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SIMULATIONS OF FISHING EFFECTS ON THE SOUTHERN BENGUELA FISH COMMUNITY USING AN INDIVIDUAL-BASED MODEL: LEARNING FROM A COMPARISON WITH ECOSIM

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By applying an individual-based model (OSMOSE) to the southern Benguela ecosystem, a multispecies analysis is proposed, complementary to that provided by the application of ECOPATH/ECOSIM models. To reconstruct marine foodwebs, OSMOSE is based on the hypothesis that predation is a size-structured process. In all, 12 fish species, chosen for their importance in terms of biomass and catches, are explicitly modelled. Growth, reproduction and mortality parameters are required to model their dynamics and trophic interactions. Maps of mean spatial distribution of the species are compiled from published literature. Taking into account the spatial component is necessary because spatial co-occurrence determines potential interactions between predatory fish and prey fish of suitable size. To explore ecosystem effects of fishing, different fishing scenarios, previously examined using ECOSIM, are simulated using the OSMOSE model. They explore the effects of targeting fish species in the southern Benguela considered to be predators (Cape hake *Merluccius capensis* and *M. paradoxus*) or prey (anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi*). Simulation results are compared and are generally consistent with those obtained using an ECOSIM model. This cross-validation appears to be a promising means of evaluating the robustness of model outputs, when separate validation of marine ecosystem models are still difficult to perform.

Key words: fishing efforts, marine ecosystems, multispecies modelling, trophic interactions

Implementation of an Ecosystem Approach to Fisheries is being encouraged by the Food and Agriculture Organization of the United Nations (FAO) and by some national and regional agencies charged with managing marine resources (FAO 2003). However, this objective is confounded by the limited knowledge available on ecosystem functioning. Independent modelling approaches focused on different processes and hypotheses are proposed to disentangle the complexity of the interactions within marine ecosystems, so hopefully contributing to development of a more integrative approach to fisheries management. Each approach might describe several aspects of ecosystem structure and function, but a common difficulty of the models remains validation of the simulation output. Comparing the results produced by different models may help to consolidate, refute or at least encourage discussion of the simulated effects of fishing on marine ecosystems. If the results from different models show similar trends, then there is more confidence in them, because they will have emerged from independent representations of the ecosystem. Moreover, even if the results are divergent, comparing model outputs can still be informative, because it allows the identification of a range of possible trajectories for the system dynamics. In this context, an application of the OSMOSE model (Object-oriented Simulator of Marine ecOSystems Exploitation; Shin and Cury 2001) to the southern Benguela ecosystem is proposed here as an alternative multispecies analysis to ECOPATH with ECOSIM (EwE), which has already been applied to the southern Benguela (e.g. Shannon *et al.* 2000, 2003).

To start, a brief description of the OSMOSE model is given, then the data and the sources of information used for calibrating the model with respect to the fish community of the southern Benguela, especially those concerning the spatial distribution of the species, are presented. A set of simulations aimed at detecting the effects of increasing fishing pressure on particular target species are then discussed. The simulations are conducted following fishing scenarios that have been implemented by Shannon *et al.* (2000), using EwE models of the southern Benguela, in order to compare the outputs of both models.

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MATERIAL AND METHODS

OSMOSE model: overview of structure and hypotheses

As a detailed description of the OSMOSE model is provided in Shin and Cury (2001, 2004), only the main outline of the model will be presented here. OSMOSE is a multispecies model that depends on the central hypothesis that fish predation is opportunistic and depending on size suitability and spatial co-occurrence between a predator and its prey. The OSMOSE size-structured and spatial model incorporates an individual-based formulation of the key processes of the fish life cycle: predation, growth, reproduction and mortality (by predation, starvation, fishing). The unit of interaction is the fish school, defined in the model as a group of fish having the same size, the same spatial coordinates, requiring similar food and belonging to the same species. Using object-orientated terminology, a fish group is represented by a class belonging to the class "cohort", which in turn belongs to the class "species". This hierarchical structure allows key variables (biomass, for example) to be tracked at different levels of aggregation. From each class, characterized by attributes (biological parameters) and functions (growth, predation), a number of objects are created that are part of the simulated system.

Only the dynamics of fish species are explicitly modelled in this application. The other trophic compartments of the ecosystem are implicitly taken into account through various model parameters. For example, phytoplankton, zooplankton and invertebrate species that constitute the prey of fish are represented through the total carrying capacity of all non-piscivorous fish included in the model. Predation of fish by top predators such as marine mammals and seabirds is taken into account by an additional natural mortality term. Step by step, different processes that affect fish species dynamics are modelled. The time-step adopted for application to the fish community of the southern Benguela is the semester (January–June, July–December). It results from a compromise between the necessity to take into account a seasonal aspect in the dynamics, and the ready availability of data. Both constraints are linked essentially to the spatial distributions of the species by age-class. Fish schools move in a two-dimensional grid, represented by a set of square cells with closed boundaries. Their dynamics and interactions are modelled through the processes described below in the order in which they are implemented within a time-step.

CARRYING CAPACITY CONSTRAINT

In OSMOSE, the carrying capacity corresponds to the upper limit of the viable biomass of all non-piscivorous fish in the system. At the beginning of each iteration, the total biomass of non-piscivorous fish in each cell of the grid is compared with the system carrying capacity. If it exceeds the carrying capacity, then the abundance of non-piscivorous fish schools is reduced to the implemented level of the carrying capacity. For the sake of simplicity, the reduction in biomass operates uniformly across the non-piscivorous schools. It means that, in each cell, each group of non-piscivorous fish undergoes the same density-dependent mortality because of a lack of food. In the results section, the total mortality of age-group 0 is re-estimated, to account for the fact that pre-recruits are more sensitive than adult fish to starvation.

SPATIAL DISTRIBUTION

Depending on species, age or size, fish are placed at the beginning of each time-step in their mean spatial distributional areas. These areas are provided as input to the model for each 6-month semester. Then, within the time-step, local movements can take place, as described below.

FORAGING AND PREDATION

This phase only concerns the piscivorous fish of the system. The order in which fish schools act is randomly set at each time-step. School displacement is directed by a search for the adjacent cell with the highest biomass of potential prey. Once each school has moved (or stayed in its cell), it proceeds to the feeding phase, so causing an explicit predation mortality for each school preyed upon. It should be noted that two criteria form the basis of the predation process: an individual predator can potentially feed on any species provided that there is spatio-temporal co-occurrence (to be considered accessible, prey fish schools have to be located in the same cell as predators) and that the predator/prey size ratio is not less than a minimal threshold (input parameter of the model). Therefore, two species can simultaneously be predator and prey of each other and there can be cannibalism (Alheit 1987, Valdès *et al.* 1987). These trophic patterns are consistent with the observations of very diversified and time-varying diets of fish in different ecosystems in the world, and especially in the southern Benguela (e.g. Crawford 1987).

Finally, when all fish schools have completed the feeding phase, a predation efficiency ξ is calculated for each fish school. This coefficient is determined as the ratio between the food biomass ingested by a school and the food biomass required to fulfil its vital functions (an input parameter of the model).

GROWTH

Mean annual growth rates (in length) are calculated using the von Bertalanffy (1938) model. This mean rate is re-adjusted to take into account the quantity of food consumed by a fish school during a timestep. A critical threshold ξ_{crit} can be determined for predation efficiency beyond which it is considered that the food ration is dedicated to fish growth. An approximation would be to consider that, if a school predation efficiency $\xi \geq \xi_{\text{crit}}$, then growth rate in length varies linearly with ξ such that for $\xi = \xi_{\text{crit}}$, the rate is zero, or for $\xi = (\xi_{\max} + \xi_{\text{crit}})/2$, with $\xi_{\max} = 1$, growth rate equals the mean growth rate calculated by the von Bertalanffy model.

OTHER SOURCES OF MORTALITY

Starvation mortality affects fish schools when the food ration is too low for fish maintenance. Beverton and Holt (1957) advocate the existence of a starvation mortality for adult stages of fish in a linear model linking rate of natural mortality to fish density. By considering that, for each species, nutritional resources are limited, this linear model is applied under the hypothesis that the greater the density of fish, the less the food ration per fish will be. Hence, starvation mortality rates of fish schools are linearly expressed in relation to predation efficiency when $\xi \leq \xi_{\text{crit}}$.

Fishing mortality rates are applied to the different species, following the classical survival equation structured by age:

$$N_{s,t+1} = N_{s,t}\ \mathrm{e}^{-Fs} \quad ,$$

where $N_{s,t}$ is the abundance of species s at time t, and F_s is the fishing mortality rate applied to species s.

REPRODUCTION

Let ϕ_s be the relative fecundity of species s, SB_s its spawning biomass, $B_{s,a}$ the biomass of age-class a, a_{Ms} its age at maturity, and A_s its longevity. Assuming that the sex ratio is 1:1 for all species, and noting $N_{s,0,t+1}$ to be the number of eggs spawned by species s at the end of the time step t, the following equation is applied:

$$N_{s,0,t+1} = \phi_s\, SB_{s,t} \quad \text{with} \quad SB_{s,t} = \frac{1}{2} \sum_{a=a_{M_s}}^{A_s} B_{s,a,t}\ .$$

Parameterization of the model

The first step in the modelling process is to select the fish species to be represented explicitly. This choice is not trivial and must be based on clear and objective criteria. Moreover, there must be a compromise between the cost-effectiveness of data collection (easily-accessible data are preferred) and the representivity of the set of species chosen in terms of ecosystem functioning and dynamics. Three criteria, considered to quantify the "importance" of the species in the ecosystem, have guided the choice of species in this study: biomass, catches and consumption (which is linked to species interactions in terms of predation or competition). In general, the importance attached to some species following the first two criteria goes hand in hand with the investment in research and data collection. Application of the OSMOSE model to the southern Benguela focuses on 12 interacting fish species in the following pelagic and demersal compartments: anchovy *Engraulis encrasicolus* (formerly *E. capensis*), sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi*, horse mackerel *Trachurus trachurus capensis*, chub mackerel *Scomber japonicus*, shallow-water Cape hake *Merluccius capensis*, deep-water Cape hake *M. paradoxus*, kingklip *Genypterus capensis*, snoek *Thyrsites atun*, silver kob *Argyrosomus inodorus*, lanternfish *Lampanyctodes hectoris* and lightfish *Maurolicus muelleri*. An application of the ECOPATH model to the southern Benguela shows that, in the 1990s, these species represented at least 76.2% of the biomass and 93.8% of the catch of all fish species (calculations based on Table I of Shannon *et al.* 2003). During the same period, the 12 species were also responsible for at least 84% of the total consumption by fish species and top predators (marine mammals and seabirds) and 72% of the consumption of small pelagic fish production (Shannon 2001). The choice of species is also determined relative to the functional group to which it belongs. For example, anchovy, sardine and round herring represented 97% of the biomass and 99.9% of the catch of small pelagic fish in the 1990s (Shannon *et al.* 2003). Snoek and silver kob represented 77.4% of the biomass and 70.6% of the catch of large pelagic fish in the 1980s (Jarre-Teichmann *et al.* 1998). Tuna were omitted from the model, despite representing a non-negligible proportion of the biomass of the large pelagic fish group, be-

Table I: Species parameters used in the OSMOSE model. There are three categories of parameters: growth, reproduction and survival parameters. L_∞, K and t_0 are the parameters of the von Bertalanffy growth model, c is the condition factor, ϕ is the annual relative fecundity (number of eggs spawned per gramme of mature female), a_{mat} is the age at maturity, a_{max} the maximal age or longevity, a_{rec} the age at recruitment, M_{add} the additional annual natural mortality (other than that due to predation by fish and starvation). Values reported in the table come from the literature (see Appendix for the list of references used). Values in bold are estimated or adapted by the authors based on cited references (see Appendix)

Species		Growth				Reproduction		Survival		
		L_∞ (cm^{-1})	K (year^{-1})	t_0 (year)	c (g cm^{-3})	ϕ (eggs g^{-1})	a_{mat} (year)	a_{max} (year)	a_{rec} (year)	M_{add} (year^{-1})
Anchovy	*Engraulis encrasicolus*	14.8	1.37	−0.03	0.007	**8 000**	1	5	1	0.406
Chub mackerel	*Scomber japonicus*	68	0.207	−0.98	0.005	**300**	3	8	*2*	0.236
Cape hake (shallow-water)	*Merluccius capensis*	230.3	0.046	−0.82	0.005	**500**	**4**	15	3	**0.312**
Cape hake (deep-water)	*M. paradoxus*	230.3	0.046	−0.82	0.005	**500**	**4**	15	3	**0.270**
Horse mackerel	*Trachurus t. capensis*	54.5	0.183	−0.65	0.009	**250**	3	8	2	**0.362**
Kingklip	*Genypterus capensis*	132.6	0.142	0.05	0.001	**500**	5	24	**3**	**0.250**
Lanternfish	*Lampanyctodes hectoris*	7	1.66	0.06	**0.008**	646	0.5	*2*	1	**0.270**
Lightfish	*Maurolicus muelleri*	6	1.15	0.06	**0.008**	334	0.5	*2*	1	**0.270**
Round herring	*Etrumeus whiteheadi*	30.1	0.71	0.28	0.009	**750**	**1**	6	**1**	0.183
Sardine	*Sardinops sagax*	21.4	0.95	−0.17	0.009	**400**	*2*	10	1	0.498
Silver kob	*Argyrosomus inodorus*	116	0.12	−1.47	0.007	**150**	2	25	3	**0.228**
Snoek	*Thyrsites atun*	115.3	0.294	**−0.1**	0.018	**130**	3	10	2	0.189

cause their oceanic spatial distribution means they do not interact as much with the selected community (see Fig. 3 in Drapeau *et al.* 2004). Finally, Cape hake, horse mackerel, kingklip, snoek and chub mackerel represented about 70% of the biomass of commercially important demersal fish species surveyed in 2001 on the West and South coasts of the Benguela and 90% of the reported demersal commercial catch over the period 1992–1999 (Marine and Coastal Management, unpublished data).

Species parameters

At model initialization, a certain number of species are created, and some attributes are assigned to them. Three types of biological parameter characterize a species in the model: growth, reproduction and survival. The values used are reported in Table I, and the data sources are listed in the Appendix. Some adaptations are used in the application of the OSMOSE model. For lanternfish and lightfish, the same value of mortality is applied because the two species are considered to be similar and constitute the main part of the "mesopelagic fish" compartment in the ECOPATH model. Silver kob are attributed the same mortality value as "other large pelagic fish", the compartment to which it pertains in ECOPATH. The values adopted for horse mackerel and both species of Cape hake are those from the adult compartments. On account of the lack of information, and because kingklip are generally not preyed upon (except when small), the additional mortality rate value adopted for kingklip is the total natural mortality rate estimated by Japp (1989). Of all the parameters, relative fecundity is the most difficult to obtain. For some species, the values used are estimated from other species belonging to the same family, and living in different ecosystems. They were only used to obtain an appropriate order of magnitude of relative fecundity for initializing the simulations. There are also a certain number of parameter values chosen to be common to all species, because data are less accessible on a species basis and because the approximation is considered to be satisfactory for a first approach. The minimal predator-prey size ratio is taken as 3.5 (Froese and Pauly 1998) and, from values available for different fish species elsewhere, it is estimated that a fish should annually consume 3.5 g of food per body gramme (Laevastu and Larkins 1981, Gislason and Helgason 1985, Longhurst and Pauly 1987).

Species spatial distributions

The geographical area studied is chosen so as to cover the distribution areas of the 12 species modelled. It is represented by a square grid, comprising 40 × 40 cells, and which extends from the Orange River on the West Coast to Port Alfred on South

Table II: References used for compiling the maps of the spatial distributions of the 12 species modelled. The literature provided two types of information, maps drawn from scientific surveys and accumulated knowledge, and descriptions of spatial distributions documented in the literature

Species	References	
	Maps	Descriptions
Anchovy	Armstrong and Thomas (1989) Armstrong *et al.* (1991) Hampton (1987, 1992) Valdes *et al.* (1987)	Armstrong *et al.* (1991) Crawford (1981) Hampton (1987, 1992) Shelton (1986)
Chub mackerel	Crawford (1989b)	Crawford (1989b)
Cape hakes	Badenhorst and Smale (1991) Payne (1989) Punt (1994) Punt *et al.* (1992)	Badenhorst and Smale (1991) Payne (1989) Punt *et al.* (1992)
Horse mackerel	Barange *et al.* (1998) Crawford (1989a) Hecht (1990)	Badenhorst and Smale (1991) Barange *et al.* (1998) Crawford (1989a) Hecht (1990) Naish *et al.* (1991) Shelton (1986)
Kingklip	Badenhorst and Smale (1991) Japp (1990) Olivar and Sabatès (1989) Punt and Japp (1994)	Badenhorst and Smale (1991) Olivar and Sabatès (1989)
Mesopelagic species	Armstrong and Prosch (1991) Hulley and Prosch (1987) Prosch (1986, 1991)	Armstrong and Prosch (1991) Prosch (1991) Prosch *et al.* (1989)
Round herring	Armstrong and Thomas (1989) Hampton (1992) Roel and Armstrong (1991)	Roel and Armstrong (1991)
Sardine	Armstrong and Thomas (1989) Hampton (1992)	Armstrong *et al.* (1987) Hampton (1992)
Silver kob	Van der Elst (1993)	Van der Elst (1993)
Snoek	Crawford (1989b) Crawford and de Villiers (1985)	Crawford (1989b) Crawford and de Villiers (1985)

Africa's south coast (26–38°S, 16–28°E). Chub mackerel and snoek belonging to 1+ age-classes were assumed to migrate to the northern Benguela during the first semester (Crawford 1989b), so their whole distribution is not represented in this grid. They interact with the other species of the model only during the second semester. The maps used in the model were compiled from the literature for each species and age-class and are presented in Figure 1. The literature provided two kinds of information (Table II): maps drawn from scientific surveys and accumulated knowledge, and descriptions of spatial distributions documented in the literature. Together, the forms of information allowed the preparation of maps that can be considered, on average, to be representative of the actual species distributions in the southern Benguela. Pecquerie *et al.* (2004) found that their maps derived from research and commercial databases generally agreed fairly well with those presented here.

Initial conditions and simulations

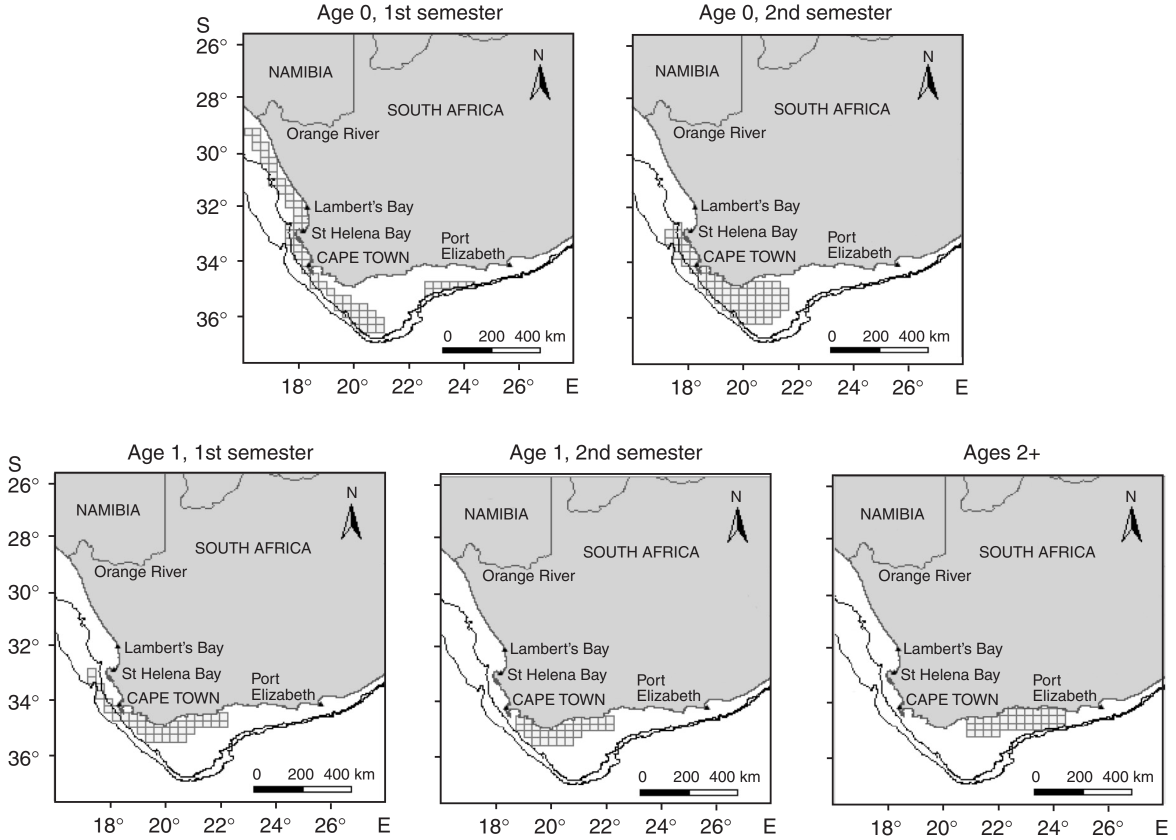
To initialize the model, the age structure of each species is constructed using the classical survival equation:

$$B_{s,a+1} = B_{s,a}\ \mathrm{e}^{-(F_s+M_s)} \quad ,$$

where $B_{s,a}$ is the biomass of species s at age a, and F_s and M_s are respectively the fishing and natural mortality rates of species s.

The 1980s was the period chosen for the state of reference of the southern Benguela ecosystem, because the simulations undertaken by Shannon *et al.*

(a) ANCHOVY



(b) CHUB MACKEREL

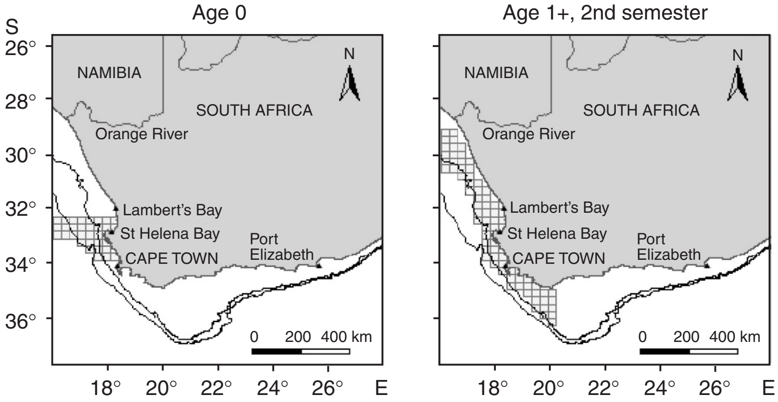


Fig. 1: Mean spatial distribution of each species and age-class included in the model. The maps are derived from the literature, directly from published maps and supplemented with information provided in the text: (a) anchovy by age-class and semester, (b) chub mackerel by age-class and semester, (c) shallow-water Cape hake by age-class, (d) deep-water Cape hake by age-class, (e) horse mackerel by age-class, (f) kingklip by age-class, (g) mesopelagic fish – lanternfish and lightfish, (h) round herring by age-class and semester, (i) sardine by age-class and semester, (j) silver kob and (k) snoek by age-class and semester

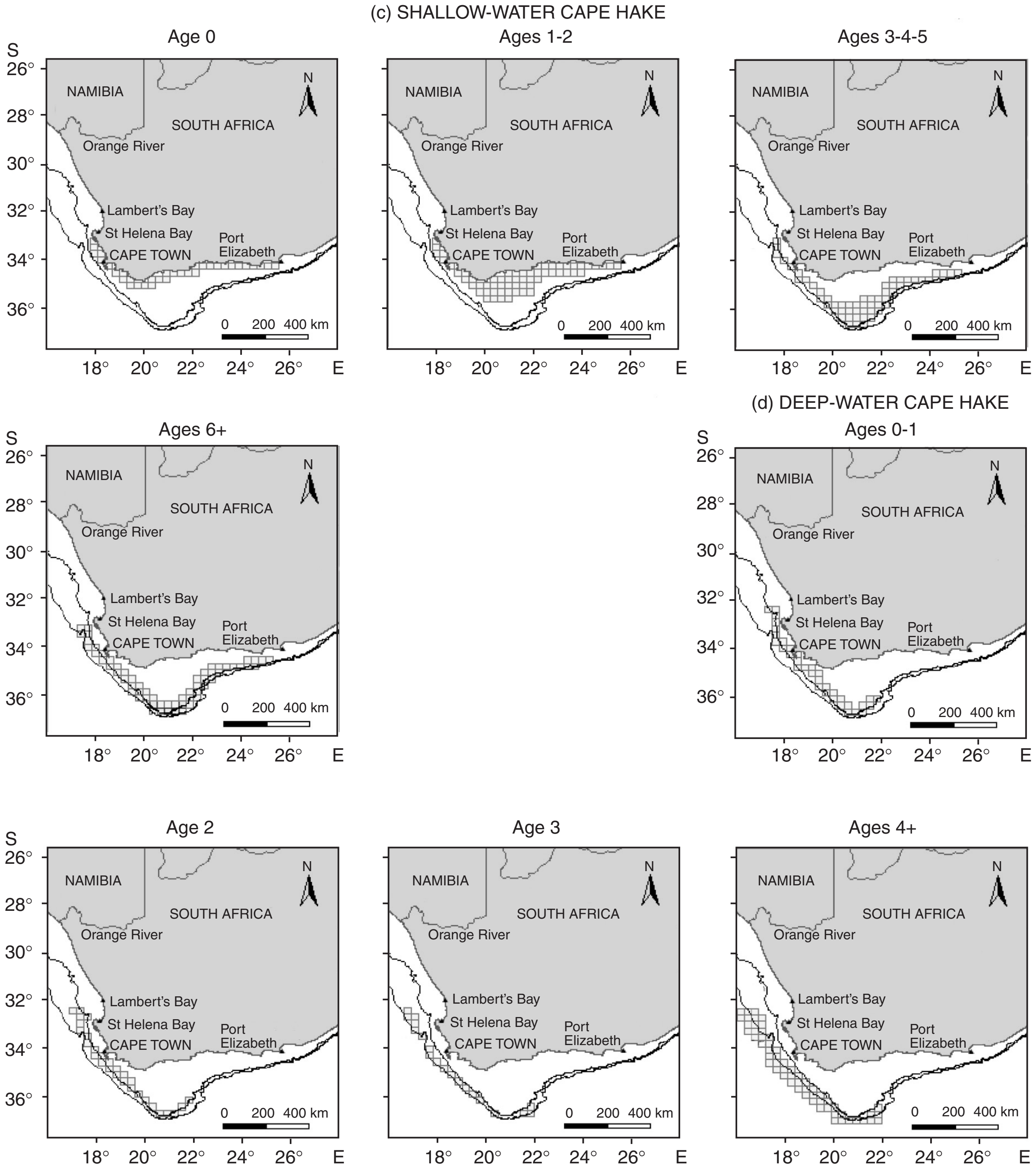
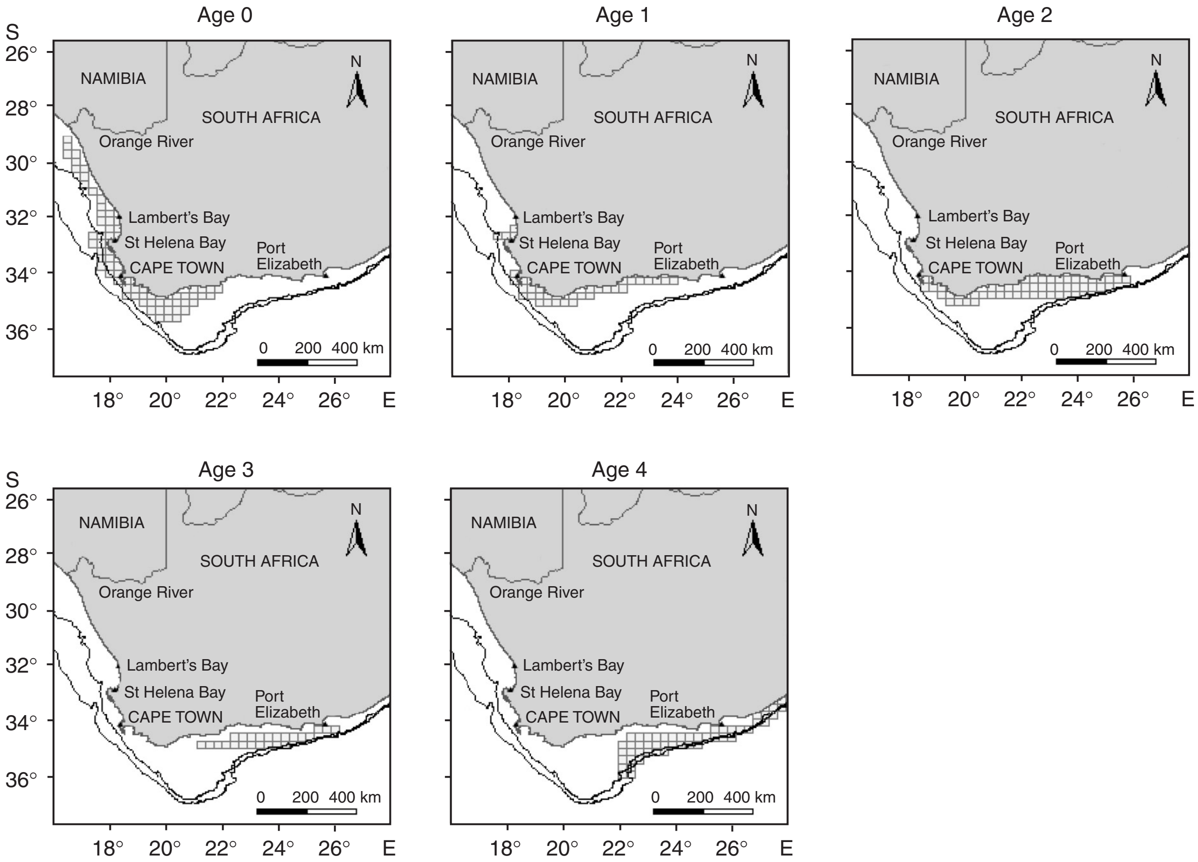


Fig. 1: (*continued*)

(e) HORSE MACKEREL


Age 0

Age 1

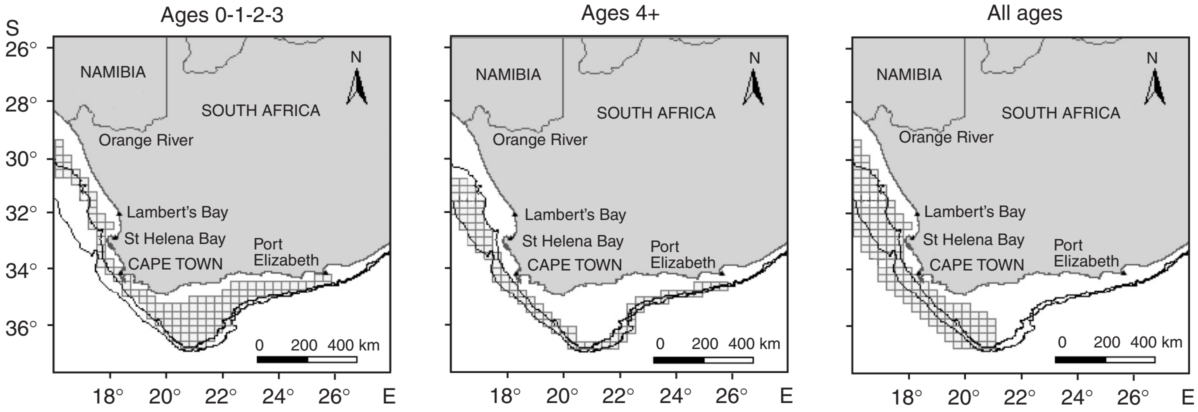
Age 2

Age 3

Age 4

(f) KINGKLIP

(g) MESOPELAGIC FISH


Ages 0-1-2-3

Ages 4+

All ages

Fig. 1: (*continued*)

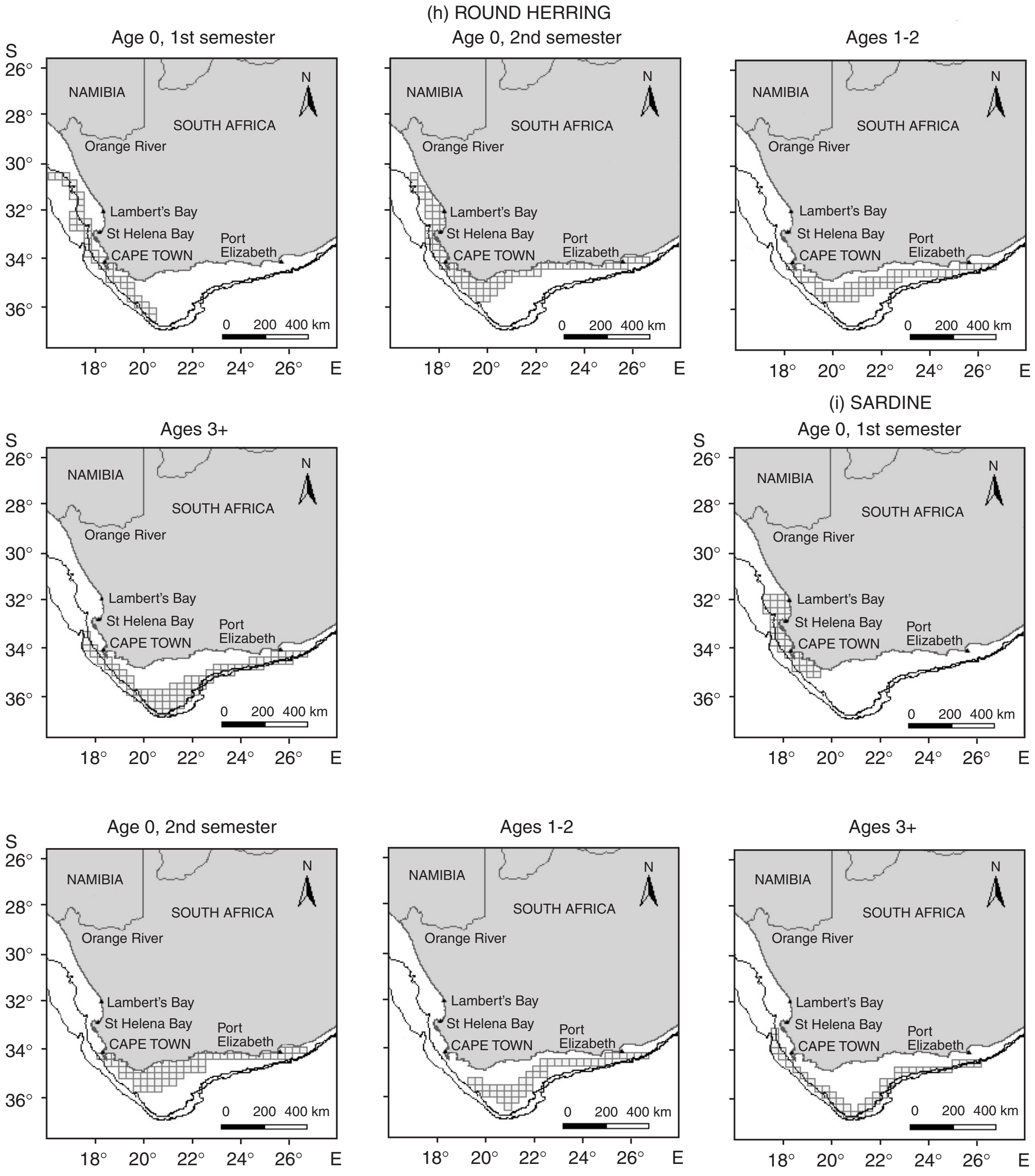


Fig. 1: (*continued*)

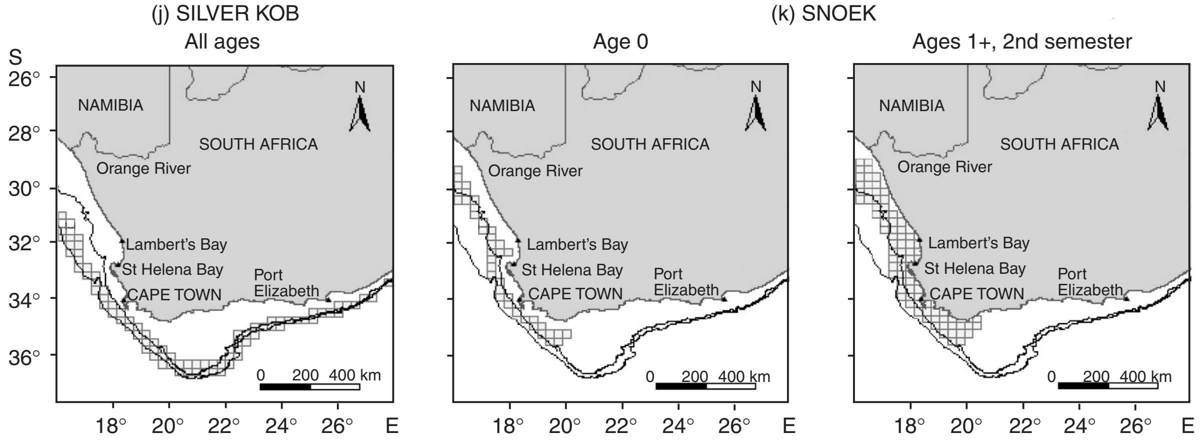


Fig. 1: (*continued*)

(2000), and to which the current results will be compared, were for the same period. Initial values used in the simulations are reported in Table III. Values in bold are estimated from other sources because they pertain to fish species that are not explicit compartments of the ECOPATH model constructed by Shannon (2001). For kingklip, *F* and *M* are estimated from Japp (1989). For the purposes of this paper, an estimation of kingklip biomass was calculated from catch values reported in Punt and Japp (1994). For silver kob, values of biomass and fishing mortality are provided by Penney *et al.* (1991). Once the model had been initialized, the state of reference of the community modelled was simulated by tuning the model to obtain mean species biomasses within the range of ±10% of the expected biomasses (Table III). The relative fecundity of the species served as the tuning parameter for the model. Two scenarios, corresponding to those simulated by Shannon *et al.* (2000) using an ECOSIM model, were then considered in order to explore the impacts of fishing. The first considered the impacts of a four-fold increase in fishing mortality on the three main small pelagic fish species (anchovy, sardine and round herring). The second considered the effects of a four-fold increase in fishing mortality on two predatory species that are (commercially) the most important fish in the southern Benguela, namely shallow-water and deep-water Cape hake. The results represent aver-

Table III: Input data used for initializing OSMOSE simulations. Biomass (mean *B*), annual natural (*M*) and fishing (*F*) mortality values are estimated or used by Shannon (2001) and Shannon *et al.* (2003) in an ECOPATH model of the southern Benguela for the 1980s period. Bold values are estimated from other sources (see text)

Species	Biomass (mean *B*, tons)	Annual natural mortality (M, year^{-1})	Annual fishing mortality (F, year^{-1})
Anchovy	1 147 500	0.894	0.301
Chub mackerel	62 500	0.579	0.113
Cape hake (shallow-water)	311 300	0.509	0.279
Cape hake (deep-water)	524 040	0.391	0.387
Horse mackerel	400 000	0.716	0.089
Kingklip	**64 773**	**0.250**	**0.110**
Lanternfish	950 620	1.184	0.004
Lightfish	950 620	1.184	0.004
Round herring	1 222 000	1.122	0.032
Sardine	129 000	0.886	0.307
Silver kob	**10 400**	0.234	**0.181**
Snoek	52 700	0.286	0.213

ages calculated over the last 100 years of 20 simulation runs, each simulating the ecosystem dynamics through 200 years for a given value of fishing mortality.

RESULTS AND DISCUSSION

Reference state

To obtain a state of reference close to the mean conditions prevailing in the 1980s, it was necessary to modify considerably the values of initial relative fecundity. This was not expected before conducting the simulations. Tuning of the model allowed assessment of the role of relative fecundity as a parameter in the modelled fish life cycles. Allowing the relative fecundity to vary appeared equivalent to adding mortality of fish eggs and larvae, because all final values of the fecundity were substantially smaller than initial values. This meant that, structurally, an important part of the mortality of fish eggs and larvae was not taken into account explicitly in the model.

Three main processes are crucial for determining the success of recruitment. First, all eggs released in the sea are not fertilized, and such a loss could not be taken into account in the model because no estimation was available. Second, the first feeding stage of larvae, a day or so after absorption of the yolk sac, is critical for larval survival (Hjort 1914, Cushing 1982). Several authors (Blaxter and Hempel 1963, Lasker *et al.* 1970) have suggested a physiological and behavioural point of no return in fish larvae: if, within a period of 2–3 days, food concentration is too low, larvae no longer feed and subsequently die. Many factors play a part in this process (Cury and Roy 1989, Bakun 1996), making it very complex to model. However, it was first thought that starvation mortality was entirely taken into account through the carrying capacity of the model. The problem is that all fish were considered to respond to the lack of food in the same way, irrespective of whether they were adults or larvae. Third, predation on fish eggs and larvae constitutes an important source of mortality. Predation by the 12 species of the model is explicit. Predation by other species of the ecosystem was implicitly taken into account by the application of the M_{add} rate of mortality. Here again, the problem is that the same mortality rate was applied to all fish belonging to the same species, whereas higher rates of mortality are more likely for fish eggs and larvae. Consequently, the mortality of fish eggs and larvae was underestimated in the structure of the OSMOSE model. Attempting to address this complex problem in a simple way, tuning the model through the relative fecundity parameter, allows compensation for such underestimation.

If the initial values of relative fecundities used (Table I) are adequate estimations, it is straightforward to estimate the total mortality undergone by age-classes 0. Let Z_0 be the total mortality rate of age-class 0 of a given species, considered to be underestimated and which can be calculated from the output of the model following the classical survival equation:

$$N_1 = N_0 \, e^{-Z_0} \quad ,$$

with N_0 and N_1 being respectively the abundance of age-classes 0 and 1 of a given species. This equation is developed as follows:

$$N_1 = \phi' \, SB \, e^{-Z_0} \quad , \tag{1}$$

where SB is the spawning biomass of the species considered and ϕ' the relative fecundity modified after tuning of the model. According to what was suggested above, an alternative equation is considered:

$$N_1 = \phi SB e^{-Z_0'} \quad , \tag{2}$$

where ϕ is the initial relative fecundity value and Z_0' the actual total mortality rate of age-class 0. Z_0' can then be estimated by equating (1) and (2):

$$Z_0' = Z_0 - \ln(\phi'/\phi) \quad .$$

These estimations are reported in Table IV. Koslow (1992) proposed that annual mortality of age-class 0 is 11–14 for marine teleosts. The current values are generally lower (4.7–12.5), but are of the same order of magnitude.

Simulations with increasing fishing mortality on small pelagic fish species

Results of increasing the fishing mortality on anchovy, sardine and round herring are illustrated in Figure 2 and are compared with those obtained using ECOSIM (Table V). In the simulations, sardine are the first to collapse (when $F = 2$), then anchovy (when $F = 2.5$). Round herring are less impacted because initial fishing mortality is much smaller. In response, snoek and silver kob, which are large pelagic fish that feed on small pelagic fish (Crawford and de Villiers 1985, Griffiths 1995, 2002), undergo a substantial decrease in their biomass. These results are consistent with those produced using ECOSIM by Shannon *et al.* (2000)

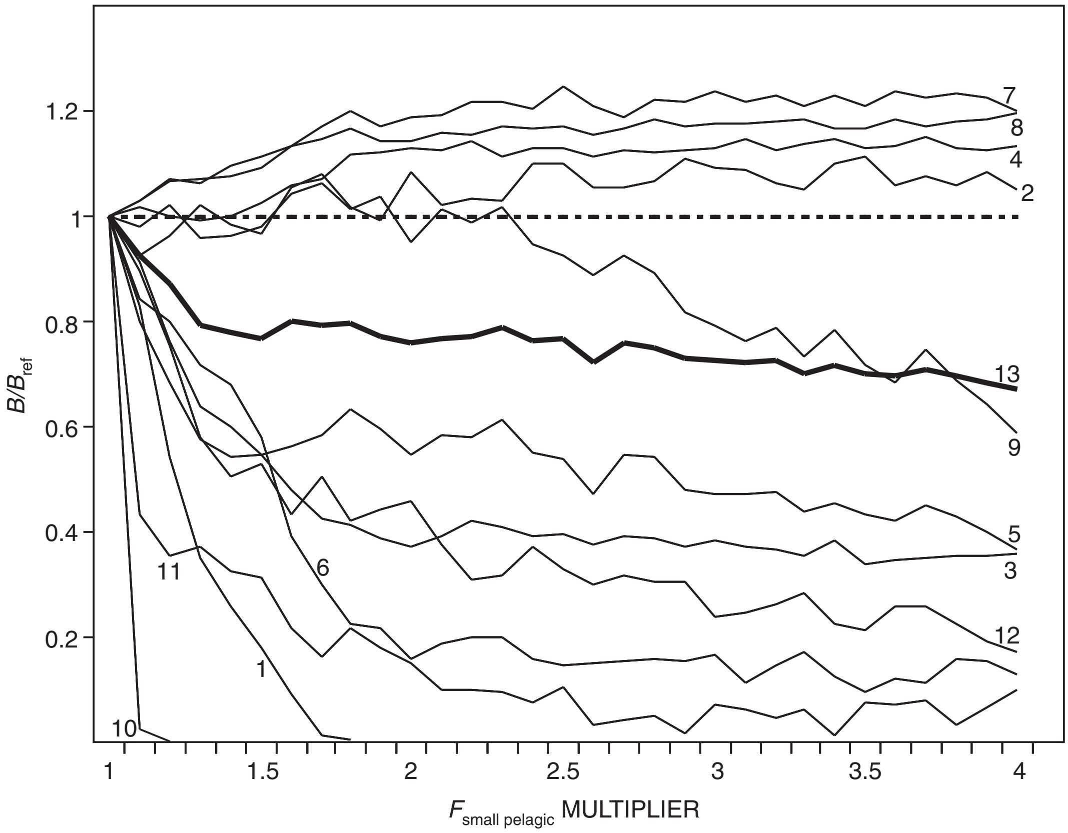


Fig. 2: OSMOSE simulation of effects on species biomass of an increase in fishing mortality of small pelagic fish (anchovy, sardine, round herring). Relative biomass (biomass/original biomass of reference) against a multiplier of fishing mortality rate applied to small pelagic species ($F_{small\ pelagic}$ multiplier). Biomass is the average biomass calculated over the last 100 years of 20 simulations, each of 200 years duration. Species are indicated by numerals – 1 = anchovy, 2 = chub mackerel, 3 = shallow-water Cape hake, 4 = deep-water Cape hake, 5 = horse mackerel, 6 = kingklip, 7 = lanternfish, 8 = lightfish, 9 = round herring, 10 = sardine, 11 = silver kob, 12 = snoek, 13 = all species

when simulating a permanent four-fold increase in fishing mortality of small pelagic fish, under mixed and wasp-waist (Cury *et al.* 2000) control scenarios. Under bottom-up control, sardine and anchovy did not collapse, but stabilized at about half their original biomass (Shannon *et al.* 2000).

While explaining the increase in chub mackerel biomass, which is clearly observed under mixed control and wasp-waist control scenarios, Shannon *et al.* (2000) suggested that this species can take advantage of reduced biomass of anchovy and sardine, competitors for zooplankton prey. Responses are similar in OSMOSE, because these species compete through the carrying capacity of the system. However, adult chub mackerel also feed on anchovy and sardine (Crawford 1989b). This last interaction, which counterbalances the effects of competition between chub mackerel and small pelagic fish, may be responsible for the increase observed in OSMOSE simulations being small.

The increase in mesopelagic fish can be explained as a response to the reduced competition with small pelagic fish when the latter are more heavily fished. In OSMOSE, competition between these non-piscivorous species emerges through the carrying capacity constraint and overlap of the spatial distributions. This is consistent with the results of the ECOPATH model of Shannon *et al.* (2003), which shows that mesopelagic

Table IV: Estimates of the total annual mortality rate of age-class 0 by species (Z_0'), based on output of the OSMOSE model for the reference state of the simulations. Pre-vailing conditions in the southern Benguela ecosystem in the 1980s served to tune the model

Species	Annual mortality rate of age-class 0
Anchovy	10.7
Chub mackerel	8.2
Cape hake (shallow-water)	7.9
Cape hake (deep-water)	8.0
Horse mackerel	4.7
Kingklip	11.8
Lanternfish	7.9
Lightfish	7.1
Round herring	10.3
Sardine	8.0
Silver kob	12.5
Snoek	11.2

Table V: Trends in species biomass when simulating a permanent four-fold increase in the fishing mortality of small pelagic fish (anchovy, sardine, round herring), using ECOSIM and OSMOSE models. Results of ECOSIM simulations that were conducted under three different scenarios of flow control (bottom-up, mixed and wasp-waist) are reported from Shannon *et al.* (2000). Narrow increasing arrows correspond to a relative increase of biomass (B/B_{ref}) between 1 and 1.5, whereas broad increasing arrows correspond to a relative increase >1.5. Narrow decreasing arrows indicate a relative decrease of biomass (B/B_{ref}) to between 0.5 and 1, whereas broad decreasing arrows indicate a relative decrease to <0.5. The absence of arrows indicates that no significant trend was ob-served. Note that in ECOSIM simulations, shallow-water and deep-water Cape hakes are combined into the single box "hake", lanternfish and lightfish are combined into the box "mesopelagic fish" and silver kob and snoek are combined into the box "large pelagic fish". Kingklip are not modelled separately in ECOSIM simulations

Species	OSMOSE	ECOSIM		
		Bottom-up	Mixed	Wasp-waist
Anchovy	⬊	↘	⬊	⬊
Chub mackerel	↗	↗	⬈	⬈
Cape hake (shallow-water) Cape hake (deep-water)	⬊ ↗	↗	↗	↗
Horse mackerel	⬊	↗	⬈	⬈
Kingklip	⬊			
Lanternfish Lightfish	↗ ↗	↗	↗	↗
Round herring	↘			
Sardine	⬊	⬊	⬊	⬊
Silver kob Snoek	⬊ ⬊	↘	⬊	⬊

fish compete with small pelagic fish for macrozooplankton and mesozooplankton (see diet compositions in their Table 2, and mixed trophic impacts in their Figure 10). Like chub mackerel, deep-water Cape hake, a major predator of mesopelagic fish (Payne 1987), increases in biomass in these simulations. On the contrary, the decrease in small pelagic fish biomass has detrimental effects on shallow-water Cape hake. These opposite trends may explain why the response of Cape hake, which were aggregated into a single box for simulations in Shannon *et al.* (2000), is small in their simulations (Table V).

Shannon *et al.* (2000) reported that horse mackerel, competing with anchovy and sardine for zooplankton prey, stabilized at a larger population size than was maintained before simulating an increased fishing pressure on small pelagic fish. By comparison, the opposite trend is observed in OSMOSE simulations, which could appear counter-intuitive. Nonetheless, it is not necessarily contradictory with ECOSIM simulations. Indeed, Shannon (2001) showed that, contrary to what was expected from static models in which horse mackerel negatively affected small pelagic fish through competition for zooplankton prey, small pelagic fish biomass was not enhanced when heavier fishing on horse mackerel was simulated. That result highlighted the potential for trajectories predicted from static models to differ from dynamic simulations, because direct and indirect effects come into play and change over time, by means of complex feedbacks. Similarly, OSMOSE results presented here suggest a large indirect effect caused by the massive decrease in small pelagic species biomass. In OSMOSE, the size-based predation rule implies that, when the biomass of a prey species (a small-sized fish species) decreases, then its predators can switch to other prey species, depending on their relative abundance in the same area. Therefore, the collapse of anchovy and sardine could have led to higher predation pressure on horse mackerel, to such an extent that its detrimental effects exceeded the direct effect of released competition.

In ECOSIM simulations, these effects are probably underestimated for two reasons. First, in EwE, only species originally estimated to contribute to the diets

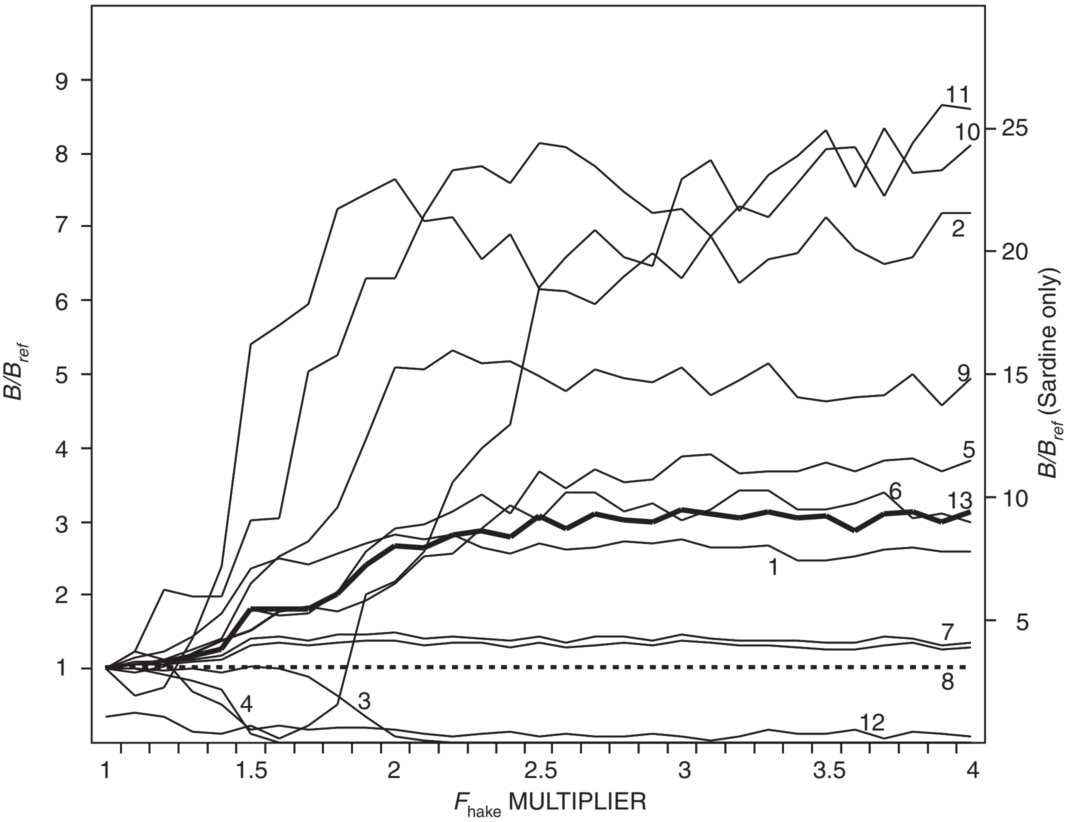


Fig. 3: OSMOSE simulation of effects on species biomass of an increase in fishing mortality of shallow-water and deep-water Cape hake. Relative biomass (biomass/original biomass of reference) against a multiplier of fishing mortality rate applied to hakes (F_{hake} multiplier). Biomass is the average biomass calculated over the last 100 years of 20 simulations, each of 200 years duration. Species are indicated by numerals – 1 = anchovy, 2 = chub mackerel, 3 = shallow-water Cape hake, 4 = deep-water Cape hake, 5 = horse mackerel, 6 = kingklip, 7 = lanternfish, 8 = lightfish, 9 = round herring, 10 = sardine, 11 = silver kob, 12 = snoek, 13 = all species. Sardine relative biomass (Species 10) should be read against the y-axis to the right

of model groups are considered in terms of increased or reduced contributions to the diets of predators, because prey abundances change over time. Second, in EwE, fish eggs and larvae are grouped, all species together, in the trophic group "macrozooplankton". This group, which also includes euphausiids, is defined according to the size of the organisms included (2–20 mm), and constitutes a major part of the diets of all 12 fish species considered in the present study. For example, in the comparative ECOPATH models used for parameterizing the ECOSIM simulations (Shannon 2001, Shannon *et al.* 2003), chub mackerel feed essentially on "macrozooplankton" (80% of the diet of chub mackerel in the ECOPATH model of the 1980s). In light of the respective spatial distributions of adult chub mackerel and larvae of other species, it is probable that horse mackerel and small pelagic fish species form a non-negligible part of the "macrozooplankton" group preyed upon by chub mackerel (Figures 1a, b, e, h, i). By comparison, in the OSMOSE model, predation by chub mackerel would be directly governed by overlaps between their spatial distribution and those of prey fish of suitable size. In the present simulations, the decrease in the biomass of small pelagic fish may induce horse mackerel to be more extensively preyed upon by chub mackerel.

Overall, alteration of small pelagic fish species biomass leads to a decrease in the total biomass of the fish community considered. In this context, these species exert a major bottom-up effect on the predatory

Table VI: Trends of species biomass when simulating a permanent four-fold increase in the fishing mortality of hakes (shallow-water and deep-water hakes) using OSMOSE and from a pulse four-fold increase in the fishing mortality of Cape hakes estimated using an ECOSIM model. Results of the ECOSIM simulations that were conducted under three different scenarios of flow control (bottom-up, mixed and wasp-waist) are reported from Shannon *et al.* (2000). Narrow increasing arrows correspond to a relative increase of biomass (B/B_{ref}) between 1 and 1.5, whereas broad increasing arrows correspond to a relative increase >1.5. Narrow decreasing arrows indicate a relative decrease of biomass (B/B_{ref}) to between 0.5 and 1, whereas broad decreasing arrows indicate a relative decrease to <0.5. The absence of arrows indicates that no significant trend was observed

Species	OSMOSE	ECOSIM		
		Bottom-up	Mixed	Wasp-waist
Anchovy	⬈			↗
Chub mackerel	⬈			⬊
Cape hake (shallow-water) Cape hake (deep-water)	⬊ ⬊	↘	⬊	⬊
Horse mackerel	⬈		↘	⬊
Kingklip	⬈			
Lanternfish Lightfish	↗ ↗	↗	⬈	⬈
Round herring	⬈			↗
Sardine	⬈			↗
Silver kob Snoek	⬈ ⬊	↗	↗	↗

fish community. This effect is not over-ridden by compensations in the density of competitive species or size-classes.

Simulations with increasing fishing mortality on Cape hake

Results of an increased fishing mortality on Cape hake are illustrated in Figure 3 and are compared with those obtained using ECOSIM (Table VI, Shannon *et al.* 2000). As expected, and as in all three-flow control scenarios simulated by Shannon *et al.* (2000), biomass of Cape hake decreases. Nonetheless, the effect is more pronounced in the simulations reported here, possibly because the increase in fishing mortality is permanent in the present scenario, whereas it is only a pulse increase in Shannon *et al.* (2000), and possibly also because the two species of hake are considered separately here. In addition, the collapse could have been accelerated by a depensation effect (Walters and Kitchell 2001). When the biomass of Cape hake decreases, their predation pressure on small species decreases concomitantly. As a result, if the biomass of small fish species increases, this can have a further detrimental effect on Cape hake because juvenile hake may compete with other small fish species, and juvenile and larval hake may also be prey to some small fish.

Overall, the biomass of the competitors of Cape hake and their prey increases in response to the decrease in hake biomass. The total modelled fish biomass is about three times higher than in the state of reference, whereas the carrying capacity did not change. This indicates a top-down effect of Cape hake on the fish community under consideration. For example, mesopelagic fish biomass increases, in accordance with results provided by Shannon *et al.* (2000) and with empirical knowledge. Indeed, deep-water Cape hake are major predators on mesopelagic fish (Prosch 1986, Payne 1987) and mesopelagic fish have a large net positive trophic impact on large deep-water Cape hake (Shannon *et al.* 2003).

Under a wasp-waist scenario, Shannon *et al.* (2000) observed an increase in the biomass of sardine and round herring, also the case in OSMOSE simulations. However, the increase in sardine biomass is very high in OSMOSE simulations. Indeed, simulation results indicate that sardine biomass increases by a factor of 25 from the state of reference to that representing a four-fold increase in fishing mortality on Cape hake. If a direct effect is responsible for this, and noting that only the biomasses of Cape hake and snoek decrease, this result suggests that adult Cape hake are major predators of sardine, and/or that juvenile Cape hake are major competitors of sardine, and/or that snoek are very important predators of sardine. Table 2 of Shannon *et al.* (2003), which reports the balanced diet composition of these species obtained from an ECOPATH model, does not provide information in support of either of the first two hypotheses. However, in the 1990s, sardine constituted 22% of the diets of snoek, whereas in the 1980s model, anchovy were the most important food item of snoek (Shannon *et al.* 2003, M. H. Griffiths, MCM, pers. comm.). Therefore, using OSMOSE, reduced predation pressure by snoek would be expected to allow species such as sardine to benefit. In addition, in the ECOPATH model of Shannon *et al.* (2003), all fish larvae in the diet of fish are generally aggregated with euphausiids in the trophic group "macrozooplankton". This could be one reason why some species do not react in the same way in OSMOSE and ECOSIM simulations.

Consulting the maps of distribution areas, adult shallow-water Cape hake clearly have a distribution that is similar to sardine, including the distribution of sardine pre-recruits (Figs 1c, i). Therefore, sardine theoretically constitute a source of food for shallow-water Cape hake. This does not necessarily imply that sardine constitute an important part of hake diet, but according to the simulations, it does suggest at least that shallow-water Cape hake are responsible for an important part of sardine predation mortality. Using an ECOPATH model for the 1990s, when sardine abundance was larger than in the previous decade, the predation mortality exerted on sardine by large shallow-water Cape hake was estimated to be 11% of the total predation mortality on sardine.

Under mixed control and wasp-waist control scenarios using ECOSIM, Shannon *et al.* (2000) obtained a lower biomass for horse mackerel than at the state of reference, and interpreted this trend as a response to increased competition for zooplankton with larger mesopelagic fish. Again, as in the previous simulations, the reverse trend was observed for this species in the current simulations. Trying to understand these different outputs can help improve understanding of the trophic interactions involving horse mackerel. Crawford (1989a) indicates that the diet of small horse mackerel is similar to that of juvenile anchovy and sardine. As the distributions of juveniles of the three species overlap (Figs 1a, e, i), there is a basis for suspecting potential competition. In addition, Crawford (1989a) noted that the diet of adult horse mackerel is similar to the diet of Cape hake of equivalent size. Further, Drapeau *et al.* (2004) showed that Cape hake and horse mackerel have large potential interaction indices. The increase in horse mackerel biomass can then be interpreted as a response to reduced competition with Cape hake as the latter decrease substantially in biomass. According to this hypothesis, the adult fraction of the horse mackerel population may well largely determine the response of the whole population. The increase in horse mackerel biomass in this simulation, and its response to altered F_{prey} in the previous OSMOSE simulation, indicate that, within the frame of simulated conditions, food is not a limiting factor for small pelagic fish.

Chub mackerel is another species that shows an opposite trend in OSMOSE and ECOSIM simulations. Because chub mackerel were heavily fished in the late 1970s and 1980s, Shannon (2001) assumed that the stock in the 1980s was likely to have consisted of young fish that were largely zooplanktivorous. However, by the 1990s, the proportion of mesopelagic fish in the diet of chub mackerel was assumed to be larger (25% compared with just 16% in the 1980s, Shannon *et al.* 2003). The decrease in chub mackerel biomass observed in ECOSIM simulations suggests that the competition with deep-water Cape hake for mesopelagic fish was not very strong in the 1980s, which was the time frame of the simulations, whereas the macrozooplankton group constituted 80% of chub mackerel diet in the 1980s model (Shannon *et al.* 2003). On the other hand, the literature indicates that sardine and anchovy can constitute an important part of chub mackerel diet under certain circumstances, because chub mackerel are considered to be opportunistic feeders (Crawford 1989b). This opportunism is explicit in the OSMOSE model, which allows predators to feed on whatever fish of suitable size are present in the same area as the predator in question, and may be responsible for the increase observed in chub mackerel biomass in response to increased biomass of small pelagic species.

The fact that the biomass of snoek decreases in OSMOSE simulations is questionable. No direct explanation can be provided. It was expected that any increase in small pelagic species would be beneficial to snoek, i.e. that snoek would show a symmetrical response as in the earlier simulations. The current results suggest that small pelagic fish were not limiting for snoek in the reference state. Moreover, it is possible that competition between snoek larvae and small pelagic fish, which are dominant at the outset of the simulations, can play a part in the decrease of snoek biomass, although further investigations would be needed to support this hypothesis.

CONCLUSION

The responses of the different species when simulating altered biomass of either small pelagic fish or Cape hake are in agreement with the main predation and competition relationships shown by empirical studies in the southern Benguela. This is a first step in evaluating the results and supports the possible use of simple local size-based predation rules for studying the dynamics of fish species in a multispecies context. The present comparison with ECOSIM output can help consolidate several results and delimit a range of the possible impacts of fishing on the fish community of the southern Benguela. Generally, mesopelagic fish, small pelagic fish and Cape hake respond in the same way in both models. Apparent contradictory results also serve to demonstrate that a better understanding is required of the trophic roles of some species in the foodweb, such as horse mackerel and chub mackerel, because their responses appear to result from more complex interactions, involving different life stages or different types of control (predation, competition), depending on the prevailing conditions.

In the OSMOSE model, predation is a size-based, opportunistic process. This provides the opportunity for examining the trophic web as a dynamic structure in which predation and competition interactions between species vary according to their relative abundances. This is a phenomenon very well illustrated by Crawford (1987), who showed that sardine constituted about 90% of the diet of snoek sampled in 1958, whereas anchovy represented 90% of snoek diet in 1979. In this context, OSMOSE potentially constitutes a tool for exploring the effects of altered fishing mortalities leading to altered species biomass. Comparing OSMOSE output with that of an ECOSIM model permits suggesting which types of interactions, under what circumstances, are likely to predominate and to control production. Through the presentation and discussion of the results, the same resource clearly appears to have been limiting under certain conditions, but not under others, so the dynamics of some species may be under the influence of competition in some instances, but driven by predation under others. This implies that the trophic role of a species can vary. This is one of the difficulties encountered when studying marine foodwebs, where two species can be predator, prey or competitor with respect to each other, depending on the stage in their life cycle. Exploring the dynamics of exploited marine ecosystems remains challenging for these reasons and necessitates various modelling approaches. A multiplicity of independent modelling approaches can lead to identification of consistent patterns that will help to move towards an ecosystem approach to fisheries.

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APPENDIX

References of the species parameters used in OSMOSE (cf. Table I)

Species	Growth		Reproduction		Survival		
	L_∞, K, t_0	c	ϕ	a_{mat}	a_{max}	a_{rec}	M_{add}
Anchovy	Waldron *et al.* (1989)	J. van der Westhuizen, pers. comm.	Melo (1994) Le Clus (1979)	Armstrong *et al.* (1991)	M. Kerstan, pers. comm.	Armstrong *et al.* (1991)	Shannon (2001)
Chub mackerel	Baird (1977)	Baird (1977)	Collette and Nauen (1983)	Crawford (1989b)	Castro Hernández and Santana Ortega (2000)	Crawford (1989b)	Shannon (2001)
Cape hake (shallow-water)	Punt and Leslie (1991)	Punt and Leslie (1991)	Kartas and Quignard (1984)	Punt and Leslie Quignard (1984)	R. W. Leslie, pers. comm.	R. W. Leslie, pers. comm.	Shannon (2001)
Cape hake (deep-water)	Punt and Leslie (1991)	Punt and Leslie (1991)	Kartas and Quignard (1984)	Punt and Leslie (1991)	R. W. Leslie, pers. comm.	R. W. Leslie, pers. comm.	Shannon (2001)
Horse mackerel	Horsten (1999)	M. Kerstan, pers. comm.	Kartas and Quignard (1984)	R. W. Leslie, pers. comm. in Butterworth and Clarke (1996)	Horsten (1999)	Hecht (1990)	Shannon (2001)
Kingklip	Japp (1990)	Japp (1990)	Cape Hakes relative fecundity	Japp (1990) Payne and Badenhorst (1989)	Japp (1990)	Punt and Japp (1994)	Japp (1989)
Lanternfish	Prosch (1986)	Haimovici and Velasco (2000)	Prosch (1991)	Prosch (1986)	Prosch (1986)		Shannon (2001)
Lightfish	Prosch (1986)	Haimovici and Velasco (2000)	Prosch (1991)	Prosch (1986)	Prosch (1986)		Shannon (2001)
Round herring	Waldron *et al.* (1991)	Geldenhuys (1978)	Baxter and Pope (1969) Kosior and Strzyzewska (1979)	Roel and Melo (1990)	M. Kerstan, pers. comm.	Roel and Armstrong (1991)	Shannon (2001)
Sardine	M. Kerstan, pers. comm.	J. van der Westhuizen, pers. comm.	Akkers (1995)	Akkers *et al.* (1996)	M. Kerstan, pers. comm.	Crawford (1980)	Shannon (2001)
Silver kob	Kirchner (1998)	Griffiths (1996)	Battaglene and Talbot (1994)	Griffiths (1997)	Griffiths (1995, 1997)	Griffiths (1997)	Shannon (2001)
Snoek	Venidiktova (1988) t_0 altered based on M. H. Griffiths, pers. comm.	M. H. Griffiths, pers. comm.	Rowling (1994) Nakamura and Parin (1993)	Griffiths (1999)	Griffiths (1999)	M. H. Griffiths, pers. comm.	Shannon (2001)

M. Kerstan, M. H. Griffiths: formerly Marine and Coastal Management (MCM)
R. W. Leslie, J. van der Westhuizen: currently MCM