COMPARING TROPHIC FLOWS IN THE SOUTHERN BENGUELA TO THOSE IN OTHER UPWELLING ECOSYSTEMS

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A balanced trophic flow model of the southern Benguela ecosystem is presented, averaging the period 1980–1989 and emphasizing upper trophic levels. The model is based largely on studies conducted within the framework of the Benguela Ecology Programme and updates the results of an expert workshop held in Cape Town in September 1989. Small pelagic fish other than anchovy *Engraulis capensis* and sardine *Sardinops sagax,* mainly round herring *Etrumeus whiteheadi* and mesopelagic fish, were important components of the food web in the southern Benguela. Severe balancing difficulties were encountered with respect to the semi-pelagic resources (hake *Merluccius* spp.) and demersal top predators (sharks), indicating the need for further research on the interaction of these groups with their ecosystem. The model is compared to other existing trophic flow models of ecosystems in major upwelling areas, i.e. the northern Humboldt Current (4–14°S), the California Current (28–42°N) and the southern Canary Current (12–25°N), and to two independently constructed models of the northern Benguela ecosystem. These models are compared using network analysis routines of the ECOPATH software, focusing on the interactions between the five dominant fish species (anchovy, sardine, horse mackerel *Trachurus trachurus capensis*, chub mackerel *Scomber japonicus* and hake) that support important fisheries in all systems. The upwelling systems rank by size rather than species dominance. The ratio of catches and primary production differs between systems, partly because of differences in fishing regimes. Predation on the five dominant fish groups by other fish in the system was the most important cause of fish mortality in all models. Fishery catches are generally a larger cause of mortality for these groups than predation by mammals. The ecological cost of fishing appears to be comparatively low in the southern Benguela, because catches are low compared with the primary production, but also because the fishery is relatively low in the foodweb. However, in view of the very tight foodweb demonstrated in the model, it is likely that an increase in fishing pressure would cause severe trade-offs with respect to other components of the southern Benguela ecosystem.

Four large coastal upwelling areas are created by eastern boundary currents along the west coasts of Africa and the Americas (Fig. 1). Upwelling regions are strongly influenced by the physical environment, which provides the nutrient-rich, bright-light conditions necessary for productive plant growth. The primary production fuels secondary production, and the great productivity of upwelling areas is evidenced by their accounting for about 38% of the marine primary production (Longhurst *et al.* 1995), and sustaining more than 30% of the world's catch of marine fish (F.A.O. 1996). Upwelling regions are characterized by similar species groupings in the marine pelagic communities (Cushing 1971, Bakun and Parrish 1981). It is therefore interesting to ask whether the dynamics of the ecosystems are also similar, or whether ecological processes differ among the systems. Given such understanding, possible impacts of changes in the ecosystems, e.g. through climate change or different

fishing regimes, could be assessed in a better way than is possible to date.

Mass-balance trophic flow models summarize information about the components of ecosystems and their functioning, and such models can be used to compare ecosystems (Jarre *et al.* 1991, Christensen and Pauly 1993, Jarre-Teichmann 1998). Such trophic flow models were developed for four ecosystems in upwelling areas, namely off northern and central Peru in the Humboldt Current (4–14°S), off California and Oregon in the California Current (28–42°N), south of Cape Blanc in the Canary Current (12–25°N) and the northern Benguela ecosystem (17–28°S, Jarre-Teichmann and Christensen in press). The models were based on documented information covering different periods from the mid-1960s to the early 1980s, corresponding to dominance regimes of small pelagic fish: anchovy, sardine or horse mackerel. Care was taken to construct them in the

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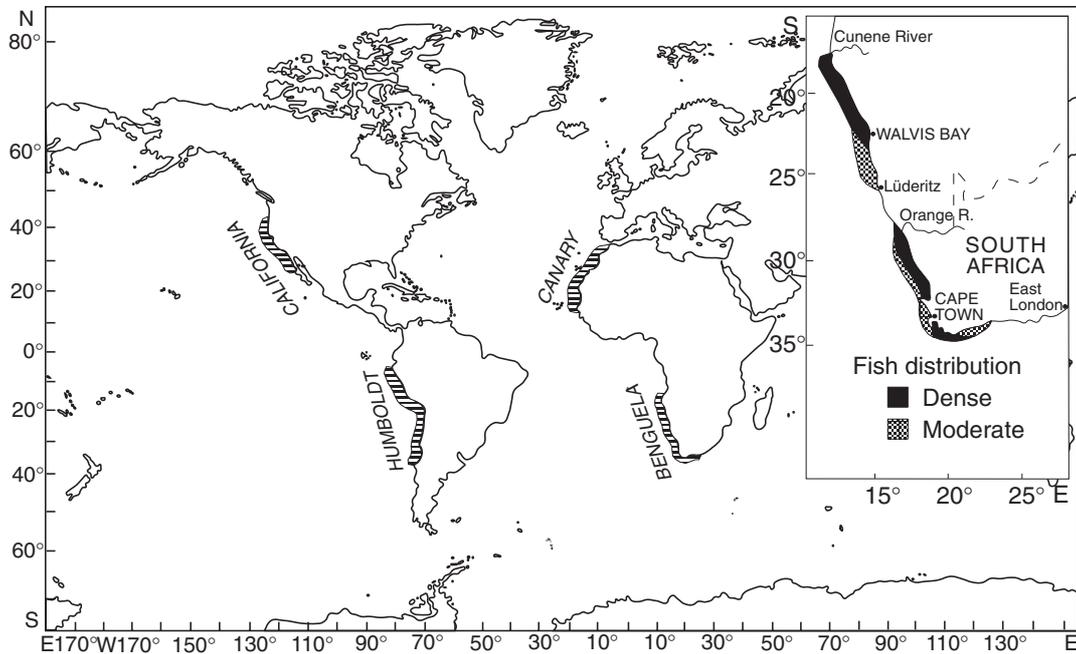
Fig. 1: Global distribution of the major upwelling areas modelled, with details of the Benguela upwelling system

same way, so that they could be compared readily, and balancing and comparison were carried out using the ECOPATH software package (Christensen and Pauly 1992, 1995).

The entire Benguela extends from Angola at 15°S, around the southern tip of the African continent, to the Agulhas Bank and farther east to about East London (28°E). It is divided into northern and southern subsystems by a strong upwelling centre off Lüderitz (25–27°S, Fig. 1). The northern and southern systems cover areas of some 179 000 and 220 000 km² respectively.

In the framework of the Benguela Ecology Programme, major data series on both the northern and southern Benguela ecosystems for the decade 1980–1989 were compiled and analysed. An attempt was undertaken in 1989 to summarize this knowledge into ecosystem spreadsheet models. Experts working on different species groups in the Benguela region were brought together in a workshop in Cape Town in September 1989, where the spreadsheet models were discussed, tested and refined. Subsequent to the workshop, the data from many of the species groups were modified and published (e.g. Armstrong *et al*. 1991, Brown *et al*. 1991, Hutchings

et al. 1991). In this paper, the aim is to incorporate these modified data into the spreadsheet model, and therefore to present a preliminary ecosystem model for the southern Benguela ecosystem for the decade 1980–1989. The paper further aims to compare the results from the southern Benguela model to those from the other four upwelling systems.

MATERIAL AND METHODS

In order to be comparable with the models already constructed (Jarre-Teichmann and Christensen in press), the major biotic components of the southern Benguela were grouped into functionally similar groups. In all, 19 categories were identified in the ecosystem. For migratory species, such as chub mackerel *Scomber japonicus* and tunas, biomass and consumption estimates were adjusted to account only for the periods they spend in the southern Benguela.

Information for the flow budgets was obtained mainly from published data, most notably from works emanating from the Benguela Trophic Functioning Symposium (Payne *et al*. 1992). Where information

was not readily available, best-guess estimates were obtained from unpublished data or personal communications.

Considering average ("steady state") conditions over an appropriate period of time, trophic interactions between the components of an ecosystem are described by a set of linear equations, wherein the production of each component equals its consumption by other components in the system (predation), its export from the system (by fishing or emigration) and a baseline mortality:

Production by (i) = All predation on (i) + Non-predatory biomass losses of (i) + Fishery catches of (i) + Other exports of (i).

The terms in this equation can be replaced by

Production by (i) = $B_i \times P/B_i$

Predatory losses of (i) = $\sum_j (B_j \times Q/Bj \times DC_{j,i})$

Other losses of (i) = $(1 - EE_i) \times B_i \times P/B_i$,

and this leads, for any component in the system, to

$$B_i \times P/B_i \times EE_i - \sum_j (B_j \times Q/B_j \times DC_{j,i}) - Ex_i = 0 \quad ,$$

where i indicates a component (stock, species, species group) of the model,

j is any of the predators of i,
B_i is the biomass of i,
P/B_i is the production of i per unit of its biomass (= total mortality under steady-state conditions),
Q/B_i is the consumption of a component per unit of its biomass,
$DC_{j,i}$ is the average fraction of i in the diet of j (in terms of mass),
EE_i is the ecotrophic efficiency of i (the fraction of the total production consumed by predators or exported from the system),
Ex_i is the export of i from the system (e.g. by emigration or fishery catch).

The energy balance of each component is given by

Consumption = Production + Respiration + Non-assimilated food,

where consumption includes that within the system as well as consumption of imports (i.e. consumption "outside the system"), and production may be consumed by predators, exported from the system or be a contribution to detritus.

This structure defines the necessary parameters for the model. As a property of a system of linear equations, one of the parameters of biomass, *P/B* ratio, *Q/B* ratio or ecotrophic efficiency may be unknown for

each of the components. The unknown parameter, along with the respiration of that component, is estimated when solving the system. If an acceptable result is reached from the inputs for each of the unknowns, the model is considered balanced and can be analysed further. The ECOPATH approach (Christensen and Pauly 1992, 1995) was used for this purpose.

Description of the model of the southern Benguela ecosystem, 1980–1989

Biomass estimates were expressed in wet mass where available. If information was provided in units of carbon, a global correction factor of 14.25 was used. This value lies between 10 and 17.2, the lower and upper limits estimated by Cushing (1971) and Ryther (1969) respectively. Bacteria were not represented in the model, because insufficient information on bacterial activity is available from the other upwelling areas. Therefore, all consumption of bacteria, and their activity, is "hidden" in the detritus box.

PHYTOPLANKTON

Brown *et al*. (1991) used all available data from the southern Benguela to derive the current best estimates of mean phytoplankton biomass and average annual primary production. Estimates for the West Coast and the Agulhas Bank from that study were combined here into one estimate for the southern Benguela. Biomass was estimated as 1.2×10^6 tons C and *P/B* as $154.4 \cdot \text{year}^{-1}$.

Sedimentation rates were obtained from sediment trap measurements, and presented as a constant fraction of net production by Brown *et al*. (1991). Total sedimentation was estimated to be 5.7×10^6 tons C, i.e. 3.1% of primary production. Although the upwelling source water is enriched by nutrients sequestered from the organic-rich sediments (e.g. Bailey 1987), this process takes place only after decomposition of the organic sediment derived from the pelagic zone. As the currency of the model is wet mass, not nutrients, these sedimentation losses were assumed to be exported from the system.

MICROZOOPLANKTON

This category consists of organisms in the size range 2–200 μm equivalent spherical diameter, including nanoflagellates, ciliates and larval stages of many zooplankton. The information was derived from data presented in Brown *et al*. (1991) and Painting *et al*. (1992). Mean biomass concentrations were

given as 6.3 mg·m⁻³ for the West Coast and 10.7 mg C·m⁻³ for the Agulhas Bank. Assuming an average water depth of 45 m in the productive region, and that the area of the Agulhas Bank is approximately 53% that of the southern Benguela (Brown *et al*. 1991), this is equivalent to a total of 8.5×10^4 tons C for the southern Benguela. Productivity was weighted according to the relative contributions of flagellates and ciliates in the microzooplankton size fraction, the relative biomasses and the relative sizes of the total areas, and *P/B* was estimated to be 482·year⁻¹.

The proportion of unassimilated food for microzooplankton was assumed to be 20% (Stoecker 1984). By definition:

Growth Growth Efficiency (*GGE*) = (Consumption – Respiration) / Consumption.

The *GGE* for microzooplankton was estimated to be 40% (Painting *et al*. 1992), which gives a respiration/consumption ratio of 60%.

Dietary information was not available for microzooplankton in the Benguela system. Consequently, it was assumed that microzooplankton were opportunistic feeders, ingesting small phytoplankton, bacteria and other microzooplankton in approximately equal proportions.

MESOZOOPLANKTON

Mesozooplankton include organisms in the size range 200–2 000 μm, which, in the Benguela, are mainly copepods. Information was obtained from Hutchings *et al*. (1991), who gave a biomass estimate of 187 600 tons C, a *P/B* of 20·year⁻¹ and gross food conversion efficiency, i.e. the ratio of production to consumption, (referred hereafter as gross efficiency) of 30% for copepods in the southern Benguela. The fraction of non-assimilated food was assumed to be 35%. Phytoplankton and microzooplankton are considered to be eaten in equal proportions (50%) by mesozooplankton (Hutchings *et al*. 1991).

MACROZOOPLANKTON

Macrozooplankton include organisms in the size range 2–20 mm. In the Benguela, most of the data for this size range was derived from euphausiids (Hutchings *et al*. 1991), although other groups such as chaetognaths and fish larvae may also be important. Hutchings *et al*. (1991) considered a biomass of 63 600 tons C, a *P/B* of 13·year⁻¹ and a gross efficiency of 41% to be appropriate for macrozooplankton in the southern Benguela. The fraction of non-assimilated food was assumed to be 35%. The diet of macrozooplankton is considered to be 60% phyto-

plankton and 40% mesozooplankton (Hutchings *et al*. 1991).

SALPS AND JELLYFISH

There is very little information on salps and jellyfish in the Benguela, but they are believed to be a potentially important component of the system (e.g. Gibbons 1997). Biomasses for the southern Benguela, determined from Bongo net catches are estimated to be 55×10^6 tons (A. J. Boyd, Sea Fisheries [SF], pers. comm.), but other observations (L. Hutchings, SF, pers. comm.) suggest that the average biomass is much lower, probably in the range of 10–50% of the combined meso- and macrozooplankton biomass, at about 10^6 tons wet mass. This lower estimate was used in the current calculations. If it is assumed that these organisms comprise 98–99% liquid, and a conversion of 0.4 from dry mass to carbon (Peters 1984) is used, a biomass of 6 300 tons C is calculated. The *P/B* for salps and jellyfish (in terms of tissue) was assumed to be half that of macrozooplankton, i.e. 6.5·year⁻¹. All remaining parameters were assumed to be the same as for macrozooplankton. Assuming that water does not need to be produced, production was computed as 6.5·year⁻¹ × 6 300 tons (= 40 950 tons C·year⁻¹), corresponding to 5.8×10^5 tons wet mass·year⁻¹ by average conversion, yielding a *P/B* of 0.584·year⁻¹. Assuming a gross efficiency of 41%, *Q/B* was estimated to be 1.42·year⁻¹. Jellyfish diet was assumed to be composed of equal proportions of four plankton categories in the carbon budget: 25% each of phytoplankton, bacteria (detritus), microzooplankton and mesozooplankton.

COMBINED ZOOPLANKTON BOX

To allow for comparisons with previous ecosystem models, the above-mentioned four zooplankton categories were combined into one single zooplankton box. The combined estimates were computed as biomass = 26.3×10^6 tons wet mass, *P/B* = 112.46·year⁻¹ and *Q/B* = 440.37·year⁻¹. The weighted diet composition resulted in 40.9% phytoplankton, 21.9% microzooplankton, 0.5% mesozooplankton and 36.7% detritus. It was noted that consumption was dominated by the dynamics of the microzooplankton, which accounted for 84% of the total consumption by the combined zooplankton group.

ANCHOVY

Anchovy *Engraulis capensis* biomass in the southern Benguela was estimated to be 1 106 000 tons for the period 1984–1988 (Armstrong *et al*. 1991). However,

a biomass estimate of 1 147 500 tons was used here, based on updated (1984–1989) acoustic estimates (M. Barange, SF, pers. comm.). Productivity was considered to be 1.2·year^{-1}, the same value as estimated for the northern Benguela (Hewitson and Cruickshank 1993). A *Q/B* of 12.3·year^{-1} was calculated from Armstrong *et al*. (1991), yielding a gross efficiency of 9.75%. Diet composition was estimated at 5% phytoplankton, 4% microzooplankton, 57% mesozooplankton and 34% macrozooplankton (Armstrong *et al*. 1991). Non-assimilated food was assumed to be 35% of consumption. The mean catch of anchovy for the 1980s was estimated to be 346 000 tons (Roel and Armstrong 1991).

SARDINE

Biomass of sardine *Sardinops sagax* in the southern Benguela was estimated at 146 000 tons (Armstrong *et al*. 1991). Revised acoustic estimates indicate a slightly lower estimate of 129 000 tons (M. Barange, SF, pers comm.). Annual productivity was estimated at 1.1·year^{-1} for the northern Benguela (Hewitson and Cruickshank 1993), a value considered appropriate for the southern Benguela. Annual consumption in the southern Benguela was estimated at 127 000 tons C (Armstrong *et al*. 1991). Using the higher biomass estimate of Armstrong *et al*. (1991) with an estimated *P/B* of 1.2·year^{-1} yielded a total annual production of 175 200 tons wet mass. Applying the global conversion factor of 14.25 from carbon to wet mass equates to a gross efficiency of 9.7%, and, correspondingly, a *Q/B* estimate of 11.3·year^{-1}, which was used for the model. Assimilation efficiency was assumed to be 65%, as for other planktivores. The diet composition of sardine was considered to be 33% zooplankton and 67% phytoplankton in the southern Benguela (Armstrong *et al*. 1991), but a consumption of 68% zooplankton and 32% phytoplankton is considered more appropriate (L. Hutchings, pers comm., Van der Lingen 1998). The mean catch of sardine for the 1980s was estimated at 40 800 tons (Roel and Armstrong 1991).

CHUB MACKEREL

Chub mackerel *Scomber japonicus* migrate between the northern and southern Benguela, spending approximately half a year in each region (Crawford and de Villiers 1984). Chub mackerel were heavily fished in the mid-1970s, severely reducing their biomass. Virtual Population Analysis (VPA) estimates are available for the southern Benguela for the period 1954–1983 (O. Centurier-Harris, formerly SF, unpublished data). Based on that VPA, an age-weighted

mean fishing mortality for the years 1971–1982 was estimated to be 0.625·year^{-1}. Biomass in the southern Benguela was subsequently estimated at 98 000 tons from the surplus production equation, with a natural mortality of 0.25·year^{-1} and a *P/B* ratio of 0.5·year^{-1}, similar to that of other predatory fish, such as snoek *Thyrsites atun*. This agrees well with the mean estimate of about 100 000 tons (for the period 1954–1976) calculated for the Western Cape (Crawford 1989). Total biomass averaged at about 18 000 tons for the years after the stock collapse (1978–1983, Crawford *et al*. 1983). It is assumed that the biomass recovered during the 1980s, but that the stock was not as large as before the collapse. Therefore, an estimate of 62 500 tons was used in the model.

Given the heavy fishing pressure on chub mackerel in the 1970s, it is considered that only small and medium-sized mackerel were present in the system during the 1980s. Based on Baird (1978), and weighting by the relative proportions obtained from VPA, the diet composition was estimated to be 81.7% zooplankton, 1.7% anchovy, 0.9% round herring *Etrumeus whiteheadi*, and 15.7% lanternfish. Assimilation efficiency was considered to be 80%.

Gross efficiency was taken to be 10%. Based on the belief that fish were smaller in the 1980s following the collapse, *P/B* was estimated to be higher at 0.6·year^{-1}, yielding a *Q/B* of 6·year^{-1}. The mean catch for the period 1986–1991 was 6 190 tons (Japp *et al*. 1994). The same value is presumed for the entire 1980s, based on Crawford and de Villiers' (1984) estimates for the early 1980s.

HORSE MACKEREL

Historical VPA estimates (Kinloch *et al*. 1986) were used to back-calculate numbers of 0- and 1-year old horse mackerel *Trachurus trachurus capensis*, using a natural mortality of 0.4·year^{-1}. Length-mass relationships were obtained from Kerstan and Leslie (1994). The total biomass was estimated to be 330 000 tons for the period 1975–1983. No major change in biomass was assumed for the 1980s.

P/B was estimated at 0.45·year^{-1} from the surplus production equation, with an *F* value of 0.18·year^{-1}, based on a mean annual catch of 46 691 tons during the period 1975–1983 (Badenhorst 1995) and an *M* value of 0.4·year^{-1}. However, on the assumption of biomass constancy, *P/B* = *F* + *M* = 0.58·year^{-1}. Both estimates are similar to the estimate of 0.5·year^{-1} calculated by Kinloch *et al*. (1986). A mean value of 0.52·year^{-1} was used for *P/B* in the model.

The diet (weighted for a fish length of 20 cm) was estimated to be 97.4% zooplankton, 0.1% cephalopods

Table I: Basic input parameters by species for the large pelagic fish box

Fish species	Biomass (tons)	*P/B* (·year⁻¹)	Gross efficiency (%)	Mean annual catch (tons) and time period
Snoek *Thyrsites atun*	52 700	0.50	10	9 246 (1980–1988) 10 339 (1975–1988)
Kob *Agrysomus inodorus*	10 400	0.36	10	1 344 (1984–1988)
Geelbek *Atractoscion aequidens*	2 500	0.53	10	487 (1985–1989)
Yellowtail *Seriola lalandi*	7 500	0.31	10	806 (1985–1989)
Tuna*	8 375	0.20	5	3 575 (1980–1989)

* Mainly longfin tuna *Thunnes alalunga*, yellowfin tuna *T. albacares* and bigeye tuna *T. obesus*

and 2.5% mesopelagic fish, values applicable to the Namibian stock (Andronov 1983, 1985). *Q/B* was estimated at 5.1·year⁻¹, based on a gross efficiency of 10%, and assimilation efficiency was considered to be 80%.

The mean catch of horse mackerel for the 1980s was 36 450 tons (Badenhorst 1995).

OTHER SMALL PELAGIC FISH AND CEPHALOPODS

Round herring *Etrumeus whiteheadi*, sometimes referred to as redeye, is an important species in the southern Benguela foodweb. Biomass was taken as 1 222 000 tons, the mean of the estimates obtained from acoustic surveys in 1986, 1987 and 1989 (Roel and Armstrong 1991).

Annual production estimates were not available, and consequently a *P/B* of 1.2·year⁻¹ was considered appropriate for this small pelagic fish. *Q/B* was estimated as 12·year⁻¹, based on an assumed gross efficiency of 10%. Assimilation efficiency was considered to be 65%, as used for other small planktivorous. Diet was estimated at 60% mesozooplankton and 40% macrozooplankton (Wallace-Fincham 1987, Armstrong *et al.* 1991). Purse seine catches of round herring averaged 39 450 tons during the 1980s (Roel and Armstrong 1991).

Saury (Scomberesocidae) and other small pelagic fish, such as flying fish (Exocoetidae), were also included in the model. Biomass of such fish in the southern Benguela during the 1980s was estimated to be 80 000 tons. *P/B* was assumed to be 0.9·year⁻¹, gross efficiency 10% and assimilation efficiency 80%. The diet was weighted according to relative biomasses of saury and flying fish. The annual mean catch of saury was calculated to be 79 tons for the 1980s.

Pelagic goby *Sufflogobius bibarbatus*, an important component of the northern Benguela foodweb, is assumed to be an insignificant component of the foodweb in the southern Benguela, and was not included in the flow budget.

A number of different species of cephalopod are present in the southern Benguela. A mean combined biomass of 40 000 tons is considered appropriate (M. R. Lipiński, SF, pers. comm.). *P/B* was assumed to be 1.5·year⁻¹, and the remaining parameters were considered similar to those for cephalopod species elsewhere. Diet was weighted according to the relative biomasses of cephalopods. The mean annual catch of squid was estimated to be 2 000 tons for the 1980s (M. R. Lipiński, pers. comm.).

MESOPELAGIC FISH

Lanternfish biomass in the southern Benguela is dominated by *Lampanyctodes hectoris*. Biomass was estimated at between 0.5 and 1.2 million tons. Following Armstrong *et al.* (1991), a value of 850 000 tons was used in the model. Hewitson and Cruickshank (1993) estimated a *P/B* of 1.2·year⁻¹ for the northern Benguela, a value considered to be appropriate also for the southern Benguela. Based on a gross efficiency of 10%, *Q/B* was estimated at 12·year⁻¹. Assimilation efficiency was assumed to be 80%. The diet composition was 40% mesozooplankton and 60% macrozooplankton (Armstrong *et al.* 1991). Annual catches averaged 6 820 tons for the 1980s (SF unpublished data).

Maurolicus muelleri, locally called lightfish, but actually a member of the hatchetfish family, is common in the southern Benguela. Armstrong *et al.* (1991) assumed similar biomasses for lightfish and lanternfish, i.e. 850 000 tons, based on data from Armstrong and Prosch (1991); cf. Hulley and Prosch (1987). *P/B* was considered to be the same as for lanternfish, i.e. 1.2·year⁻¹ and a gross efficiency of 10%, as well as an assimilation efficiency of 80%. No commercial catches of lightfish have been reported.

LARGE PELAGIC FISH

Dominant, large pelagic fish in the southern Benguela include snoek, kob *Agyrosomus inodorus*, geelbek *Atractoscion aequidens*, yellowtail *Seriola lalandi*,

Table II: Catches and biomass breakdowns by species and size-class of hake *Merluccius capensis* and *M. paradoxus*, 1980−1989

Size group/species	M. capensis		M. paradoxus	
	Mean annual catch (tons)	Biomass (tons)	Mean annual catch (tons)	Biomass (tons)
Small (age 0–2 years)	11 161	106 154	26 125	233 379
Large (age 3+ years)	50 865	135 105	51 539	149 209

and tuna *Thunnus* spp. (Table I). The *P/B* for snoek was based on the assumption that *P/B* = *Z*, where *Z* is the sum of natural mortality (*M*) and fishing mortality (*F*). *M* was estimated and *F* was calculated from catches.

The combined biomass of large pelagic fish in the southern Benguela is 81 475 tons. A *P/B* of 0.434·year^{-1}, a *Q/B* of 4.6·year^{-1} and a gross efficiency of 9.5% were estimated, weighted by biomass. Diet was weighted by biomass rather than by consumption of single groups, because it was considered that the data were not sufficiently sound for a more elaborate estimate. The resulting overall diet was 14% zooplankton, 40% anchovy, 7.1% sardine, 1.2% chub mackerel, 2.9% horse mackerel, 12.5% other small pelagic fish, 0.1% large pelagic fish, 1.1% macrobenthos, 1.5% large deep-water hake *Merluccius paradoxus*, 2.7% small *M. paradoxus*, 1.3% large shallow-water hake *M. capensis*, 1.1% small *M. capensis*, 10.7% other demersal fish and 3.8% mesopelagic fish. The diet of snoek was based on Dudley's (1987) data, but recalculated to account for seasonal inshore-offshore migration of male and female snoek and the relative contributions to the overall diet of the snoek sampled in the West and South coasts. Assimilation efficiency was assumed to be 80%, the same as for other carnivorous fish. Annual mean catches were taken as 15 458 tons (SF unpublished data).

HAKES

There are two commercially important species of hake in the Benguela region, the shallow-water species *Merluccius capensis* and the deep-water species *M. paradoxus*. Because of the important role of hake as predators and the predominance of hake-on-hake predation in the southern Benguela, four groups, i.e. small and large *M. capensis* and small and large *M. paradoxus*, were modelled and later combined into a single hake box for comparison with the other models of upwelling systems.

Annual catches during the 1980s averaged 139 785 tons (wet mass) for all age-classes of both species of hake on the West and South coasts combined (Punt 1994). This value was rounded to 140 000 tons for

the model. To allocate the total catches to the four boxes, it was assumed that all small hake caught on the West Coast were *M. paradoxus* and that all large hake caught on the South Coast were *M. capensis* (R. W. Leslie, SF, pers. comm.). Annual biomasses per age-class of hake trawled on the West Coast (1980–1989), i.e. 27% of 0−2 year-olds and 73% of 3 years and older, were taken from Leslie (1997). The breakdown of the total catches is given in Table II.

Biomass estimates of hake were obtained by means of a production model (R. W. Leslie, unpublished data). For the purpose of this paper, both species were combined because they are managed together, but separate estimates of the combined hake biomass were also made for the West and South coasts.

Research hake survey data from January/February cruises on the West Coast and from the May/June cruises on the South coast were used to derive the relative proportions of the two hake species on each coast for the period 1980–1989. These were estimated to be 25% *M. capensis* and 75% *M. paradoxus* on the West Coast and 91% *M. capensis* and 9% *M. paradoxus* on the South Coast. From these, total biomass estimates of both species on the two coasts were estimated separately.

Species-specific numbers per age-class and year were derived from numbers-at-length and age-length keys for the period 1985−1988 for the West Coast. Such data were not available for the South Coast, but it was assumed that the proportions of age-classes were the same for both coasts. Also, the estimates for the period 1985−1988 were assumed to be representative of the decade of the 1980s.

The proportions of the total biomass of 1−2 years (small) and 3 year-old and older (large) hake were calculated for each species. These fractions were multiplied by the total biomass estimated for each species on each coast. The combined biomass estimates for the two species for each coast were then added to the total biomass estimate for the southern Benguela. The resulting biomass breakdown is given in Table II.

A total mortality of 0.6 year^{-1} was assumed for large hake, similar to other predatory fish, and a value of 1.2 year^{-1} was taken for small hake, in line

Table III: Diet composition by mass (%) of hakes *Merluccius capensis* and *M. paradoxus* by size-group and species

Food category	Diet composition by mass (%)			
	M. capensis		*M. paradoxus*	
	Small	Large	Small	Large
Zooplankton	39	8	35	14
Anchovy	21	13	0	1
Sardine	0	1.25	0	0
Other small pelagic fish	6	16.25	2	18
Chub mackerel	0	1.25	0	0
Large pelagic fish	0	1.25	0	0
M. paradoxus	2	28	0	21
M. capensis	0	12	0	0
Demersal fish	25	15	2	10
Mesopelagic fish	7	4	61	36

with the *P/B* for small pelagic fish. The consumption rate was estimated assuming a gross efficiency of 15% for small hake and 25% for large hake, in accord with estimates for other demersal fish (Livingston and Goiney 1984). Assimilation efficiency was assumed to be 80% for all size-classes.

Based on data from the period 1988–1994, diets were calculated from Punt *et al.* (1992), who gave the proportion by mass, prey species and predator age separately for both hake species. The percentages were weighted by the mean proportion of each age-group (of each species) in the size-classes of the four species (Table III). Combined, these gave an overall hake diet of 24.8% zooplankton, 33.5% mesopelagic fish, 6.6% anchovy, 0.3% sardine, 9.6% other small pelagic fish, 0.3% large pelagic fish, 0.3% chub mackerel, 14% hake (cannibalism or hake-on-hake predation) and 10.6% other demersal fish.

DEMERSAL FISH

This category includes a wide variety of species, which include Agulhas sole *Austroglossus pectoralis*, West Coast sole *A. microlepis*, kingklip *Genyptenus capensis*, rattails (mainly *Malacocephalus laevis* and *Caelorinchus simorhynchus*), John Dory *Zeus* spp., panga *Pterogymnus laniarius*, gurnard *Chelidonichthys* spp., monkfish *Lophius vomerinus*, red sea harder *Emmelichthys nitidus*, cardinal fish *Epigonus* spp., jacopever *Helicolenus dactylopterus* and ribbonfish *Lepidopus caudatus*. Combined biomass for the southern Benguela was estimated to be 232 061 tons, and the *P/B* was assumed to be 1.0·year⁻¹, the gross efficiency 10% and the assimilation efficiency 80%. Diets were weighted according to relative biomasses of the different species. This resulted in a breakdown of 32.6% macrobenthos, 25.7% zooplankton, 17.2%

demersal fish, 4.1% mesopelagic fish, 3.5% *M. paradoxus*, 2.3% *M. capensis*, 0.1% anchovy and 14.5% other small pelagic fish. Combined catches were calculated to be 25 214 tons, although not all species are retained by the fishery.

SHARKS

Sharks are caught mainly as a bycatch by demersal trawling, and their biomass is estimated to be 188 727 tons in the southern Benguela (Wilkinson *et al.* 1994). This is likely an underestimate, because pelagic sharks are not included in the estimate, and neither is the proportion of sharks which inhabit untrawlable areas. However, sharks inhabiting soft-bottom substrata (trawlable areas) are likely to have been overestimated through extrapolation over large areas, which would include some rocky substrata unsuitable for these species. It was considered appropriate to increase the biomass by 75% to 330 272 tons. Cliff *et al.* (1996) estimated *Z* to be 0.53·year⁻¹ for the great white shark *Carcharodon carcharias*, implying a *P/B* of 0.5·year⁻¹. Assuming a gross efficiency of 25%, the same as for large demersal fish, a *Q/B* of 2·year⁻¹ was estimated. Assimilation efficiency was assumed to be that of carnivores, i.e. 80%.

Based on relative biomass estimates for sharks belonging to different feeding guilds (A. J. Penney, formerly SF, pers. comm.) and assuming that the apex predators (e.g. great white sharks) have a biomass similar to that of benthic carnivorous fish, a weighted diet was calculated to be 9.3% anchovy, 1.2% sardine, 18.5% chub mackerel, 1.2% horse mackerel, 10.5% other pelagic fish (and squid), 38.5% demersal fish, 20.5% hake, 0.35% macrobenthos, 0.23% seals and 0.47% sharks (within-group predation). As the predation on chub mackerel appeared grossly overestimated and the within-group predation appeared very low (M. Kroese, SF, pers. comm), the fraction of chub mackerel in shark diet was reduced to 1.5 % and the difference was attributed to shark within-group predation.

Annual catches of sharks average 3 000 tons in the southern Benguela (M. Kroese, SF, pers. comm.), but again not all are retained for commercial purposes.

SEABIRDS

Information was obtained from Crawford *et al.* (1991). Biomass was estimated at 3 257 tons for the southern Benguela, with a production of 400 tons·year⁻¹ using a *P/B* of 0.12·year⁻¹. Total annual consumption was estimated to be 26 913 tons wet mass (converted from carbon values in Crawford *et al.* 1991), yielding a gross efficiency of 0.104% and a *Q/B* of 118·year⁻¹. An assimilation efficiency of 74% was assumed

(Crawford 1991).

Diet information is expressed in percentage contributions for each prey item in each region (Crawford *et al*. 1991). The resulting diet composition was 10.5% zooplankton, 36.5% anchovy, 8.4% sardine, 0.8% horse mackerel, 14.5% other small pelagic fish and squid (6.5% squid, 1.9% round herring, 0.6% pelagic goby and 5.5% other species, e.g. saury), 0.2% large pelagic fish, 17.2% hake (assuming that seabirds eat mainly small hake in proportion to the biomass estimates: 9.5% small *M. paradoxus*, 7.7% small *M. capensis*), 0.7% demersal fish, 0.2% marine birds, 0.4% seals and 10.3% mesopelagic fish.

SEALS

Biomass of the Cape fur seal *Arctocephalus pusillus pusillus* was estimated at 29 180 tons for the southern Benguela (1989 workshop). Annual production was estimated as the mean of the low and high values (1989 workshop), giving an estimate of 27 607 tons·year^{-1} for the southern Benguela. A *P/B* of 0.946·year^{-1} was derived assuming a gross efficiency of 4.9%, and total consumption was estimated to be 563 408 tons. The assimilation efficiency for most carnivorous mammals is around 80% (Furness 1984), a value considered appropriate for seals in the model.

Diet was given as annual consumption of prey species (David 1987) for two areas of the southern Benguela. The weighted diet composition for the southern Benguela was 25.2% anchovy, 2.8% sardine, 1.3% chub mackerel, 3.2% horse mackerel, 23.9% other small pelagic fish, 1.5% large pelagic fish, 6.5% macrobenthos (rock lobster and other crustaceans), 24.1% hake (assuming seals eat hake of different size-classes in proportion to prey biomass estimates: 5.8% large *M. paradoxus*, 8.9% small *M. paradoxus*, 5.3% large *M. capensis* and 4.1% small *M. capensis*), 10.9% demersal fish and 0.6% mesopelagic fish.

WHALES AND DOLPHINS

Biomass estimates are not available for most species of whale and dolphin off southern Africa. The biomass of Bryde's whale *Balaenoptera edeni* was estimated to be 6 300 tons (Best 1984), and the combined biomass of dusky dolphin *Lagenorhynchus obscurus*, common dolphin *Delphinus delphis* and Heaviside's dolphin *Cephalorhynchus heavisidii* was considered to be 2 350 tons (1989 workshop). A weighted *P/B* estimate of 0.6·year^{-1} was used for the southern Benguela. The assimilation efficiency was estimated as 79% (Gaskin 1982) and gross efficiency was assigned a value of 8%. The diet of Bryde's whale was obtained from Best (1967), and diets of all dolphin species from Sekiguchi *et al*. (1992). This resulted in

a weighted diet composition of 6.6% zooplankton, 30.1% anchovy, 7.4% sardine, 26.8% horse mackerel, 20.4% other small pelagic fish, 4.3% hake (assuming whales and dolphins consume hake of different size-classes in proportion to prey biomass estimates: 1.1% large *M. paradoxus*, 1.6% small *M. paradoxus*, 1.0% large *M. capensis* and 0.7% small *M. capensis*) and 4.3% mesopelagic fish.

BENTHOS

Macrobenthos is important food for demersal fish, but the information available is very limited. The minimum biomass necessary to sustain the food requirements was computed for the other system components based on an ecotrophic efficiency (*EE*) of 95%. The remaining parameters were assumed to be the same as for those used in the models of the other upwelling systems, i.e. a *P/B* of 1.2·year^{-1} for macrobenthos and 4.0·year^{-1} for meiobenthos. For both groups, a gross efficiency of 12% was assumed. Benthos consists mainly of browsers or suspension feeders, and only occasionally carnivores. Little primary production can be expected in water depths greater than 20 m. The diet of macrobenthos was therefore assumed to consist of 5% benthic producers, 8% meiobenthos, 7% macrobenthos and 80% detritus. The diet of meiobenthos was assumed to consist of 5% benthic producers and 95% detritus. Biomass of benthic producers was estimated based on the grazing demand by benthos and an *EE* of 50%, taking into account that benthic producers such as macroalgae are often only consumed after decaying.

DETRITUS

The detritus category receives inputs from other categories in the form of faecal material, or through residual mortality. No other information was included in the budgets for this category.

RESULTS

Balancing the model

The original model was severely unbalanced with respect to zooplankton (*EE* = 1.65), hake (*EE*s between 1.04 and 1.6, and an *EE* of 3.7 for large *M. paradoxus*) and demersal fish (*EE* = 5.1). An *EE* >1 means that more production is consumed or exported from the system than is produced. The following sections describe how these components were changed in order to balance the model. Further changes were made to the diets of other small pelagic fish, and in

Table IV: Estimated parameters of the mass-balance model of the southern Benguela ecosystem, 1980−1989

Functional group	Estimated parameter	Value
Phytoplankton	*EE*	0.44
Benthic producers	*B* (*EE* = 0.50)	10.5
Zooplankton	*EE*	0.97
Anchovy	*EE*	0.99
Sardine	*EE*	0.99
Chub mackerel	*EE*	0.96
Horse mackerel	*EE*	0.96
Other small pelagic fish	*EE*	0.94
Large pelagic fish	*EE*	0.97
Meiobenthos	*B* (*EE* = 0.95)	19.6
Macrobenthos	*B* (*EE* = 0.95)	93.0
Hakes	*B* (*EE* = 0.99)	4.0
Demersal fish	*B* (*EE* = 0.99)	6.8
Seabirds	*EE*	0.96
Seals	*EE*	0.14
Whales and dolphins	*EE*	0.00
Mesopelagic fish	*EE*	0.94
Sharks	*EE*	0.96
Detritus	*EE*	0.49

B = Biomass (tons wet mass·km^{-2})
EE = Ecotrophic efficiency

balancing the impact of shark predation in the system. The estimated parameters for the balanced model are given in Table IV. The inputs to the balanced model are summarized in Table V.

ZOOPLANKTON

The dynamics of the combined zooplankton box were strongly dominated by microzooplankton. The combined gross efficiency of the zooplankton box was raised from 0.21 to 0.26, closer to the efficiency reported for meso-and macrozooplankton, which corresponded to an increase in gross efficiency of microzooplankton from 0.20 to slightly below 0.26. The fraction of microzooplankton in microzooplankton diet was also lowered from 33 to 25%, the remainder was distributed in equal parts to the other two food items, phytoplankton and detritus (bacteria), resulting in an estimate of 37.5% for each of them.

SARDINE

In the case of sardine, *EE* = 1.265, indicating that the *P/B* ratio was too low. Therefore, the *P/B* was raised slightly from 1.1 to 1.2·year^{-1}, in line with that of anchovy.

OTHER SMALL PELAGIC FISH

The diet proportions of sardine (0.4%) and other

small pelagic fish (0.1%) in the diet of other small pelagic fish and squid were swapped around, because there were not enough sardine in the system to account for predation by small pelagic fish.

DEMERSAL FISH

Meyer and Smale (1991) investigated the diet of some trawled demersal fish, finding macrobenthos as the dominant food item. They also reported extensive predation on other small demersal fish, such as the dragonet *Paracallionymus costatus*, the biomass of which was originally not included in the model. No diet information could be obtained for that species, but other dragonets, such as *Callionymus lyra*, are known to feed on small crustaceans and molluscs (Muus and Dahlstrøm 1964). Meyer and Smale (1991) also reported feeding stanzas in some benthic feeding species, with small benthic crustaceans dominating the prey of smaller fish.

It was therefore assumed that the bulk of the biomass missing in the original model consisted of small demersal species, which would predominantly feed on macrobenthos. The *P/B* was consequently raised from 1.0 to 1.2·year^{-1}, because small species tend to have high mortalities, and the gross efficiency was increased to 15%, in line with that of small hake. For the change in diet composition, no further consumption was assumed for hake, because only large, motile benthic fish would feed on them. Such large fish would be included in bottom trawl samples and therefore in the original biomass estimates. It was also assumed that 25% of the additional biomass of demersal fish would feed on the various groups of the system, as originally reported (except on hake, the diet proportion of which was redirected to macrobenthos), and that 75% of the additional biomass would feed on macrobenthos exclusively. A minimum biomass was then estimated based on an *EE* of 0.95, emphasizing the importance of demersal fish as prey in the system.

HAKE

The major fraction of predation mortality of large *M. paradoxus* was caused by cannibalism and predation by large *M. capensis*. Because it was difficult to reconcile that large *M. paradoxus* could prey so severely on smaller fish of the same species, the cannibalism fraction was reduced considerably from 13 to 2.5%. Because the fraction of small *M. paradoxus* in the diet of large *M. paradoxus* was already relatively high (8%), the difference was redirected to anchovy and other small pelagic fish in equal parts. Similarly, the fraction of large *M. paradoxus* in the diet of large

Table V: Biomass (*B*), *P/B*, gross efficiency (*P/Q*), export (Exp) and ecotrophic efficiency (*EE*) used in the ECOPATH model of the southern Benguela. Where parameters or diets have been adjusted during the balancing of the model, modified values are also given. Export of phytoplankton is through sedimentation, whereas export of other groups is through harvesting

Functional group	Parameter	Parameter values	Source	Modified parameters (balancing of model)
Phytoplankton	*B*	1.69×10^7 tons	Brown *et al.* (1991)	
	P/B	154.4·year^{-1}	Brown *et al.* (1991)	
	Exp	8.10×10^7 tons	Brown *et al.* (1991)	
*Microzooplankton	*B*	1.22×10^6 tons	Brown *et al.* (1991), Painting *et al.* (1992)	
	P/B	428·year^{-1}		
	P/Q	20%	Stoecker (1984)	Adjusted to 26%
Mesozooplankton	*B*	2.67×10^6 tons	Hutchings *et al.* (1991)	
	P/B	20·year^{-1}	Hutchings *et al.* (1991)	
	P/Q	30%	Hutchings *et al.* (1991)	
Macrozooplankton	*B*	9.06×10^5 tons	Hutchings *et al.* (1991)	
	P/B	13·year^{-1}	Hutchings *et al.* (1991)	
	P/Q	41%	Hutchings *et al.* (1991)	
Salps and jellyfish	*B*	5.5×10^7 tons	1989 workshop	Adjusted to 1.0×10^6 tons
	P/B	0.3705·year^{-1}		
	P/Q	41%		
Anchovy	*B*	1.15×10^6 tons	M. Barange, SF, unpublished data	
	P/B	1.2·year^{-1}	Hewitson and Cruickshank (1993)	
	P/Q	9.8%	Armstrong *et al.* (1991)	
	Exp	3.46×10^5 tons	Roel and Armstrong (1991)	
Sardine	*B*	1.29×10^5 tons	M. Barange, SF, unpublished data	Adjusted to 1.2·year^{-1}
	P/B	1.1·year^{-1}	Hewitson and Cruikshank (1993)	
	P/Q	9.7%	Armstrong *et al.* (1991)	
	Exp	4.08×10^4 tons	Roel and Armstrong (1991)	
Chub mackerel	*B*	6.25×10^4 tons		
	P/B	0.6·year^{-1}		
	P/Q	10%		
	Exp	6.2×10^3 tons	Japp *et al.* (1994)	
Horse mackerel	*B*	3.32×10^5 tons		
	P/B	0.52·year^{-1}		
	P/Q	10%		
	Exp	3.65×10^4 tons	Badenhorst (1995)	
*Round herring	*B*	1.22×10^6 tons	Roel and Armstrong (1991)	
	P/B	1.2·year^{-1}		
	P/Q	10%		
	Exp	3.95×10^4 tons	Roel and Armstrong (1991)	
Saury and flying fish	*B*	8.00×10^4 tons	1989 workshop	
	P/B	0.9·year^{-1}		
	P/Q	10%		
	Exp	79 tons	1989 workshop	
Cephalopods	*B*	4.00×10^4 tons	1989 workshop	
	P/B	1.5·year^{-1}		
	P/Q	10%		
	Exp	2.00×10^3 tons		
Lanternfish	*B*	8.50×10^5 tons	Armstrong *et al.* (1991)	Adjusted to 9.50×10^5 tons
	P/B	1.2·year^{-1}	Hewitson and Cruickshank (1993)	
	P/Q	10%		
	Exp	6.82×10^3 tons	SF unpublished data	
Lightfish	*B*	8.50×10^5 tons	Armstrong *et al.* (1991)	Adjusted to 9.50×10^5 tons
	P/B	1.2·year^{-1}		
	P/Q	10%		
	Exp	None		

Table V (continued)

Functional group	Parameters	Parameter values	Source	Modified parameters (balancing of model)
Large pelagic fish	B P/B P/Q Exp	8.15×10^4 tons $0.43 \cdot$year^{-1} 9% 1.55×10^4 tons	A. J. Penney, SF, pers. comm. 1989 workshop A. J. Penney, SF, pers. comm.	
Small *M. capensis* (age 0–2 years)	B P/B P/Q Exp	1.06×10^5 tons $1.2 \cdot$year^{-1} 15% 1.12×10^4 tons		†
*Large *M. capensis* (age 3+ years)	B P/B P/Q Exp	1.35×10^5 tons $0.6 \cdot$year^{-1} 25% 5.09×10^4 tons		†
Small *M. paradoxus* (age 0–2 years)	B P/B P/Q Exp	2.33×10^5 tons $1.2 \cdot$year^{-1} 15% 2.61×10^4 tons		†
*Large *M. paradoxus* (age 3+ years)	B P/B P/Q Exp	1.49×10^5 tons 25% 5.15×10^4 tons	$0.6 \cdot$year^{-1}	†
*Demersal fish	B P/B P/Q Exp	2.32×10^5 tons $1.0 \cdot$year^{-1} 10% 2.52×10^4 tons	1989 workshop 1989 workshop	† Adjusted to 1.2·year^{-1} Adjusted to 15%
*Sharks	B P/B P/Q Exp	3.30×10^5 tons $0.5 \cdot$year^{-1} 25% 3.00×10^3 tons	Cliff *et al.* (1996) M. Kroese, SF, pers. comm.	
Seabirds	B P/B P/Q Exp	3.26×10^3 tons $0.12 \cdot$year^{-1} 0.10% None	Crawford *et al.* (1991) Crawford *et al.* (1991) Crawford *et al.* (1991)	
*Seals	B P/B P/Q Exp	2.92×10^4 tons $0.95 \cdot$year^{-1} 4.9% None	1989 workshop 1989 workshop	
*Whales and dolphins	B P/B P/Q Exp	8.65×10^3 tons $0.6 \cdot$year^{-1} 6% None	Best (1984) and 1989 workshop 1989 workshop	
Macrobenthos	EE P/B	0.95 $1.2 \cdot$year^{-1}		
Meiobenthos	EE P/B	0.95 $4.0 \cdot$year^{-1}		
Benthic producers	EE P/B	0.50 $15 \cdot$year^{-1}		

* Diet adjusted
† Biomass re-estimated by the model

M. capensis was reduced from 11 to 2.8%, and the difference was also redirected to anchovy and other small pelagic fish in equal parts. It was also noted that the predation mortality on hake caused by seals alone was very high (more than one-third of the total mortality), so, the fraction of large *M. paradoxus* in the diet of seals was decreased by half and the difference was redirected to other small pelagic fish. This resulted in the predation mortality of large *M. paradoxus* caused by large hake, demersal fish and seals being the same order of magnitude, and the total predation mortality of large *M. paradoxus* being approximately 50% higher than their fishing mortality. Despite these changes, the *EE* of large *M. paradoxus* was >1,
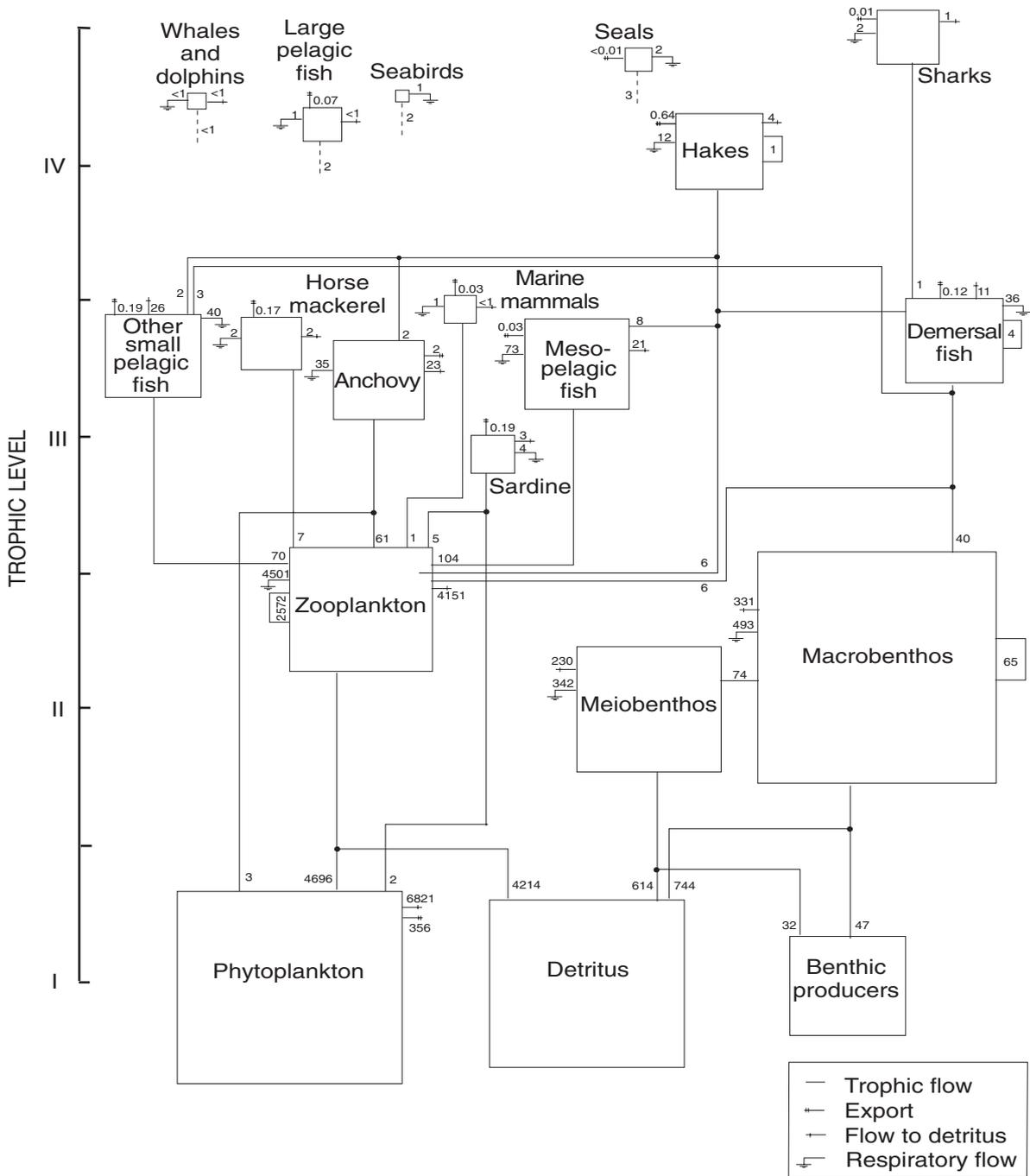
Fig 2: Diagram of the trophic flows in the southern Benguela, 1980–1989. The size of the boxes is proportional to the biomass of the components, if the boxes are envisaged as cubes instead of squares. Boxes are arranged along the vertical axis according to their trophic level, defined as 1 for primary producers and detritus, and as 1 plus the mean trophic level of their prey items for consumers, weighted according to their fraction in the consumer's diet. Flows are in units of tons·wet mass·km-2·year^{-1}. Flows leave the boxes in their upper half and enter them in their lower half. Flows of at least 1 ton·km-2·year^{-1} were rounded to the nearest integer, those below to one digit. Trophic flows of < 0.1 ppt of the total consumption in the system, corresponding to about 0.4 tons·km-2·year^{-1}, were omitted for clarity. Detritus mass is a rough guess only. Biomass of zooplankton excludes wet mass of jellyfish

so a minimum biomass of this predatory fish was calculated, based on an *EE* of 0.99. A minimum biomass was then estimated for the other hake groups based on an *EE* of 0.99, which resulted in an increase in total hake biomass in the southern Benguela ecosystem by almost 30%.

SHARKS

Sharks seem to be important predators in the southern Benguela, and they influenced the balancing of the model to a major extent. Predation of hake by sharks was lowered considerably, to a diet proportion of 0.4%. The predation on macrobenthos was increased by 10%, and the within-group predation to a total of 23.4%. The latter is an overestimate of within-group predation, but such an adjustment was necessary for balancing the model. Demersal fish in the diet of sharks were increased from 38.5 to 41.5%, and 0.4% of the diet of sharks was allocated to large pelagic fish. The *EE* of demersal fish was set to 99%, emphasizing the heavy feeding pressure on them in the system. Biomass of mesopelagic fish was subsequently increased to 950 000 tons each for lanternfish and lightfish, well within the range of 0.5–1.2 million tons estimated for each of the groups (cf. Hulley and Prosch 1987).

The model assumes that the published shark biomass is underestimated by 75%. If the underestimate was only 50%, and consequently a value of 1.27 tons·km^{-2} was used instead of the 1.5 tons·km^{-2} used in the model, the model outputs for biomass of macrobenthos and demersal fish would be lower by 5%. Consequently, 1–1.5% less anchovy and sardine and 3% less other small pelagic fish would be consumed in the system. Based on these cascading effects in the foodweb from a seemingly important top predator group, a more accurate biomass estimate of sharks in the southern Benguela could be of importance to a general understanding of the foodweb.

SEABIRDS

It should be noted that it was necessary to reduce the within-group consumption of seabirds from 0.2 to 0.1%. To balance the model, the extra 0.1% was reallocated to anchovy, because this was the prey item consumed in the greatest quantitites by the seabirds.

Problems in balancing hake and demersal fish boxes

Demersal fish, including hake, were particularly problematic in the model of the southern Benguela. The best way to balance the model was by setting *EE* to 0.99 for the demersal fish and all four hake boxes, and estimating the biomass which would then be required to support the other components of the system. This was done after the proportion of one or more of those components in the diets of some predators had already been reduced substantially (for example, hake consumed by sharks had to be reduced by a large amount). Demersal fish biomass was then required to be 6.5 times greater than the estimated biomass, and it was necessary for hake biomass to be 30% higher than estimated. These adjustments in turn had repercussions through the rest of the system, because prey species were consumed in far greater quantities.

The outcome of this model is that the ratio of pelagic : demersal : mesopelagic fish was 7 : 5 : 4. This excludes sharks. Benthic producers, micro- and macrobenthos were all higher than would be expected from a traditional upwelling system, but not unusually high for a shelf ecosystem. This may be explained partially by the fact that, in the model of the southern Benguela, it was necessary to include marine components in the area from along the West Coast to the South Coast as far as East London. However, the main upwelling region is only along the West Coast, and the remaining area is largely a shelf ecosystem. It was important that the Agulhas Bank be included to account for the fact that many of the commercially important fish species (and their prey) in the southern Benguela spend part of their life on the Agulhas Bank. For example, anchovy spawn on the Agulhas Bank and their eggs and larvae are transported by currents up the West Coast, where they recruit before returning to the Agulhas Bank as one year olds to spawn (Hutchings 1992). Hake are distributed both on the West Coast and the Agulhas Bank. It would be possible to split the modelled region into South and West Coast regions for some species, but for others, whose migratory patterns are less well known, it would be problematic, not only in terms of estimating biomass, but also for their dietary components. Therefore, fish resources in the wider region were integrated and modelled as one ecosystem.

Trophic flow diagram

The trophic flows in the southern Benguela are shown in Figure 2. The components of the system are structured along the vertical axis according to trophic level. Primary producers and detritus are placed on Trophic Level 1 by definition. The trophic level of consumers is computed from the average trophic level of their prey, weighted by the consumer's diet composition, plus one. Accordingly, the planktonic and benthic invertebrate groups are situated
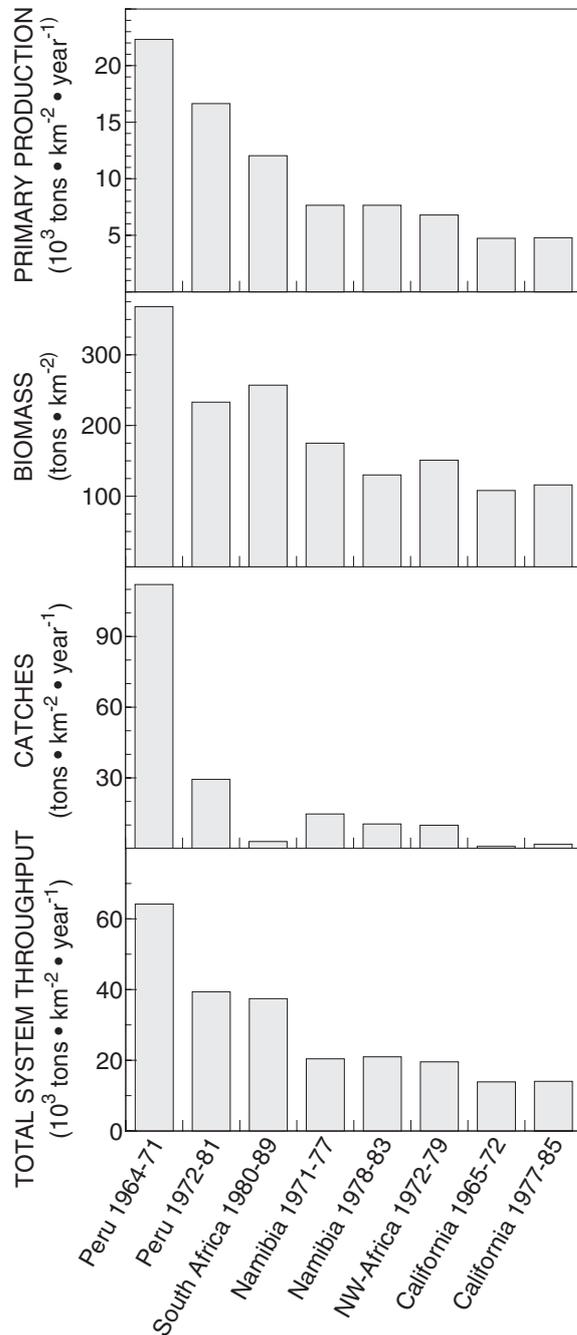
Fig. 3: Summary statistics of the models of upwelling areas regarding the size of the systems. Note that the systems are arranged in geographical rather than in regime-specific order, and that the similar trend in primary production, biomass (excluding detritus) and total system throughput is not followed by the catches

between Trophic Levels 2 and 3, because the bulk of their diet consisted of primary producers and/or detritus (including bacteria). Of the vertebrates, sardine fed lowest in the foodweb, followed by anchovy, mesopelagic fish and other small pelagic fish and squid. Horse mackerel and demersal fish were placed slightly higher in the foodweb, but on comparable trophic levels, depite their widely differing diet. Chub mackerel, although predatory, were situated only slightly higher, because it was assumed that the stock consisted mainly of planktivorous juveniles during the 1980s. Hake clearly stood out as a predator, whereas large pelagic fish were the top teleosts. Their trophic position was exceeded only by sharks, whales, seals and seabirds. These top predator groups fed almost entirely on the groups of small pelagic or demersal fish.

Not surprisingly, the major flows in the system were among the lower trophic levels. Further important flows were channelled via anchovy and other small pelagic fish towards hake, and via other small pelagic fish to demersal fish. Predation by sharks, particularly on demersal fish, was also important, and sharks therefore appeared to have been important top predators by the magnitude of their consumption. Sardine and chub mackerel played only a marginal role in the period under investigation.

Summary statistics

Statistics pertaining to the size of the southern Benguela ecosystem, compared to other upwelling systems modelled, are shown in Figure 3. In terms of primary production and catches, the Peruvian system is the largest of the upwelling systems. However, that system had been considerably larger during the 1960s, before the collapse of the Peruvian anchovy *Engraulis ringens* fishery at the beginning of the 1970s. Also, the Peruvian system experienced the most pronounced changes during the periods modelled. With respect to total biomass sustained in the system and total system throughput, the size of the Peruvian system during the 1970s is comparable to that of the southern Benguela during the 1980s. Primary production in the southern Benguela was intermediate between primary production off Peru and in the northern Benguela. However, fish catches were much smaller in the southern Benguela. They were also smaller than the catches in the northern Benguela and north-west African systems, and only higher than those in the California upwelling system. Nevertheless, the Peruvian and southern Benguela systems appear to have been rather similar in terms of system size, although the Peruvian system underwent a regime shift from anchovy *Engraulis ringens* to sardine
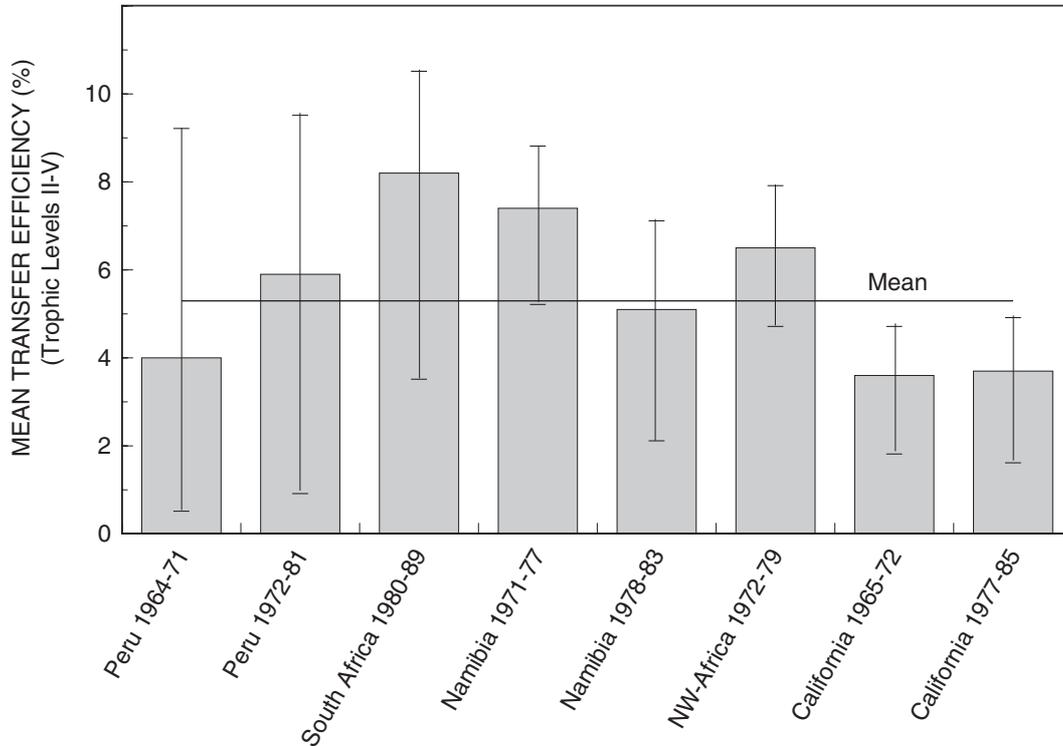
Fig. 4: Mean transfer efficiency from discrete Trophic Levels II (herbivores) to V (fifth order carnivores) for all systems modelled. Note that the mean transfer efficiencies are lower than the global estimate of 10% (Pauly and Christensen 1995) in every system, and that the mean over the upwelling systems is only slightly more than half of the global value. Bars denote standard deviation

Sardinops sagax, whereas the Benguela was dominated by anchovy. However, a comparison may be possible, because anchovy in the Peruvian upwelling system are more productive (and herbivorous) than sardine. Although Peruvian anchovy are not strictly herbivorous, they consumed about 70% phytoplankton (by mass) in non-*Niño* years during the late 1960s and the 1970s (Jarre-Teichmann 1992). The opposite appears to be the case for the system off southern Africa.

Both the Peruvian and Benguela systems were dominated by their less productive species of small pelagic fish during the periods under comparison here. Jarre-Teichmann and Christensen (1998) noted that the four upwelling systems they compared were separated by size rather than by species dominance, and that the southern Benguela appeared to be no exception. The southern Benguela ranks second (in terms of biomass, primary production and total system throughput) after the Peruvian upwelling system, followed by the northern Benguela. The north-

west African and Californian systems are the smallest, but it is noteworthy that both are strongly seasonal upwelling systems, compared to the more protracted upwelling in the southern Benguela.

Transfer efficiency

Transfer efficiencies between discrete trophic levels were calculated following Ulanowicz (1995), and the mean transfer efficiencies for discrete Trophic Levels II–V (herbivores to third order carnivores) are given in Figure 4 for all upwelling systems analysed. Again, the southern Benguela was no exception to the rule that, in general, upwelling systems are highly inefficient; the global average transfer efficiency is around 10% (Pauly and Christensen 1995), whereas the average of the upwelling systems compared here was only 5.4%. Although the average transfer efficiency in the southern Benguela was higher than in the

Fig. 5: Trophic pyramids of the southen Benguela upwelling ecosystem (1980−1989) and the northern-central Peruvian ecosystem (1973−1981). The volume of each discrete trophic level is proportional to the throughput at that level. The top angle of the pyramid is inversely proportional to the mean system transfer efficiency. The bottom compartment represents throughput at discrete Trophic Level 2 (herbivory)

other systems, with respect to the wide range of the transfer efficiencies, the differences between the Peruvian system in the 1970s, the Benguela and the north-west African systems are not significant.

A closer look at the distribution of flows between the discrete trophic levels (Fig. 5) shows that the throughput at Trophic Level II (herbivores) was larger in the southern Benguela ecosystem than off Peru, whereas the thoughput at Trophic Level III (zoo-planktivores) was larger off Peru than South Africa. It therefore appears that the energy transfer from primary producers to small pelagic fish was less efficient in the southern Benguela, one possible explanation for the smaller magnitude of total fish production. This is dealt with further in the discussion.

Mixed trophic impacts

The structure of the foodwebs in the southern Benguela and Peruvian systems was further compared (Fig. 6) using mixed trophic impact analysis (Ulanowicz and Puccia 1990). Whereas zooplankton strongly favoured all principal groups in the southern Benguela, it had no impact on Peruvian anchovy, and its positive effect as anchovy prey was largely counteracted by its competition with anchovy for phytoplankton. Zooplankton production was also less limiting for the top predators off Peru than off southern Africa.

Anchovy, the dominant small pelagic fish in the southern Benguela, had a less pronounced impact on its system than Peruvian anchovy. On the other hand, the impact of other small pelagic fish (e.g. round herring) is stronger in the Benguela than that of other small pelagic fish in the Peruvian system. Potential beneficial effects of anchovy on its predator groups, e.g. hake, in the southern Benguela were levelled out

by mutual predation on, and hence competition for, zooplankton. However, anchovy was a competitor with horse mackerel in the Benguela system, whereas it is a food source for horse mackerel off Peru. Along the same lines, other small pelagic fish strongly competed with horse mackerel in the Benguela, but not off Peru, where horse mackerel appear to have been more piscivorous. Seabirds were more dependent on anchovy off Peru than in the Benguela.

Hake had little influence on small pelagic fish in both systems, but hake-on-hake competition was more pronounced in the Benguela. Hake favoured the top predators in the Benguela, whereas it competed with seabirds (for small pelagic fish) and did not impact marine mammals in the Peruvian system. It should be noted that mesopelagic fish appear to play no role in the Peruvian upwelling system, whereas they are important food items for the higher trophic levels in the Benguela system and compete slightly with anchovy and sardine for food.

Fisheries are detrimental to most of the groups in both the Benguela and Peruvian systems. It should be noted that the detrimental impact of the fishery on hake was stronger in both systems than the fishery on small pelagic fish. Further, the impact of the fishery on seabirds and seals is larger than can be expected from direct exploitation alone, and results from competition of the fishery with seabirds and mammals for their prey.

Partitioning of total fish production

The partitioning of the total production of the five dominant groups (anchovy, sardine, chub mackerel, horse mackerel and hake) by predatory fish (chub mackerel, horse mackerel, hake, other pelagic and
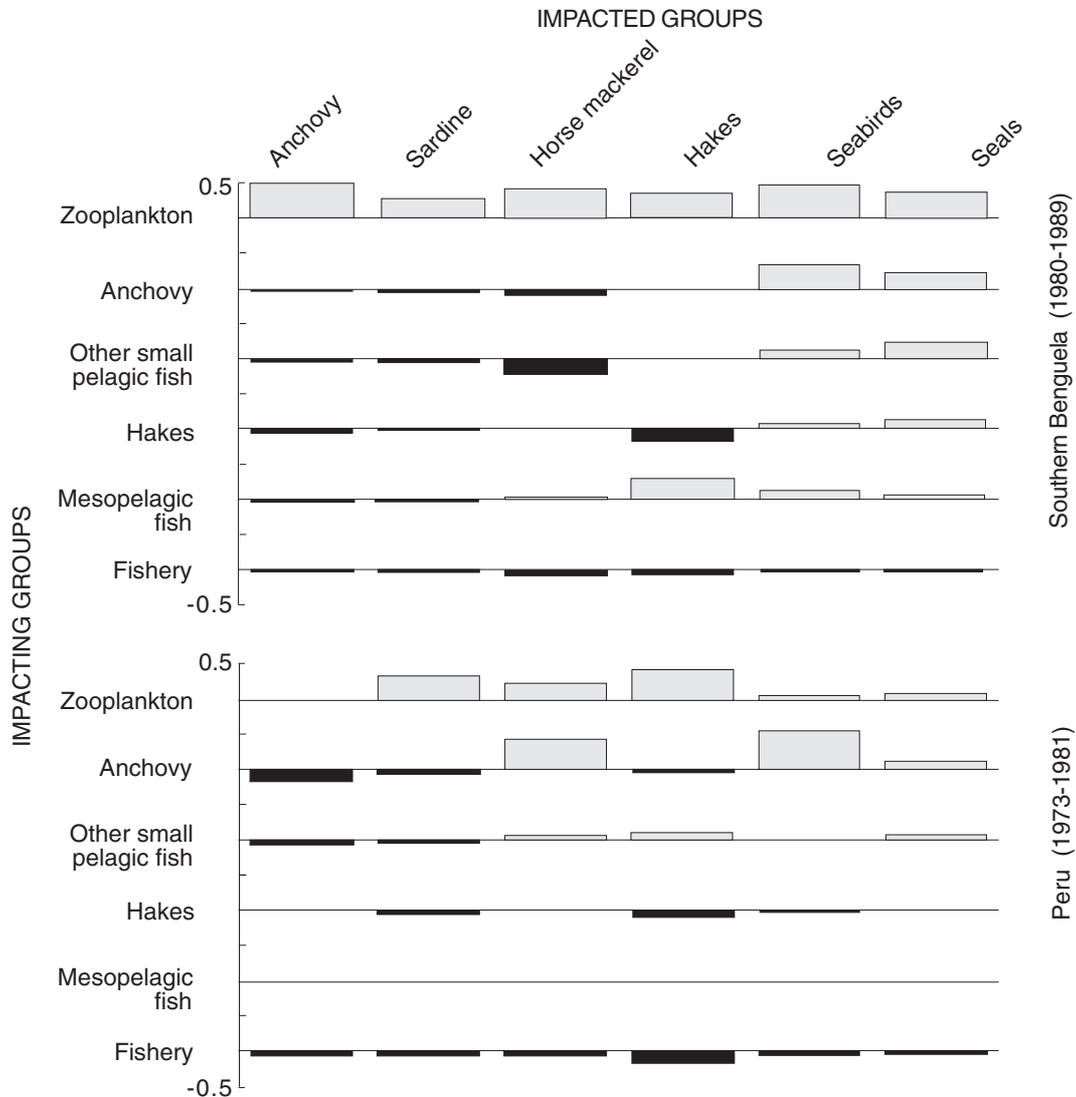
Fig. 6: Mixed trophic impacts of selected groups in the southern Benguela (1980–1989) and the northern-central Peruvian ecosystems (1973–1981). The computed impacts are relative on a scale of −1 to +1, where 0 indicates no impact

demersal fish), mammals, other top predators (large pelagic fish, sharks and seabirds) and the fishery is given in Figure 7. Some 41.7% of the fish production of the five dominant groups is consumed by fish in the southern Benguela, 14.6% by mammals, 18.9% by other top predators, 23.0% by the fishery, and only 1.8% die of other causes. Both the northern and southern Benguela share the property that less than

half of the production of the five groups is consumed by fish. However, it should be noted that other small pelagic fish (e.g. round herring) were important components in the foodwebs of both systems and are not part of this comparison.

Predation by mammals on the five groups was most important in the southern Benguela, followed by the Peruvian and Californian systems. The consumption
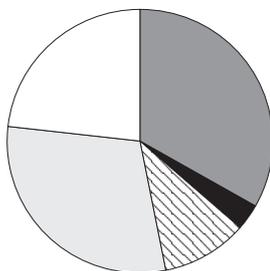
Peru 1973-1981
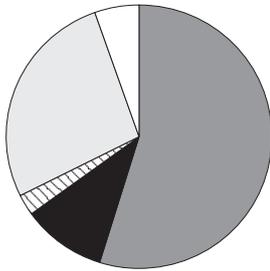
South Africa 1980-1989
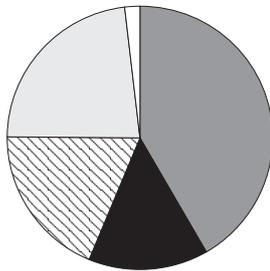
Namibia 1978-1983

California 1977-1985

Fish

Mammals

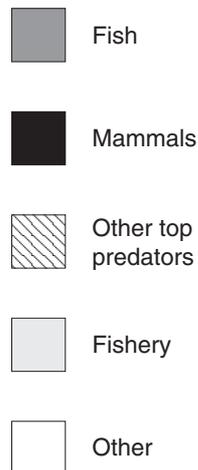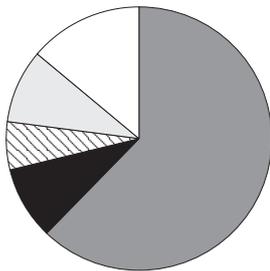Other top predators

Fishery

Other

Fig. 7: Partitioning of the production of the five dominant fish species (anchovy, sardine, chub mackerel, horse mackerel and hake) during the late 1970s or 1980s, between fish, mammals, other top predators and the fishery

by other top predators was much more important in the southern Benguela than in all other systems. This was mainly a result of the explicit inclusion of sharks in the Benguela model, and the fact that the Agulhas Bank is considered here as being part of the southern Benguela upwelling system, although it is more characteristic of a shelf system, with higher biomasses of demersal fish groups than on the West Coast. The fishery took approximately 25% of the production of the five dominant groups in the southern and northern Benguela, but less than half of this fraction off California. However, it should be kept in mind that the fishing bans on sardine and mackerel off California had just been lifted, and strict management was enforced.

With respect to the "other" destination of production, it should be noted that the southern Benguela was the tightest of all systems. This could probably be an artefact attributable to the overestimation of fish consumption at the higher trophic levels, notably by large hake and sharks, which showed during the model-balancing process. Further investigation on trophic impact, especially of sharks, in the system is advisable.

Fraction of primary production needed to sustain the fishery

Fisheries in different areas can have catches of similar size, but their species composition can be rather different, based both on the availability of fish and on the fishing strategy. The exploitation of fish at higher trophic levels is ecologically more costly, because the transfer efficiency of energy up the food-web is very inefficient (Fig. 4). Therefore, a common currency needs to be established before the ecological cost of fishing can be estimated. Pauly and Christensen (1995) suggested primary production equivalents where, after the removal of cycles in the system, the end flow of each path in the system (e.g. fishery catch of a particular species) is traced back through the foodweb using, for each group encountered on the way down the foodweb, that group's gross efficiency (production/consumption ratio) as a raising factor for the required total flow. The primary production required to sustain the fishery in upwelling systems calculated in this way is given in Figure 8, both in absolute terms and relative to the production available in the corresponding system.

Although the requirements in absolute values resemble the size of the fishery, changes in the fishing strategy are clearly reflected. Although the magnitude of the catches off Peru was reduced by a factor of more than three between the mid-1960s and the 1970s, the
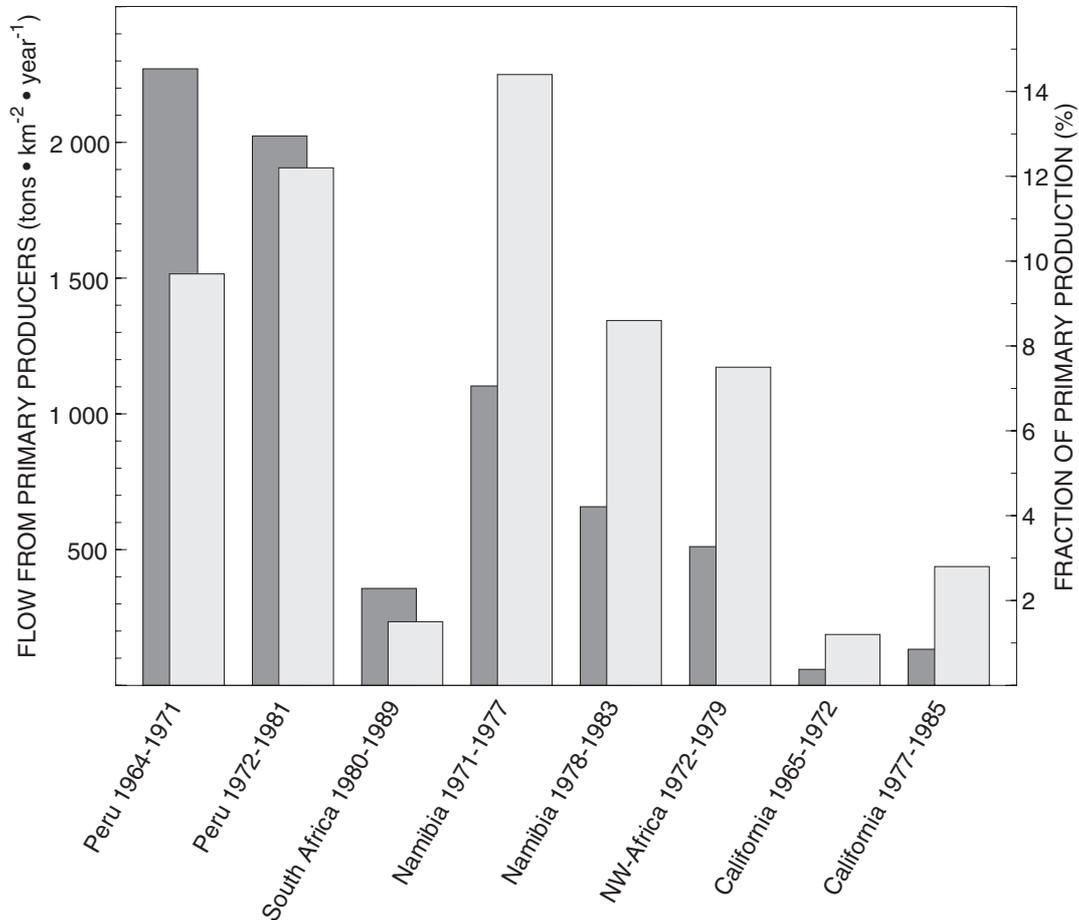
Fig. 8: Primary production required to sustain all catches in the upwelling systems and periods modelled

primary production required to sustain the fishery in the latter period decreased only marginally, because hake and sardine, which are both higher in the foodweb than Peruvian anchovy, were increasingly fished.

Whereas the fishery off Namibia (northern Benguela) required the largest share of the available primary production in the 1970s, and a relatively high one during the 1980s, the fraction of the primary production of the southern Benguela was very low. Not only was the fishery rather small in terms of absolute landings, but fishing took place low in the foodweb.

DISCUSSION

The model presents an update from the model of

the southern Benguela ecosystem presented by Baird *et al.* (1991). The models differ in that those authors explicitly included bacteria, micro- and mesozooplankton. In turn, the present model takes the demersal components of the system, including sharks, into account as additional top predators. As the periods modelled are also different (Baird *et al.* 1991 built their model on work published in the mid-1980s, whereas the model here describes the period 1980–1989) it is not straightforward to compare network statistics and flow patterns of the two models.

The present study has shown that the mesopelagic fish populations on the West Coast, although only lightly fished, play an integral role in the foodweb of the southern Benguela, particularly as a connecting link between zooplankton and hake. In terms of ecosystem considerations, this group is far from being

underexploited, as shown by their high ecotrophic efficiency, indicating that a high proportion of mesopelagic fish production is consumed as prey by other species in the system.

In the Benguela and similar systems, many of the more numerous species at various trophic levels are opportunistic feeders, with the result that species often have overlapping diets. When a particular food item is abundant, it is frequently preyed upon by a number of species (Crawford 1987). Therefore, it was suggested that, as with seabirds and other predators, species at lower trophic levels could take advantage if the food supply increased (Crawford *et al*. 1987). Mixed trophic impacts analysis of the present model showed that, indeed, zooplankton stongly favour all consumer groups in the Benguela, either directly or indirectly. However, there is also an indication of negative impact by competition, e.g. between round herring (the dominant component in the "other pelagic fish" group) and horse mackerel, and between anchovy and hake. The positive impact of anchovy as prey for hake is balanced by the negative impact through their competition for zooplankton. The trophic structure of the system therefore does not allow a straightforward interpretation of increases in primary or secondary production feeding directly into fish yield.

Top predators are relatively important in the southern Benguela system. The model indicates that the food-web on the upper trophic levels is rather tight, such that there may well be strong competition for food in years when small pelagic fish, particularly anchovy, are less abundant. Breeding success of penguins and cormorants in the southern Benguela is known to depend on food availability, whereas gannets are affected to a lesser extent (Crawford 1991). Marine mammals are estimated to consume relatively more in the southern Benguela than in other systems considered here. The relatively small fish yields in the southern Benguela, compared with those in the northern Benguela, Peru and north-west Africa, are balanced by greater consumption by mammals and seabirds in the southern Benguela.

As opportunistic generalists, the species in the southern Benguela are adapted to variability, and as such they are survivors, not optimal exploiters of their upwelling ecosystem. Therefore, less efficient pathways through the foodweb should be expected (L. Hutchings, pers. comm.). Indeed, the present results show that the transfer rates on the lower trophic levels were particularly low, and only 3–15% of the primary production was used to sustain catches in upwelling areas. The catches off California and South Africa were particularly low. This could also be due to the fact that ecosystem benefits other than fish yield, such as tourism (e.g. whale- and seabird-watching) and recreational activities such as sportfishing, may be considered more strongly in the management of the fisheries in these two ecosystems than in the others considered here.

Primary production in the southern Benguela peaks in summer, when light and upwelling-favourable winds are strongest. However, in summer, anchovy and sardine are found on the Agulhas Bank, where they spawn (Hampton 1992). Fish populations in upwelling areas are generally constrained by suitable spawning habitats (Parrish *et al*. 1983). Those authors postulate that, off Peru, the large Rossby radius, corresponding to a large extension of the offshore area directly influenced by upwelling, and a wide shelf off the anchovy's historically major spawning ground may counterbalance the strong offshore transport prevailing in that area, which allows a larger anchovy stock to be sustained there than in other upwelling systems. In turn, there appears to be a strong mismatch between fish reproduction and maximum food availability in the southern Benguela, explaining in part why the energy transfer from primary producers to small pelagic fish is so low in that region. The lower production of predatory fish there compared to the Peruvian system is a logical consequence, because there may simply not be enough food for more predators in the Benguela region.

It has been suggested that the environment favours either epipelagic fish species or groundfish species in the Benguela system, but not both simultaneously (Shannon *et al*. 1988). The model here shows that the 1980s was a period when the trophic impacts of semipelagic species (hake) and demersal fish, including sharks, were very important for the trophic flows, and the coupling between the upwelling system off the South African west coast and the shelf ecosystem on the South Coast appeared to have been very tight. The present results, together with the observations of demersal-pelagic counterbalance in several shelf systems (Daan 1980, Koslow 1984), emphasize the mixed properties of the southern Benguela region as an upwelling ecosystem with dominance of small pelagic fish, but also as a shelf ecosystem with important demersal flows.

Jarre-Teichmann and Christensen (1998) list a number of properties of upwelling systems that appeared to be global characteristics, from their comparison of the Peruvian, Californian, north-west African and northern Benguela ecosystems. These are:

(i)   general species composition and major flow patterns;
(ii) important role of small pelagic fish as a basis for the foodweb;
(iii) the total fraction of primary production required to sustain the fish groups in the ecosystem;
(iv) general correlation between total catch and the

trophic level of the fishery, and the primary production;

(v) low mean transfer of energy up the foodweb;

(vi) overall low system maturity.

The total mortality of small pelagic fish was estimated as being generally higher than in this model for the southern Benguela. However, with respect to the overall foodweb structure and energy flow, the Benguela does not appear to have any exceptional system properties which would render comparison with other upwelling areas invalid. Possible reasons for the particularly low fishery yield, in spite of high primary production and a relatively low trophic level of the fishery, have been discussed above.

Data series exist for the southern Benguela which will allow construction of similar trophic models for the 1990s, and render temporal comparisons in this ecosystem possible. For the northern Benguela, models are available, in principle, covering the 1970s and the 1980s up to the mid-1990s (Jarre-Teichmann and Christensen in press, 1971–1977 and 1978–83; Shannon and Jarre-Teichmann in prep. a, b, 1980–1989; Heymans 1996, 1990–1995), and these can be compared to the southern Benguela system after standardization. In addition, plans are underway to work up unpublished data on the northern Benguela. These data will be collated and analysed in an attempt to improve the models. Spatially linked models could also be possible, allowing separation of the characteristic properties of the South African south and west coast systems, and linking the northern and southern Benguela through the migrations of their shared stocks. The Benguela Ecology Programme laid the basis for understanding trophic flows in the Benguela ecosystem, and many of its results have been used in this model. An improved understanding of the trophic structure of the Benguela region from an ecosystem viewpoint, such as begun here, will also make it easier to model its dynamic response with respect to different management scenarios.

ACKNOWLEDGEMENTS

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