

MODELLING STOCK DYNAMICS IN THE SOUTHERN BENGUELA ECOSYSTEM FOR THE PERIOD 1978–2002

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An ecosystem model of the southern Benguela was fitted to available time-series data for the period 1978–2002, to explore how changes in target fish populations in this ecosystem can be attributed to feeding interaction terms and population control patterns, the impact of fishing, and environmental forcing. Fishing patterns were estimated to explain only 2–3% of the variability in the time-series, whereas an estimated productivity forcing pattern applied to phytoplankton explained 4–12% of the variance represented by the sum of squares. Model settings describing prey vulnerability to their predators could explain around 40% of the variability in the time-series. Modelled stock dynamics in the southern Benguela ecosystem more closely represent observed time-series when wasp-waist control by small pelagic fish is simulated. Overall, model simulations suggest that almost half the variance in the time-series can be explained based on a combination of fishing, vulnerability settings and productivity patterns. Variation in mortalities and prey preferences over time, as well as model fits in relation to available effort series, are discussed. The study advances a model with improved parameterization and credibility to assist with an ecosystem approach to South African fisheries management.

Key words: ecosystem modelling, environmental forcing, fishing patterns, southern Benguela, stock dynamics, wasp-waist

A global appreciation of, and move towards, an ecosystem approach to fisheries (e.g. Sinclair *et al.* 2002, Sinclair and Valdimarsson 2003) has led to particular attention being drawn to the tools available to help achieve it. By their very nature, ecosystem models have large inherent uncertainties and are therefore perceived to have serious limitations, sometimes being passed off as academic exercises and lacking predictive power and robustness. Substantial progress has been made in the ecosystem modelling arena, a promising approach being the ECOPATH with ECOSIM model (EwE, Christensen and Pauly 1992, Walters *et al.* 1997), which now has the capacity to fit ecosystem models to available time-series data (Christensen and Walters 2004, Walters and Martell *in press*). This paper presents one such example, in support of the potential of using ecosystem models to contribute to fisheries management advice in the future.

A previous study simulated stock changes in the southern Benguela from the 1980s to the 1990s (Shannon *et al.* 2004). That study considered simulations in which rates of fishing mortality of sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus* (formerly *E. capensis*) and horse mackerel *Trachurus trachurus capensis* were manipulated to represent changes in their fisheries and in the stocks from the 1980s to the 1990s. Results showed that it would be

unlikely that observed changes in the fishing mortality during the two decades were the primary driving factors of the observed changes in stock sizes of anchovy and sardine in the southern Benguela. On the other hand, model simulations in which the susceptibility of phyto- and zooplankton to feeding by anchovy and sardine were simulated, suggested that the observed anchovy–sardine changes in the system may have been driven largely by changes in the availability of mesozooplankton prey to these small pelagic fish, mediated by means of environmental forcing (Shannon *et al.* 2004). Between the 1950s and the 1990s, there was a long-term increase in zooplankton abundance off the west coast of South Africa. Copepod biomass increased 10-fold and copepod abundance increased 100-fold, with the proportion of small cyclopoid copepods (favourable food for sardine) increasing and the relative abundance of large calanoid copepods (preferred prey of anchovy) decreasing (Verheye and Richardson 1998, Verheye *et al.* 1998). However, on a shorter, more recent time scale, there was a notable reduction in copepod abundance in the St Helena Bay region of the West Coast in the later part of the 1990s (H. M. Verheye, Marine & Coastal Management [MCM], pers. comm.). This may be an indication of strong predation of zooplankton by small pelagic fish (Verheye *et al.* 1998, Cury *et al.* 2000). Further, there have been indications that density-dependent effects

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Table I: Summary of model groups and the corresponding time-series used to simulate their dynamics in the southern Benguela

Model group	Data series used	Comments	Used to force model dynamics	Used to compare to model outputs
Anchovy	Total biomass	Representative of biomass		✓
	Purse-seine catch		✓	✓
	Fishing mortality (<i>F</i>)			
Sardine	Spawner biomass	Representative of biomass		✓
	Purse-seine catch			✓
	Fishing mortality (<i>F</i>)		✓	
Seabirds	Gannet abundance	Representative of seabird biomass		✓
Seals	Seal pup abundance	Representative of seal biomass		✓
Cephalopods	Total chokka squid catch (jig + demersal trawl catches)	Directed jig fishery only started in 1985. Chokka squid caught as bycatch in demersal trawl fishery		✓
	Chokka squid jig effort		✓	
	Chokka squid trawl effort		✓	
Horse mackerel	Total catch of large horse mackerel (midwater trawl catch + demersal trawl catch; South African and foreign fleets)	Large horse mackerel in midwater and demersal trawls		✓
	South African midwater trawl effort	South African directed midwater trawl fishery only started in 1990	✓	
	Demersal trawl effort	Demersal trawl effort for trawls directed at horse mackerel	✓	
Hake	Biomass indices from surveys, estimated for: small/large <i>M. paradoxus</i> (summed for both coasts, 0–500-m isobaths) and small/large <i>M. capensis</i> (summed for both coasts, 0–500-m isobaths)	Representative of hake biomass		✓
	Model estimates of exploitable biomass of <i>M. capensis</i> on South Coast and <i>M. paradoxus</i> on West Coast	Representative of biomass of large hake		✓
	Total catch of large <i>M. capensis</i> , total catch of large <i>M. paradoxus</i> and total catch of small <i>M. paradoxus</i>	Consists of West Coast offshore trawl catch; South Coast offshore trawl catch; South Coast inshore trawl catch; West Coast long line catch; South Coast longline catch; South Coast handline catch		✓
	<i>M. capensis</i> offshore trawl effort	Fishery operative on South Coast	✓	
	<i>M. paradoxus</i> offshore trawl effort	Fishery operative on South Coast	✓	
	West Coast hake trawl effort	Catches both species	✓	
Snoek and other large pelagic fish	Total snoek catch (line + trawl)			✓
	Linefish effort	Applied to snoek and other large pelagics	✓	
	Demersal trawl effort for snoek	Calculated for demersal trawls directed at snoek	✓	

are influencing the current large biomasses of anchovy and sardine. For example, anchovy spawners have been in poorer condition in recent years (P. Fréon and C. D. Van der Lingen, MCM, pers. comm.), sardine recruits are substantially smaller than recorded when stock sizes were lower (Coetzee *et al.* 2003) and sardine reproductive parameters reflect density-dependence changes (Van der Lingen *et al.* *subm.*). It is generally

agreed that the present abundance of anchovy, sardine and round herring *Etrumeus whiteheadi*, estimated at three times the average biomass in the 1980s, is unsustainable in the long term, and that there will likely be a shift to a regime dominated by sardine in line with the current structure of the zooplankton community.

In this paper, the intention is to explore how changes in target fish populations of the southern Benguela

can be attributed to feeding interaction terms and population control patterns, impact of fishing and environmental forcing. In addition, the study will attempt to:

- (1) further evaluate the wasp-waist hypothesis, i.e. whether model fits are improved under wasp-waist parameter settings;
- (2) identify problems/underestimates, and highlight importance of particular fishing effort series/catch series;
- (3) provide a model with improved parameterization for use in exploring alternative fishing scenarios/management options for South African fisheries.

COLLATION AND PREPARATION OF TIME-SERIES

A critical step in the development of credible models for policy analysis is to show that they can at least reproduce observed historical responses to disturbances such as fishing. This necessarily involves an iterative exercise in “fitting” the model to data, by correcting parameter estimates and time-series-forcing information to show what values (or ranges of values, or alternative hypotheses about key processes) could explain the observed historical patterns. For any such fitting exercise, it is critical to have as long a reference period, with as many different disturbance patterns, as possible.

The southern Benguela ecosystem was considered for this model to extend from the Orange River on the West Coast (29°S), southwards and eastwards, to span the Agulhas Bank and South Coast as far east as East London (28°E), covering the shelf out to approximately the 500-m isobath, following Jarre-Teichmann *et al.* (1998). Information on biomasses and catches of model ecosystem components over time was used to modify model variables based on summed-squared residuals (Table I). The data series used were selected from the many available series on the basis of reliability and representivity, to avoid introducing additional uncertainties and biases into the model-fitting procedure. Where catch per unit effort (*cpue*) series were used, they were applied to derive effort series to drive the model fishing patterns, not as indices of relative abundance of the resources.

Small pelagic fish

Anchovy and sardine spawner and recruit biomass estimates and purse-seine catches were available for the period 1984–2001/02. Anchovy fishing mortality rates F were estimated as catch divided by the estimated

biomass in May (the middle of the fishing season), where biomass was estimated as follows: spawner biomasses were forward-calculated from estimates obtained during research cruises undertaken in November each year, reducing these by the equivalent of half a year of natural mortality M (where M is 0.9 year⁻¹; De Oliveira 2002), and adding to these biomasses the recruit biomasses estimated from research surveys undertaken in May of the following year. Catch, as a proportion of this estimated anchovy biomass, was used to provide an estimate of anchovy F . Total biomass was used for anchovy because the anchovy fishery targets mainly recruits. Sardine fishing mortalities were estimated as catch divided by model spawner biomass. Biomass estimates were not available for either anchovy or sardine during the period 1978–1983, so F -values for these years were assumed to be the same as in 1984. Estimates of South African sardine spawner biomass using Virtual Population Analysis (Armstrong *et al.* 1983) were only available until 1980 and were not used in model fitting.

Seabirds

Estimates of Cape gannet *Morus capensis* abundance (number of breeding pairs) were available from 1978 to 1997. This series is the longest and most continuous of the available South African seabird series. Gannets feed pelagically and their numbers are strongly associated with fluctuations in the anchovy stock (Crawford and Dyer 1995). Gannet abundance was used as a relative estimate of seabird abundance when fitting the time-series for the ecosystem model.

Seals

Seal pup counts were available for South African colonies (south of the Orange River) for several years. Pups were counted from aerial photographs taken in December for the years 1979, 1982, 1985, 1988, 1992, 1994, 1995, 1996 and 1997. Pup numbers were used as representative indices of abundance of seals at the colonies in the following year.

Chokka squid

Chokka squid *Loligo vulgaris reynaudii* dominate commercial catches of cephalopods in South African waters. Catches of chokka in the jig fishery were available from 1983 to 1996 (Roel 1998, Roel *et al.* 1998) and updated for the years 1997–2001 (MCM, unpublished data). Squid jig effort (standardized for boats with 2–20 men on board) was estimated for the period

1985–1996 by Roel (1998) and revised using a GLM-standardized *cpue* series (expressed as kg chokka caught per fisher per hour, J. Glazer, MCM, pers. comm.). Chokka squid are also caught as bycatch in the South Coast demersal trawl fishery. Catch data were again obtained from Roel (1998) and updated from MCM unpublished reports, and Roel's (1998) trawl fishery effort series was updated using updated *cpue* and catch data. Effort was expressed per hour trawled.

Some biomass indices data were available for squid from bottom trawl research surveys between 1988 and 1997 using swept-area estimates, as described in Badenhorst and Smale (1991). Because these were not available for several years and did not fully cover the range and depths occupied by squid, they were not considered sufficiently reliable to be representative series of cephalopod biomass for model fitting.

Horse mackerel

Biomass indices for horse mackerel are available for some years from demersal surveys using swept-area estimates. However, because small horse mackerel are pelagic, it is likely that small fish were under-represented in the surveys. Further, interannual variability in swept-area survey biomass indices is large, because large horse mackerel range within the water column and are not always available to bottom trawl gear. In addition, there are large uncertainties associated with splitting such indices to estimate biomass for the small (≤ 20 cm long, 2 years old) and large horse mackerel model components. Therefore, estimates of horse mackerel biomass were not used in fitting the model in this study.

Horse mackerel catches were separated into those taken by (1) the purse-seine fishery, (2) the midwater trawl fishery, and (3) the demersal trawl fishery (inshore and offshore combined, mainly on the South Coast). Although some large horse mackerel were caught historically in the purse-seine fishery, the amount is assumed to be minimal, and current purse-seine catches are of small horse mackerel. The data on pelagic catches of small horse mackerel were from MCM unpublished catch records. Large horse mackerel are caught in trawl fisheries. Midwater trawl catches were obtained from Horsten (1999). Japanese midwater trawling in South African waters was gradually reduced from 1987 and stopped altogether in 1992 (Punt and Leslie 1990), subsequently being replaced by the South African midwater trawl fleet. Midwater trawl effort was obtained from MCM unpublished data on midwater trawls targeting horse mackerel (recorded as 85-mm mesh size trawl catches). Effort, in standard fishing hours (standardized using a factor representing vessel power), was available for the years

1990–1999 for the South African midwater fleet. Inshore- and offshore-directed South African demersal trawl efforts (and catches) were extracted from the MCM database and, in the absence of other effort estimates, were used as representative of the effort series for demersally trawled horse mackerel. Trawl effort is in standard fishing hours and available from 1980 onwards.

Hake

Two species of Cape hake are found in the southern Benguela, shallow-water *Merluccius capensis* and deep-water *M. paradoxus*. Understanding of the stock structures and recruitment variability of these hakes is still incomplete and further research is required. The two species closely resemble one another and are not separated in commercial catches, though because their depths of distribution vary, fishing depth can be used to estimate catches by species.

Summed biomass indices from demersal trawl surveys undertaken on both the West and South coasts in depths up to 500 m were available for *M. capensis* from 1985 to 1997, excluding 1988 and 1989, and for *M. paradoxus* from 1985 to 1999, excluding 1988, 1989 and 1998. Model estimates of exploitable hake biomass were provided by R. Rademeyer (University of Cape Town), using the method described in Rademeyer (2003). Hake catches on the West Coast (mainly *M. paradoxus*) are approximately double those on the South Coast (mainly *M. capensis*). As an example, in 1978 the proportions of *M. capensis* in the total hake catch was 13 and 82% on the West and South coasts respectively. Model estimates of exploitable biomass for trawls targeting *M. paradoxus* on the West Coast and for inshore trawls targeting *M. capensis* on the South Coast were used as representative hake biomass series for the ecosystem model fitting (Table I). These were used in addition to biomass indices from research surveys, because the model estimates are continuous, integrated series that were considered to assist in improving the overall fit of the ecosystem model, rather than adding more uncertainty to it.

Records of Cape hake catches are available for West and South Coast offshore trawls (both fisheries catch large *M. capensis*, and both small and large *M. paradoxus*), South Coast inshore trawls (catching small and large *M. capensis*), West Coast longlines (catching large *M. capensis* and large *M. paradoxus*), South Coast longlines (catching large *M. capensis*) and South Coast handlines (catching large *M. capensis*).

Three effort series were selected for modelling Cape hake dynamics. These were as follows:

- (1) Effort was calculated for offshore trawling of *M. capensis* on the South Coast, using a GLM-standard-

- ized *cpue* (kg min⁻¹) series (Glazer and Butterworth 2004) and the total catches of *M. capensis* on the South Coast (Butterworth and Rademeyer 2004), to obtain a standard effort (thousands of minutes fishing) that would have been required if all *M. capensis* caught on the South Coast had been taken in *M. capensis*-directed trawls using a standard offshore vessel;
- (2) Similarly, effort was calculated for offshore trawling of *M. paradoxus* on the South Coast, from the *cpue* series for *M. paradoxus* (Glazer and Butterworth 2004). As in the previous estimation, standard effort (in thousands of minutes fishing) was estimated to be the effort that would have been required if all *M. paradoxus* caught on the South Coast were taken in *M. paradoxus*-directed trawls using a standard offshore vessel. Total catches of *M. paradoxus* on the South Coast were obtained from Butterworth and Rademeyer (2004);
 - (3) Trawl effort (thousands of minutes fishing) for West Coast Cape hake trawls was available from *cpue* (Glazer and Butterworth 2004) and trawl catch series (Butterworth and Rademeyer 2004). However, fishing selectivity changed between 1985 and 1992, so catchability was not constant over the full time-series.

In addition to effort series, fishing mortality estimates were available for *M. capensis* on the South coast and for *M. paradoxus* on the West Coast (R. Rademeyer, University of Cape Town, pers. comm.). These provided an alternative to hake fishing effort series for fitting the ecosystem model to hake biomass and catch time-series.

Large pelagic fish

Large pelagic fish considered in ECOPATH models of the southern Benguela (Shannon *et al.* 2003) include snoek *Thyrsites atun*, silver kob *Argyrosomus inodorus*, geelbek *Atractoscion aequidens*, yellowtail *Seriola lalandi* and tuna *Thunnus* spp. Owing to its commercial importance and abundance, snoek was modelled as a separate group. The other species were grouped into the model group "other large pelagic fish", for which model input parameters were estimated by weighting parameters for each species according to their relative biomasses estimated to have been located within the boundaries of the modelled region (adjusted to account for seasonal migrations of tuna species). Pelagic sharks were modelled as a separate group (Shannon *et al.* 2003), but time-series data were not available, so sharks were not used in the model fitting undertaken for this study.

Large pelagic fish are caught in the linefishery.

Effort was available as number of boats fishing (on all linefish, including snoek) per year from 1986 to 1999. Effort for snoek caught in trawls was estimated from the combined effort series estimated for offshore trawls for *M. capensis* on the South Coast, and for Cape hake on the West Coast, scaled by the percentage of demersal trawls targeting snoek. Snoek trawl data were obtained from MCM's demersal trawl database, considering all areas (although snoek are caught mainly on the West coast) and all depths, and an overall percentage of commercial demersal trawls that contained >1 ton of snoek (i.e. trawls in which snoek may have been targeted, as opposed to being caught incidentally) was estimated.

METHODS

Setting up a base model for the southern Benguela

To initiate simulations of the dynamics of the southern Benguela ecosystem from 1978, a model for 1978 was prepared based on the 1980s model of the southern Benguela ecosystem (Shannon *et al.* 2003) using the ECOPATH with ECOSIM 5.1 (2004 version) software (Christensen and Pauly 1992, Walters *et al.* 1997, 2000, Christensen and Walters 2004). Initial estimates for production per unit biomass (*P/B*) and production per unit consumption (*P/Q*; Shannon 2001, Shannon *et al.* 2003), notably for small Cape hake, were revised in line with the standardized values agreed upon at an upwelling ecosystems modelling workshop held in Cape Town in November 2002 (Moloney and Jarre 2003, Moloney *et al.* subm.). Wherever possible, average catches in the 1980s were replaced by actual catches reported for 1978. For sardine, this resulted in an ecotrophic efficiency (proportion of production used in or exported from the system) of >1, indicating that model production of sardine in the 1980s was insufficient to sustain the combined predation and catches of sardine for 1978. Therefore, the 1978 model was used to estimate the sardine biomass required to sustain sardine catches and predation. Sardine biomass in the 1978 model was required to be 0.824 tons km⁻² year⁻¹ compared with the average of 0.586 tons km⁻² year⁻¹ estimated for the years 1980–1989. The higher biomass for 1978 is in line with expectations, given the larger catches in that year.

In view of test simulation results using these time-series data, the following adjustments were made to update some of the parameters previously used by Shannon (2001) and Shannon *et al.* (2003), because the original parameter settings caused problems in the simulations:

- (i) *Predation on cetaceans*: cetaceans initially constituted 15% of apex chondrichthyan diet (Shannon *et al.* 2003), but this caused unsustainable mortality on the model cetacean group and was reduced here to 4%, with a corresponding 11% increase in the proportion of the dominant prey group, benthic-feeding chondrichthyans, in the diet of apex chondrichthyans.
- (ii) *Predation on snoek*: test simulations of the time-series model showed that snoek biomass and yield were grossly overestimated in the model. This was presumed to be related to unrealistically high predation of snoek by certain of its predators, such as chondrichthyans and seals. However, there is large uncertainty around the diet composition estimates for those predator groups, and the settings used in this study are not thought to be any less realistic than the original settings used by Shannon (2001). Subsequently, snoek was reduced from 7 to 1% in the apex chondrichthyan diet, and from 0.5 to 0.1% in the pelagic-feeding chondrichthyan diet, and compensated for by increasing the proportion of benthic chondrichthyans (the dominant prey group for apex chondrichthyan predators) consumed by these two other chondrichthyan groups. In addition, the proportions of snoek and other large pelagic fish were reduced in the diet of seals from 0.5 to 0.1% each, with an additional 0.4% being allocated to each of the pelagic-feeding and benthic-feeding demersal groups. Similarly, snoek in the diet of large *M. paradoxus* was reduced from 0.5 to 0.1%, the small consumption remaining being attributed instead to cephalopods;
- (iii) *Predation by cephalopods*: predation of anchovy and round herring by cephalopods proved unsustainably high in the long-term model simulations examined. Most diet information on cephalopods is for chokka squid, whereas the cuttlefish, *Sepia* spp., probably constitute a higher biomass than squid and are likely to feed more benthically (on macrobenthos) than pelagically. Therefore, anchovy and round herring in the diet of cephalopods were reduced from 5 to 1%, and the extra 8% of the diet was assumed to be macrobenthos (up from 38 to 46%);
- (iv) *Consumption of microzooplankton*: test simulations using time-series data showed that microzooplankton was poorly linked in the initial foodweb, presumably partly because macrozooplankton did not consume microzooplankton in the original models (Shannon *et al.* 2003). Microzooplankton are eaten by some macrozooplankton (Gibbons *et al.* 1992). Therefore, in the revised model used here, microzooplankton, phytoplankton and mesozooplankton were assumed to constitute equal portions of the diet of macrozooplankton (L. Hutchings, MCM, pers. comm.). Large within-group consumption by microzooplankton (“cannibalism”) resulted in consumption of microzooplankton being higher than the production of that group, and was reduced from 20 to 5%, with the balance attributed to increased detritus consumption;
- (v) *The P/B for seals* was reduced from an unrealistically high 0.946 year⁻¹ (Shannon *et al.* 2003) to 0.25 year⁻¹, in line with the revisions reported by Moloney and Jarre (2003). This meant that the large mortality of seals caused by the apex chondrichthyan model group was unsustainable. Consequently, the proportion of seals in the diet of apex chondrichthyans was reduced from 20 to 3% and the additional 17% added to the proportion of benthic chondrichthyans in the apex chondrichthyan diet composition. Cetacean *P/B* was also reduced from 0.6 year⁻¹ to a more realistic 0.15 year⁻¹ (Moloney and Jarre 2003);
- (vi) To reflect the fact that sardine biomass was assumed to be falling in 1978, whereas anchovy biomass was increasing, model parameter settings representing relative biomass accumulation rates of -5 and +5% of biomasses were used for the two species respectively. These settings only pertained to model initialization (start year).

In the southern Benguela, midwater trawling by South African vessels for horse mackerel only began in the 1990s (although catches were made by the Japanese fleet prior to this; total catches by South African and foreign fleets have been used – see Table I), the squid jig fishery only began in 1985, and an experimental fishery for hake using longlines (targeting large *M. capensis* on the South Coast) started in the mid-1990s. In order that catch series for the first of these two fisheries could be included in the time-series simulations starting in 1978, and catches of hake by longlines could be reflected, very small “token” catches were allocated to these three fisheries in the baseline 1978 model for years prior to the start of the fisheries. Catches by these fisheries were set to 10⁻⁶ tons km⁻² year⁻¹ for large *M. capensis*, 10⁻⁵ tons km⁻² year⁻¹ for squid, and to 0.0994 tons km⁻² year⁻¹ for horse mackerel, the latter being the 1978 midwater catch made by Japanese vessels. Midwater trawl effort prior to 1990 was assumed to be equivalent to that exerted by the South African midwater trawl fishery at the start of the 1990s. Because an effort series for the chokka squid jig fishery was used to force squid catches, the jig effort series was rescaled so that a relative value of 1 was used in the years prior to the start of the jig fishery (i.e. 1978–1984), along with a minimal catch, and effort was then increased to a relative value of 1000 in 1985, when the fishery opened.

The model incorporates trophic ontogeny, allowing adults and juveniles of three species to be linked:

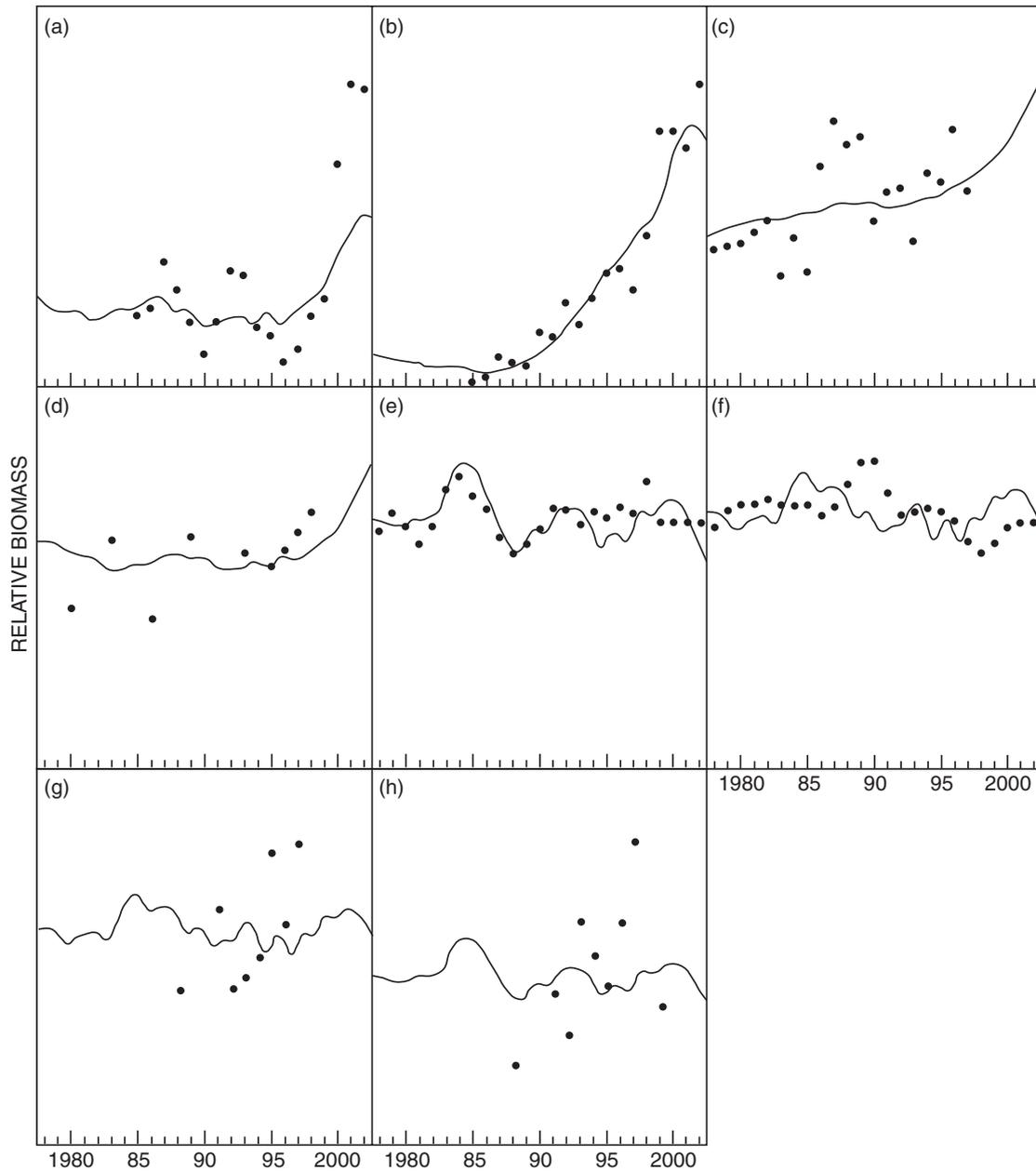


Fig. 1: Time-series trends estimated by ECOSIM (lines) and from time-series data (dots) for the period 1978–2002. The time-series are treated as relative biomasses only, and are hence scaled to match the ECOSIM model series: (a) estimated total biomass of anchovy compared with modelled biomass of anchovy (ECOSIM); (b) sardine spawner biomass (surveys) compared with sardine biomass (ECOSIM); (c) pairs of breeding gannets off South Africa compared with biomass of seabirds (ECOSIM); (d) seal pups in the southern Benguela (census data) compared with seal biomass (ECOSIM); (e) exploitable biomass (modelled) of *M. paradoxus* on the West Coast compared with large *M. paradoxus* biomass (ECOSIM); (f) exploitable biomass (modelled) of *M. capensis* on the South Coast compared with large *M. capensis* biomass (ECOSIM); (g) estimated combined biomass of small and large *M. capensis* on both West and South coasts (from surveys) compared with large *M. capensis* biomass (ECOSIM); (h) estimated combined biomass of small and large *M. paradoxus* on both West and South coasts (from surveys) compared with large *M. paradoxus* biomass (ECOSIM)

Table II: Parameters used to model the growth of juvenile/small horse mackerel and Cape hake into adults

Parameter	Horse mackerel	<i>M. capensis</i>	<i>M. paradoxus</i>
Age at transition from juvenile/small group to adult/large group	2 years	3 years	3 years
Average adult weight as a proportion of average weight at transition	3.5	3	3
K (von Bertalanffy growth coefficient)	0.183	0.046	0.046

Sources of information: M. Kerstan (formerly MCM, pers. comm.) for horse mackerel; Punt and Leslie (1991) and Leslie (1998a, b) for Cape hake

- (a) juvenile and adult horse mackerel;
- (b) small and large shallow-water Cape hake;
- (c) small and large deep-water Cape hake.

A delay-differential model is used to model the recruitment of juveniles/small individuals into the adult/large size pool (Walters *et al.* 1997), based on parameters tabulated (Table II). Using this approach, it is possible to keep track of recruitment as feeding conditions change (Christensen and Walters 2004). Individuals in each group are subjected to total mortality that can change over time, depending on the sum of the amounts consumed by their predators, including fisheries. Natural mortality excluding predation ("baseline mortality") is calculated from the steady-state ECOPATH balance in which P/B is input, and is assumed to remain constant in ECOSIM simulations.

Tuning the model to time-series data

ECOSIM models can be "driven" by changes in fishing mortality, fleet effort, and productivity patterns. In addition, fitting to time-series depends on the settings for trophic interaction patterns, i.e. flow control or vulnerability settings. The relative role of these factors for the southern Benguela ecosystem model is explored.

RELATIVE ROLES OF FISHING, FEEDING INTERACTION CONTROL AND SYSTEM PRODUCTIVITY

The following procedure was applied to explore how the southern Benguela model could be fitted to the available time-series (Figs 1, 2) described above and listed in Table I, and to test the relative roles of fisheries, feeding interaction control (vulnerabilities) and system productivity in explaining the variability in the time-series:

- (1) The time-series data file was read from Excel, and stored in the EwE database;
- (2) All fisheries catches and fishing mortalities for each year of the simulation were reset to the ECOPATH baseline value (for 1978). A baseline good-

ness-of-fit (sums of squares, SS) was estimated following Christensen and Walters (2004) as the sum of squared log ratios of biomass and predicted biomasses, the log ratios of fishing mortality rates and predicted fishing mortality rates, and the log ratios of catches and predicted catches for all series listed in Table I;

- (3) The time-series was re-read (to set fishing rates again);
- (4) The "fit to time-series" module of ECOSIM was next used to search for the predator-prey interactions most sensitive to changes in vulnerabilities. Once obtained, searches for the interactions estimated to be the most sensitive were marked for vulnerability searches. In addition, vulnerabilities of small pelagics (anchovy, sardine, round herring and small horse mackerel) as prey (i.e. prey-predator interactions) as well as consumers were marked for vulnerability searches (to see if a wasp-waist pattern of vulnerabilities would be estimated);
- (5) A vulnerability search was next run to estimate vulnerabilities for the interactions marked in Procedure 4 above that would minimize the SS s;
- (6) A combined vulnerability and production anomaly was run to estimate vulnerabilities and a forcing function (impacting phytoplankton P/B) that would minimize the SS s;
- (7) Procedures 4–6 above were also reversed to estimate productivity pattern first, then vulnerabilities.

FLOW CONTROL (VULNERABILITIES)

In ECOSIM, values are allocated to simulate the vulnerability of prey groups to their predators. For a given predator-prey interaction, a vulnerability of 2 (default setting; vulnerabilities rescaled to range from 0 to 1 in previous versions of EwE; see Christensen and Walters (2004) for conversion formula) indicates that, if the predator biomass increases drastically, it will at most be able to double the predation mortality on the prey in question. Relative sensitivities of the goodness-of-fit (weighted SS , of log biomasses, or catch, from log predicted biomass, or catch) to vulnerabilities used for the model groups can be used in a search routine to estimate vulnerability settings.

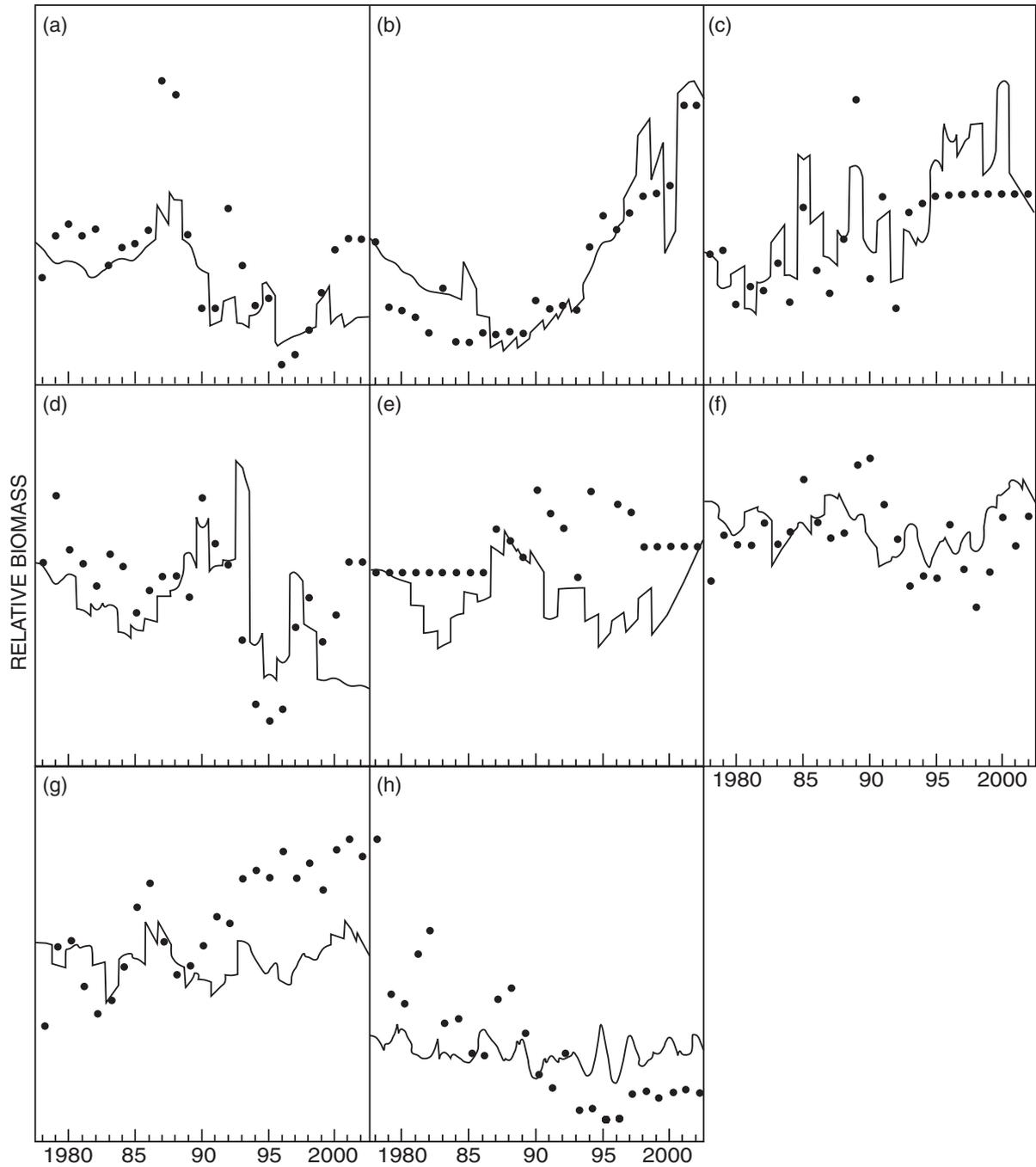


Fig. 2: Total catches (combined gears) as estimated by ECOSIM (lines) and from time-series data (dots) for the period 1978–2002. Catches are scaled similarly ($\text{tons km}^{-2} \text{ year}^{-1}$) for both types of information: (a) anchovy; (b) sardine; (c) chokka squid; (d) large horse mackerel; (e) snoek; (f) large *M. capensis*; (g) large *M. paradoxus*; (h) small *M. paradoxus*

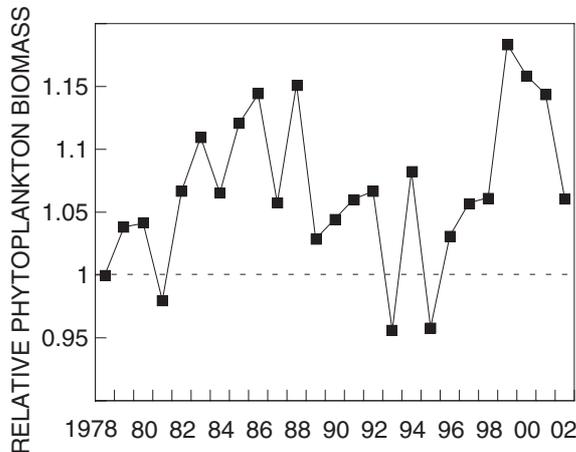


Fig. 3: Phytoplankton biomass (when an environmental forcing function was fitted after vulnerabilities had been tuned) estimated by ECOSIM for the period 1978–2002, expressed as relative to biomass estimated for 1978

In the base model for this study, vulnerability values were set to the default of 2, representing mixed control type (bottom-up and top-down influences acting simultaneously). Subsequent simulations were undertaken in which wasp-waist flow control for the main small pelagic fish was incorporated, namely for anchovy, sardine, round herring and small horse mackerel.

ENVIRONMENTAL FORCING

The time-series fitting routine of EwE 5.1 was used to explore which simulated environmental forcing function would generate modelled residual stock dynamics that best fitted those observed in the system over the period 1978–2002.

EFFECT ON UNCERTAINTY IN ECOPATH INPUT PARAMETERS

The model with fitted parameters as described in the section above was used with a Monte Carlo routine in ECOSIM, to evaluate if *SS* could be further reduced by allowing the biomasses, production and consumption rates to vary within $\pm 20\%$ and the biomass accumulation rates within $\pm 10\%$ of the original values estimated.

RESULTS AND DISCUSSION

Using forcing by fishing to drive stock dynamics

Changes in fishing patterns are important drivers for

ecosystem models of the type analysed here. However, the fishing patterns do not appear to contribute much towards explaining trends in the southern Benguela ecosystem. It is estimated that a reduction of only 2–3% of the baseline *SS* (Step 2 in the procedure described above) could be achieved using these fishing effort series alone (i.e. ignoring vulnerabilities and environmental forcing). This finding may reflect relatively constant fishing pressure in the system over the time period studied. However, the information on changes in fishing mortality and fishing effort was far from complete, and the time span covered was fairly short. With longer time-series, and with more fishing driving variables, fishing pressure may have been more variable, and hence the contribution of the fishing pattern towards explaining time-series trends would probably increase. Considering that ranges of some species are likely to shrink at low stock sizes, catchability for some species may be density-dependent. However, from the model fitting here, there are no indications that density-dependent catchability is important in explaining population trends.

Vulnerability tuning

A search routine was used to estimate vulnerabilities for predator-prey interactions. An initial search was made to determine how sensitive predator-prey vulnerability settings were. The 15 interactions for which the vulnerabilities had the strongest impact on the *SS* were then selected, which included anchovy and sardine as both prey and predators, and seabirds preying on snoek and on seabirds. In addition, it was ensured that small pelagic fish species (anchovy, sardine, round herring and small horse mackerel) were included both as consumers and as prey, and that predation on small hake and consumption of macrozooplankton by small hake were also marked (small hake may operate in a similar manner to small pelagic fish, because their diets are $>70\%$ macrozooplankton).

The results indicated top-down settings (Vulnerability >3) for anchovy, sardine, round herring and juvenile horse mackerel predation on zooplankton. In addition, the following interactions were found to be top-down controlled: predation on small *M. paradoxus* and juvenile horse mackerel, and predation on snoek by seabirds. Estimated vulnerabilities were low ($=1$), indicating bottom-up control for predation on anchovy, sardine, round herring and small *M. capensis*. Bottom-up control was also estimated for macrozooplankton consumption by small hake, and for seabird–seabird predation. In summary, the model simulations showed that modelled stock dynamics in the southern Benguela ecosystem more closely represent observed time-series when zooplankton was top-down controlled by anchovy, sardine, round herring and ju-

venile horse mackerel, and when anchovy, sardine, round herring and small *M. capensis* exerted bottom-up control over their predators. This supports the hypothesis of wasp-waist flow control (see Cury *et al.* 2000). However, plankton dynamics are not modelled well in EwE models (Moloney and Jarre 2003, Moloney *et al.* *subm.*), and the findings here need to be compared with the results of other modelling approaches representing plankton dynamics more explicitly. These estimated vulnerability settings reduced the baseline *SS* by 40% (in addition to the 2–3% explained based on fishing patterns).

Exploring environmental forcing in the southern Benguela

Estimating productivity forcing patterns and applying these to phytoplankton can result in a further decrease in the *SS*. This explained around 4–6% of the variance represented by the *SS* when vulnerabilities had been tuned, and around 12% when an environmental forcing function was used to improve model fitting in the absence of any vulnerability tuning. In the latter case, however, the environmental forcing function was, by necessity, of larger amplitude, because trophic interactions had not been tuned to account for flow controls. Both fitted environmental forcing functions increased in the late 1990s, and that estimated after the vulnerability tuning (Fig. 3) also showed an overall increase from 1981 to 1988.

Shannon *et al.* (1992) reported a period of increased equatorward wind stress from 1977 to 1983. This was followed by a period of lower than average equatorward wind stress, during which the sea level rose along the entire south-western African coast (Shannon *et al.* 1992). Around 1991, east-west progressive wind anomalies (plotted as deviation from the long-term average for the years 1960–1990) changed from negative to positive (see Cury and Shannon 2004). It is possible that these changes could have affected spawning by pelagic fish, and/or reduced offshore advection of pelagic fish eggs and larvae, resulting in large numbers of recruits reaching the nursery areas along the West Coast (Shannon *et al.* 1996, Boyd *et al.* 1998). Indeed, recruitment of anchovy and sardine has been particularly good recently (Coetzee *et al.* 2003). From the mid-1990s, the southerly wind component measured off Cape Point in the Cape Peninsula was stronger than the average north/south wind component for the period 1960–1991 (MCM, unpublished data). This may suggest more intensive upwelling in the last few years of the time period modelled, possibly facilitating sufficient plankton production to support large stocks of small pelagic fish in the late 1990s–early 2000s. Roy *et al.* (2001) believe the large stock sizes of anchovy and sardine in 2001 resulted from a suitable

timing and frequency of environmental events off South Africa in 1999/2000:

- (i) in December 1999, there was a warm event characterized by weak upwelling, which assisted anchovy eggs and larvae to reach the West Coast nursery areas;
- (ii) this event was followed by a cold event, a period of intense upwelling, which enhanced productivity, so increasing survival and growth of small pelagic fish.

Given the above, the primary productivity forcing required to improve the present model fit may well correspond to wind/temperature patterns off the South African coast (influencing upwelling intensity, retention nearshore, etc.), although such relationships can only be considered speculative and qualitative at this stage, at least until further analysis of the causal mechanisms has been undertaken.

Overall effects

A model-fitting sequence of fishing patterns, vulnerabilities and environmental forcing function resulted in a total reduction in *SS* of 46%, i.e. close to half the variance in the time-series could be explained on the basis of a combination of fishing, vulnerability settings and productivity patterns. A total reduction in *SS* of 40% was obtained when the order of fitting was reversed (an environmental forcing function was fitted before vulnerability tuning was undertaken).

It is debatable whether 40–46% is a “significant” reduction in *SS*, but such a discussion would suffer from a lack of objective criteria against which to evaluate the model performance. It is clear, however, that many of the time-series do not show much trend over time, some series even contradicting others. The question arises as to which ones should be trusted? In the absence of an answer, it may be best to explore alternative hypotheses, e.g. did hake biomass increase in the 1980s (as suggested from research surveys, Figs 1g, h), or not (as suggested from time-series of trawlable biomass assessments, Figs 1e, f)? It is beyond the scope of this paper to explore such questions further, but such simulations are both meaningful and of interest for use of the ecosystem model to evaluate ambiguity in trends from the more traditional stock assessment and survey series. Indeed, the Marine Stewardship Council Certification Report for the South African Hake Trawl Fishery (Powers *et al.* 2004) highlights major shortcomings in knowledge with respect to the structure of the stocks, as well as ecosystem relations, and suggests, *inter alia*, a liaison between ecosystem and stock assessment modelling. It is believed that the approach pursued and results

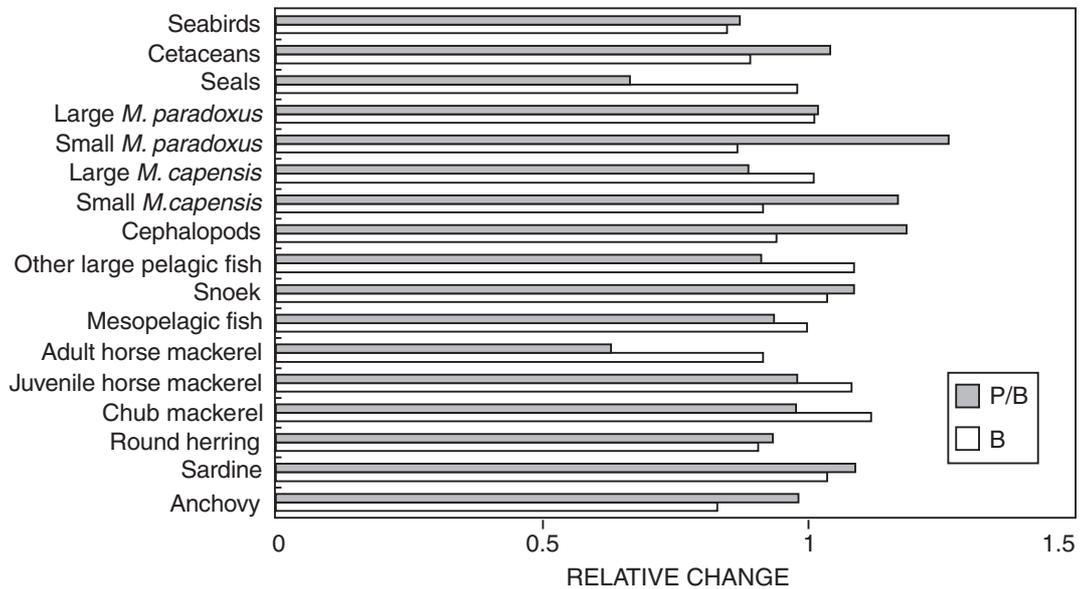


Fig. 4: Changes in biomass (B) and mortality (P/B) of selected groups in a "best-fit" Monte Carlo run (expressed as relative to original biomasses and annual mortality rates)

presented here represent a step towards this goal. For the model groups in which there are clear trends in the time-series, e.g. for sardine and anchovy, model fitting leads to fairly good fits (see Figs 1a, b, 2a, b).

Effect of uncertainty

Using the approaches above, 44% of the variability in the time-series could be explained. The effect of changes in input parameters (biomass, production/biomass, consumption/biomass, catch and diet) were estimated further using a Monte Carlo approach in ECOSIM to investigate whether an improved fit to the time-series data could be obtained. Based on 1 000 runs, a configuration was derived in which 55% of the variability in the data set could be explained. Monte Carlo simulations were run using default variability as explained earlier. An example of Monte Carlo-derived biomasses and mortality rates, presented relative to the original biomasses and mortality rates, is given in Figure 4. It is apparent that a variety of parameter combinations may give "plausible" fitting to the time-series data. However, the main question is not whether it is better to use one biomass or another, but rather what effect the varying parameter settings have on the important policy questions that applications of the model would seek to evaluate? It is important to

focus on the effect of uncertainties in model parameter estimates on the results obtained in addressing such questions, rather than to focus on particular individual estimates.

Mortality rates

Mortality rates estimated by ECOSIM vary over time as a function of fishing intensity, feeding conditions and predation pressure. For the southern Benguela model, total mortalities vary considerably over time, for most fish groups, but without any clear trend (Fig. 5), with the exceptions of anchovy (total mortality declines from 1.4 to 1.2 year⁻¹ over the period modelled) and sardine (total mortality declines from 1.2 to 1.0 year⁻¹). It is a common misperception (caused by the use of time-invariable parameters in some early applications) that EwE models are constrained by the steady-state assumptions, notably with regards to instantaneous mortality rates (P/B or Z). This is, however, incorrect. Where information on variability over time is available, be it through changes in fishing, environmental conditions, mediating groups, feeding or predator conditions, it will be reflected in the ECOSIM run, as indicated by Figure 5.

There is limited independent information to evaluate the estimated mortality rates. However, a time-series

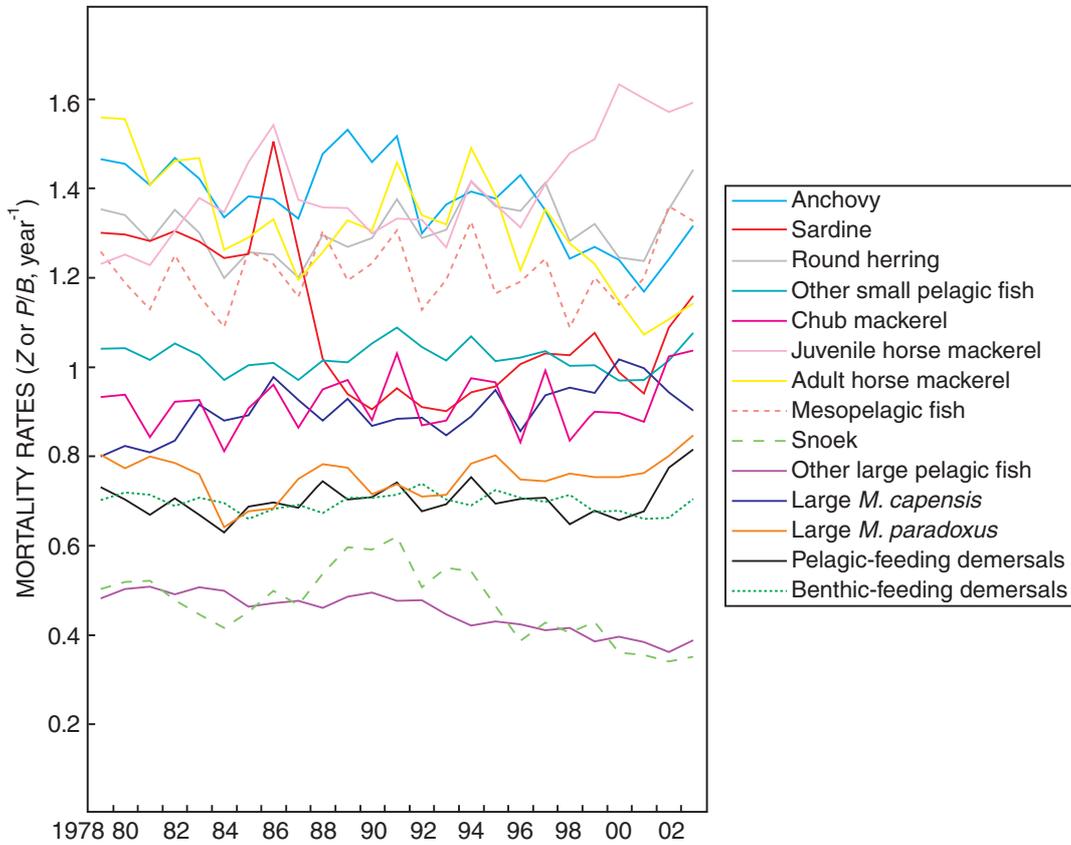


Fig. 5: Estimated mortality rates (Z or P/B , year⁻¹) for the major fish species in the southern Benguela model, 1978–2002

of predation mortality for sardine and anchovy as a result of Cape gannet predation is available (R. J. M. Crawford, MCM, unpublished data). A comparison of ECOSIM-evaluated sardine and anchovy predation mortality by piscivorous birds with the estimates for predation mortality by Cape gannets is shown in Figure 6. Predation mortalities for anchovy indicate variation in a qualitatively similar fashion for both series, whereas ECOSIM estimates a continuously increasing trend for sardine while the gannet estimates do not. Other southern African seabird species are also strongly linked to fluctuations in the availability of pelagic fish prey. Crawford (2003) reported a significant relationship between the numbers of swift terns *Sterna bergii* breeding off South Africa's Western Cape and the combined biomass of anchovy and sardine. Further, the number of African penguin chicks fledging was significantly correlated with anchovy biomass between 1984 and 1992 (Crawford and

Dyer 1995). Cape cormorants *Phalacrocorax capensis* accounted for the largest proportion (about one-third) of the consumption of fish by seabirds off south-western Africa in the 1980s (Crawford *et al.* 1991), and anchovy abundance affected the number of Cape cormorants attempting to breed during the period 1984–1992 (Crawford and Dyer 1995).

Prey preference

Predator-prey selectivity varies in ECOSIM as predator and prey abundances change over time. This is illustrated in Figure 7 for apex chondrichthyans as predators, and its most important prey groups. The apex chondrichthyan group is poorly known and was selected purely for illustration. In this example, some groups became more suitable prey as their abundances increased, whereas others became less suitable. Overall,

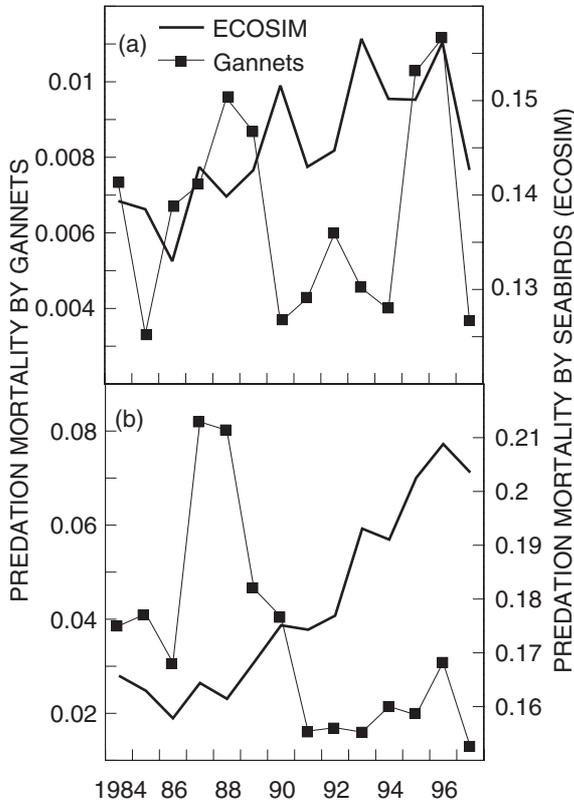


Fig. 6: Predation mortality caused by Cape gannets feeding on (a) anchovy and (b) sardine, compared with modelled predation mortality caused by seabirds (ECOSIM)

though, it appears that variability in suitability is large for most higher trophic level consumers, whereas there is little variation in suitabilities for lower trophic level consumers, e.g. for all small pelagic fish and for microzooplankton. A closer examination, however, reveals that this is an artifact caused by the number of prey groups specified for a given consumer group. If <5 prey types are specified, the standard error of suitabilities is low (<0.1), but it is higher for groups with more prey types. Because the number of prey is a function of how the model is specified, care should be taken when interpreting variation in suitabilities for a consumer group.

Further investigation of effort series for hake

Although neither the South Coast nor West Coast trawl effort series, nor fishing mortality estimates for *M. paradoxus*, showed large increases over the last decade,

total large *M. paradoxus* catches have increased since 1990 (Fig. 2). This trend is mainly because trawlers have moved into deeper waters (Glazer and Butterworth 2002) on the West Coast, so taking larger *M. paradoxus*. High total mortality estimates for older hakes are required to balance hake biomass models, one possible reason being that catches (fishing mortalities) of older hake may be underestimated. The catchability of hake trawls on the West Coast changed between 1983 and 1992 (Rademeyer 2001), and is a likely explanation for the poor model fit to large *M. paradoxus* catches post-1985. An additional factor partly explaining the underestimation of model yield of *M. paradoxus* compared with observed catches is that there is under-reporting of hake caught by longline – there are likely substantial, but unquantified, losses of hake from longlines before they are retrieved, as well as unreported discarding of 3- and 4-year-old hake in favour of larger (6- and 7-year-old) hake.

The model generally overestimated small *M. paradoxus* catches from 1993 onwards (Fig. 2h). It is likely that large quantities of small hake were caught in commercial trawls before 1985, when small-meshed liners were widely used, and that these were discarded and therefore unreported. Further, as the handline and longline fishing sectors developed, and the market for high quality large hake developed, it is possible that small hake were discarded, a practice that certainly went unreported (R. W. Leslie, MCM, pers. comm.).

This study draws on the split of total catches, according to area and gear type, into small (0-, 1- and 2-year-old hake) and large (older than 2 years) size-classes based on the estimated relative proportions of the two size-classes in demersal landings data (Leslie 1998a, b). Of the total trawl catches of *M. paradoxus* on the West and South coasts, approximately 60% were allocated to the small size-class of *M. paradoxus*. This proportion was an average for the period 1980–1989, and may account for the slight overestimation of small *M. paradoxus* model yield and underestimation of large *M. paradoxus* model yield in later years, underlining the importance of generating size/age disaggregations of Cape hake in the catches.

When two hake fishing effort (*F*) series (*M. capensis* on the South Coast, *M. paradoxus* on the West Coast) were used to force the modelled hake fisheries in place of the three fishing effort series, similar trajectories (not shown) were obtained, but model fits were poorer. However, using those *F* series, modelled yield of *M. capensis* was overestimated (by about a factor of two) compared with reported catches. If *M. capensis* on the West and South coasts constitute a single stock (Le Clus 2004), not all the *M. capensis* resource would be available to the South Coast fisheries. Therefore, applying the total *F* series estimated for

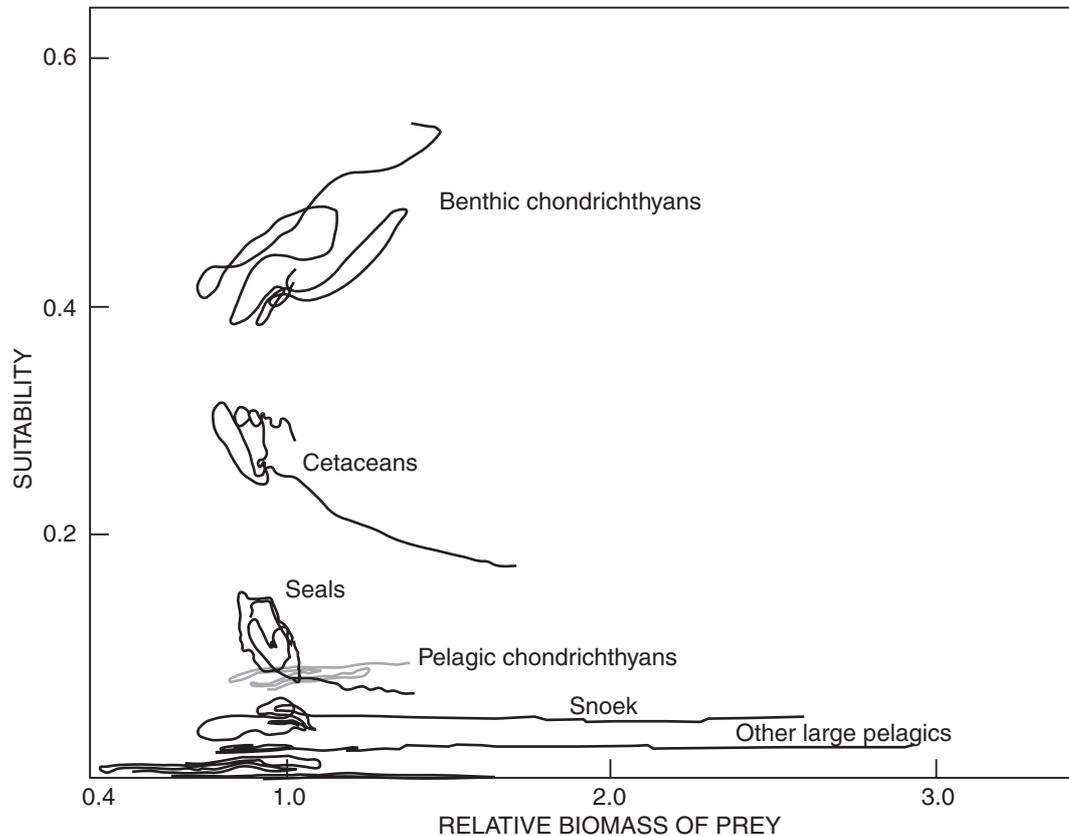


Fig. 7: Relative suitabilities (preference) for apex chondrichthyans as predators. Suitability as prey for benthic and pelagic chondrichthyans, as well as for other large pelagics increase with relative abundance, while cetaceans and seals become less preferred as their abundances as potential prey increase

M. capensis fisheries on the South Coast to the whole *M. capensis* stock may explain the overestimation of *F* and hence the overestimation of model *M. capensis* yields.

Pending revision of anchovy and sardine abundance series

Anchovy and sardine spawner biomass and recruitment estimates from acoustic surveys, and anchovy and sardine stock assessments, are currently being revised (Cunningham and Butterworth 2004a, b). These revisions follow refinements in the processing of acoustic survey data, and indicate that the resources may have been underestimated substantially in past assessments (of the order of an average of 30–50% over the period 1984–2003). It will only be

possible to incorporate such corrected abundance and fishing mortality estimates into the current dynamic analyses once the underlying ECOPATH model has been revised to account for these large discrepancies. The revised data-series may necessitate another iteration of the analyses. It is noteworthy that Shannon (2001) reported difficulties in balancing the initial models of the southern Benguela in the 1980s and 1990s, related to estimated model consumption of anchovy and sardine by their predators exceeding the model inputs of anchovy and sardine production.

CONCLUSIONS

The present study supports the conclusion of Shannon *et al.* (2004), who, using dynamic simulations from

mass-balanced models of the southern Benguela, in the absence of time-series data, found that fishing played a small role in explaining the ecosystem changes observed from the 1980s to the 1990s. It was found here that variation in fishing pressure has little explanatory power with regard to the variance in the time-series used in this model of the southern Benguela. This reflects the fact that fishing pressure for the various groups has been generally constant though large changes in biomasses have been observed. This makes a case for expanding the scope of stock dynamics to look beyond fishing as the main driving force for the population dynamics of many exploited species in the southern Benguela. This is being widely discussed for other marine ecosystems experiencing pronounced variations in environmental conditions (e.g. mutual anchovy-hake inhibition off northern central Peru (Sandoval de Castillo *et al.* 1989), the influence of oxygen concentrations on cod *Gadus morhua* recruitment in the Baltic Sea (Jarre-Teichmann *et al.* 2000), and the dependence of Barents Sea cod on capelin *Mallotus villosus* availability (Tjelmeland and Bogstad 1998, Gjøsæter *et al.* 2002).

For Cape hake, targeted by more than one fishery, using effort series to drive the fisheries in the model may be advantageous over use of fishing mortality series. In the model configuration used here, individual fisheries can be handled separately in the case of effort series, whereas fishery-specific F series cannot be applied to the four hake groups currently specified in the model. This is because it has not yet been possible to split the stock into separate sub-components according to the fishery operating on it. This could be a future consideration, to improve on and to avoid some of the assumptions required to split the stock into size and species groups.

This study has not taken into account spatial considerations, which would likely account for at least some of the deviations found between model and observed time-series. Understanding of the functioning of marine ecosystems would be improved by more detailed analyses of spatial considerations such as migration and the spatial overlaps or co-occurrences of species. The need for spatially explicit modelling approaches has been recognized as a priority (e.g. Livingstone and Juroda-Molina 2000) and the increasing number of studies focusing on spatial aspects of ecosystem research in the southern Benguela is encouraging (e.g. Pecquerie *et al.* 2004, Drapeau *et al.* 2004, Shin *et al.* 2004, Fréon *et al.* *in press*).

Shannon *et al.* (2004) found that environmental effects mediated through zooplankton prey availability likely played a larger role than fishing in driving changes in many groups in the southern Benguela ecosystem in the last couple of decades. Indeed, in the

present study, an environmental forcing pattern explained more of the variance represented by the SS in model fitting than forcing by fishing. However, vulnerabilities describing flow control patterns between groups in the ecosystem were simultaneously explored, and this was the largest source of improvements in fitting the model to data.

Cury *et al.* (2000) found support for the hypothesis that the southern Benguela upwelling system is largely wasp-waist controlled, i.e. that small pelagic fish control their zooplankton prey (top-down control) while simultaneously exerting bottom-up control on their predators. Similarly, the time-series fitting routine of EwE suggested vulnerabilities in line with wasp-waist control. While the possibility of this resulting from a modelling artifact cannot be discounted, these results nevertheless increase the evidence for the wasp-waist hypothesis. Recent comparative studies on trophic flow control (e.g. Moloney *et al.* *in press*) will help in exploring the question as to the extent to which this is a general feature of upwelling ecosystems, all of which show strong fluctuations in their principle small pelagic species. Continued improvement in understanding trophic flow control has been highlighted as an important research area (Cury *et al.* *in press*), supporting scientific advice for an ecosystem approach to fisheries management. The present study demonstrates the value of using the trophic modelling approach EwE as a tool in facilitating the EAF process for the southern Benguela.

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