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Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s

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Abstract

The northern Benguela ecosystem has been overfished and physically challenged over the past three decades. Ecopath with Ecosim was used to construct three ecosystem models (1971–1977, 1980–1989, and 1990–1995) and to compare differences in ecosystem structure. In the 1970s, the system sustained high catches, and had large populations of a few planktivorous fish. In the 1980s, the planktivorous fish species were expanded (horse mackerel, mesopelagic fish, and other small pelagics), although anchovy and sardine biomass was reduced. Catches remained high in the 1980s and the system was well connected. In the 1990s, the system was severely stressed, catches were much lower and omnivory was reduced. Most of the energy flowed through few pathways in the 1990s, and the energy was not transferred as efficiently up the trophic chain as in the 1980s. The fishery operated at the highest trophic level during the 1980s and there are some indications of “fishing down the foodweb” in this ecosystem between the 1980s and the 1990s. The high catches of sardine and hake in the 1970s are reflected in the high primary production required (PPR) by those compartments; the high catches of horse mackerel in the 1980s are shown by the high PPR for horse mackerel. The overall PPR for the fishery was highest in the 1980s, when the system was fished at nearly the same intensity as the 1970s, but the species taken were from higher trophic levels, requiring larger concentrations of primary production for their own existence. The importance of ecosystem–environmental interactions are highlighted by the abundance of horse mackerel, mesopelagics, small pelagics, and hake in the 1980s and the reduced biomass of most species in the 1990s, not only due to overfishing, but also due to the Benguela Niño that occurred in 1995. The system changed from an efficient ecosystem dominated by only two planktivores (anchovy and sardine) in the 1970s, to a system of large resilience and a varied planktivore population during the 1980s. However, the system’s resilience was lower, but its connectance was higher in the 1990s, where sardine was making a comeback and the marine mammals were doing well until the Benguela Niño reduced the system to a state of lower maturity.

Keywords: Northern Benguela; Upwelling; Ecopath; Flow network analysis; Trophic interactions; Foodweb

1. Introduction

Towards the end of the last century, it was recognized that ecosystem models are invaluable in the field of fisheries science (e.g. Mercer, 1982; Sherman and Alexander, 1986; Pauly et al., 1998). Using ecosystem models, changes in the species groups within an ecosystem can be summarized and viewed

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as part of a whole, where both direct and indirect effects of species on others within an ecosystem can be explored and the overall functioning of ecosystems can be compared. Ecosystem models include the budget type models (Rose et al., 1996), which describe energy or biomass flows between species and facilitate assessment of ecosystem-level properties, following the theories of Odum (1969), Finn (1976), and Ulanowicz (1986). Budget (or mass-balanced) models enable comparisons between different ecosystems or the same ecosystem during different time periods (Christensen and Pauly, 1993a).

The northern Benguela ecosystem, off the coast of Namibia in Southwest Africa, has changed dramatically over the past three decades (1970s, 1980s, and 1990s). In some instances these changes represented ecosystem variability, but fishing practices in the northern Benguela ecosystem have also changed with changes in fishing policy, political changes in the country, etc. As with most upwelling systems, the northern Benguela ecosystem is very productive and its living marine resources have been exploited for nearly a century. Historically, the system has been very important as a fishing ground in the southern African region, and was controlled by South Africa until 1990 when Namibia became independent and took control of the fishing industry and research.

The northern Benguela ecosystem has been relatively well studied during the past three decades by, among others, Siegfried and Field (1982), Macpherson and Roel (1987), Payne et al. (1987), Lluch-Belda et al. (1989), Barange et al. (1991a,b), Brown et al. (1991), Crawford et al. (1991), Macpherson and Gordoa (1992), Timonin et al. (1992), Hewitson and Cruickshank (1993), Pages (1992), and Stuttaford (1997). The knowledge of the various ecosystem components has been combined into three trophic flow models spanning the period from the early 1970s to the mid-1990s (Jarre-Teichmann, 1998; Jarre-Teichmann and Christensen, 1998; Shannon and Jarre-Teichmann,

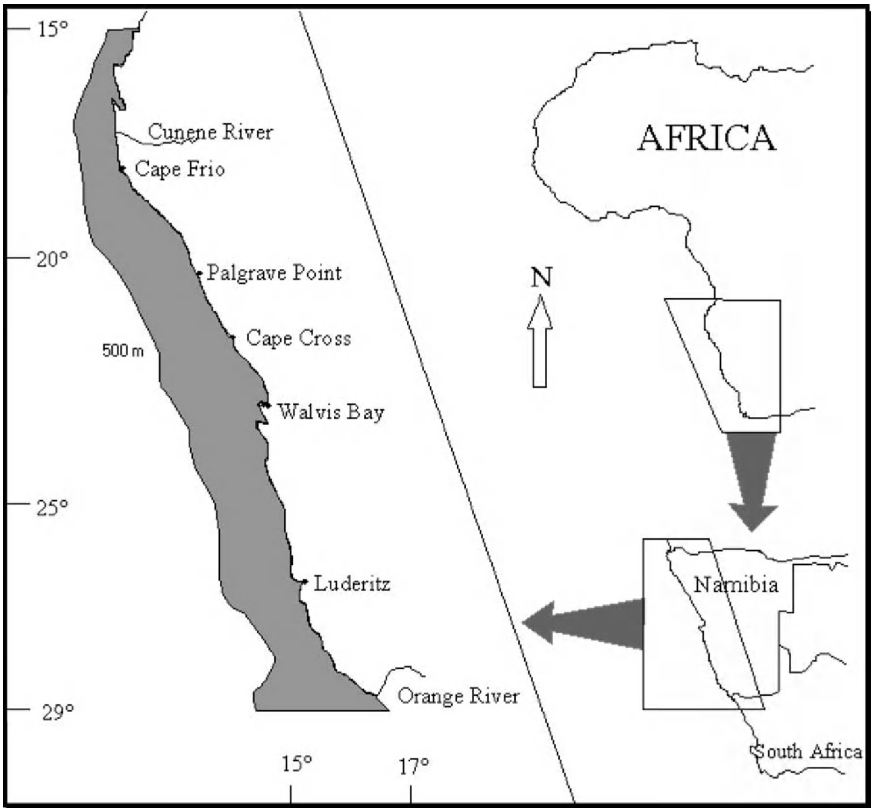

Fig. 1. Schematic representation of the northern Benguela ecosystem showing the 500 m depth contour.

1999a,b; Heymans and Baird, 2000a,b). This paper aims to compare these models by using the ecosystem analysis software Ecopath (Christensen et al., 2000) and to discuss the changes in the northern Benguela upwelling system during these three decades.

2. Study site

The Benguela upwelling system is situated along the West Coast of Africa in the South-East Atlantic Ocean. It is comprised of two major ecosystems (the southern and northern Benguela), separated by the principal upwelling center in the vicinity of Lüderitz (∼27°S:15°E), where upwelling-favorable winds blow throughout the year (Shannon and Pillar, 1986). It has been suggested that the upwelling core in the vicinity of Lüderitz may provide an environmental barrier to the interchange of biota between the northern and southern parts of the system due to the cold water and high wind speed (Crawford et al., 1987).

The northern Benguela ecosystem extends from 15 to 29°S. The system is bounded by the Angolan gyre in the north, which is considered to form part of the Angolan ecosystem, and extends to south of the Lüderitz upwelling center (Fig. 1). The areal extent of the system is approximately 179,000 km^2, covering the shelf from the coast to 500 m depth (Hewitson and Cruickshank, 1993). It is a typical eastern boundary current large marine ecosystem (LME), and forms the eastern boundary of the South Atlantic intercontinental gyre (Bakun, 1993). The area between 17 and 25°S in the northern Benguela is characterized by perennial upwelling, although it is less intense than in the Lüderitz area, with a maximum during late winter and spring and a minimum during late summer (Shannon, 1985). The rate of upwelling off central Namibia has been reported to be as high as $2.2 \times 10^{-3}\,\text{cm}\,\text{s}^{-1}$ during periods of vigorous upwelling (Stander, 1964).

3. Methods and data

Trophic flow models of the northern Benguela ecosystem were constructed and analyzed using Ecopath with Ecosim Version 4, called Ecopath hereafter (Christensen and Pauly, 1992, 1995; Christensen et al., 2000; Christensen and Walters, 2004) Ulanowicz (1986) has shown that a greater number of compartments would increase the development capacity of a system, and comparing systems of different structure is problematic. When comparing a system where for instance the microbial loop is well defined (i.e. detritus, bacteria, heterotrophic microflagellates, microzooplankton) with a system where this system is embedded in the detritus pool, the number of flows, recycling and network analysis indices such as total systems throughput of those systems would be very different. Thus, the models were modified as described below, to allow for comparisons. In most instances, aggregations of top predators were made based on trophic similarities, with species belonging to similar niche being aggregated. However, in some circumstances, viz. zooplankton, it was necessary to aggregate three different trophic levels into one because data were not available for all three different zooplankton communities for the three different time periods. Comparisons of system level indices between the three models with these communities aggregated in one model and not aggregated in the other two would have been erroneous. The importance of a probable jellyfish explosion in this ecosystem was unfortunately masked by these aggregations. However, without any information of jellyfish abundances before the 1980s it was not sensible to incorporate jellyfish as an independent compartment.

Data availability differed for the three time periods, with data in the 1980s being the most prevalent. Data on various commercially important species were available from the Ministry of Fisheries and Marine Resources of Namibia for the most recent time period, and from Sea Fisheries Research Institute (now Marine and Coastal Management) in South Africa for the earlier time periods. Data for non-commercial species were not always available for all three periods, and had to be inferred from other ecosystems or from other periods.

3.1. General Ecopath methodology

Based on the original work of Polovina (1984), Ecopath was developed by Christensen and Pauly (1992, 1995) and Christensen et al. (2000). Recently, a dynamic simulation module, Ecosim, has been developed that facilitates the simulation of fishing effects on ecosystems (Walters et al., 1997).

The Ecopath model is structured around a system of linear equations for expressing mass-balance. The linear equation was given by Christensen and Pauly (1992) for an arbitrary period, as

$$B_{(i)}\left(\frac{P}{B}\right)_{(i)}\mathrm{EE}_{(i)}=C_{(i)}+\sum_{(j)}\left[B_{(j)}\left(\frac{Q}{B}\right)_{(j)}\mathrm{DC}_{(ij)}\right],$$

where, $B_{(i)}$ is the biomass of component *i* during the period covered, $(P/B)_{(i)}$ is the production of a component *i* per unit biomass of *i*, $\mathrm{EE}_{(i)}$ is the ecotrophic efficiency (the fraction of the total production consumed by predators or exported from the system) of component *i*, $C_{(i)}$ is the catch of component *i*, $B_{(j)}$ is the biomass of each of the *j* predators of *i*, $(Q/B)_{(j)}$ is the consumption of component *j* per unit biomass, and $\mathrm{DC}_{(ij)}$ is the average fraction of *i* in the diet of *j* (in terms of weight).

The components in the system are linked by flows between them from prey to predators. Consumption by predators can be described by: consumption = production + non-assimilated food + respiration (Winberg, 1956). Consumption includes consumption within the system and from outside the system, termed import. The model is mass-balanced, i.e. mass is “conserved.”

3.2. Model descriptions

3.2.1. 1971–1977

The model of the northern Benguela system during 1971–1977 was constructed as part of a set of trophic models of the world’s four large marine upwelling systems (Jarre-Teichmann, 1998; Jarre-Teichmann and Christensen, 1998). As these models were designed in strictly the same manner to allow for straightforward comparisons, fewer groups could be detailed than in the subsequent models of the northern Benguela ecosystem. For example, pelagic goby (*Sufflogobius bibarbatus*) is important in the northern Benguela system but not in the other upwelling ecosystems, and was included along with other small pelagics. The original model constructed by Jarre-Teichmann (1998) for the period 1971–1977 was modified in the following way:

- The area of the northern Benguela upwelling system, previously calculated from Rossby radii and alongshore extension, was modified to the agreed 179,000 km^2, and biomasses and catches per unit area were recalculated.
- The original annual productivity estimate of phytoplankton (250 per year) was revised to 35.7 per year as used by Shannon and Jarre-Teichmann (1999a) for the 1980s. The original estimate of pelagic primary production of 7650 tonnes wet mass$\cdot$km$^{-2}\cdot$year^{-1} was retained, and phytoplankton biomass was recalculated accordingly.
- The original annual productivity estimate for zooplankton (65 per year) was revised to 35 per year, which is similar to the biomass-weighted productivity of the zooplankton groups in Shannon and Jarre-Teichmann (1999a).

The revised model is given in Tables 1 and 2.

3.2.2. 1980–1989

The model for 1980–1989 was based largely on data presented at a workshop held under the auspices of the Benguela Ecology Programme (BEP) in South Africa in 1989, attended by experts on the various ecosystem components. These data were updated using additional publications, and are described in detail by Shannon and Jarre-Teichmann (1999a,b).

For the comparative purpose of this study, aggregations of groups in the original model were modified in two steps. Firstly, the chondrichthyans were incorporated into the large pelagic and ‘other demersal’ groups. As no data were available on chondrichthyans in the northern Benguela system, this was achieved by analogy to the southern Benguela system (Shannon, 2001). Accordingly, 3% of the total chondrichthyan biomass was estimated to be apex predators (included with large pelagics), 40% of the remainder was estimated to be pelagic predators (also included with large pelagics), and 60% of the remainder was estimated to be demersal predators (included with demersal fish). Condrichthtyan diets were re-allocated by assuming that: (1) apex chondrichthyans prey on fish, such as chub mackerel (*Scomber japonicus*), large pelagics and seals (*Arctocephalus pusillus pusillus*); and (2) other pelagic chondrichthyans feed on the smaller pelagic fish groups, such as anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*), squid and horse mackerel (*Trachurus trachurus capensis*). Demersal chondrichthyans feed on the bottom dwelling species such as macrobenthos, demersals and hake

Table 1
Balanced parameter estimates for the northern Benguela model for the period 1971–1977

Group	Biomass	*P/B*	*Q/B*	EE	GE	Unassim.	Harvest
1. Phytoplankton	214.286	35.700	–	0.297	–	n.a.	–
2. Benthic producers	1.656	15.000	–	0.500	–	n.a.	–
3. Zooplankton	15.000	35.000	175.000	0.836	0.200	0.350	–
4. Meiobenthos	3.402	4.000	33.000	0.800	0.121	0.350	–
5. Macrobenthos	13.610	1.200	10.000	0.900	0.120	0.350	–
6. Anchovy	3.313	2.220	16.000	0.829	0.139	0.200	1.092
7. Sardine	8.257	1.177	15.000	0.980	0.078	0.200	2.380
8. Chub mackerel	0.486	0.860	8.500	0.980	0.101	0.200	0.121
9. Mesopelagics	1.470	2.000	10.000	0.601	0.200	0.200	–
10. Small pelagics	3.395	1.600	15.000	0.950	0.107	0.200	0.045
11. Horse mackerel	8.939	0.520	7.000	0.849	0.074	0.200	1.128
12. Hake	6.809	0.526	4.000	0.950	0.132	0.200	1.732
13. Large pelagics	0.032	1.700	11.600	0.712	0.147	0.200	0.035
14. Demersal fish	0.846	0.350	2.917	0.950	0.120	0.200	0.022
15. Marine birds	0.004	0.100	60.000	0.000	0.002	0.200	–
16. Marine mammals	0.020	0.070	32.000	0.000	0.002	0.200	–
17. Detritus	–	–	–	0.067	–	–	–

Biomass is in tonnes wet weight per square kilometer, *P/B* is production/biomass ratio (per year), *Q/B* is consumption/biomass ratio (per year), EE is ecotrophic efficiency (the proportion of production consumed or exported as harvest), GE is production/consumption ratio, unassim. is percentage unassimilated food and harvest is in tonnes wet weight per square kilometer per year.

(*Merluccius capensis* and *M. paradoxus*). Intra-group predation of chondrichthyans was re-distributed on the target groups after weighting by biomass.

A second step allowed for comparison with the model of the 1970s, and was carried out by:

- combining the micro-, meso-, and macrozooplankton boxes, as well as gelatinous zooplankton, into a single zooplankton box;
- combining pelagic goby and cephalopods with "other small pelagics"; and

Table 2
Diet composition for the 1971–1977 model of the northern Benguela ecosystem

	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0.820			0.550	0.550			0.510						
2		0.050	0.050											
3	0.100			0.400	0.400	0.665	1.000	0.400	0.900	0.380	0.400	0.350		
4			0.080											
5			0.070							0.150		0.440		
6						0.055		0.010	0.020	0.100	0.250	0.010	0.200	0.200
7								0.030	0.040	0.100	0.160	0.020	0.300	0.330
8										0.010	0.010			0.020
9						0.250				0.020	0.040	0.070		
10						0.030			0.040	0.080	0.060	0.050	0.150	0.200
11										0.100	0.070			0.110
12										0.060			0.050	0.040
13											0.010			
14												0.050	0.300	0.100
15														
16														
17	0.080	0.950	0.800	0.050	0.050			0.050				0.010		

The number of each compartment corresponds to those in Table 1. Rows represent prey and columns represent predators.

Table 3
Balanced parameter estimates for the northern Benguela model for the period 1980–1989

Group	Biomass	*P*/*B*	*Q*/*B*	EE	GE	Unassim.	Harvest	Sedimentation
1. Phytoplankton	203.664	35.700	–	0.808	–	n.a.	–	228.0
2. Benthic producers	3.210	15.000	–	0.500	–	n.a.	–	–
3. Zooplankton	71.923	36.398	151.503	0.758	0.240	0.252	–	–
4. Meiobenthos	5.957	4.000	33.333	0.950	0.120	0.200	–	–
5. Macrobenthos	28.296	1.200	10.000	0.950	0.120	0.200	–	–
6. Anchovy	1.408	1.160	11.717	0.996	0.099	0.350	0.732	–
7. Sardine	0.749	1.100	11.000	0.927	0.100	0.350	0.296	–
8. Chub mackerel	0.349	0.600	6.000	0.913	0.100	0.250	0.174	–
9. Mesopelagics	9.274	1.230	12.300	0.991	0.100	0.350	0.006	–
10. Small pelagics	9.109	0.918	9.184	0.981	0.100	0.345	0.001	–
11. Horse mackerel	13.966	0.520	5.200	0.913	0.100	0.300	3.382	–
12. Hake	7.263	1.000	4.545	0.997	0.220	0.200	1.676	–
13. Large pelagics	1.017	0.492	2.249	0.963	0.219	0.200	0.175	–
14. Demersal fish	4.107	0.920	6.097	0.986	0.151	0.200	0.202	–
15. Marine birds	0.010	0.160	120.300	0.000	0.001	0.260	–	–
16. Marine mammals	0.317	0.945	18.244	0.042	0.052	0.201	0.008	–
17. Detritus	840.000	–	–	0.728	–	–	–	–

Biomass is in tonnes wet weight per square kilometer, *P*/*B* is production/biomass ratio (per year), *Q*/*B* is consumption/biomass ratio (per year), EE is ecotrophic efficiency (the proportion of production consumed or exported as harvest), GE is production/consumption ratio, unassim. is percentage unassimilated food, harvest is in tonnes wet weight per square kilometer per year and sedimentation of phytoplankton as emigration is in tonnes wet weight per square kilometer per year.

- combining whales, dolphins, and seals into a "marine mammals" box.

The balanced parameters and diet matrix of the revised, re-aggregated 1980s model used in this study are tabulated in Tables 3 and 4.

3.2.3. 1990–1995

This model was originally constructed in mgC·m^{-2}·d^{-2} based on data for commercial species obtained from the Namibian Ministry of Fisheries and Marine Resources, and supplemented with published information on other species (Heymans, 1997;

Table 4
Diet composition for the 1980–1989 model of the northern Benguela ecosystem

	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0.580			0.330	0.560			0.808						
2		0.050	0.050											
3	0.160			0.670	0.440	0.817	1.000	0.145	0.966	0.536	0.172	0.398	0.046	
4			0.080											
5			0.070					0.002		0.088	0.005	0.375		
6						0.017				0.010	0.087		0.180	0.020
7											0.079		0.045	0.040
8											0.007		0.001	
9						0.157		0.030	0.025	0.180	0.041	0.019	0.053	0.018
10						0.009		0.006	0.009	0.041	0.393	0.042	0.547	0.538
11								0.005		0.045	0.025		0.005	0.222
12								0.005		0.049	0.055	0.101	0.103	0.129
13										0.001	0.035		0.003	0.033
14										0.050	0.100	0.065	0.015	
15														
16											0.001		0.002	
17	0.260	0.950	0.800											

The number of each compartment corresponds to those in Table 3. Rows represent prey and columns represent predators.

Table 5
Conversion factors and references used to recalculate the 1990 model of the northern Benguela ecosystem

Compartment	Conversion factor	Reference
Phytoplankton	Same as the 1980s data	Brown et al. (1991), Shannon and Jarre-Teichmann (1999)
Benthic producer	Added to the model by using data from the 1980s model	Shannon and Jarre-Teichmann (1999)
Zooplankton	Include micro-, meso-, and macrozooplankton, jellyfish and larval fish. Wet mass:carbon ratio for zooplankton = 0.04	Hutchings et al. (1991)
Meiobenthos	Added using *P/B* and EE for the 1980s model	Shannon and Jarre-Teichmann (1999)
Macrobenthos	Include deep see crabs and rock lobster. Biomass estimated by using *P/B* and EE for the 1980s model, and *Q/B* of 8.6	Shannon and Jarre-Teichmann (1999), De La Cruz-Aguero (1993).
Anchovy	Converted from C to wet weight	Heymans and Baird (2000b)
Sardine	Converted from C to wet weight	Heymans and Baird (2000b)
Chub mackerel	Added using *P/B* and EE for the 1980s model	Shannon and Jarre-Teichmann (1999)
Mesopelagics	Lanternfish and lightfish	Heymans and Baird (2000b)
Small pelagics	Gobies, other small pelagics, and squids. Used *P/B* and other energetics values for the 1980s model	Heymans and Baird (2000b)
Horse mackerel	Converted from C to wet weight	Heymans and Baird (2000b)
Hake	Converted from C to wet weight	Heymans and Baird (2000b)
Large pelagics	Snoek, tuna, various pelagic carnivorous fish—1980s data	Shannon and Jarre-Teichmann (1999)
Demersal fish	Benthic feeding fish and carnivorous fish scaled for area of 127,000 km^2	Heymans and Baird (2000b)
Marine birds	Converted from C to wet weight	Heymans and Baird (2000b)
Marine mammals	Include seals, whales, and dolphins	Heymans and Baird (2000b), Shannon and Jarre-Teichmann (1999)
Detritus	DOC + suspended POC + bacteria + hetereotrophic microflagellates. Bacteria C:wet biomass ratio = 0.1. Bacteria biomass = 17.5% of phytoplankton biomass. DOC and suspended POC calculated using Ecoempire	Ducklow (1983), Linley et al. (1983)

Heymans and Baird, 2000a,b). It consisted of 24 compartments and for this paper the model was aggregated and recalculated in tonnes wet weight km^{-2} per year, using the conversion factors and references given in Table 5. At first, the two detritus compartments (dissolved organic carbon and suspended particulate carbon) were aggregated and sediment detritus added. The detritus pool was then calculated using the Ecoempire routine in Ecopath, with an euphotic zone of 35 m, primary production of 510 g C m^{-2} and the methodology reported in Shannon and Jarre-Teichmann (1999a,b).

Benthic producers, meiobenthos, chub mackerel, other small pelagics and cetaceans were added to the original model, by using the *P/B*, *Q/B*, and EE values from Shannon and Jarre-Teichmann (1999a) as inputs, and allowing Ecopath to calculate their biomass. Some compartments were aggregated: 'fish larvae' was added to macrozooplankton; deep sea crab (*Chaceon maritae*) and rock lobster (*Jasus lallandi*) were combined into one compartment called 'macrobenthos'; and snoek (*Thyrsites atun*), tuna (*Thunnus* sp.), and other pelagics were added into a large pelagics compartment. The model was then balanced, before further aggregations were made. Additionally, bacteria and heterotrophic microflagellates were incorporated into detritus. Micro-, meso-, and macrozooplankton compartments were aggregated into a zooplankton compartment that also contained jellyfish. Gobies, cephalopods, and other small pelagics were combined into a compartment called small pelagics, while cetaceans and seals were combined into a marine mammals compartment (Table 5). The input data and diet composition used for the aggregated 1990s model of the northern Benguela ecosystem are given in Tables 6 and 7.

4. Results

The cumulative biomass of the major fish groups (Fig. 2) was lower in the 1990s (approximately 28 tonnes wet weight km^{-2} per year) than in either the

Table 6
Balanced parameter estimates for the northern Benguela model for the period 1990–1995

Group	Biomass	*P*/*B*	*Q*/*B*	EE	GE	Biomass accumulated	Unassim.	Harvest
1. Phytoplankton	204.000	30.300	–	0.405	–	0.000	n.a.	–
2. Benthic producers	0.128	15.000	–	0.800	–	0.000	n.a.	–
3. Zooplankton	146.928	7.949	28.329	0.696	0.281	0.000	0.350	0.009
4. Meiobenthos	0.381	4.000	33.000	0.950	0.121	0.000	0.350	–
5. Macrobenthos	2.103	1.200	8.600	0.950	0.140	0.000	0.350	0.013
6. Anchovy	0.947	1.200	12.300	0.506	0.098	0.000	0.350	0.229
7. Sardine	2.040	1.100	12.400	0.562	0.089	0.000	0.350	0.480
8. Chub mackerel	0.512	0.500	5.000	0.800	0.100	0.000	0.350	–
9. Mesopelagics	4.469	0.718	6.921	0.590	0.104	0.000	0.350	–
10. Small pelagics	3.596	0.873	7.900	0.435	0.110	0.000	0.350	–
11. Horse mackerel	8.939	0.850	8.500	0.677	0.100	0.000	0.350	2.067
12. Hake	3.655	0.800	20.000	0.583	0.040	0.000	0.200	0.510
13. Large pelagics	0.370	0.434	4.568	0.254	0.095	0.000	0.200	0.005
14. Demersal fish	2.809	1.000	10.000	0.460	0.100	0.000	0.200	0.118
15. Marine birds	0.012	0.140	118.269	0.000	0.001	0.000	0.200	–
16. Marine mammals	0.237	0.111	18.883	0.197	0.006	−0.004	0.200	0.010
17. Detritus	840.000	–	–			–	–	–

Input data include biomass (in tonnes wet weight per square kilometer), production/biomass (*P*/*B*) (per year), consumption/biomass (*Q*/*B*) (per year), EE is ecotrophic efficiency (the proportion of production consumed or exported as harvest), GE is production/consumption ratio, biomass accumulated (in tonnes wet weight per square kilometer per year), percentage unassimilated food (unassim.) and harvest (in tonnes wet weight per square kilometer per year).

1980s or the 1970s (Table 8). The reduction in cumulative biomass was in part due to the decrease in anchovy and sardine over the three decades, with sardine biomass being virtually zero during the 1980s and anchovy being very low in the 1990s (Fig. 2). However, horse mackerel, hake, demersal fish and mesopelagic fish were all more abundant in the 1980s than in the 1970s and 1990s.

Table 7
The diet matrix of the northern Benguela ecosystem for the 1990s

	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0.596			0.150	0.324			0.536						
2		0.050	0.050											
3	0.136			0.850	0.676	0.992	1.000	0.423	0.992	0.952	0.797	0.952	0.967	0.055
4			0.080											
5			0.030							0.017	0.072	0.017		
6						0.001				0.001	0.006	0.001	0.002	0.044
7										0.003	0.012	0.003	0.003	0.088
8										0.001	0.003	0.001	0.001	0.019
9						0.004		0.007	0.008	0.004	0.018	0.004	0.004	0.126
10						0.003		0.007		0.004	0.019	0.004	0.005	0.139
11								0.016		0.010	0.041	0.010	0.010	0.298
12								0.006		0.004	0.016	0.004	0.004	0.114
13											0.001			0.007
14								0.006		0.004	0.015	0.004	0.004	0.111
15														
16														
17	0.268	0.950	0.840											

The number of each compartment corresponds to those in Table 6. Rows represent prey and columns represent predators.

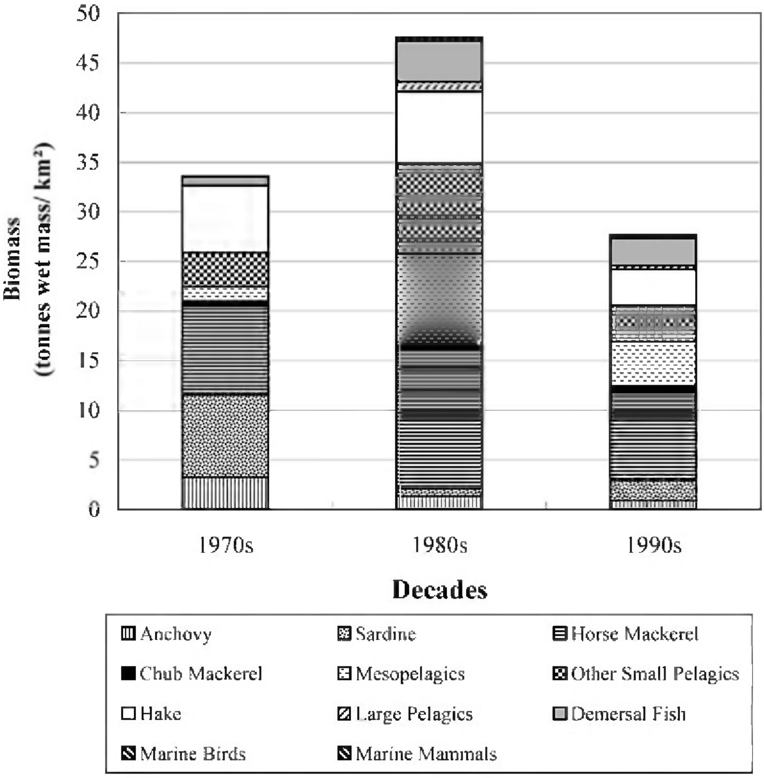

Fig. 2. Biomass (tonnes wet weight per square kilometer) of predators in the northern Benguela ecosystem for the three decades.

Table 8
Statistics summarizing biomass and major flows during the three decades

Summary statistics	1971–1977	1980–1989	1990–1995
Trophic level of fishery	2.85	3.25	3.1
Efficiency of fishery	0.0009	0.0009	0.0006
Total landings	6.6	6.7	3.4
Total biomass excluding detritus	281.5	360.6	381.2
Total net primary production	7674.8	7319.0	6183.1
Total consumption	3213.5	11742.6	4477.3
Total export	6124.4	1221.2	4452
Total respiration	1550.4	6069.9	1731.1
Total production	8264.2	10036.0	7479.3
Throughput	17443.2	23495.0	16251.5
Net production	6124.4	1249.1	4452.0
Total flows to detritus	6554.8	4460.8	5591.1
Zooplankton biomass	15.0	71.9	146.9
Zooplankton production	525.0	2617.9	1167.9
Total fish biomass	33.5	47.2	27.3
Total fish production	30.9	41.2	23.5
Connectance index	0.258	0.285	0.301
Systems omnivory index	0.152	0.172	0.117

Biomass is in tonnes wet weight per square kilometer and flows in tonnes wet weight per square kilometer per year.

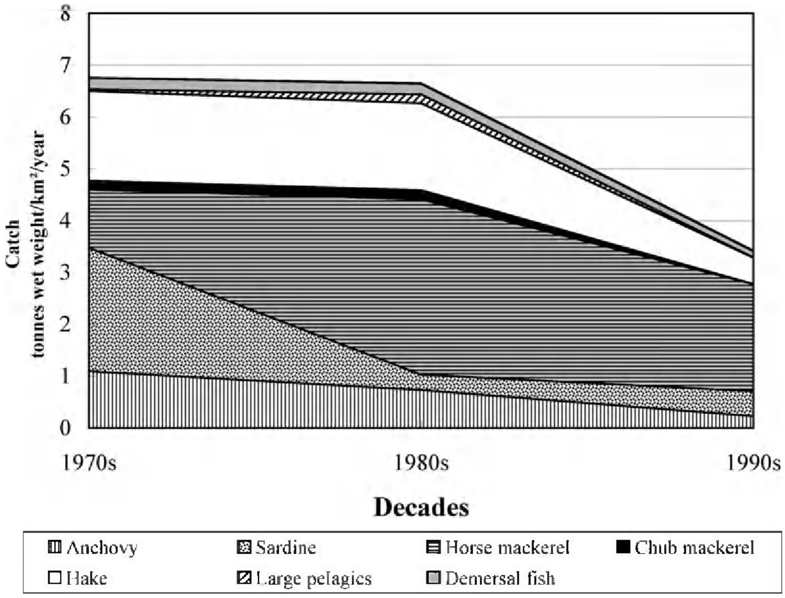

Fig. 3. Catches (tonnes wet weight per square kilometer per year) of commercial fish in the northern Benguela ecosystem for the three time periods.

Annual catches in the 1970s and 1980s were just over 6.5 tonnes wet weight km^{-2} per year, nearly twice the approximately 3.5 tonnes wet weight km^{-2} per year of the 1990s (Fig. 3). There has been a steady decline in anchovy catches over the three decades, while the catches of sardine declined dramatically from the 1970s to the 1980s, and increased slightly in the 1990s. The decline in the sardine catches was counterbalanced by the catch of horse mackerel in the 1980s, although the catch of this species has also decreased into the 1990s. The catch of chub mackerel decreased marginally from the 1970s to the 1980s, and there were no records of catches of chub mackerel in the 1990s. Catches of hake and other demersal species remained relatively constant over the first two decades but decreased into the 1990s, when hake catches declined to one third those of the 1980s.

4.1. *Internal indices*

Internal indices are used to compare different groups or species over time, rather than comparing the whole ecosystem. These indices include the effective trophic level of each group, the transfer efficiency between distinct trophic levels, and the primary production required (PPR) for the catch and production of each predator.

The effective trophic level of a compartment is a weighted average of the number of steps a living component is from the primary producers or non-living components of the system (Odum and Heald, 1975; Field et al., 1989). An analysis of the effective trophic levels of the various compartments in this ecosystem shows that the primary consumers in this ecosystem include zooplankton, meiobenthos, macrobenthos, anchovy, other small pelagic fish and sardine (Table 9). The secondary consumers include mesopelagics, horse mackerel, chub mackerel, hake, demersal fish and large pelagic fish (Table 9). The top consumers are marine birds and mammals (Table 9). The effective trophic level of the main primary consumers changed over time, with that of anchovy increasing from 2.4 to 2.8 to 3.0 and that of sardine from 2.4 to 2.5 to 2.8. Thus, anchovy and sardine are now feeding higher in the foodweb than they did in the 1970s and 1980s. Conversely, some of the secondary consumers, such as chub mackerel, large pelagics, hake, demersal fish, and marine birds feed lower in the foodweb than in previous decades (Table 9).

Table 9
Effective trophic level of each compartment over the three different time periods

		1971–1977	1980–1989	1990–1995
1	Phytoplankton	1.0	1.0	1.0
2	Benthic producers	1.0	1.0	1.0
3	Zooplankton	2.1	2.2	2.2
4	Meiobenthos	2.4	2.8	3.0
5	Macrobenthos	2.4	2.5	2.8
6	Anchovy	3.4	3.4	3.2
7	Sardine	3.1	3.2	3.2
8	Chub mackerel	3.4	3.6	3.3
9	Mesopelagics	2.5	2.3	2.6
10	Small pelagics	2.0	2.0	2.0
11	Horse mackerel	2.2	2.2	2.1
12	Hake	3.4	3.6	3.2
13	Large pelagics	3.3	3.4	3.2
14	Demersal fish	3.8	3.6	3.2
15	Marine birds	3.7	3.7	4.0
16	Marine mammals	3.1	3.2	3.2
17	Detritus	1.0	1.0	1.0

The transfer efficiency of each discrete trophic level is defined as a measure of the fraction of input to each of the aggregated trophic levels that is passed on to the next level (Ulanowicz, 1987), i.e. the fraction that is either consumed by predators or harvested. Transfer efficiencies tend to decrease as one ascends the trophic pyramid (Christensen and Pauly, 1993b; Shannon and Jarre-Teichmann, 1999a,b) and they are generally lower in upwelling ecosystems (Jarre-Teichmann et al., 1998). The 1970s and 1990s models are no exception (Fig. 4). However, during the 1980s, transfer efficiencies from the second discrete trophic level were lower than those of the third and the fourth levels, whereas they declined steadily in the 1970s and 1990s. The transfer efficiency was calculated by estimating the total matter flowing from each trophic level (including detritus, respiration, and export) divided by that flowing into each trophic level, rather than using that calculated by Ecopath, as there seems to be a discrepancy between these calculations. Thus, the transfer efficiency was calculated to the fifth trophic level even though the highest effective trophic level for any group is 4-marine mammals in the 1990s (Table 9). The transfer efficiency is calculated using recycled pathways as well as straight-through pathways, which cause the discrete trophic levels used in the Lindeman trophic analysis to be higher than the effective trophic levels of the groups.

Pauly and Christensen (1995) relate PPR to the potential net primary production used in terrestrial systems by Vitousek et al. (1986). According to Christensen et al. (2000), PPR is similar to H.T. Odum's concept of energy, and proportional to Wackernagel and Rees' (1996) ecological footprint. The fractions of PPR to sustain the predators are highest for most groups in the 1980s, with the exception of anchovy, sardine and chub mackerel, which are higher in the 1970s, and marine mammals, which

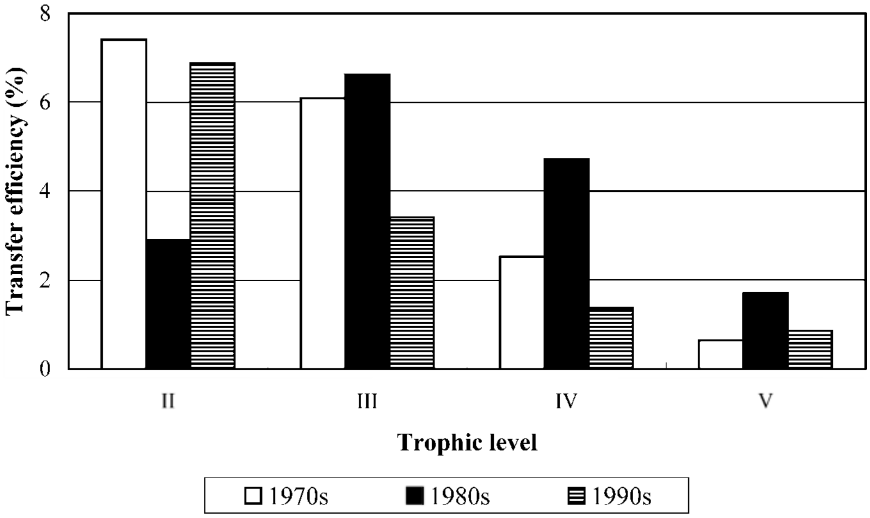

Fig. 4. Transfer efficiencies of the northern Benguela ecosystem during the 1970s, 1980s, and 1990s.

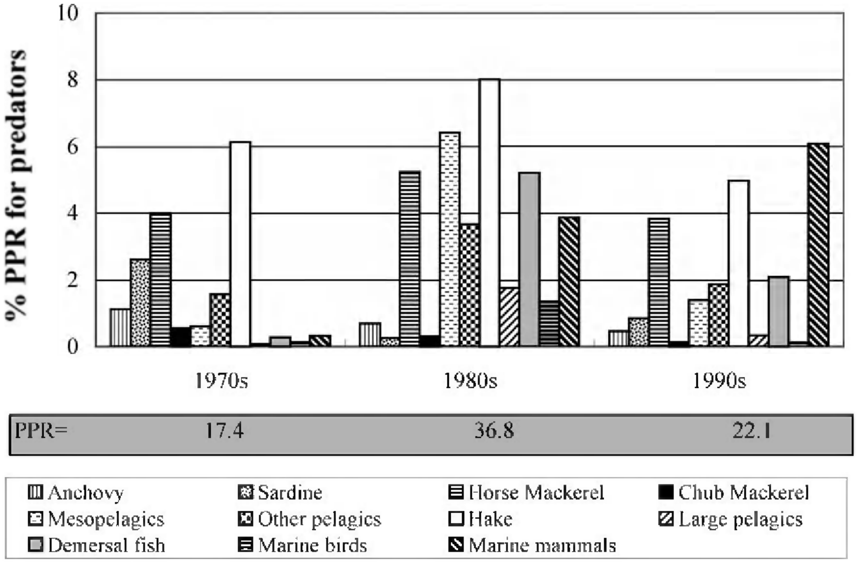

Fig. 5. The percentage of primary production required (%PPR) to sustain the predators of the northern Benguela ecosystem for the three decades.

is higher in the 1990s (Fig. 5). The percentages of total PPR needed to support the catches during the three decades are shown in Fig. 6. The higher total PPR for the fishery in the 1980s (5.7 tonnes km^{-2} per year) reflects the higher landings in that decade (Table 8), while the lower PPR for the fishery in the 1990s (4.3 tonnes km^{-2} per year) is also observed in the lower catches in that time period. However, the PPR for the fishery in the 1970s (4.9 tonnes km^{-2} per year) is still lower than that of the 1980s, even though the total catch was similar (Fig. 3; Table 8).

4.2. Total system indices

The total system indices include summary statistics such as the trophic level of the fishery, total biomass

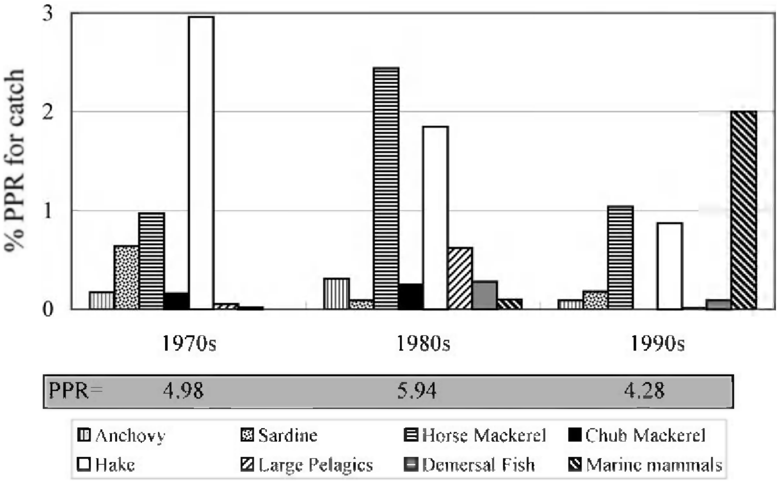

Fig. 6. The percentage of primary production required (%PPR) to sustain the harvest of commercially exploited fish in the northern Benguela ecosystem.

excluding detritus, total consumption, respiration, production, total systems throughput, connectance, and the systems omnivory index (Table 8). The trophic level of the fishery has increased from the 1970s to the 1980s after which it decreased to the 1990s. Total biomass excluding detritus grew from the 1970s to the 1990s, while the net primary production decreased over that time (Table 8). Conversely, total consumption, respiration, production, and consequently throughput was much higher during the 1980s than in either the 1970s or the 1990s (Table 8). The total systems throughput increases with the amount of material flowing through the system (Ulanowicz, 1986; Field et al., 1989), and is a measure of the size of the system (Ulanowicz, 1986). Thus, the total throughput was greatest in the 1980s, and least in the 1990s when total biomass was small. The high total net primary production in the 1970s is reflected in the high net systems production. Similarly, the higher net systems production in the 1990s is also due to the higher primary production (Table 8). The higher net primary production in the 1980s and the high zooplankton turnover rates are reflected in the high total systems throughput in the 1980s model.

The connectance of a foodweb is the number of connections in the ecosystem as a proportion of the total possible trophic connections (Ulanowicz, 1986). It has a strong bearing on the upper limit of the growth of a system and it includes feeding on detritus (Christensen and Pauly, 1992). The connectance index (C.I. in Table 8) increases from the 1970s to the 1990s, while the systems omnivory index was highest in the 1980s and lowest in the 1990s (Table 8). The systems omnivory index is the average group omnivory index weighted by the logarithm of total food consumption and an alternative to the connectance (Christensen and Pauly, 1992).

Other total systems indices used to compare the ecosystem over time include the Finn Cycling Index, mean path length, ascendency, development capacity, and systems overhead.

The Finn (1976) cycling index (FCI) is defined as the recycled fraction of an ecosystem's throughput. The FCI was shown to be an indication of the recovery time of the ecosystem by developing routes for nutrient conservation (Vasconcellos et al., 1997). In Ecopath, it is expressed as a percentage of the total flows (Christensen, 1996). The FCI of the 1980s is an order of magnitude larger than that of the 1970s and twice as high as that of the 1990s (Table 10).

Finn's mean path length is similarly related to the recovery time of the ecosystem (Vasconcellos et al., 1997). The mean path length was also higher in the 1980s, again showing that the 1980s ecosystem would likely recover more quickly than the 1970s or 1990s. The predatory cycling index is the percentage of throughput cycled after detritus has been removed (Christensen, 1996). It was very high in the 1980s and 1990s models, although it is about half those values in the 1970s (Table 10). This indicates larger connectance in the 1980s and 1990s than in the 1970s (Table 8).

Ascendency, a measure of the average mutual information in a system, scaled by system throughput, is derived from information theory (Ulanowicz, 1986; Ulanowicz and Norden, 1990). It is a measure of the network's potential for competitive advantage over other network configurations (Ulanowicz, 1986, 1987). The upper limit to ascendency is the development capacity, and the difference between the capacity and the ascendency is system overhead (Ulanowicz, 1986). The systems overhead reflects the system's reserved strength, from which it can draw to meet unexpected perturbations (Ulanowicz, 1986). Thus, a system with high ascendency will be highly developed, and will be very diversified. Conversely, a system with high overhead is more resilient and has strength in reserve (Heymans and Ulanowicz, 2002).

Table 10
Network analysis indices of the northern Benguela ecosystem for the three decades

Parameter	1971–1977	1980–1989	1990–1995
Finn's cycling index (% of total systems throughput)	2.8	22.1	9.5
Predatory cycling index (% of throughput without detritus)	6.3	12.1	11.2
Finn's mean path length	2.3	3.2	2.6
Ascendency (% of capacity)	41.7	23.9	31.7
Overhead (% of capacity)	58.3	76.1	68.3

The overhead and development capacity were highest in the 1980s model, while the ascendancy was highest in the 1970s model (Table 10).

Sensitivity analyses of the three models to input data were conducted, and the models seem relatively robust with regards to input data (Appendix A).

5. Discussion

The dominant species in the northern Benguela ecosystem changed over time. The dominant pelagic fish in the 1980s and 1990s was horse mackerel (Table 6), while in the 1970s the biomass of sardine was as high as that of horse mackerel and the biomass of anchovy was still relatively high (Table 7). Additionally, the effective trophic level of the pelagic species also changed: The effective trophic level of anchovy and sardine increased over time (Table 9), indicating that they now seem to feed higher in the foodweb than in the 1970s and 1980s. In the 1990s, anchovy and sardine consumed large proportions of zooplankton (James, 1988), whereas in the 1970s and 1980s, it is believed that phytoplankton may have been more important in their diet (King and Macleod, 1976). Conversely, some of the secondary consumers, such as chub mackerel, large pelagics, hake, demersal fish, and marine birds now appear to feed lower in the foodweb than in previous decades (Table 9).

These differences between decades could be due to the effective trophic levels of the species being dependent on diet compositions estimated from available data for the three decades. One species that was important in the diet composition of fish is zooplankton. An order of magnitude increase in zooplankton over the three decades from 15 tonnes wet weight km^{-2} per year in the 1970s to 147 tonnes wet weight km^{-2} per year in the 1990s (Table 8) is largely due to an increase in the observed jellyfish biomass from the earlier decades to the 1990s, and uncertainties about turnover rates pertaining to this group. Data on the abundance of gelatinous plankton were patchy at best, with King and O'Toole (1973) reporting gelatinous zooplankton for the fist time in the 1970s, although no indication of abundance was available until a study by Fearon et al. (1992). A more comprehensive study on jellyfish abundance in the northern Benguela was made in 1997 and 1998 by Spark et al. (2001) but their study falls outside the timeframe of these models. The lack of relevant reliable data on gelatinous plankton for the periods in question forced their inclusion in the zooplankton compartment, although it would be interesting to study the effect of these predators further (Spark et al., 2001).

The comparison of total annual zooplankton production (as the product of biomass and annual productivity), which in part remedies this uncertainty, yielded the highest value for the 1980s, and the lowest value for the 1970s. The higher production of zooplankton in the 1980s would be necessary to sustain the higher biomass of fish (Fig. 2) in that decade, and is reflected in the higher PPR for the predators and the fishery (Figs. 5 and 6), as well as the higher production of fish in the 1980s (Table 8).

The fractions of PPR to sustain the predators are highest for most groups in the 1980s, with the exception of anchovy, sardine, and chub mackerel, which are higher in the 1970s, and marine mammals, which is higher in the 1990s (Fig. 5). This is an indication of the high biomass of anchovy and sardine in the 1970s and the reduced biomass (Fig. 2) of these species in the 1980s and 1990s. Similarly, the reduced fraction of PPR to sustain the predators of all the commercially important fish in the 1990s is due to the low biomass of those groups, with only hake and horse mackerel still maintaining relatively high biomass in the 1990s (Fig. 2). During the 1980s, mesopelagics, small pelagics, horse mackerel, and hake were more abundant (Fig. 2) and therefore greater proportions of total primary production were required to sustain their consumption (Fig. 5). Despite lower abundance in the 1990s than in the 1980s (Tables 3 and 6), PPR to sustain seals was higher during the 1990s (Fig. 5), because their abundance was higher relative to that of their prey and they fed at higher trophic levels during that time (Table 9). However, hake occupied a slightly lower trophic level (Table 9) and was less abundant in the 1990s, which explains the lower fraction of PPR to sustain hake (Fig. 5).

Over the three decades, the total catch also increased from the 1970s to the 1980s, after which it decreased in the 1990s (Fig. 3). The increase in catch from the 1970s to the 1980s of horse mackerel, which has a higher effective trophic level (Table 9), and the decrease in anchovy and sardine catches in the 1980s compared to the 1970s, are reflected in the higher trophic level of the fishery in the 1980s (Table 8). Similarly, the increase in sardine catches in the 1990s compared to the reduction in total catches is reflected in the lower mean trophic level of the fishery in the 1990s compared to the 1980s (Table 8). The fishery was also less efficient in the 1990s than in the two previous decades, and it operated at the highest trophic level during the 1980s (Table 8).

Pauly et al. (1998) showed that in many aquatic ecosystems, there has been an increase in recent decades in the proportion of catches taken from lower trophic levels. This trend has been termed "fishing down the foodweb." The northern Benguela ecosystem shows some indications of "fishing down the foodweb," with the trophic level of the fishery decreasing from the 1980s to the 1990s (Table 8). This is in contrast to what has been found for the southern Benguela ecosystem, where fishing was at a slightly higher trophic level in the 1990s than in the 1980s (Shannon, 2001).

The inefficient transfer of energy from one trophic level to the next causes the exploitation of fish at lower trophic levels to be less expensive in ecological terms than those at higher trophic levels (Jarre-Teichmann, 1998). The lower PPR for the fishery in the 1970s (Fig. 6) corresponds to the lower trophic level of the fishery in the 1970s than in the 1980s. Fig. 3 also reflects the increased fraction of horse mackerel and hake in the total catch of the 1980s, which have higher trophic levels, and are therefore more expensive in ecological terms, as shown in the higher PPR for the fishery in that decade. Although the PPR for the fishery in the 1990s is much lower than in the previous decades, it is still quite large (Fig. 6) compared to the relatively low catch (Fig. 3). This is a consequence of the different diet compositions used in the periods modeled, in particular those of anchovy and sardine (Tables 2, 4, and 7) as well as the higher relative importance of horse mackerel and hake in the total catch during the 1990s (Fig. 3).

In addition to high predator biomass and total catch in the 1980s, the 1980s model also had the highest total systems throughput, omnivory index (Table 8), FCI, Finn's mean path length, and systems overhead (Table 10). The high omnivory index indicates that the ecosystem was more web-like (with many different paths along which the energy could be transferred up the foodweb) and therefore stable during the 1980s (Christensen and Pauly, 1992). The high FCI (Table 10) observed in the 1980s is due to the large amount of recycling which is an indication of systems maturity (*sensu* Odum, 1969) and that the system's recovery time was quicker than in any other decade (Vasconcellos et al., 1997). The high overhead in the 1980s again confirms the system's stability and resilience and indicates that the system was in a state of diverse interaction.

In contrast to the 1980s, which seems to be most diverse and connected, the 1970s model has the least number of trophic connections. Even though the predator biomass is not the lowest in the 1970s, the total biomass excluding detritus is the lowest of the three periods modeled. However, the net production and net primary production is the highest in the 1970s model (Table 8). Another indication of low trophic connection in the 1970s is the high flow to detritus, which is reflected in that decade having the lowest Finn cycling index and the highest ascendency. The high ascendency in the 1970s indicates a state of severe channeling during that time, where energy flowed largely through only a few links, and very few alternative routes of energy flow were available. This again is due to the low connectance in the system, which led to the high flow to detritus, and a low Finn path length (Table 10). The low connectance but higher omnivory index in the 1970s compared to the 1990s is probably due to the low dependence on and connectance to detritus (i.e. detritivory) during the 1970s, while detritivory was estimated to have been higher in the 1990s.

Even though the throughput, predator biomass and omnivory index were lowest in the 1990s, that model seems to be situated between the 1980s and the 1970s on the stability and resilience ladder. The FCI and overhead is higher than that of the 1970s, but still lower than those of the 1980s. The reduction of the FCI and overhead from the 1980s to the 1990s is likely to make the system more susceptible to stress-induced changes. The smaller resilience (small system overhead, Table 8) in the 1990s compared to that of the 1980s could be due to overfishing, "fishing down the foodweb" *sensu* Pauly et al. (1998) and the physical constraints of the system, which was under a severe Benguela Niño in 1995.

In the 1990s, the biomass of pelagic fish decreased substantially due to the southward advection of oxygen poor water in 1994 that was combined with sulfur eruptions and a Benguela Niño event in 1995 (Gammelsrød et al., 1998). The 1995 Benguela Niño comprised a warming of the coastal waters off the northern Benguela down to Lüderitz due to the intrusion of warm Angolan Current water (Gammelsrød et al., 1998). These events caused high starvation-induced mortalities of adult seals due to high pelagic fish mortality. The starvation of the adult seals also caused seal pup mortalities and there was recruitment failure of sardine and anchovy by the end of 1995.

Benguela Niños occurred in 1963 and 1984 as well as in 1995 (Gammelsrød et al., 1998). However, no Benguela Niños occurred between 1971 and 1977, although a cooling event was recorded in 1970 (Tauton-Clark, 1990). Subsequent to the 1984 Benguela Niño, summer phytoplankton and zooplankton densities were on average four times lower than during the summer of 1982–1983, but this was counteracted by a warming event in 1986, which was reported to have improved the survival of eggs and larvae for some pelagic species (Gammelsrød et al., 1998). In contrast, the time period modeled in the 1990s only included 1995, and no data thereafter. Thus, a recovery of the ecosystem post-1995 was not included in this model, which may explain the reduced resilience and stability in the 1990s model compared to the earlier models.

The increase in jellyfish biomass, with the reduction in zooplankton production (Table 8) could also be a reason for the lack of resilience in the system, because jellyfish are not consumed as widely as other planktivores. All energy that flows to jellyfish, therefore, would probably flow directly to detritus, thereby channeling energy back to the primary producers. This is also noticeable in the lower transfer efficiencies between the trophic levels in the 1990s (Fig. 4), compared to those of the 1980s or 1970s. The lower transfer efficiencies in the 1990s indicate that the system is not as effective at delivering energy up the foodweb as it was in the 1970s or the 1980s.

6. Summary

The northern Benguela ecosystem has undergone some dramatic changes over the past three decades. In the 1970s, the system sustained high catches, and had large populations of a few planktivorous fish (mainly anchovy and sardine). In the 1980s, the planktivorous fish species expanded (anchovy, sardine, horse mackerel, mesopelagic fish, and other small pelagics) and catches remained high. Transfer efficiencies to higher trophic levels were highest during the 1980s. Finally, in the 1990s, the system was more stressed, catches were lower and omnivory was reduced. In the 1990s, most of the energy flowed through few pathways, and the energy was not transferred as efficiently up the trophic chain as in the 1980s.

The structure of the ecosystem also changed. Anchovy and sardine were the dominant planktivores in the 1970s, while horse mackerel, mesopelagics, and other small pelagics dominated in the 1980s. The dominance of horse mackerel continued in the 1990s with a small increase in sardine during that time. The increase in sardine catches in the 1990s compared to the reduction in total catches is reflected in the lower mean trophic level of the fishery in the 1990s. The fishery operated at the highest trophic level during the 1980s and there are some indications of "fishing down the foodweb" in this ecosystem between the 1980s and the 1990s.

The trophic levels of some of the key species in this ecosystem have changed over the past three decades. Anchovy and sardine fed at higher trophic levels in the 1990s than in the previous two decades, while some of the secondary consumers, such as chub mackerel, large pelagics, hake, other demersals, and marine birds fed lower in the foodweb than in previous decades. Catches decreased marginally from the 1970s to the 1980s, but then more noticeably in the 1990s, due to both natural effects such as Benguela Ninos and strong fishing pressure.

This is reflected in less PPR to sustain the fishery in the 1990s. The high catches of sardine and hake in the 1970s are reflected in the high PPR by those compartments. The high catches of horse mackerel in the 1980s are shown by the high PPR for horse mackerel. The overall PPR for the fishery was highest in the 1980s, when the system was fished at nearly the same intensity as the 1970s, but the species taken were from higher trophic levels, requiring larger concentrations of primary production for their own existence.

The northern Benguela ecosystem increased dramatically in biomass, throughput, systems omnivory and resilience in the 1980s, probably due to favorable environmental conditions before and after the 1984 Benguela Niño. The system was however, severely depleted in the 1990s, probably due to both overfishing and environmental changes. These changes are seen in the reduced PPR to support the catches and predators and in the reduced cycling and overhead in the 1990s. The importance of ecosystem–environmental interactions are highlighted by the abundance of horse mackerel, mesopelagics, small pelagics, and hake in the 1980s and the reduced biomass of most species in the 1990s, not only due to overfishing, but also due to the Benguela Niño in 1995. This aspect warrants further investigation using dynamic simulations (Ecosim) with respect to environmental and fisheries forcing, and may well be possible in the near future given the recent availability of newly analyzed catch data (Willemse, 2002).

In conclusion, the northern Benguela ecosystem seems to have gone through various anthropogenic and physical changes over the past three decades. It changed from a structured, channel-like ecosystem in the 1970s, when anchovy and sardine were the most important planktivores, and hake was important as a predator, to a system of large resilience during the 1980s. Finally, in the 1990s, the system's resilience was lower, but its connectance was higher; sardine was making a comeback and the marine mammals were doing well until the Benguela Niño reduced the system to a state of lower maturity.

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Appendix A. Sensitivity analysis

The sensitivity of ecosystem models to input data is always of concern. Some sensitivity analyses were therefore done on the three models, to see if changes in input data (viz. the changes made while re-organizing the models for comparison purposes) would affect the results obtained in this study. As the data available for the 1980s model was the most complete, most of the changes were made to the 1970s and 1990s models. Four different scenarios were run for the 1970 model:

(1) The model was rerun with the original *P*/*B* ratio for zooplankton (65 per year);
(2) The model was also rerun with the original *P*/*B* ratio for phytoplankton (250 per year);
(3) The diet of zooplankton was changed to be similar to their diet in the 1980s (59.6% phytoplankton, 13% zooplankton, and 27.4% detritus). This diet was not 100% the same as that used in the 1980s and 1990s models, as it had to be adapted slightly to balance the model;
(4) The *P*/*B* and *Q*/*B* ratios of anchovy and sardine were changed to be more similar to those obtained in the other two models (anchovy: $P/B = 1.9$ per year, $Q/B = 12$ per year and sardine: $P/B = 1.2$ per year, $Q/B = 12.4$ per year). As in scenario 3, the *P*/*B* and *Q*/*B* ratios were not identical to those used in the other two models, as they had to be adapted to balance the model. The *P*/*B* ratio of anchovy in particular was required to be substantially higher than the values used in the 1980s and 1990s model, in order that anchovy production was sufficient to sustain estimated catches and consumption during that time.

Three different scenarios were run for the 1990 model:

(5) The addition of benthic producers, meiobenthos, macrobenthos and chub mackerel to the 1990s model were done by using similar biomasses as those obtained for the 1980s. The effect of this was tested by removing their biomass estimates, and using ecotrophic efficiencies of 0.5 each for these groups;
(6) The *P*/*B* ratio of horse mackerel was reduced to 0.58 per year (which is similar to that of horse mackerel in the other two models, but again not

Table A.1
Sensitivity analyses results: summary statistics, ascendency, overhead, development capacity, and cycling indices for 1970s, 1980s, and 1990s models as well as the seven sensitivity scenarios (see text for details)

Indices	1970s	Scenario 1	Scenario 2	Scenario 3	Scenario 4	1980s	1990s	Scenario 5	Scenario 6	Scenario 7
Sum of all consumption	3214	5464	3214	3214	3179	11743	4477	4556	4477	4419
Sum of all exports	6124	5112	52046	6124	6151	1021	4452	4420	4450	4499
Sum of all respiratory flows	1550	2563	1550	1550	1524	6070	1731	1772	1734	1684
Sum of all flows into detritus	6555	5722	52476	7064	6580	3973	5591	5629	5589	5638
Total system throughput	17443	18861	109286	17952	17434	22806	16251	16378	16249	16240
Sum of all production	8264	8714	54185	8264	8263	9808	7379	7397	7376	7379
Mean trophic level of the catch	2.85	2.85	2.85	2.87	2.85	3.25	3.1	3.1	3.1	3.1
Gross efficiency (catch/net p.p.)	0.0009	0.0009	0.0001	0.0009	0.0009	0.0009	0.0006	0.0006	0.0006	0.0006
Calculated total net primary production	7675	7675	53596	7675	7675	7091	6183	6192	6183	6183
Total primary production/total respiration	4.95	3.00	34.57	4.95	5.04	1.17	3.57	3.49	3.57	3.67
Net system production	6124	5112	52046	6124	6151	1021	4452	4420	4450	4499
Total primary production/total biomass	27	27	190	27	27	20	16	16	16	16
Total biomass/total throughput	0.016	0.015	0.003	0.016	0.016	0.016	0.023	0.024	0.023	0.023
Total biomass (excluding detritus)	282	282	282	282	282	361	381	387	381	381
Total catches	6.555	6.555	6.555	6.555	6.555	6.652	3.441	3.441	3.441	3.441
Connectance index	0.258	0.258	0.258	0.258	0.258	0.285	0.301	0.301	0.301	0.301
System omnivory index	0.152	0.152	0.152	0.164	0.151	0.172	0.117	0.111	0.117	0.122
Total market value	6.56	6.56	6.56	6.56	6.56	6.65	3.44	3.44	3.44	3.44
Ascendency	41.7	35.9	74.9	39.1	42.1	24.1	31.7	31.1	31.7	32
Overhead	58.3	64.1	25.1	60.9	57.9	75.9	68.3	68.9	68.3	68
Capacity	46512	55287	155569	48410	46028	68922	46794	48314	46788	46003
Throughput cycled (excluding detritus)	274	499	274	353	274	1766	567	568	567	567
Predatory cycling index	6.32	6.73	6.32	9.22	6.41	12.12	11.19	11.09	11.18	11.42
Throughput cycled (including detritus)	56	54	59	42	56	33	37	36	37	36
Finn's cycling index	2.82	4.86	0.42	4.73	2.83	23.03	9.50	9.63	9.50	9.64
Finn's mean path length	2.27	2.46	2.04	2.34	2.27	3.26	2.63	2.65	2.63	2.63
Finn's straight-through path length without detritus	2.61	2.69	2.61	2.23	2.61	2.11	2.60	2.56	2.59	2.61
Finn's straight-through path length with detritus	2.21	2.34	2.03	2.23	2.21	2.51	2.38	2.39	2.38	2.37

the same, as the model had to be re-balanced); and finally

(7) The *Q*/*B* of hake was reduced from 20 to 4 per year, to be similar to those obtained in the two other models.

The summary statistics, ascendency, overhead, development capacity, and cycling indices of all seven of these scenarios, as well as those of the three unchanged models, are given in Table A.1.

Scenario 1 did increase the sum of all consumption and sum of all respiration, as well as the development capacity of the 1970s model to values higher than those obtained for the 1990s, which subsequently reduced the total primary production/total respiration ratio to lower than that obtained for the 1990s. Similarly, in scenario 2, the total systems throughput, total production, and development capacity in the 1970s model was higher than that of the 1980s model, while the gross efficiency was much lower than any of the other two models. Scenario 3 only increased the development capacity marginally, although it was now higher than that of the 1990s model, whereas for the original 1970s model, it was lower, and the Finn's straight-through path length (without detritus) was lower than that of the 1980s model. Scenario 4 did not cause any changes that affected any of the systems indices or their interpretations. Changes made to the 1990s model had less of an impact on the interpretation than the changes made to the 1970s model. Scenarios 5 and 6 did not affect the interpretation at all, while scenario 7 decreased the development capacity of the 1990s model to marginally lower than that of the 1970s model.

Only one of these scenarios, namely scenario 2 in which phytoplankton *P*/*B* was changed back to the original (much higher) value of the 1970s model, seems to be sensitive in terms of overall systems resilience (overhead). Scenarios 1, 2, and 3 showed that system maturity (FCI) may be sensitive to parameter values for phytoplankton and zooplankton in the 1970s model. However, in no instance did any of the changes made to the ecosystem parameters drive the overhead or FCI to be so different that it would change the interpretation of the results. The overhead and FCI of the 1970s scenarios were always lower than those of the 1980s or 1990s models. Similarly, the overhead and FCI of the 1990s scenarios were never lower than that of the 1970s or higher than that of the 1980s.

Finally, it was not possible to test changes in the marine mammal diet without extensive changes to the models to re-balance them. Thus, the sensitivity of the models to the consumption by marine mammals was tested by calculating the total consumption of each group and the proportion of fish consumed by marine mammals. In the 1980s model, marine mammal consumption is about 1% of the total consumption by predators, and marine mammal consumption of fish is 4% of the total fish production consumed by predators in the system. These ratios are reduced to 0.2 and 0.4%, respectively, in the 1990s and 0.002 and 0.3% in the 1970s models. These values include the export of prey and all interactions that include detritus. Thus, very different diet compositions of marine mammals during the three models are unlikely to effect the overall indices as consumption my mammals is very small. It is also improbable that the diet would be similar over the three time periods, as the abundance of the different fish species have changed and marine mammals are generalists that would feed on whatever is available.

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