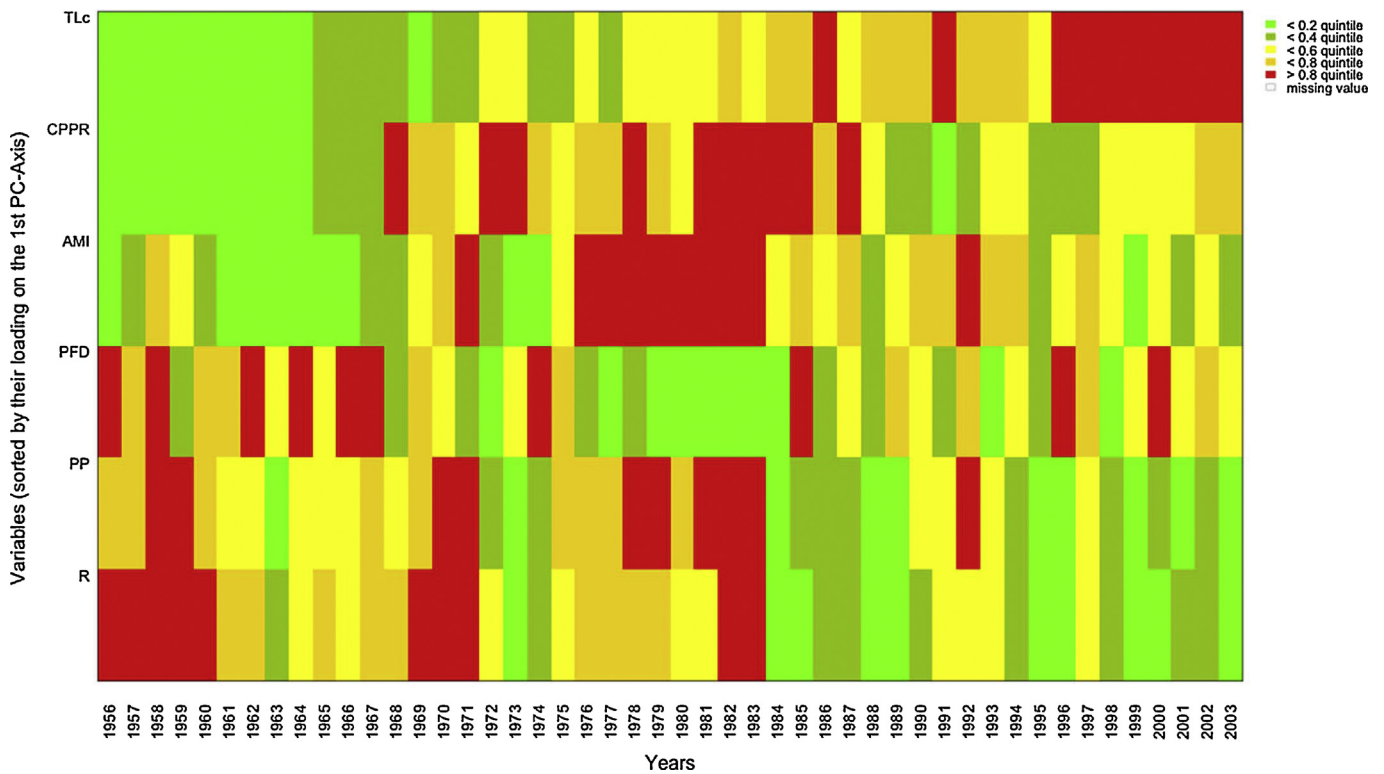


**Fig. 5.** Energy flow through the main (a) demersal and (b) pelagic fish compartments during three time periods: 1956–1973; 1974–1983 and 1984–2003. Blue arrows indicate feeding, black arrows flows to predators and red arrows fishing pressure, plotted with the main environmental driver (sea surface temperature SST) and the PCA values on main drivers of change in those parts of the ecosystem: PC1 for demersal (Fig. 5a) and PC2 for pelagic (Fig. 5b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

and shark catches, while being negatively correlated with the sardine catches and purse seine effort.

#### 4. Discussion

Regime shifts have been shown in various ecosystems including the southern Benguela (Blamey et al., 2012). However, in this study we described how the changes in the drivers of the ecosystem (fishing effort of different fleets, catch and changes in sea surface temperature) have reorganised the ecosystem, such that the main demersal species was impacted and the pelagics were reorganised between the main fished species (anchovy and sardine) and the less commercially viable gobies and jellyfish. It is evident that the development of the ecosystem consisted of three time periods, before the early 1970s, after the mid-1980s and the intervening period where the system changed. During the early period much of the flow in the ecosystem went through the sardine/anchovy food chain, and the demersal fleet did not significantly impact the hake stocks. During this time the pelagic fishery only took about 1/6th of the energy that flows between sardine/anchovy and gobies/jellies. During this time there were two Benguela Niño events (1963 and 1972), but



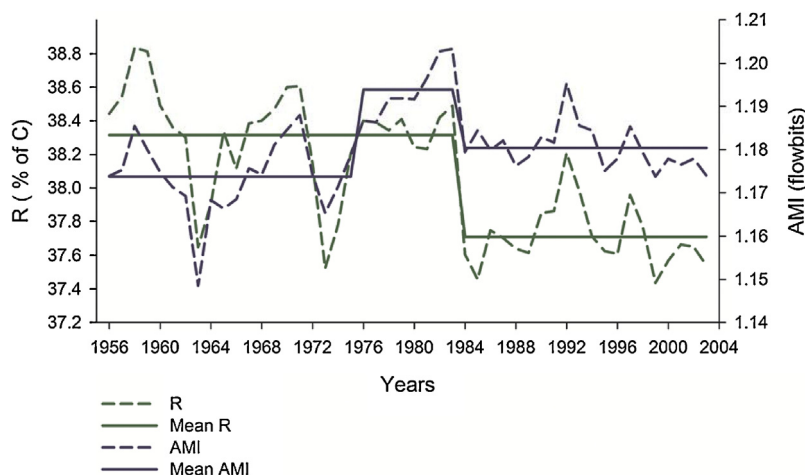
**Fig. 6.** Traffic light plots of ENA indicators for the northern Benguela ecosystem sorted by loading on the 1st PCA axis. TLC=trophic level of the catch; CPPR=primary production required for the catch; AMI=average mutual information; PFD=proportion of flow to detritus; PP=primary production; R=redundancy.

only the second event impacted the organisation and resilience of the ecosystem.

Between the mid-1970s and the mid-1980s the ecosystem was being reorganised, with anchovy/sardine and hake biomasses being reduced, hake catches became a more significant part of the hake production and the energy flow from sardine/anchovy to gobies/jellies was reduced significantly, although catches were still high. Subsequent to 1984 however, the system was reduced with more energy flowing from primary producers to gobies/jellyfish and the ratio of catches to production still similar to the previous time-period but much reduced in magnitude.

Although sea surface temperature (the main environmental driver) was not important as a main driver in the changes of the ecosystem (Fig. 3a), and did not impact the overall structure of

the ecosystem, the large fluctuations in primary production caused by significant Benguela Niño events in 1972 and 1984 did correlate with the changes in the emergent properties of the system. Specifically the 1972 and 1984 events were evident in the redundancy and AMI of the system (Fig. 7) due to the cumulative effect of the increased fishing pressure and the lack of primary production in those years. Both indices showed large fluctuations during Benguela Niño, which affects the AMI in 1974 but the redundancy of the system was only affected after 1984. An increase in AMI is indicative of a simplification of the food web (Latham and Scully, 2002), which was evident from the changes in the pelagic food web (Fig. 5b). The significant fishing pressure prior to the mid-1970s combined with the Benguela Niño in 1972 changed the internal structure of the ecosystem, indicated by the increase in AMI. The



**Fig. 7.** STARS analysis of emergent ecosystem descriptor: Redundancy as a percentage of development capacity, and average mutual information (flowbits) over time.

system was losing redundancy (diversity of flows among the different pathways) from the start of the fishery to the 1984 Benguela Niño, when the system abruptly changed to a new state, with lower energy distribution through both the demersal system and the sardine/anchovy section of the pelagic system. The decrease in AMI was due to the increase in gobies/jellies that have taken over the anchovy/sardine niche, leaving the system with a lower AMI and lower redundancy. Gobies and jellyfish were both not well linked to the rest of the food web or the fishery, with few animals predating jellyfish, and gobies not very important in the fishery. Jellyfish had become the major zooplankton consumers in the northern Benguela since the collapse of the sardine (Roux et al., 2013). Gobies were only caught as a bycatch of the purse-seine fishery (Roux et al., 2013) and are now the major prey for most top predators in the system. They are also able to live in and feed on benthos in the large anoxic layers of the ecosystem as well as being able to feed on jellyfish (Utne-Palm et al., 2010).

Thus the ecosystem has been reorganised by the large fisheries for small pelagics and demersal fish, to such an extent that a once-off lack of primary production due to the 1984 Benguela Niño reduced the resilience of the ecosystem and created a system where most of the pelagic energy flow was redirected to the jellyfish/gobies, that were not as important as prey for top predators as sardine/anchovy was prior to the mid-1970s. The ecosystem has reorganised to such an extent that the SST anomaly is more important as a driver of change in the ecosystem, with both the redundancy and the AMI following the SST anomaly more closely. The decrease in AMI, which is an indicator of increased stability in the food web complexity (Latham and Scully, 2002), means that the ecosystem will be very difficult to get out of this “reduced fishing” minimum *sensu* Folke et al. (2004) as the number of links in the ecosystem are reduced.

Despite the fact that the model reproduces shifts in given functional groups relatively well, and that the integrated analyses (Table 2 and Figs. 3 and 4) compare well to the results of a study on the regime shifts in the demersal community in the 1990s (Kirkman et al., 2015), we are aware of the limitations of our analyses, such as high cross-, and auto-correlation, the lack of seasonality and natural noise, as well as the aggregated and simplified food-web structure. As an upwelling system the Northern Benguela ecosystem is relatively simple, but our representation of the system (Fig. 2) does aggregate the food web structure, as we do not explain the microbial loop very well, which might be important in this system. Recently the need for ecological indices has become very important, with the EU Marine Strategy Framework Directive encouraging the study of food-webs through network indices (Rombouts et al., 2013). The estimations of species interactions often benefit the understanding of ecosystem response to perturbations (Bascompte, 2009), but the impact of network structure on the community may differ between different interaction types (Thébault and Fontaine, 2010). Consequently, the ENA analysis depends strongly on model quality and structure. The number of functional groups and model structure both have an impact on the number of flows and system properties (Pinnegar et al., 2005).

Ecopath with Ecosim (Christensen and Walters, 2004) is a commonly used approach that has been broadly discussed. It has been well vetted by authors such as Plagányi and Butterworth (2004); Coll et al. (2009) and Walters et al. (1997) who described the pros and cons of the methodology, which has been taken into account during the building, fitting and evaluation of this model. Specifically, model topology has been shown to be very important when comparing ecosystems and when deciding on which indicators to use (Heymans et al., 2014). In addition, data uncertainties may translate to uncertainties in modelled trophic control and hence results, as has been seen in the Baltic (Niiranen et al., 2012). However in this study the model was well fitted for several trophic levels

and we have confidence in the model and data (Heymans, 2004; Heymans et al., 2009), which represent changes in biomasses and ecosystem dynamics well.

## 5. Conclusion

The Northern Benguela ecosystem has moved from a regime with high redundancy and lower internal structure into a system with higher internal structure and less resilience due to significant fishing pressure and two specific catastrophic events, Benguela Niños that occurred in the early 1970s and the early 1980s. This caused:

- (1) Increasing pressure, high sardine biomass/tuna/hake/linefish, low gobies/jellies/small pelagics (birds, snoek, sharks, mammals) biomass and high primary production, high flow via sardine to fisheries—high resilience, lower AMI—then significant environmental pulse (Benguela Niño) disturbing the system.
- (2) Benguela Niño and highest pressure (linefish, hake, purse seine effort), changing biomass (lower sardine—higher gobies/jellies/small pelagics), changes in the flows of energy going to gobies/jellies/s pelagics, from primary production, through food web to fishery, highest AMI—flows are more evenly distributed in the food web—with *R* still high (seen as a transitional period).
- (3) Another important ecosystem disturbance (Benguela Niño), combined with changes in AMI, causes the 2nd shift—where we have lower AMI due to a reduction in flows through sardine, as well as lower sardine biomass, higher gobies/jellies/small pelagics biomass, lower PP and very low resilience. The system seems to have a significant reduction in *R*.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.10.027>.

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