A MODEL OF TROPHIC FLOWS IN THE NORTHERN BENGUELA UPWELLING SYSTEM DURING THE 1980s

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A model of trophic flows through the northern Benguela between 1980 and 1989 was constructed using the ECOPATH approach. The model serves to close the temporal gap between models of the system for the 1970s and 1990s. The aim is to provide a workable model, with the intention of encouraging scientists working on different components of the ecosystem to collaborate to improve and update the model for more recent years. Ultimately, this type of model may form a basis for multispecies management approaches in the region. By the 1980s, sardine *Sardinops sagax* and hake *Merluccius* spp. stocks in the northern Benguela had both undergone a decline, yet were still heavily fished. Horse mackerel *Trachurus trachurus capensis* had increased over the previous decade and was the dominant pelagic species during the 1980s, with high catches. Production by some groups, such as goby *Sufflogobius bibarbatus*, mesopelagic fish and demersal fish, was insufficient to sustain other components of the system. In all, 1.5 million tons of goby, 1.7 million tons of mesopelagic fish and 0.7 million tons of demersal fish (excluding hake) were required to support predators in the northern Benguela. Total biomass in the northern Benguela during the 1980s was high, comparable to that of the Peruvian system in the 1960s and almost double that of the northern Benguela during the 1970s. Horse mackerel and hake catches were both high, with fishing on hake being ecologically more expensive. Biomass of benthic producers, meio- and macrobenthos were a quarter of the total biomass of these groups in the southern Benguela. The sensitivity of the model to parameter estimates is highlighted. Uncertainty about some of the parameters, thought to have major influences on the functioning of the model, is explored.

The Benguela upwelling system is one of the four major upwelling regions of the world. Situated off the west coast of Southern Africa, the system may be sub-divided into two oceanographic areas; a northern and southern region. The northern Benguela extends from 15 to 29°S. To date, only a few attempts have been made to model the trophic flows through the northern Benguela ecosystem. Using the ECOPATH modelling approach (Christensen and Pauly 1992), trophic functioning of the northern Benguela system has been examined for two periods, 1971–1977 and 1978–1983 (Jarre-Teichmann 1998, Jarre-Teichmann and Christensen 1998, in press). Heymans (1996) and Heymans and Baird (in prep. a, b) have modelled the flow of carbon through the system during the 1990s. The present study attempts to model trophic flows in the system between 1980 and 1989, using an alternative set of data, and closing the temporal gap between the previous models. Input data to this model are described and the main results presented.

At a workshop held in Cape Town in 1989, experts working on different species groups in the Benguela came together to discuss spreadsheet models for the 1980s, and to test and refine data. A preliminary model of the trophic flows in the southern Benguela system during that decade has been constructed (Jarre-Teichmann *et al*. 1998). The present paper documents a first attempt at an ECOPATH model for the northern Benguela, covering the decade 1980–1989, based on estimates used at the workshop and additional data published thereafter. What were perceived to be the most relevant and useful data were used, serving as a compilation of data on the components of the northern Benguela ecosystem, to show how the ecosystem is structured trophically. However, there is large uncertainty around many of the parameter estimates used in the model. The comparison with other models of the region, pertaining either to different periods of time, or to models of the southern Benguela, will form part of a larger comparative study of trophic flow models of the northern Benguela system. This paper aims to present an updated, workable "straw dog" model, to encourage scientists with specialized knowledge of components in the region to suggest improvements and to update these estimates for more recent years. By combining available expertise, a more representative model can be developed to assist in answering pertinent management questions in an ecosystem context. For a comparison of the model to those of the northern Benguela during other periods, readers are directed to Heymans *et al*. (in prep.), and to Shannon and Jarre-Teichmann (in press) for a

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comparison of the model to a similar model of the southern Benguela during the 1980s.

MATERIAL AND METHODS

The ECOPATH model

A widely-used ecosystem modelling tool called ECOPATH, originally based on the model of Polovina (1984), has been developed since 1987 by the International Centre for Living Aquatic Resources Management (ICLARM). The steady-state approach was recently extended to a dynamic simulation tool called ECOSIM (Walters *et al.* 1997).

A trophic flow budget is constructed using ECOPATH, creating a balance for each component ("box") in the model, and a balance for the flows between compartments. The box balance is based on Winberg's (1956) equation:

Consumption (*Q*) = Production (*P*) + Respiration (*R*) + Unassimilated food (*U*).

This means that, for each living group of organisms in a system in steady state over a given period of time, input balances output. A set of simultaneous linear equations describes the interactions between groups within the ecosystem:

Production of group (*i*) is balanced by the sum of predation on the group by other groups, export from the system (fishing or emigration) and other mortality:

Production by (*i*) = All predation on (*i*) + non-predatory biomass losses of (*i*) + fishery catches of (*i*) + other exports of (*i*) .

By re-expressing these terms as follows, a balance is established for each interaction of (*i*) with predator (*j*):

$$\text{Production by } (i) = B_i \times P/B_i$$
$$\text{Predatory losses of } (i) = \sum_j (B_j \times Q/B_j \times DC_{j,i})$$
$$\text{Other losses of } (i) = (1 - EE_i) \times B_i \times P/B_i \quad,$$

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_j is the consumption per unit of its biomass for consumer *j*,
$DC_{j,i}$ 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).

Therefore, for each group *i* within the ecosystem,

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

where Ex_i is the export of (*i*) from the system (e.g. by emigration or fishery catch).

The model requires the following input data for each component of the ecosystem: biomass (*B*), production per unit biomass (*P/B*), total consumption per unit biomass (*Q/B*), assimilation efficiency, diet composition, exports (mortality and other exports), ecotrophic efficiency (*EE*). One of *B*, *P/B*, *Q/B* or *EE* may be unknown, and will be estimated, as is respiration, through solving of the linear equations. A model is considered to be in mass-balance once acceptable results for the unknown parameter and respiration are obtained. Further analysis may then be undertaken.

ECOPATH has recently been expanded into "ECOPATH with ECOSIM", which incorporates a new dynamic simulation routine (Walters *et al.* 1997) that builds on the steady-state model of the mass-balance ECOPATH approach. Most important, this simulation routine facilitates exploring the dynamic effects of changes in the fishery on all components in the ecosystem, and thus to addressing questions of resistance and/or resilience of the ecosystem towards different fisheries management regimes.

For this paper, the alpha version of ECOPATH with ECOSIM (1998 version) was used to model trophic flows through the northern Benguela ecosystem. Preliminary results of ECOSIM simulations to study the effects of altered fishing strategies are presented elsewhere (Shannon and Jarre-Teichmann in press).

Data used to model the trophic flow of the northern Benguela

The northern Benguela model covers the shelf to approximately the 500-m depth contour, extending from 15 to 29°S, an area of 179 000 km². The period modelled is from 1980 to 1989. Unless otherwise stated, parameter values are presented in tons wet mass. Where literature-derived values of biomass, production or consumption were given in units of carbon, a conversion factor of 14.25 was used (Jarre-Teichmann *et al.* 1998). This value lies between 10 and 17.2, the lower and upper limits estimated by Cushing (1971) and Ryther (1969) respectively. For most groups, 20% of the food consumed was assumed to be unassimilated. Groups such as anchovy *Engraulis capensis*, sardine *Sardinops sagax*, goby *Sufflogobius bibarba-*

tus, other small pelagic fish and mesopelagic fish, which feed largely on plankton, were assumed to assimilate only 65% of food consumed. Bacteria were not an explicit part of the model, because insufficient information on bacterial activity is available for the northern Benguela system. Therefore, bacterial activity and consumption of bacteria remain "hidden" in the detritus compartment, as has been the case in other models (e.g. Christensen and Pauly 1993).

PHYTOPLANKTON

During the 1980s, phytoplankton biomass and production were estimated to be 2 558 300 tons C and 77 416 608 tons C·year^{-1} respectively (Brown *et al.* 1991). At the 1989 workshop, this value for production was increased by 18% to account for production of particulate dissolved organic carbon (PDOC), giving a *P/B* of 35.7·year^{-1}. *R/Q* was assumed to be 11.7%, and percentage export (by advection out of the system, i.e. not contributing to detritus) was taken as 3.7% of estimated primary production, i.e. 228 tons·km^{-2} (Brown *et al.* 1991).

MICROZOOPLANKTON (<200 μm)

As for the model of the southern Benguela (Jarre-Teichmann *et al.* 1998), most data for microzooplankton were based on information in Painting *et al.* (1992) and estimates made during the 1989 workshop. In accordance with higher meso- and macrozooplankton densities off Namibia (see below), microzooplankton was assumed to have higher densities there than along the west coast of South Africa, at 8 mg C·m^{-2} (cf. 6.3 mg C·m^{-2} in the southern Benguela, Jarre-Teichmann *et al.* 1998). Assuming an average water depth of 35 m in the productive region off Namibia, this is equivalent to a microzooplankton biomass of 50 120 tons C. *P/B* was estimated as 354·year^{-1} and gross growth efficiency (equal to 1-respiration/consumption) as 40%. Unassimilated food was assumed to be 20% (Stoecker 1984). In the absence of dietary information, microzooplankton were assumed to consume 40% phytoplankton, 40% bacteria (detritus box) and 20% microzooplankton, similar to values used for the southern Benguela (Jarre-Teichmann *et al.* 1998).

MESOZOOPLANKTON (200–2 000 μm)

Most of the data for this group were derived from copepods. Biomass was estimated at 179 000 tons C, *P/B* at 40·year^{-1} and *P/Q* at 30% (Hutchings *et al.* 1991). Assuming the ratio of carbon : wet mass is 0.04, as adopted by Hutchings *et al.* (1991) for meso-

zooplankton (from Parsons *et al.* 1984), biomass equates to 25 tons·km^{-2}. The diet of mesozooplankton consists of equal proportions of phytoplankton and microzooplankton (Hutchings *et al.* 1991).

MACROZOOPLANKTON (2–20 mm)

Most of the data from this group was derived from euphausiids. Hutchings *et al.* (1991) estimated the biomass at 107 400 tons C, *P/B* at 13year^{-1} and *P/Q* at 41%. Converting from carbon to wet mass (as for mesozooplankton), biomass equates to 15 tons·km^{-2}. Diet is comprised of 60% phytoplankton and 40% mesozooplankton (Hutchings *et al.* 1991).

GELATINOUS ZOOPLANKTON

Jellyfish, mainly *Chrysaora* sp., are abundant over the inner shelf zone off Namibia (Belkovich *et al.* 1986). Biomass of jellyfish and salps was assumed to be 1 million tons (wet mass) in the southern Benguela (Jarre-Teichmann *et al.* 1998). However, there is much uncertainty around this estimate. In the northern Benguela, jellyfish and salps are considered to be about five times the biomass in the southern Benguela, i.e. 5 million tons (wet). It was assumed that these organisms consist of 99% liquid, constituting 50 000 tons dry mass. Using a conversion factor of 0.4 from dry mass to carbon (Peters 1984), biomass is equivalent to 20 000 tons C. Following the method used in Jarre-Teichmann *et al.* (1998), *P/B* was calculated to be 0.371·year^{-1} and *P/Q* was assumed to be 41%, giving a *Q/B* of 0.904·year^{-1}. Diet was assumed to be 25% each of phytoplankton, bacteria (detritus), microzooplankton and mesozooplankton, as assumed for the southern Benguela.

ANCHOVY, SARDINE AND GOBY

Information on these small pelagics was taken from Hewitson and Cruickshank (1993), supplemented with estimates made during the 1989 workshop. The three groups were modelled separately. Biomass estimates for anchovy, sardine and goby were 252 000, 134 000 and 600 000 tons respectively. Their respective catches were 131 000, 53 000 and 216 tons·year^{-1}. For anchovy, *P/B* was 1.16·year^{-1} and *P/Q* was 9.98%. For sardine and goby, *P/B* was considered to be 1.1 and 0.9·year^{-1} respectively. *P/Q* was 10% for both sardine and goby.

Diet was estimated from the relative consumption of prey by juvenile and adult anchovy (see Table VII in Hewitson and Cruickshank 1993) from a dietary study off Namibia by King and MacLeod (1976). Anchovy diet comprised 33% phytoplankton, 4% mi-

crozooplankton, 31% mesozooplankton and 32% macrozooplankton.

King and MacLeod (1976) estimated consumption of sardine to be 56% phytoplankton, 8% microzooplankton, 18% mesozooplankton and 18% macrozooplankton. Information on the diet of gobies in the northern Benguela was taken from Crawford *et al*. (1985); 93% phytoplankton, 1% mesozooplankton and 6% macrozooplankton.

HORSE MACKEREL

Off Namibia, biomass of horse mackerel *Trachurus trachurus capensis* was estimated to have been 2.4 million tons in 1980, dropping to 2 million tons in 1984/1985 (Babayan *et al*. 1986, Vaske *et al*. 1988). In 1986, the stock was estimated to be between 3.46 and 5.67 million tons (Shcherbich *et al*. 1986). For the northern Benguela model, 2.5 million tons was considered representative of the horse mackerel biomass in the 1980s.

Mean annual catches from the period 1980–1984 were 605 344 tons·year^{-1} (Shcherbich *et al*. 1986). However, such high catches were considered unsustainable following the major decline of 66% in horse mackerel biomass between the early and mid 1980s. Subsequently, Bergh *et al*. (1986) recommended a total allowable catch (*TAC*) of only 232 000 tons·year^{-1}. Despite this, catches seem to have remained at a high level. By subtracting catches of horse mackerel in the southern Benguela (Marine and Coastal Management [MCM], unpublished data) from mean annual catches of horse mackerel in the South-East Atlantic (F.A.O. 1989, 1992), catches in the northern Benguela during the 1980s were estimated at around 600 000 tons·year^{-1}, the value used in the model.

A *P/B* value of 0.52·year^{-1} was used in the northern Benguela model, the same value used for the southern Benguela (Jarre-Teichmann *et al*. 1998). The daily ration for 24–32 cm horse mackerel from Namibian waters was estimated at between 6.6 and 12.5% of fish body mass (Andronov 1985), corresponding to a very high annual *Q/B* of about 35·year^{-1}. However, given that this value does not include the larger size-classes, a *Q/B* of 5.2·year^{-1}, corresponding to a *P/Q* of 10%, was taken to be representative of the horse mackerel population. Assimilation efficiency was taken to be 70%, based on a diet of zooplankton, which constituted more than 80% of their food.

Small horse mackerel (16–17 cm) consume mainly mesozooplankton (copepods), whereas larger (38–40 cm) fish consume macrozooplankton (euphausiids) and fish such as lanternfish *Lampanyctodes hectoris*, anchovy and sardine (Andronov 1985, Konchina 1986). For the model, the proportion of prey in the diet of horse mackerel was allocated according to

Andronov (1983), who reported diet composition by mass for four different size-classes, corresponding to ages 1, 2, 3 and 4–6 years. Based on the stock sizes in those age-classes, estimated by Shcherbich *et al*. (1986) for the period 1980–1985, the mean proportion of the total estimated biomass for age-classes 1–6 years was calculated, and used to weight Andronov's (1983) diet compositions. The weighted diet for fish aged 1–6 years is 17.9% mesozooplankton, 78.7% macrozooplankton, 0.1% cephalopods, 0.8% goby and 2.5% lanternfish. Because only 7% of the Namibian horse mackerel stock were of fish aged seven years and older (Shcherbich *et al*. 1986), the diet of fish aged 1–6 years was considered to represent that of the whole stock.

MESOPELAGIC FISH

Hewitson and Cruickshank (1993) gave a lower biomass limit of 800 000 tons for lanternfish (Myctophidae) in the northern Benguela. Production and consumption were estimated at 69 200 and 691 700 tons C·year^{-1} respectively, corresponding to a *P/B* of 1.23·year^{-1} and a *P/Q* of 10% (Hewitson and Cruickshank 1993). Mean annual catches of lanternfish in Namibian waters were taken to be 1 000 tons·year^{-1} (1989 workshop). Hewitson and Cruickshank (1993) assumed the diet composition to be 40% mesozooplankton and 60% macrozooplankton.

A biomass of 10 000 tons of lightfish *Maurolicus muelleri* is assumed for the northern Benguela (1989 workshop). Values of *P/B*, *P/Q*, *U* and dietary composition were assumed to be the same as for lanternfish. There are no records of commercial catches of lightfish in the region.

OTHER SMALL PELAGIC FISH

Information is scarce on other small pelagic fish, such as flying fish (Exocoetidae) and saury (Scomberesocidae) in the northern Benguela (Hewitson and Cruickshank 1993). The biomass of this group was estimated at 33 000 tons (1989 workshop) and *P/B* and *P/Q* were assumed to be 0.9·year^{-1} and 10% respectively. Catches of other small pelagic fish off Namibia are negligible in Namibian waters. The diet of saury and flying fish was considered to consist of 81% mesozooplankton, 14% macrozooplankton, 3% jellyfish and 2% other organisms, such as polychaetes and crustaceans.

Round herring *Etrumeus whiteheadi*, also known locally as redeye, is not of commercial importance in Namibian waters and there is little information on the species from that region. It is considered to be of little importance to the trophic flow of the northern

Benguela and was not assigned to a separate functional group in the model. Where data existed on consumption of round herring (in very small quantities) by other species, it was directed to the small pelagics group in the model.

CHUB MACKEREL

Chub mackerel *Scomber japonicus* are believed to migrate between the southern and northern Benguela systems (Crawford and de Villiers 1984). It is assumed here that they spend equal time in each system, i.e. that the biomass in the northern Benguela is equivalent to the estimated 62 500 tons used in the southern Benguela model (Jarre-Teichmann *et al.* 1998). Values for *P/B* and *P/Q* were taken as 0.6·year^{-1} and 10% respectively, as assumed for the southern Benguela (Jarre-Teichmann *et al.* 1998). The mean annual catch in the northern Benguela was 45 000 tons·year^{-1} for the period 1971–1982 and 37 000 tons·year^{-1} for the period 1980–1982 (Crawford and De Villiers 1984). Between 1982 and 1989, mean annual catches in the South-East Atlantic were 37 545 tons·year^{-1} (F.A.O. 1989, 1992). Off South Africa, annual catches of chub mackerel during the 1980s averaged 6 364.4 tons·year^{-1} (MCM unpublished data). Subtracting this value from the total annual catches taken in the South-East Atlantic gives an mean annual of 31 181 tons·year^{-1} for the northern Benguela for the 1980s.

Heavy fishing pressure on chub mackerel in the 1970s was considered to have depleted their biomass in the Benguela system. Using relative proportions obtained from Virtual Population Analysis (O. Centurier-Harris, formerly MCM, unpublished data) to weight Baird's (1978) diet for small and medium-sized mackerel, the diet was estimated to consist of 80.3% macrozooplankton, 1.4% mesozooplankton, 1.7% anchovy, 0.9% round herring and 15.7% lanternfish. Taking into account the greater proportion of young fish eating zooplankton, assimilation efficiency was assumed to be 75%. Typically, carnivorous fish assimilate 80% of food consumed (Winberg 1956).

HAKE

Two species of Cape hake are found off southern Africa, the deep-water hake *Merluccius paradoxus* and the shallow-water species *M. capensis*. Mean annual biomass of *M. capensis* in the region north of 25°S (ICSEAF Divisions 1.3 and 1.4) was between 784 000 tons for the period 1968–1984 and 714 400 tons for the period 1980–1984 (Schumacher 1987). Between 20 and 29°S (ICSEAF divisions 1.4 and 1.5), total hake biomass between 1983 and 1987 was around 980 000 tons (Abelló *et al.* 1988). For the same

region and period, Gordoa and Macpherson (1989) estimated hake biomass to be 930 000 tons, consisting of 61% *M. capensis* and 39% *M. paradoxus*. In the model, a combined mean annual hake biomass of 1.3 million tons was assumed for the whole northern Benguela region (ICSEAF divisions 1.3, 1.4 and 1.5 combined) during the 1980s.

Mean annual catches of Cape hakes in the region north of 29°S (ICSEAF divisions 1.3, 1.4 and 1.5) were 280 050 and 445 740 tons·year^{-1} for the periods 1980–1984 and 1974–1984 respectively (Andrew and Butterworth 1987). By subtracting catches of hake off South Africa (Leslie 1998a, b) from the hake catches in the South-East Atlantic (F.A.O. Fishery Statistics 1989 and 1992), catches of 350 000 tons·year^{-1} were assumed for the northern Benguela. Taking all estimates into account, annual catches in the northern Benguela during the 1980s were taken to be around 300 000 tons·year^{-1}.

Using Kogan's (1987) method for calculating daily ration of *M. capensis*, Andronov (1987) estimated that hake of 25–28 cm consume between 2.0 and 4.7% of their body mass per day. This corresponds to *Q/B* values of between 5.9 and 17.2·year^{-1} for young hake. Hake of this size would be mostly one-year-olds (Leslie 1998a). Jarre-Teichmann *et al.* (1998) used a *Q/B* value of 2.4·year^{-1} for hake aged 3 years and older and 8.0·year^{-1} for younger hake.

Excluding cannibalism, natural mortality of Cape hake off Namibia was estimated to be between 0.48 and 0.70·year^{-1} (95% confidence levels, Gasyukov and Dorovskikh 1989a). More specifically, instantaneous natural mortality rates were estimated to be in the range 0.5–0.6·year^{-1} for hakes aged 3 years and 0.7·year^{-1} for hakes aged 4 years (Gasyukov and Dorovskikh 1989b). For 1985, fishing mortality for ages 3–7 years was estimated at 0.514·year^{-1} (Schumacher 1987). Under equilibrium conditions, *P/B* is equivalent to the sum of natural and fishing mortality (in the present case 0.5 + 0.5·year^{-1}), equal to 1.0·year^{-1}. By assuming *Q/B* to be 5.0·year^{-1} for the northern Benguela hake population, *P/Q* would be 20%. However, because large hake would have been removed through heavy fishing pressure during the period modelled, it is likely that *P/Q* was higher, at 22%. *Q/B* is then 4.545·year^{-1}, the value used in the model.

Andronov (1983) and Roel and Macpherson (1988) investigated the diet of hake off Namibia. Andronov (1983) presented feeding data for three size-classes of *M. capensis*, corresponding to hake aged 0–1, 2 and 3 years. *M. capensis* aged 4 years and older accounted for only 8% of the total biomass in 1984. Therefore, it was reasonable to assume that the diet of 4+ year-olds was the same as for 3-year-olds.

Using mean mass-at-age data for 1984, (Schumacher 1987) and number-at-age data for 1984 (Gordoa and Macpherson 1989), biomass of *M. capensis* in each age-class was expressed as a proportion of total biomass. This gave an indication of the relative proportions of biomass likely to have constituted the three size-groups in 1982, the year for which detailed feeding data were available. The proportions were used to weight Andronov's (1983) diet for the three size/age-classes, in order to provide a mean weighted diet (% by mass) for *M. capensis* off Namibia: 1.6% mesozooplankton, 77.1% macrozooplankton, 2.7% jellyfish, 0.1% cephalopods, 0.9% anchovy, 0.1% lanternfish, 5.6% *M. capensis*, 5.6% goby, 3.7% macrobenthos and 2.7% digested remains.

Roel and Macpherson (1988) presented the frequency of prey items in the stomachs of a number of size groups of both *M. capensis* and *M. paradoxus* off Namibia for the period 1981–1986. Following the same procedure as described above for Andronov's (1983) data, weighted diets for both hake species were calculated for the data of Roel and Macpherson (1988). To convert length-classes to age-classes, average age-length data for both hake species combined (Leslie 1997) were used. Diet composition for both species were combined, based on the relative proportion of each species (*M. capensis* and *M. paradoxus* constituted 69 and 31% respectively – Abelló *et al*. 1988). This resulted in a frequency of prey items in the stomachs of 61.9% macrozooplankton, 19.0% mesopelagic fish, 3.6% hake, 14.4% other fish and 1% cephalopods. Other fish included gobies, snoek, horse mackerel and many species of demersal fish.

Konchina (1986) reported that, off Namibia, hake aged 3 years and older consume mainly fish, such as goby, their own young, horse mackerel, myctophids and jacopever *Helicolenus dactylopterus*. In the southern Benguela model (Jarre-Teichmann *et al*. 1998), hake diet consisted of considerably less zooplankton (25%), a greater proportion of mesopelagic fish (34%) and 11% demersal fish, excluding hake.

Considering all of the above, modelled hake diet (% mass) was considered to consist of 50% macrozooplankton, 3% jellyfish, 1% cephalopods, 1% anchovy, 6% hake, 6% goby, 4% macrobenthos, 18% mesopelagic fish, 10% other demersal fish and 1% horse mackerel.

OTHER DEMERSAL FISH

This group includes West Coast sole *Austroglossus microlepis*, kingklip *Genypterus capensis*, rattails (e.g. *Malacocephalus laevis* and *Coelorinchus simorhynchus*), gurnard *Chelidonichthys* spp., jacopever, ribbonfish *Lepidopus caudatus* and monkfish, *Lophius*

spp. Biomass was estimated to be 155 834 tons, catches at 35 847 tons·year^{-1}, *P/B* at 1.0·year^{-1} (as for hake) and *P/Q* at 10% (1989 workshop). Unpublished dietary information was weighted according to biomass estimates of the various prey species, giving a mean dietary composition of 8.3% mesozooplankton, 32.4% macrozooplankton, 1% round herring, 0.5% lanternfish, 1.4% lightfish, 2.2% goby, 4.7% other small pelagics, 10.6% hakes, 10.6% other demersal fish, 13.3% cephalopods and 15% benthic macrofauna.

CEPHALOPODS

This group consists mainly of the squids *Loligo vulgaris reynaudii* and *Todarodes angolensis*. Biomass was estimated to be 30 000 tons, catches at 20 tons·year^{-1}, *P/B* at 1.5·year^{-1} and *P/Q* at 10% (1989 workshop). Diet was weighted by relative biomasses of various species, resulting in a diet consisting of 10% macrozooplankton, 10% horse mackerel, 5% lightfish, 50% lanternfish, 10% goby, 5% hake and 10% cephalopods (1989 workshop). This diet is similar to that of the Angola flying squid *Todarodes angolensis* reported for the northern Benguela by Lipiński (1992).

LARGE PELAGIC FISH

Tuna — The biomass of tuna *Thunnus* spp. was estimated to be 4 500 tons in the northern Benguela, and catches (recreational and commercial combined) of albacore *T. alalunga*, yellowfin *T. albacares* and bigeye *T. obesus* amounted to 1 800 tons·year^{-1} (Penney *et al*. 1991a). Tuna have very fast metabolic rates, equivalent to those of mammals of similar size (Graham and Laurs 1982). Natural mortality (*M*) was assumed to be 0.2·year^{-1}, the value estimated for *T. alalunga* from the North Pacific, as calculated from Pauly's (1980) regression and using values for K and L_∞ taken from Laurs and Wetherall (1981). Using F.A.O. catch data, and the biomass estimates given in Penney *et al*. (1991a) for the three tuna species combined, fishing mortality (*F*) was estimated to be 0.27·year^{-1} in the South-East Atlantic, so that *P/B* = *F* + *M* = 0.47·year^{-1}. *P/Q* was assumed to be 5%. Diet composition was calculated according to that reported for the southern Benguela by Penney *et al*. (1991b): 20% zooplankton, 3% lanternfish, 4% lightfish, 2% goby, 4% saury, 15% anchovy, 15% sardine, 7% round herring, 5% horse mackerel, 5% chub mackerel, 15% cephalopods and 5% hake. However, because round herring are uncommon in the northern Benguela, this proportion was split equally between anchovy, sardine, other small pelagic fish and gobies.

Snoek — Off Namibia, biomass of snoek *Thyrsites*

atun was estimated at 139 900 tons and catches for the period 1980–1988 at 28 203 tons·year^{-1} (Penney *et al*. 1991a). *P/B* was calculated to be approximately 0.5·year^{-1} based on a fishing mortality of 0.23·year^{-1} and natural mortality of 0.25·year^{-1}. *P/Q* was assumed to be 10% (1989 workshop). As suitable diet data were not available for snoek in Namibian waters for the 1980s, Dudley's (1987) diet data for the southern Benguela were used. Taking into account the seasonal inshore-offshore migration and the relative contributions to the overall diet of the snoek sampled inshore and offshore, the resulting diet was 17.1% macrozooplankton, 3.5% lanternfish, 1.2% lightfish, 47.9% anchovy, 3.2% sardine, 6.3% round herring (re-allocated in equal parts to anchovy, sardine, other small pelagics and goby), 1.4% horse mackerel, 0.5% cephalopods, 7.8% hake and 11.1% other demersals.

Kob — *Agyrosomus inodorus* biomass was estimated at 9 600 tons and catches for the period 1984–1988 at 1 220 tons·year^{-1} (Penney *et al*. 1991a). *P/B* and *P/Q* were assumed to be 0.36·year^{-1} and 10% respectively (1989 workshop). The diet of kob has not been reported for the northern Benguela, so the diet described for kob in the southern Benguela (Penney *et al*. 1991b) was used: 6.8% zooplankton, 51% anchovy, 0.6% sardine, 3.3% horse mackerel, 1.1% chub mackerel, 6.1% cephalopods, 8.8% macrobenthos, 8.2% hake, 0.4% kob and 13.7% other demersal fish.

Tuna, snoek and kob were grouped into the large pelagic fish component, with a combined biomass of 154 000 tons and catches of 31 223 tons·year^{-1}. The weighted (by biomass) estimates of *P/B* and *P/Q* were estimated at 0.49·year^{-1} and at 9.9% respectively. Weighted diet for large pelagic fish was 16.5% macrozooplankton, 3.3% lanternfish, 1.2% lightfish, 0.1% goby, 0.1% other pelagics, 47.1% anchovy, 3.4% sardine, 5.9% round herring, 1.6% horse mackerel, 1.3% cephalopods, 7.6% hake, 0.2% chub mackerel, 10.9% demersal fish and 0.5% macrobenthos. The round herring portion was split equally among anchovy, sardine, other small pelagic fish and goby.

CHONDRICHTHYANS

Estimates of shark biomass or catches are not available for Namibian waters. Therefore, it was assumed that the biomass concentration there approximated that of the west coast of South Africa, i.e. around one-quarter of the total biomass of chondrichthyans in the southern Benguela model (Jarre-Teichmann *et al*. 1998). Scaling this to the relative area of the northern Benguela gave a biomass of 67 180 tons of chondrichthyans and a catch of 610 tons·year^{-1}. Diet composition was assumed to be the same as the adjusted diet of chondrichthyans in the southern Benguela: 9.3% anchovy, 1.2% sardine, 1.5% chub mackerel, 1.2% horse mackerel, 9% round herring, 0.5% small pelagic fish, 0.4% large pelagic fish, 10% cephalopods, 41.5% demersal fish, 0.4% hake, 10.4% macrobenthos, 0.2% seals and 23.4% sharks (Jarre-Teichmann *et al*. 1998). *P/B* was assumed to be 0.5·year^{-1} and P/Q to be 25%, as used in the southern Benguela model.

SEABIRDS

Data on seabirds were taken from Crawford *et al*. (1991). Biomass was estimated at 1 867 tons, production at 219 tons·year^{-1}, giving a *P/B* of 0.16·year^{-1}. Total consumption was estimated at 15 764 tons C·year^{-1} (Table XVI in Crawford *et al*. 1991), giving a *Q/B* of 120.3·year^{-1} and *P/Q* of 0.13%. Assimilation efficiency for seabirds was assumed to be 74% (Crawford *et al*. 1991). Seabirds in the northern Benguela consume prey in the following proportions by mass (Crawford *et al*. 1991): 0.3% mesozooplankton, 4.3% macrozooplankton, 4.4% cephalopods, 1.1% sardine, 21.4% anchovy, 0.7% round herring, 0.5% horse mackerel, 2.4% lightfish, 2.9% lanternfish, 46.6% goby, 2.4% saury, 0.6% other planktivorous fish, 10.3% hake, 1.5% other demersal fish, 0.3% snoek, 0.2% seals, 0.1% seabirds and <0.1% chub mackerel.

SEALS

Biomass of the Cape fur seal *Arctocephalus pusillus pusillus* was estimated at 51 763 tons and production as 48 437 tons·year^{-1} (1989 workshop), giving a *P/B* of 0.94·year^{-1} and an estimated catch of 1 512 tons·year^{-1}. *P/Q* was assumed to be 4.9%. Assimilation efficiency was considered to be 80%, the same as that for carnivorous mammals (Furness 1984). The diet composition for seals off Namibia for the period 1974–1985 was reported by David (1987) to be 3.6% anchovy, 23.6% horse mackerel, 2.6% sardine, 0.7% lanternfish, 52.9% goby, 4.6% snoek, 3.5% hake and 8.4% cephalopods.

WHALES AND DOLPHINS

Biomass estimates are not available for most species of whale and dolphin off southern Africa. A total of around 1 220 tons was estimated for dusky *Lagenorhynchus obscurus* and Heaviside's *Cephalorhynchus heavisidii* dolphins in the northern Benguela (1989 workshop). Although not as numerous as off South Africa, other dolphin species and migratory whales are also common in Namibian waters. The biomass was quadrupled to account for other cetaceans. A *P/B* of 1.0·year^{-1} was used for the model. This

Table I: Parameters used to model the northern Benguela upwelling system during the 1980s; the ratio of production to biomass (*P/B*), consumption per unit biomass (*Q/B*), gross efficiency (*P/Q*), ecotrophic efficiency (*EE*), the proportion of production used in the system for predation and catches

Group	Biomass (tons·km^{-2})	Annual catch (tons·km^{-2}·year^{-1})	*P/B* (·year^{-1})	*Q/B* (·year^{-1})	*P/Q* %	*EE*
Phytoplankton	203.664	0.000	35.700	0.000		0.912
Benthic producers	3.210	0.000	15.000	0.000		0.500
Microzooplankton	3.990	0.000	354.000	1 770.000	20	0.977
Mesozooplankton	25.000	0.000	40.000	133.333	30	0.437
Macrozooplankton	15.000	0.000	13.000	31.707	41	0.843
Gelatinous zooplankton	27.933	0.000	0.371	0.905	41	0.115
Anchovy	1.408	0.732	1.160	11.717	10	0.997
Sardine	0.749	0.296	1.100	11.000	10	0.934
Goby	8.076	0.001	0.900	9.000	10	0.990
Horse mackerel	13.966	3.382	0.520	5.200	10	0.917
Mesopelagic fish	9.274	0.006	1.230	12.300	10	0.990
Other small pelagic fish	0.754	0.000	0.900	9.000	10	0.990
Cephalopods	0.279	0.000	1.500	15.000	10	0.956
Chub mackerel	0.349	0.174	0.600	6.000	10	0.911
Hake	7.263	1.676	1.000	4.545	22	0.998
Other demersal fish	3.670	0.200	1.000	6.667	15	0.990
Large pelagic fish	0.860	0.174	0.490	2.450	20	0.977
Seabirds	0.010	0.000	0.160	120.300	0.1	0.000
Seals	0.289	0.008	0.940	19.184	4.9	0.044
Cetaceans	0.028	0.000	1.000	12.658	7.9	0.000
Chondrichthyans	0.375	0.003	0.500	2.000	25	0.952
Meiobenthos	5.957	0.000	4.000	33.333	12	0.950
Macrobenthos	28.296	0.000	1.200	10.000	12	0.950
Detritus	840.000	0.000				0.761

value was higher than that used in the southern Benguela model, because fewer whales are believed to live in Namibian waters, but lower than the value of 1.6·year^{-1} used at the 1989 workshop for dolphins alone. Assimilation efficiency was estimated at 79% (Gaskin 1982) and gross efficiency was assigned a value of 8%. Diets of dolphin species were obtained from Sekiguchi *et al*. (1992). The weighted diet composition was estimated to be 1.4% anchovy, 1.4% sardine, 19.3% lanternfish, 6.9% goby, 11.7% other small pelagics, 27.5% hake and 31.8% cephalopods.

BENTHOS

There is little information on this component in the northern Benguela ecosystem. Therefore, parameters and diet compositions were assumed to be similar to those in other upwelling systems, i.e. a *P/B* of 1.2·year^{-1} for macrobenthos and 4.0·year^{-1} for meiobenthos, a *P/B* of 15·year^{-1} for benthic producers and a *P/Q* of 12% for both macrobenthos and meiobenthos (Jarre-Teichmann *et al*. 1998). The minimum biomass necessary to sustain the food requirements for the other system components was computed, assuming an ecotrophic efficiency of 95%. Diet composition of macrobenthos consisted of 5% benthic producers, 8% meiobenthos, 7% macrobenthos and

80% detritus. The diet of meiobenthos consisted of 5% benthic producers and 95% detritus. Biomass of benthic producers was estimated based on the grazing demand by benthos and an ecotrophic efficiency of 50%, taking into account that benthic producers such as macroalgae are often only consumed after decaying.

DETRITUS

This category receives inputs from other groups in the form of faecal material, or through residual mortality. Using the method of Pauly *et al*. (1990), Regier *et al*. (1990) and Pauly *et al*. (1993) for a euphotic zone depth of 35 m and primary production of 510.23g C·m^{-2}, the biomass of detritus in the northern Benguela was calculated to be 59.027g C·m^{-2} (corresponding in wet mass to 841 tons·km^{-2}). Additional information was not included in the model.

RESULTS AND DISCUSSION

Balancing the model

Values of parameters for which the model was balanced are shown in Table I.

ZOOPLANKTON

Phytoplankton biomass in the northern Benguela was 2.5 times more than in the southern Benguela during the 1980s. Therefore, it was assumed that modelled diets of micro- and mesoplankton should be altered to reflect greater phytoplankton consumption, so that microzooplankton consumed 50% phytoplankton, 10% microzooplankton and 40% detritus, and mesozooplankton consumed 75% phytoplankton, 20% microzooplankton and 5% mesozooplankton. The diet of macrozooplankton was unaltered.

MESOPELAGIC FISH

If biomass of lightfish is assumed to be 10 000 tons, as estimated at the 1989 workshop, biomass of mesopelagics in the northern Benguela is insufficient to support feeding by other groups. The model was used to estimate the biomass required, given an ecotrophic efficiency of 99%. The modelled system required 1.66 million tons of mesopelagic fish. If, as in the southern Benguela system (Armstrong *et al*. 1991), lightfish are assumed to be present in equal proportion to lanternfish in the northern Benguela system, then this equates to a biomass of 830 000 tons each for these mesopelagic fish. This is an acceptable value for lanternfish, given that Hewitson and Cruickshank (1993) considered 800 000 tons to be a reasonable lower limit to the biomass of lanternfish in the northern Benguela. Mesopelagic fish biomass is considered to be around 1.5 million tons in Namibian waters (L. Hutchings, MCM, unpublished data).

GOBY

There was insufficient goby to support consumption by other groups in the model. The model-estimated biomass of 1.45 million tons is more than double that estimated by Hewitson and Cruickshank (1993), who caution that little was known about the goby stock during the period. It seems likely that goby, like horse mackerel, were able to take advantage of the increase in the availability of plankton food when anchovy and sardine became less abundant during the 1980s. Crawford (1987) suggested that more than one species may benefit from energy made available when another fish resource collapses.

LARGE PELAGIC FISH

Making use of dietary composition data for large pelagic fish derived for the southern Benguela caused problems in the smaller pelagic species in the northern Benguela model. In the southern Benguela model, anchovy, sardine, goby and other small pelagic fish constituted 56.6% of the diet of large pelagic fish. The relative proportions of those groups in the modelled diets of large pelagic fish (tuna, snoek and kob) were recalculated to reflect the relative proportion of anchovy and sardine production in the northern Benguela during the 1980s. This resulted in large pelagic fish consuming 9.5% anchovy, 4.8% sardine, 38.6% goby and 3.7% other small pelagic fish. Further adjustments were required, so that anchovy constituted 7% and sardine 7.3%. The fraction of cephalopods was reduced from 1.3 to 0.2%, and the remainder was added to the proportion of macrozooplankton consumed in the model. Modelled consumption of hake was reduced from 7.7 to 6%, with 0.7% added to horse mackerel and the remainder added to macrozooplankton.

CHONDRICHTHYANS

The relative proportions of anchovy and sardine in the modelled diets of chondrichthyans were changed to 6.8 and 3.7% respectively, to reflect the relative production of the two prey species.

CEPHALOPODS

Ecotrophic efficiency for cephalopods was estimated in the initial realization of the model to be >700%, indicating that requirements by other components in the model substantially exceeded simulated cephalopod production. This was because large quantities of cephalopods are consumed by hake, other demersal fish, cephalopods, seals and chondrichthyans. Because squid beaks tend to be retained in the stomachs of predators, it is likely that the contribution of cephalopods to diets of predators was overestimated. Given that hake were much more abundant in the northern than in the southern Benguela in the 1980s, much of the consumption of cephalopods was attributed instead to hake. The proportion of cephalopods in the diet of hake was reduced from 1 to 0.1%, in agreement with dietary composition by percentage mass (Andronov 1983), and the remainder was added to the proportion of macrobenthos consumed. The fraction of cephalopods in the diet of other demersal fish was reduced from 13.3% to only 0.1%. The fraction of cephalopods in the diet of seals was reduced to 1% and the remainder added to hake. The proportion of cephalopods consumed by chondrichthyans was switched with the fraction of hake consumed, so that chondrichthyans consumed 0.4% cephalopods and 10.5% hake. Cephalopods and hake in the diet of cephalopods were switched, and the proportion of cephalopods further reduced to 1% (within group predation), with the
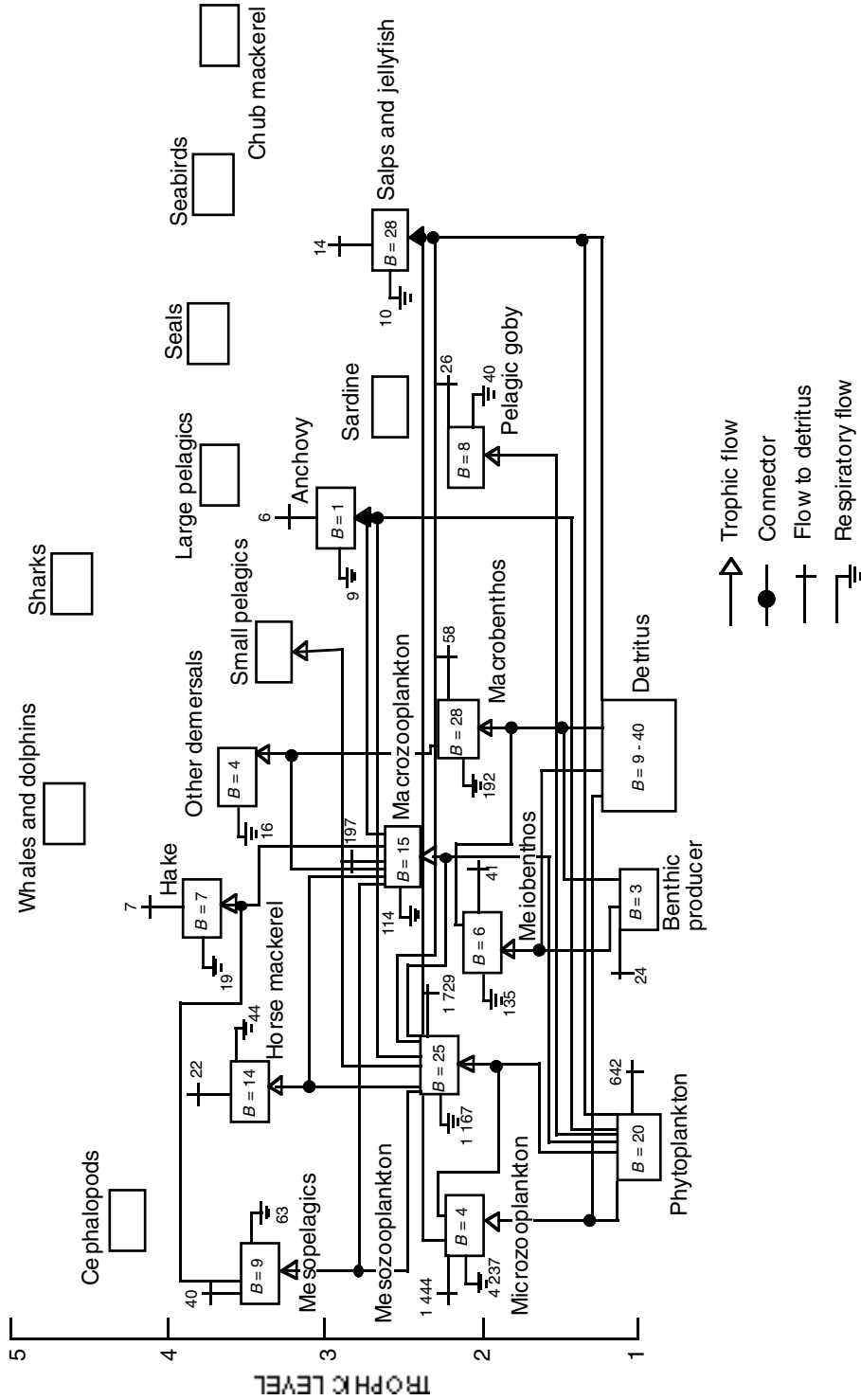
Fig. 1: Diagram of trophic flows in the northern Benguela for the 1980s. Boxes are arranged along the vertical axis according to their trophic level. Flows are in tons (wet mass)·km^{-2}·year^{-1}. Biomass of a component is denoted by B where B >1 ton·km^{-2}. Flows leave the boxes in the upper half and enter in the lower half. Values are indicated for respiration and flows to detritus, with those <5 tons·km^{-2}·year^{-1} (i.e. 0.4 ppt of total consumption) omitted for clarity

Table II: Summary statistics for the trophic model of the northern Benguela upwelling system in the 1980s

Parameter	Biomass (tons·km⁻²)	Flow (tons·km⁻²·year⁻¹)
Total biomass (excluding detritus)	360	
Sum of all consumption		11 743
Sum of all exports		1 254
Sum of all flows to detritus		4 265
Total system throughput		23 327
Sum of all production		10 034
Net system production		1 254
Sum of all respiratory flows		6 065
Total net primary production		7 319
Total catches		7

remainder re-allocated to mesopelagic fish. Hake then constituted 10% of the diet of cephalopods.

The biomass of *Todarodes angolensis* was estimated to have ranged between 8 401 and 25 600 tons between 1983 and 1988 (Lipiński 1992). As other cephalopod species also occur in Namibian waters, a total biomass of 50 000 tons for the northern Benguela was not considered an overestimate.

HAKE

In order to balance the model, it was necessary to readjust the proportions of the various pelagic fish groups in the diet of hake. The diet of hake was adjusted to 1.6% mesozooplankton, 49% macrozooplankton, 3% jellies and salps, 18% mesopelagic fish, 0.1% cephalopods, 1% anchovy, 8.8% macrobenthos, 4% goby, 4.5% horse mackerel, 0.1% large pelagics (snoek), 4.9% hake and 5% other demersal fish.

OTHER DEMERSAL FISH

It was necessary to allow the model to estimate the biomass of this poorly known group, assuming ecotrophic efficiency of 99%, given the heavy feeding pressure on this group in the Benguela system (Jarre-Teichmann *et al*. 1998). Modelled biomass of other demersal fish was required to be 657 000 tons, i.e. half that of hake. This was considered to be a reasonable estimate. *P/Q* was increased to 15% to account for smaller fish originally omitted from the model estimates, as was the case for the southern Benguela (Jarre-Teichmann *et al*. 1998). Diet of other demersal fish is not very well known. This group caused high predation mortality on itself and on other small pelagics and cephalopods. The situation was improved by reducing the proportion of other small pelagics in the modelled diet of demersal fish from 5.7 to 2%, reducing cephalopods in the diet of demersals from 13.3 to 0.1%, and

reducing demersals feeding on themselves from 10.6 to 10%. The remaining dietary components were added to macrobenthos. Macrobenthos then constituted 38.1% of the diet of demersals, equivalent to about half the proportion of macrobenthos in the diet of demersal fish in the southern Benguela system. This is plausible, given the oxygen deficient benthic environment in the northern Benguela.

OTHER SMALL PELAGIC FISH

The initial model did not include sufficient small pelagic fish to support the system. Therefore, biomass was estimated by the model, assuming a high ecotrophic efficiency of 99%, indicating the high demand of small pelagic fish as prey items for larger fish in the model. Biomass required is about four times that initially used, i.e. 135 000 tons.

SEALS

The model showed that seals caused high mortality of large pelagic fish, in particular snoek. Snoek in the diet of seals was reduced to 3.5% and the remainder was added to hake, which constituted 12% of the model seal diet. The proportion of anchovy in the diet of seals was reduced from 3.6 to 2% and the remainder added to sardine, which was more abundant in the system.

SEABIRDS

The modelled consumption of anchovy by seabirds was too high and was reduced from 21.4 to 18%. The remainder was added to sardine to reflect the relative production of these two small pelagic species in the system.

Summary statistics

Summarized flows through the northern Benguela model for the 1980s are shown in Table II. Total biomass (excluding detritus) in the northern Benguela during the 1980s was comparable to that off Peru in the 1960s, and was high in comparison to other upwelling systems modelled by Jarre-Teichmann and Christensen (1998). The biomass in Namibian waters was double that for the periods 1971–1977 and 1978–1983 (Jarre-Teichmann and Christensen 1998). Despite the higher biomass, flows were all comparable to those obtained for the region in the earlier periods modelled. This reflects the assumption in the earlier models that the productivity, rather than the biomass, of small pelagic fish needed to be increased in order

to meet the high food demand of predatory fish. The approach pursued here is consistent with the belief that the northern Benguela sustains high biomasses, but its productivity is lower than that of other up-welling regions (L. Hutchings, MCM, pers. comm.).

The mean path length (*sensu* Finn 1976) of 3.19 was short and similar to the value of 3.02 estimated for the southern Benguela model for the same system components during the 1980s (Shannon and Jarre-Teichmann, in press).

Flow diagram

Placement of the various groups according to trophic levels is shown in Figure 1. By definition, producers are assigned to Trophic Level I. Consumers are assigned to Trophic Level I plus the average trophic level of their prey, weighted by the proportion in the predator's diet. Goby, a species with high biomass that feeds largely on phytoplankton, was situated low in the food-web. Although it is an important prey species for many groups in the northern Benguela, individual flows from this group to others were small, and like all flows <5 tons·km^{-2}year^{-1}, were omitted from the flow diagram for the sake of clarity (Fig. 1).

Anchovy and sardine feed on zooplankton and phytoplankton and were found at higher trophic levels than goby. Higher still were zooplanktivorous meso-pelagic fish, and horse mackerel, which supplement their zooplanktivorous diet with a small proportion of fish. Hake and other demersal fish occupied high trophic levels and were abundant.

Primary production required

Primary production equivalents are used to compare effects of fishing at different trophic levels (Pauly and Christensen 1995). Catches of horse mackerel and hake were large, both requiring substantial proportions of total primary production (Fig. 2). However, harvesting hake at a higher trophic level required more primary production per unit of yield than harvesting horse mackerel at a lower trophic level (Fig. 2). Therefore, fishing for hake is ecologically more expensive than fishing for horse mackerel. This is also true economically. For example, for 1994, N\$ 3 500[1] were obtained per ton of hake exported, compared to N\$ 1 300 per ton of horse mackerel exported (Stuttaford 1997).

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[1] N\$ 6.1 = US\$ 1 in June 1999

Catches of large pelagic fish were smaller than those of other demersal fish, but because large pelagics were at a higher trophic level, and transfer of energy up the foodweb is inefficient, a larger proportion of primary production is required to support the fishery of large pelagic fish (Fig. 2). Primary production required to sustain all fisheries off Namibia during the 1980s was 5.8% (annual catches totalled 7 tons·km^{-2}·year^{-1}, Table II). This is about half that required to sustain the fisheries in the previous decade (Jarre-Teichmann *et al*. 1998), when total catches were closer to 10 tons·km^{-2}·year^{-1}, with severe fishing pressure on hake and horse mackerel.

Trophic aggregation

Trophic aggregation is a method that aggregates components of the system into discrete trophic levels (Lindeman 1942). Transfer efficiency is the fraction of total throughput at a discrete trophic level that is either exported or transferred to another trophic level (through consumption). In the northern Benguela during the 1980s, biomass was concentrated in Trophic Level I, i.e. the producer level (Table III). Transfer efficiencies were low, as expected in upwelling eco-systems (Jarre-Teichmann 1992, Christensen and Pauly 1993, Jarre-Teichmann and Pauly 1993). Most of the throughput at Trophic Level I (producers) was consumed by predators (Table III), whereas at higher trophic levels this proportion was much reduced, with larger proportions being returned to detritus or exported as catches.

Mixed trophic impact assessment

Mixed trophic impact assessment is a technique for measuring the relative impact of a change in the biomass of one component on other components of the eco-system, under the assumption that the diet compositions remain constant (Ulanowicz and Puccia 1990). Figure 3 shows that microzooplankton compete with most groups for phytoplankton food, thereby having a net negative impact on them. As a result of competition between mesozooplankton and goby for phyto-plankton food, an increase in mesozooplankton would have a negative impact on goby. However, mesozoo-plankton serve as prey for many other groups, which would benefit should mesozooplankton proliferate. Being very abundant, a further increase in horse mackerel would have large negative effects on groups competing with them for zooplankton prey. Despite being preyed upon by hake, horse mackerel compete
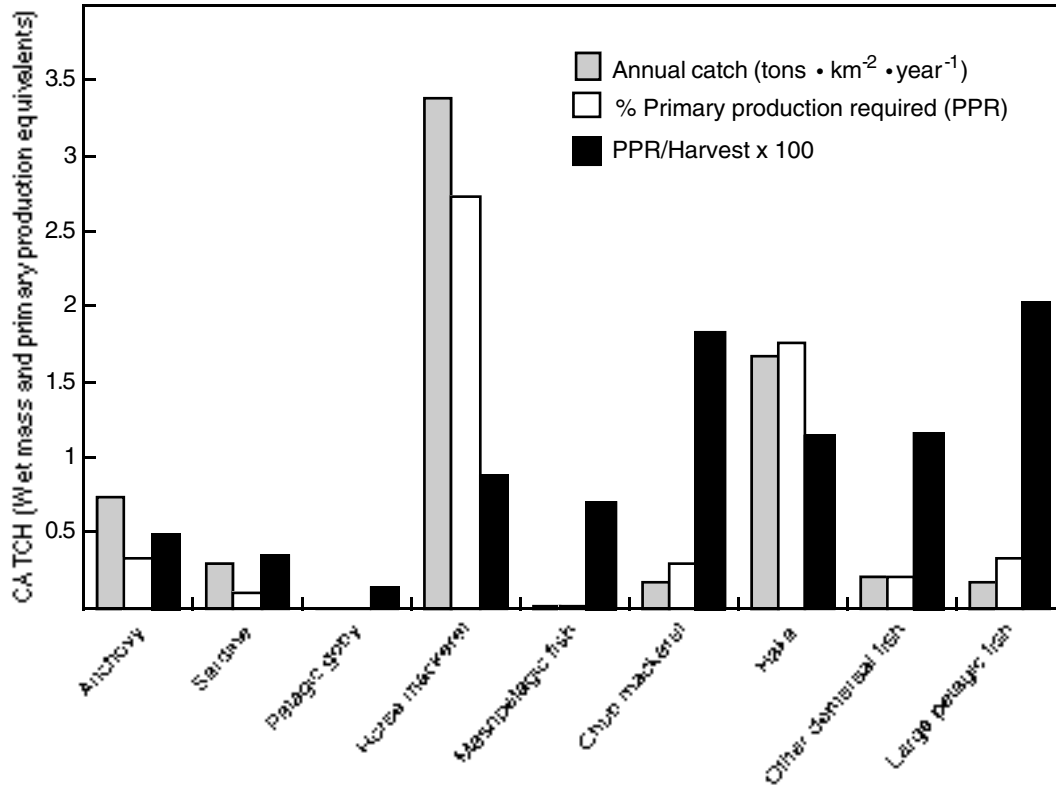
Fig. 2:   Comparison of harvested fish groups in the northern Benguela during the 1980s, showing the mean annual catches, % of total primary production (tons·km^{-2}·year^{-1}) required to sustain the catches, and the primary production required to sustain catches per unit harvested (dimensionless ratio). The latter is scaled by a factor of 0.01 for ease of graphic presentatio

strongly with hake for zooplankton prey, and an increase in horse mackerel biomass would have a net negative impact on hake.

Investigating alternative estimates of some parameters

There was uncertainty about many of the parameter estimates used in the initial realization of the balanced model. A selection of alternative scenarios was modelled to explore the influences of some of the parameters that are likely to be important in structuring the model, and for which estimates may deviate from those initially used. Because it was mainly dietary compositions that were altered in the initial balancing of the model, alterations to diets were not further explored.

However, it should be borne in mind that the allocation of diet compositions in the model has a major influence over how the model system functions trophically.

ALTERNATIVE ESTIMATE OF PHYTOPLANKTON PRODUCTIVITY

An alternative scenario was modelled in which phytoplankton productivity was not increased by 18%, as initially agreed upon during the 1989 workshop. Instead of adopting a *P/B* of 35.7 year^{-1}, it was calculated to be 30.3.year^{-1} from original *P* and *B* estimates given in Brown *et al*. (1991). Assuming the lower *P/B*, the ecotrophic efficiency of phytoplankton is 108%, indicating insufficient production of phytoplankton to support modelled consumption of phytoplankton by other groups in the system, and lending

Table III: Trophic aggregation in the northern Benguela upwelling system in the 1980s

Trophic level	Biomass (tons·km^{-2})	Transfer efficiency (%)	Proportion of throughput consumed by predators (%)
I	206.87		83.5
II	86.91		10.6
III	48.83	10.6	12.0
IV	14.55	12.3	15.9
V	3.02	17.5	6.5
VI	0.22	9.2	4.5
VII	0.01	7.3	1.8
VIII	0.00	3.0	0
IX	0.00	2.9	0
X	0.00	0.2	0

support to the decision at the 1989 workshop to adopt a higher productivity.

ALTERNATIVE ESTIMATE OF GELATINOUS ZOO-PLANKTON BIOMASS

If, instead of the present estimate of 5 million tons for gelatinous zooplankton in the northern Benguela during the 1980s, a higher estimate of 28 million tons was assumed (as suggested at the 1989 workshop), the model outputs are similar to those presented above, with the exception of total system biomass and parameters directly dependent on total biomass. This is because gelatinous zooplankton, consisting mainly of liquid, has low *P/B* and *Q/B* ratios. Further, because only a small amount of gelatinous zooplankton is consumed in the system, availability has little impact on other components. Running the model, assuming this higher biomass, caused the ecotrophic efficiency of mesozooplankton to increase from 43.7 to 46.6%. Similarly, those of microzooplankton, phytoplankton and detritus increased by small amounts, from 97.7 to 99.8%, 91.2 to 91.6% and 76.1 to 77.1% respectively. Results were similar if, instead of consuming equal portions of phytoplankton, bacteria, microzooplankton and mesozooplankton, gelatinous zooplankton were assumed to consume these prey groups in proportion to their relative biomasses. These modelling experiments show that gelatinous zooplankton are relatively unimportant in the trophic functioning of the northern Bengeula.

ALTERNATIVE ESTIMATE OF HORSE MACKEREL BIOMASS

Literature-derived biomass estimates of horse mackerel in Namibian waters varied and a fairly conservative biomass of 2.5 million tons was used in the
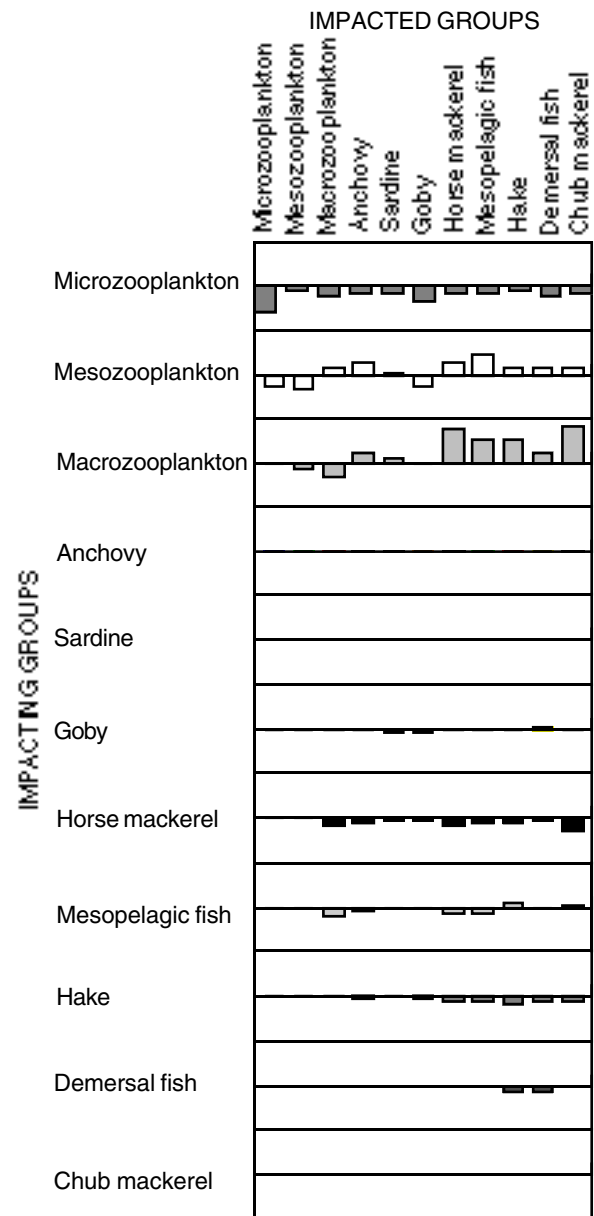

Fig. 3: Mixed trophic impacts of selected groups in the northern Benguela during the 1980s. Relative impacts are scaled from −1 to +1, where 0 indicates no net impact

initial model. The model was re-run using the upper estimate of 5.67 million tons estimated by Shcherbich *et al*. (1986). The model was unbalanced, showing an ecotrophic efficiency of 129% for macrozooplankton,

Table IV: Biomass estimated by the model when alternative scenarios are considered

Alternative scenario	Biomass (tons·km⁻²)			
	Goby	Mesopelagic fish	Other small pelagic fish	Other demersal fish
Initial balanced model	8.076	9.274	0.754	3.670
Horse mackerel biomass increased to				
3.05 million tons	8.218	9.598	0.754	3.670
P/B of hake lowered to 0.9·year⁻¹	7.887	8.760	0.717	3.418
Q/B of hake raised to 10·year⁻¹	10.351	15.444	1.206	6.686

indicating that there was insufficient production of macrozooplankton to support the food requirements for other groups. The highest possible biomass of horse mackerel that could be supported by the balanced model system was 3.04 million tons (17.0 tons·km^{-2}). Using that biomass, the model showed that more goby and mesopelagic fish could be supported (Table IV). These changes relate to greater quantities of cephalopods being consumed by the larger horse mackerel stock, making available more macrozooplankton to mesopelagic fish and goby. Corresponding to these changes was an increase in the ecotrophic efficiency from 84.3 to 91.9% for macrozooplankton and from 95.6 to 99.4% for cephalopods.

ALTERNATIVE ESTIMATE OF *P/B* FOR HAKE

It is possible that natural mortality of hake in the northern Benguela was overestimated, so that *P/B* was lower than the value of 1.0·year^{-1} initially assumed. The model was re-run assuming an alternative *P/B* of 0.9·year^{-1}, the value used in the southern Benguela model (Jarre-Teichmann *et al.* 1998), but keeping *P/Q* at 22% as before. Hake production was then insufficient to support cannibalism of small hake by larger hake, reflected in the ecotrophic efficiency of hake at 106% for the new model. Consumption by hake was reduced from 36.3 to 29.1 tons·km^{-2}·year^{-1}, as *Q/B* was adjusted down to account for the reduced *P/B*, and *P/Q* remained constant. Predation by hake on goby, mesopelagic fish and demersal fish was reduced, corresponding to larger amounts of food being required to support the same sizes of these stocks. Subsequently, smaller prey stocks could be supported by the modelled system (Table IV).

ALTERNATIVE ESTIMATE OF *Q/B* FOR HAKE

The possible range for *Q/B* of hake is large. The model was re-run assuming a *Q/B* of 10·year^{-1} (compared to 5·year^{-1} in the initial model) for *P/B*s of 1.0 and 0.9·year^{-1}. Because consumption was identical in both runs, both showed increases of the same magnitudes in the biomasses of other groups. When

Q/B was 10·year^{-1}, larger stocks of goby, mesopelagic fish and demersal fish were supported by the system because greater quantities of these groups were needed to support the increased consumption of hake (Table IV). Similarly, a larger biomass of demersal fish allowed a larger biomass of small pelagic fish (prey for demersal fish) to be supported by the system. However, the model was not balanced for these higher standing stocks, reflected in ecotrophic efficiencies exceeding 100% for macrozooplankton, anchovy, horse mackerel, cephalopods and large pelagic fish. The ecotrophic efficiency of hake was 171 and 154% for *P/B*s of 0.9 and 1.0·year^{-1} respectively. In fact, if *Q/B* is higher than the value of around 5·year^{-1}, assumed for the present model and that for the southern Benguela (Jarre-Teichmann *et al.* 1998), the diet of hake would need to be reassessed and extensively altered from that used to initially balance the present model.

To summarize, it was necessary to re-adjust the biomass of some groups in order that the model was mass-balanced. This ensured that production was sufficient to support the consumption of predatory groups in the system. For example, it was necessary to double Hewitson and Cruickshank's (1993) estimates of goby. Cephalopod production was insufficient to support the consumption reported for many of the groups, and therefore that component was reduced in the diet of several groups. Biomass of the demersal fish group was required to be half that of hake. Likewise, because there is little available data on benthos, the model was used to estimate that required to sustain other components of the system. Meiobenthos, macrobenthos and benthic producers were required to be 25% of the biomasses of those groups in the southern Benguela. This is reasonable, given the frequent occurrence of low oxygen water along the Namibian shelf (Bailey 1991) and the fact that the southern Benguela system not only includes the upwelling region, but also extends over the Agulhas Bank with its wider shelf. Not only did exploring the ranges in the estimates of some parameters serve to highlight areas of uncertainty in the model, but it also improved confidence in the estimates of others.

ACKNOWLEDGEMENTS

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