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QUANTIFICATION AND REPRESENTATION OF POTENTIAL SPATIAL INTERACTIONS IN THE SOUTHERN BENGUELA ECOSYSTEM

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This work explores the potential spatial interactions between 13 key commercial species of the southern Benguela ecosystem: sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus*, round herring *Etrumeus whiteheadi*, horse mackerel *Trachurus trachurus capensis*, chub mackerel *Scomber japonicus*, chokka squid *Loligo vulgaris reynaudii,* kingklip *Genypterus capensis*, Cape hake *Merluccius* spp., silver kob *Argyrosomus inodorus*, snoek *Thyrsites atun*, albacore *Thunnus alalunga*, bigeye tuna *Thunnus obesus* and yellowfin tuna *Thunnus albacares*. It is based on distribution maps per species after combining available commercial and research databases. The resulting 78 pairs of potential interactions are quantified using three indices: the overlap in area, the overlap in biomass and the weighted kappa index. From additional information on the diet of the different species and trophic models, the main trophic interactions (predation or competition) were identified and mapped. The results are discussed with regard to methodological limitations, habitat selection, fish assemblages, the need for spatial resolution of trophic models and the ecosystem approach to fishery management.

Key words: ecosystem indicators, Geographical Information System, kappa index, spatio-temporal interactions, southern Benguela, upwelling system

Given that about half of the global marine living resources is fully exploited and a quarter is overexploited (FAO 1997, Garcia and de Leiva Moreno 2003), the need for an ecosystem-based management of the world's fisheries in addition to single stock resource management is commonly recognized among scientists and managers (Larkin 1996, Jennings and Kaiser 1998, Hall 1999, Gislason *et al*. 2000, Sinclair *et al*. 2002, Sinclair and Valdimarsson 2002, Moloney *et al*. 2004).

In its Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem in 2001, the Food and Agriculture Organization (FAO) confirmed that the objective of including ecosystem considerations in fisheries management is to contribute to long-term food security and to human development, and to assure the effective conservation and sustainable use of the ecosystem and its resources. The identification and description of the interactions among species are priorities in building the scientific basis for incorporating ecosystem considerations into management (May *et al*. 1979). The need for spatially resolved modelling approaches becomes obvious when considering that the spatial and temporal distributions of trophically interacting species do not always coincide. Spatial dynamics of ecosystems are considered in very few trophic models, such as ECOSPACE, an extension of ECOPATH with ECOSIM (Christensen and Walters 2000, Pauly *et al*. 2000), or OSMOSE (Shin 2000, Shin and Cury 2001). In both models, biomass per species is allocated dynamically over the defined spatial grid. Horizontal movement is modelled between cells, depending on the location of preferred habitat and predation risk per species group. Ecosystem management of fisheries also requires some indicators of the present status of the ecosystem as well as a definition of ecosystem reference points. This was the aim of SCOR/IOC WG 119 on "Quantitative Ecosystem Indicators for Fisheries Management" (http://www.ecosystemindicators.org).

The Benguela Current off the south-western coast of Africa (15–37°S), one of the four major eastern boundary current systems, has been extensively studied for more than a century (Payne and Lutjeharms 1997) and is therefore a suitable case study for quantifying interactions. The present study focuses on the southern Benguela ecosystem, which is assumed to extend seawards to a depth of 2 000 m from 29°S (in the vicinity of the Orange River mouth) southwards along the west coast of South Africa and eastwards to 28°E (East London). It covers an area of 360 000 km^2 and incorporates the Agulhas Bank and the south and west coasts of South Africa (Shannon and O'Toole 1998, Shannon *et al*. 2003).

Studies have been undertaken over the past decade to understand the structure and functioning of the southern Benguela ecosystem and, in comparison with other upwelling ecosystems elsewhere (Baird *et al*. 1991, Smale 1992, Jarre-Teichmann *et al*. 1998, Shannon and Jarre-Teichmann 1999, Shannon 2001),

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Table I: Qualitative representation of predation by, and competition between, each group on the 12 others considered in this study: heavy predation (P), medium predation (p), strong competition for food (C) and medium competition (c). Instances of occasional or light predation or competition are not shown. The number following the prey name indicates the trophic level

Prey (rows)	Predators (columns)												
	Sd	An	Rh	Hm	Cm	Ck	Kk	Hk	Sk	Sn	Al	Be	Yt
Sardine (Sd) 3.0	■	C	C	pc	pc*	pc		pc*	p	Pc*	p		
Anchovy (An) 3.5	C	■	C	pc	pc*	p		pc*	P	Pc*	p		
Round herring (Rh) 3.6	C	C	■	pc	pc*	p		pc*		Pc*			
Horse mackerel (Hm) 3.7	c	c	c	■	c	p	p	Pc		pc	c	c	c
Chub mackerel (Cm) 3.9	c*	c*	c*	c	■			p		pc	c	c	c
Chokka squid (Ck) 3.8	c					P		Pc		p	P	p	P
Kingklip (Kk) 3.4				c	c		■	c		c	c	c	c
Cape Hake (Hk) 4.4	c*	c*	c*	c	c	pc	pc	P		pc	c	Pc	pc
Silver kob (Sk) 4.5									■				
Snoek (Sn) 4.5	c*	c*	c*	c	c		c	c		■	c	c	pc
Albacore (Al) 4.5				c	c		c	c		c	■	c	c
Bigeye tuna (Be) 4.5				c	c		c	c		c	c	■	c
Yellowfin tuna (Yt) 4.5				c	c		c	c		c	c	c	■

* Predation mainly by juvenile stages or competition mainly between juvenile stages

to study trophic interactions between species (Navarrete and Menge 1996). Recent studies have used the ECOPATH model (Christensen and Walters 2000), but ECOSPACE, which is spatially resolved, has not been used for the Benguela ecosystem. The main purpose of the current study is to evaluate how crucial the need is to resolve trophic models spatially. A secondary objective is to initiate the first step towards defining ecosystem indicators. To achieve these aims, some spatio-temporal overlapping between the geographical distributions of several pairs of species are described and quantified, using basic indices derived from the distribution maps of 13 key species, drawn from various and heterogeneous sources of information (commercial and scientific data).

MATERIAL AND METHODS

Density maps

The study is restricted to 13 key species of the southern Benguela (in reality, 14 species, given that there are two species of hake, which are assessed and managed as unit stocks): three small pelagic fish species (sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus* and round herring *Etrumeus whiteheadi*), two medium-sized pelagic fish species (horse mackerel *Trachurus trachurus capensis* and chub mackerel *Scomber japonicus*), one squid species (chokka) *Loligo vulgaris reynaudii*, three demersal species (kingklip *Genypterus capensis*, Cape hake *Merluccius* spp. and silver kob *Argyrosomus inodorus*) and four large pelagic species (snoek *Thyrsites atun*, albacore *Thunnus alalunga*, bigeye tuna *Thunnus obesus* and yellowfin tuna *Thunnus albacares*). Data and methods used to draw the density maps of each species are fully described in Pecquerie *et al*. (2004). In summary, six different sources of data are combined on a 10´ × 10´ cell grid in a Geographical Information System (GIS): acoustic and demersal surveys conducted by Marine and Coastal Management (MCM) from 1988 to 2001, and pelagic, demersal (including midwater trawl data), hake-directed and tuna-directed longline commercial data collected by MCM from 1985 to 2001. In order to facilitate comparisons between datasets of different spatial resolution (see Table I in Pecquerie *et al*. 2004), a 10´ × 10´ cell grid was used. The resulting indices of relative biomass were sorted by descending order

Table II: Classification of the possible combinations of cells on the interaction maps and their associated weights (w_{ij})

		Species 2				
	Classes	1	2	3	4	Not observed
Species 1	1	(w_{11} = 1) Species 1 ≈ Species 2	(w_{12} = 0.96)	(w_{13} = 0.84) Species 1 > Species 2 (in relative biomass)	(w_{14} = 0.64)	Species 1 only
	2	(w_{21} = 0.96)	Species 1 ≈ Species 2 (w_{22} = 1)	(w_{23} = 0.96)	(w_{24} = 0.84)	
	3	(w_{31} = 0.84) Species 2 > Species 1 (in relative biomass)	(w_{32} = 0.96)	(w_{33}=1) Species 1 ≈ Species 2	(w_{34} = 0.96)	
	4	(w_{41} = 0.64)	(w_{42} = 0.84)	(w_{43} = 0.96)	Species 1 ≈ Species 2 (w_{44} = 1)	
	Not observed	Species 2 only				

of cumulative frequencies of abundance and classified by quartiles: (1) 0–25% of total biomass (high densities), (2) 25–50% (medium densities), (3) 50–75% (low densities) and (4) 75–95% (very low densities), given that only 95% of the biomass has been represented to prevent an overestimation of the total distribution area as a result of outliers (see Fig. 3 of Pecquerie *et al*. 2004).

Initially, overlapping distributions were examined on the basis of semesters (April–September and October –March), in order to take into account the migration of juvenile small pelagic fish from the West Coast to the Agulhas Bank. Unfortunately, the paucity of pelagic survey data in offshore areas during the first semester (April–September) prevented studying seasonally resolved overlaps. Therefore, aggregated data from 1985 to 2002 were used to describe the geographical location of species. The impact of combining both semesters is discussed, as well as the impact of combining the two periods from the 1980s (there was a change in pelagic species dominance, Shannon *et al*. 2003).

Representation of overlapping distributions by pairs of species

For the purpose of this study, a potential interaction between two species was defined as the spatial and temporal co-occurrence of these two species on a horizontal plane at the 10´ × 10´ cell spatial resolution. Because neither the trophic links nor the vertical distributions of these species were considered, potential interactions were termed "overlapping distributions". Nonetheless, from the 78 pairs of species resulting from the matrix of overlapping distributions of the 13 species, only those likely to involve significant competition or predation interactions were selected, according to published prey consumption data (Nepgen 1979, Crawford *et al.* 1987, Prosch *et al.* 1995, Shannon 2001, Griffiths 2002, Shannon *et al*. 2003) and interviews with scientists from MCM and the Institut de Recherche pour le Développement in the case of tuna species (Table I).

Most common measurements of similarity/dissimilarity are computed by means of a contingency matrix (Couto 2003). The GIS software Arcview 3.2a was used to perform cross-tabulations analysis, in which the categories (high to very low densities) of one species' distribution are compared with those of a second species' distribution. The result can be mapped and provides a spatial distribution of overlap displaying the locations of all combinations as well as a contingency table. To represent overlapping distributions, the different combinations of cells were classified into five classes according to the contingency table presented in Table II: (i) Species 1 only, (ii) Species 1 > Species 2 (in terms of relative biomass), (iii) Species 1 ≈ Species 2, (iv) Species 2 > Species 1, (v) Species 2 only.

Quantification of spatial overlaps by pairs of species with three basic indices

PERCENTAGE OF DISTRIBUTION AREA OF ONE SPECIES THAT OVERLAPS WITH ANOTHER

The first index (*OA*) calculated was the ratio of the overlap in area between the two species (intersection) to the total distribution area of one of the two species

Table III: Contingency table of observed frequencies of cells containing species 1 (rows) and species 2 (columns)

Species 2

	Classes	1	j	4	Total
Species 1	1	f_{11}	f_{1j}	f_{14}	$\sum_j f_{1j}$
	i	f_{i1}	f_{ij}	f_{i4}	$\sum_j f_{ij}$
	4	f_{41}	f_{4j}	f_{44}	$\sum_j f_{4j}$
	Total	$\sum_i f_{i1}$	$\sum_i f_{ij}$	$\sum_i f_{i4}$	$\sum_i \sum_j f_{ij}$

Table IV: Probability distribution of classified abundances for Species 1 and 2. P_{ij} is the probability that the joint distribution of Species 1 and 2 falls in Class i for Species 1 and Class j for Species 2

Species 2

	Classes	1	j	4	Marginal probability
Species 1	1	p_{11}	p_{1j}	p_{14}	$p_{1.}$
	i	p_{i1}	$p_{ij} = f_{ij} \big/ \sum_i \sum_j f_{ij}$	p_{i4}	$p_{i.} = \dfrac{\sum_j f_{ij}}{\sum_i \sum_j f_{ij}}$
	4	p_{41}	p_{4j}	p_{44}	$p_{4.}$
	Marginal probability	$p_{.1}$	$p_{.j} = \sum_i f_{ij} \big/ \sum_i \sum_j f_{ij}$	$p_{.4}$	1

(A_1 or A_2). This is therefore an asymmetrical index; two values of this index were determined for overlap between each pair of species:

$$OA_{1/2} = \frac{A_1 \cap A_2}{A_1} \text{ and } OA_{2/1} = \frac{A_1 \cap A_2}{A_2} \quad . \qquad (1)$$

PERCENTAGE OF BIOMASS OF ONE SPECIES THAT OVERLAPS WITH ANOTHER

The second index (*OB*) is the ratio of the overlap in biomass between the two species (intersection) to the total biomass of one of the two (B_1 and B_2). This is also an asymmetrical index:

$$OB_{1/2} = \frac{B_1 \cap B_2}{B_1} \text{ and } OB_{2/1} = \frac{B_1 \cap B_2}{B_2} \quad . \qquad (2)$$

WEIGHTED KAPPA INDEX

The kappa index is widely used in land and vegetation contexts and has been applied recently in ecological studies of animal populations and plant species (Bollinger *et al.* 2000, Guisan and Zimmermann 2000, Boyce *et al.* 2002, Pearson *et al.* 2002).

Given that the spatial distributions of both species of a given pair have exactly the same number of categories for comparison of their distribution (i.e. five, including absence – Table II), a measure of association called the Generalized Kappa Index of Agreement was computed. The kappa index is one of numerous similarity/dissimilarity, or agreement measurement indices, based on categorical data analysis, and is commonly used in remote sensing (Congalton and Mead 1983). The index is a refinement of the Jacquard index (Legendre and Legendre 1998) for matched pairs (observations or subjects being the grid cells). Values range from 0 (indicating no spatial matching) to 1 (indicating perfect similarity). A Chi-squared statistic is calculated for the kappa index. The calculation of this index permitted description and quantification of the agreement between the spatial distribution of two species: comparable densities of two species have the same spatial distribution when the kappa index equals 1. In contrast to the *OA* and *OB* indices, which are expressed as percentages, this index is symmetrical, i.e. a single value characterizes the overlap between two species.

The software IDRISI32 Release 2 was used to determine the contingency tables (Tables III and IV) and to calculate the kappa index. The contingency tables contained the frequency distributions of the classified cells belonging to the i^{th} class ($i \in$ *Card*(*I*); *Card*(*I*) being the cardinality of I = [quartiles classes]), for Species 1 and the j^{th} class ($j \in$ *Card* (*J*)) for Species 2.

If p_{ij} denotes the probability that the joint distribution of Species 1 and 2 falls in class i for Species 1 and class j for Species 2, then $\sum_{I=j} p_{ij}$ is the probability of agreement (or similarity) for the distributions. If $\sum_{I=j} p_{ij}$ = 1, the two species have the same spatial distribution, i.e. the contingency table is a diagonal matrix. If the distribution of the species was statistically independent, then $p_{ij} = p_i p_j$ (with $p_{i.}$ and $p_{.j}$ being the marginal probabilities or probability).

Therefore, $\sum_{I=j} p_{ij} - \sum_i \sum_j p_i p_j$ is the excess of similarity in the distribution above that expected purely by chance (i.e. if distributions were statistically independent). Therefore, the conventional kappa index *KI* is defined as:

$$KI_{A/B} = KI_{B/A} = \frac{\sum\limits_{i=j} p_{ij} - \sum\limits_{i}\sum\limits_{j} p_i p_j}{1 - \sum\limits_{i}\sum\limits_{j} p_i p_j} \quad , \qquad (3)$$

where the value 1 in the denominator is the maximum possible value of $\sum_{i=j} p_{ij}$, corresponding to perfect similarity of distribution for the two species. This index is designed for nominal classification (Agresti 1990). The performance of the kappa analysis was improved by weighting the original kappa index. All mismatched classes (Table II) between the two species cannot be considered of equal importance. Co-occurrence of high density for Species 1 and medium density for Species 2 indicates closer association of the two species than a spatial overlap of high density for Species 1 and low or very low density for Species 2. Because different degrees of mismatch should be taken into account, and classes are ordinal (high-density > medium-density > low-density), it was more appropriate to measure a weighted kappa index (*WKI*), using weights (w_{ij}) to describe the proximity of the classes (with weights satisfying $0 \le w_{ij} \le 1$; $w_{ij} = w_{ji}$; $w_{ij} = 1$, when $i = j$). Then, the probability of similarity is $\sum_i\sum_j p_i p_{ij}$ and the *WKI* is:

$$WKI = \frac{\sum\limits_{i}\sum\limits_{j} w_{ij} p_{ij} - \sum\limits_{i}\sum\limits_{j} w_{ij} p_{i.} p_{.j}}{1 - \sum\limits_{i}\sum\limits_{j} w_{ij} p_{i.} p_{.j}} \quad , \qquad (4)$$

where $w_{ij} = 1 - \frac{(i-j)^2}{(Card(I))^2}$, with the similarity being greater for cells nearer the main diagonal in the contingency table.

Cluster analysis

Two cluster analyses were performed and compared in order to obtain a global picture of the overlaps between the 13 species. First, the raw relative abundance data per species per grid cell were used as an input for a Ward clustering analysis. Second, the matrix of distances between species (*WKI*) was used as an input for the same analysis. In this second case, the distance matrix between the species was based on the kappa index (correlation index). The amalgamation rule used to determine distances between clusters was Ward's method (Ward 1963). This method uses an analysis of variance approach to evaluate the distances between clusters by minimizing the sum of squares of any two (potential) clusters that can be formed at each step. This method is very efficient in the case of a small number of variables, such as in this study.

RESULTS

Each species considered can potentially interact with nearly all the other 12 to a certain degree, except for tuna species and silver kob. Tuna species are found mainly offshore and can potentially interact mainly among themselves and with silver kob. Kob were confined to two small inshore areas of the South Coast, and potentially interact with only a few species, such as round herring, horse mackerel and chokka squid (Figs 1, 3). The average of overlap indices based on area (*OA*) was 0.35, with a maximum value of 0.96 for kingklip and hake; indices based on biomass (*OB*) peak at 0.93 (again, kingklip and hake), with an average of 0.37. These two indices were always similar (Wilcoxon test on matched pairs, $p < 0.035$), and approximately in proportion to the *WKI*. The coefficient of determination between *OA* and *WKI* was 64% and between *OB* and *WKI* 61%. Notable exceptions to the rough proportionality between *WKI* and *OA* or *OB* were the overlaps between species that had different (mismatched) total areas of distribution, such as silver kob in comparison with other species and, to a lesser extent, bigeye and albacore tuna in comparison with species other than tuna. In most of these overlaps, *WKI* was very low, whereas *OA* or *OB* had a low (tuna species) or high (silver kob) value. Hereafter, only *WKI* results will be interpreted, although the merits of all three indices are discussed later.

The highest overlaps were those between kingklip and hake (*WKI* = 0.75), and between chokka squid and horse mackerel (0.66), round herring (0.53) and anchovy (0.51; Fig. 1).

The clusters of relative abundances of species within grid cells showed three major groups (Fig. 2a): the three tuna species (albacore, bigeye tuna and yellowfin tuna), silver kob, and the rest of the species. This is because of the offshore distribution of tuna, and because the other species occur mainly on the continental shelf, with silver kob in the present dataset occupying two restricted coastal areas (<100 m depth) on the South Coast. Within the larger cluster containing species other than tuna and silver kob, two subgroups were apparent:

(i) the predatory subgroup consisting of snoek, kingklip and hake, which was distributed mainly between the 100 and 500 m isobaths all along the coast,

(ii) the subgroup of low or intermediate trophic level species, comprising chub mackerel, round herring, horse mackerel, chokka squid, sardine and anchovy, which were found mainly within the 200 m isobath all along the coast.

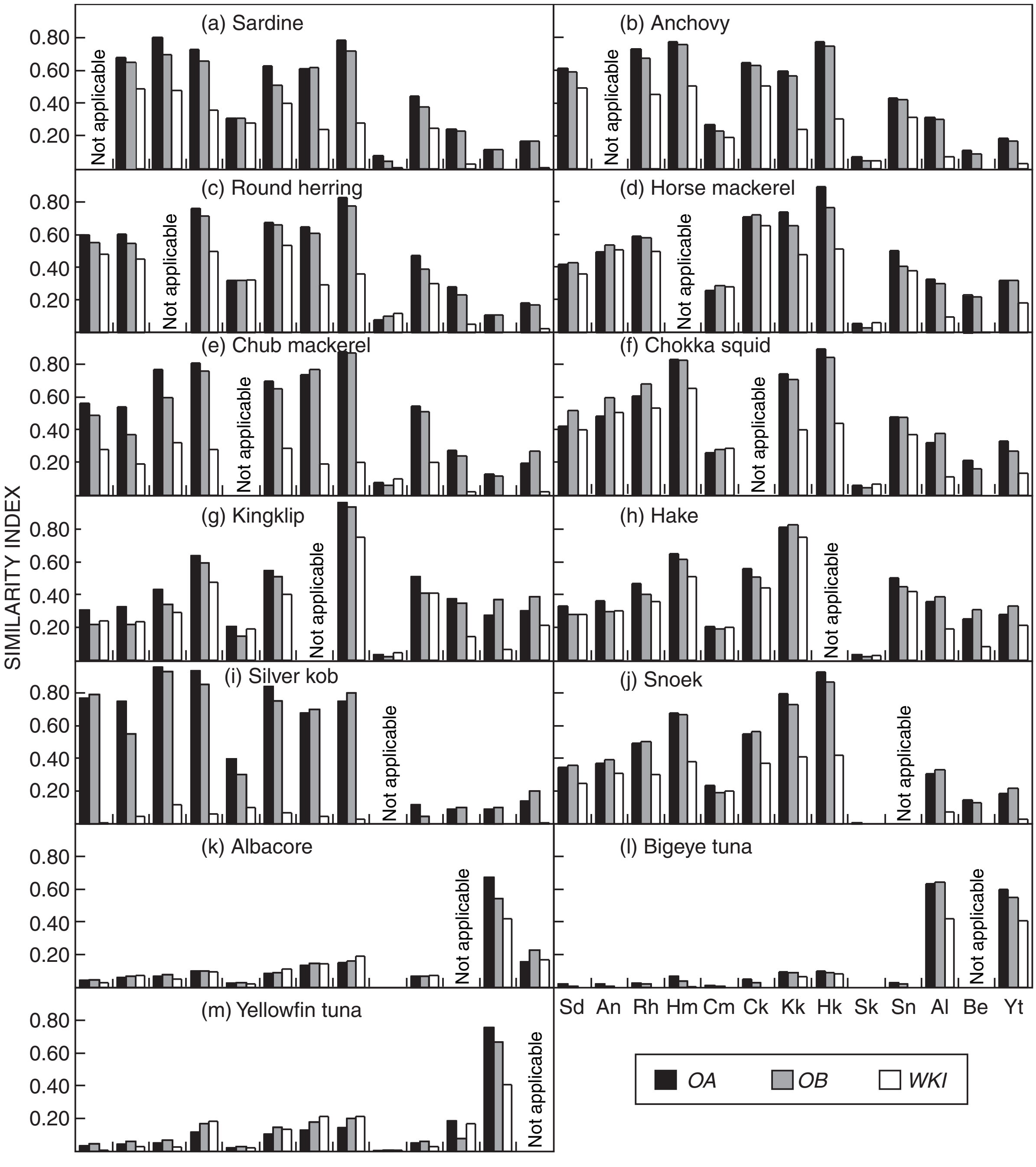

Fig. 1: Three different indices presented on a species-by-species basis, describing overlaps between (a) sardine, (b) anchovy, (c) round herring, (d) horse mackerel, (e) chub mackerel, (f) chokka squid, (g) kingklip, (h) Cape hake, (i) silver kob, (j) snoek, (k) albacore, (l) bigeye tuna, (m) yellowfin tuna, and each of the 12 other species; proportion of overlap in area (*OA*), of overlap in biomass (*OB*) and a weighted kappa index (*WKI*). See Table I for species abbreviations

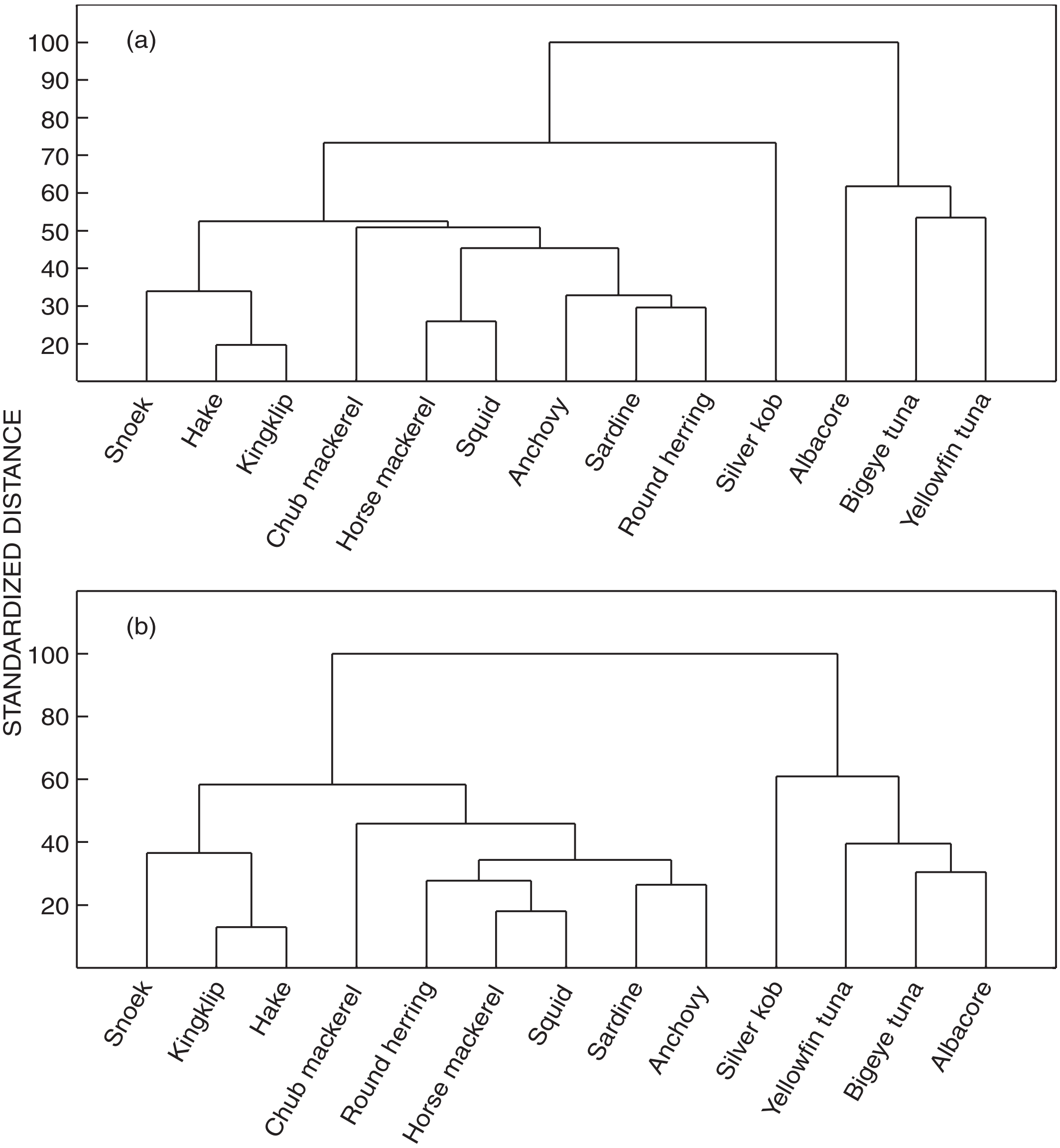

Fig. 2: Cluster analysis of the distribution of the 13 species (Ward aggregation) (a) using the raw relative abundance data per species and per grid cell (3 867 cells of 10´ × 10´) and (b) using the matrix of distances between species (*WKI*)

At a more disaggregated level, the first subgroup of predatory fish can be clearly subdivided into snoek on the one hand, and kingklip and hake on the other. The index can be interpreted as the intra-group variability within each group (kept at the minimum at each step) from a null variance for individual to 100 (standardized) for one group. Disaggregation clearly identified clusters made of similar species distributions, whereas a high level of aggregation dissociated clusters that were very distinct within the ecosystem. It was found that the addition of snoek to the hake/kingklip cluster increased the variance of this group by 50%. Hake and kingklip were widely distributed in the study area, whereas snoek were scarce on the eastern part of the South Coast. Chub mackerel were found within the next sub-cluster, distributed close to the shelf break (between 100 and 500 m), mainly in two large areas: off the Orange River and at the southern tip of the Agulhas Bank. It was isolated from the two other species of intermediate trophic level (horse mackerel and chokka squid) and from the group of low trophic level species (anchovy, sardine and round herring; see trophic levels in Table I). These other five species were relatively widely distributed compared with chub mackerel (see Figs 3a, b, c, f, g and h of Pecquerie *et al.* 2004).

The cluster of the matrix of *WKI*s was similar to that using the raw relative abundance data, which indicates the robustness of the methods and gives confidence in the results (Fig. 2b). The only substantial differences using *WKI* were the position of silver kob, which is clustered with the tuna group (because of the presence of a small patch of tuna west of Port Elizabeth), and round herring, which was clustered closer to horse mackerel and chokka squid than to sardine and anchovy. This is because of its more offshore distribution compared with that of the two other small pelagic species.

In all, 28 maps of overlapping distributions are presented in Figure 3 and detailed below.

Small and medium-sized pelagic fish

There was a high degree of overlap among sardine, anchovy, round herring, horse mackerel and chub mackerel. The values of the corresponding 10 weighted kappa indices ranged from 0.19 to 0.50, with an average of 0.39. The lowest of these were the four involving chub mackerel (average value 0.27, Fig. 1e), as a result of the scattered distribution records for that species (Fig. 3d), which has a low catchability in all types of fishing gear. The overlap between sardine and anchovy is mainly restricted to a coastal band (<150 m depth) from south of Hondeklip Bay to 100 km east of Port Elizabeth (Fig. 3a). The overlap between round herring and anchovy was predominantly between St Helena Bay and the central part of the Agulhas Bank, mainly between the coast and 200 m deep (Fig. 3b). In contrast, horse mackerel and round herring distributions overlapped mainly on the South Coast from the coast to 100 m deep, and in limited areas elsewhere, from the 100 to the 500 m isobath (Fig. 3c).

Chokka squid and other species

Because chokka squid live mainly on the South Coast, their distribution areas overlapped mostly with those of other species in that region. In the case of small pelagic species such as horse mackerel, round herring, anchovy and sardine (Figs 3e, f, g and h), there was a large overlap in distribution from the coast to a depth of 200 m, whereas the distributions of chokka squid and offshore tuna species such as albacore and yellowfin tuna overlapped at depths of 100–500 m (Figs 3x, y). Chokka squid and hake distributions overlapped on the South Coast and to a lesser extent in a smaller area between the Orange River and Hondeklip Bay (Fig. 3n).

Hake and other species

Hake distribution overlapped with those of sardine, anchovy and round herring over a large portion of the continental shelf (<200 m) between Hondeklip Bay and Port Elizabeth (Figs. 3i, j and k). Large areas with no overlap were offshore, especially off the West Coast, where the three pelagic species are not abundant, or offshore on the Agulhas Bank, where sardine was scarce. Nonetheless, overlap between hake and anchovy on the West Coast was more inshore than for the other pelagic species. The latter potential interaction is likely to involve mainly *Merluccius capensis* (shallow-water Cape hake) rather than *M. paradoxus* (deep-water Cape hake), because the latter species is seldom found in water shallower than 100 m (Badenhorst and Smale 1991, Payne 1995).

Chub mackerel and hake overlap was limited to small patches widely scattered between the coast and at least the 500 m isobath (Fig. 3m). In contrast, horse mackerel and chokka squid distributions overlapped with hake over large areas, in particular between the coast and the 500 m isobath on the South Coast and between 150 and 400 m deep from the Orange River mouth to Hondeklip Bay (Figs 3l, n).

Hake and kingklip distributions were closely matched, except for a narrow coastal band on the West Coast, where kingklip were less abundant than hake (Fig. 3o). In contrast, hake and snoek distributions overlapped mainly along an extensive band orientated northwest-southeast around the 200 m isobath along the West Coast and between 100 and at least 500 m deep from St Helena Bay to the outer edge of the Agulhas Bank (Fig. 3p).

Silver kob and other species

Silver kob was recorded in just two coastal areas of the South Coast (Fig. 3q). However, it is common on untrawlable (using bottom trawls) areas in False Bay, south of Cape Town (Griffiths 1997). Silver kob distributions overlapped with those of most coastal species, e.g. anchovy (Fig. 3q), but overlaps were limited between silver kob and tuna species, snoek and, to a lesser extent, sardine (Fig. 1).

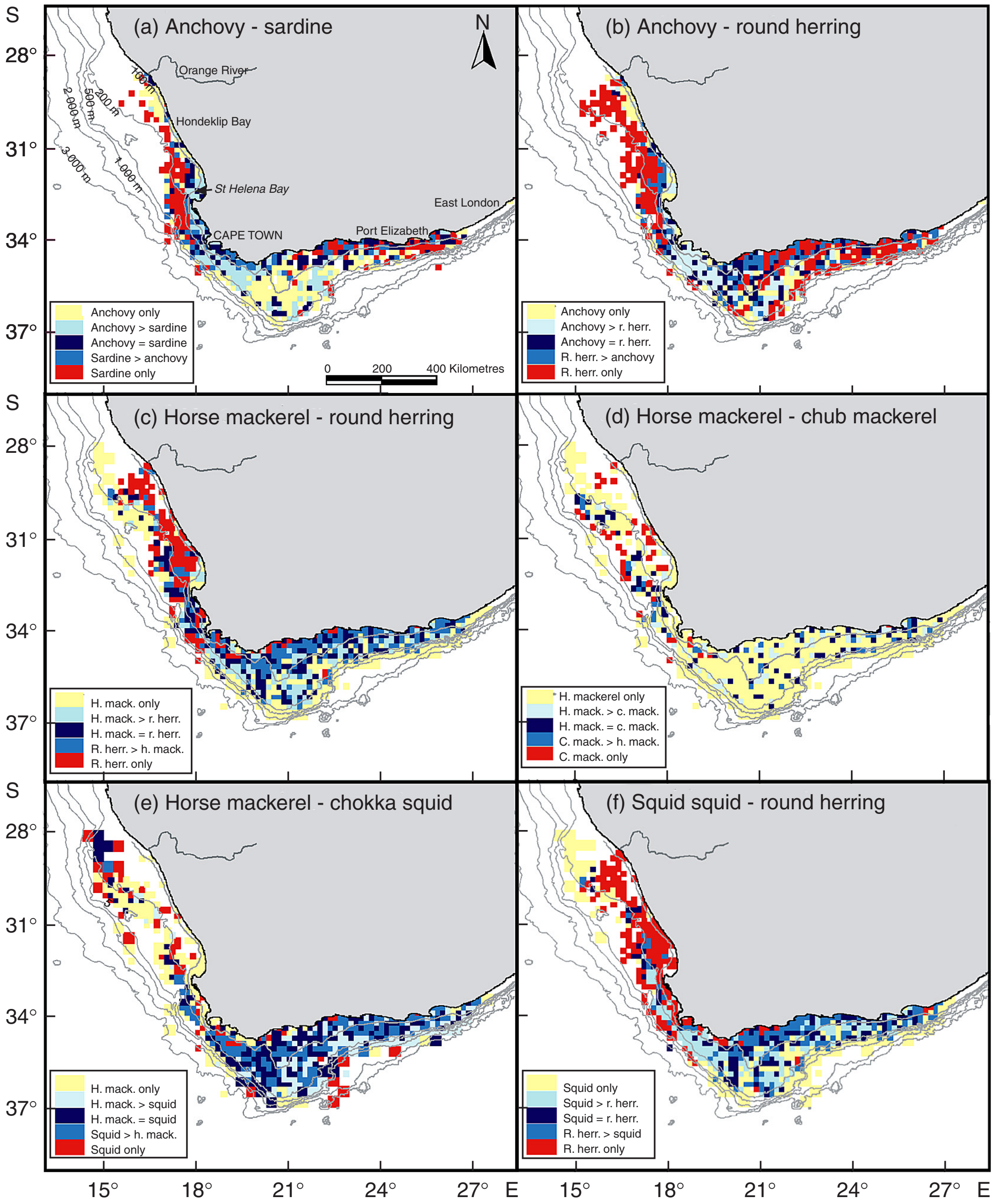

Fig. 3: Maps of overlaps (in relative biomass) between (a) anchovy and sardine, (b) anchovy and round herring, (c) horse mackerel and round herring, (d) horse mackerel and chub mackerel, (e) horse mackerel and chokka squid, (f) chokka squid and round herring, (g) chokka squid and anchovy, (h) chokka squid and sardine, (i) sardine and Cape hake, (j) anchovy and Cape hake, (k) round herring and Cape hake, (l) horse mackerel and Cape hake, (m) chub mackerel and Cape hake, (n) chokka squid and Cape hake, (o) kingklip and Cape hake, (p) snoek and Cape hake, (q) anchovy and silver kob, (r) snoek and chub mackerel, (s) snoek and horse mackerel, (t) snoek and round herring, (u) snoek and anchovy, (v) snoek and sardine, (w) albacore and sardine, (x) albacore and chokka squid, (y) yellowfin tuna and chokka squid, (z) yellowfin tuna and snoek, (α) yellowfin tuna and albacore, (β) bigeye tuna and albacore

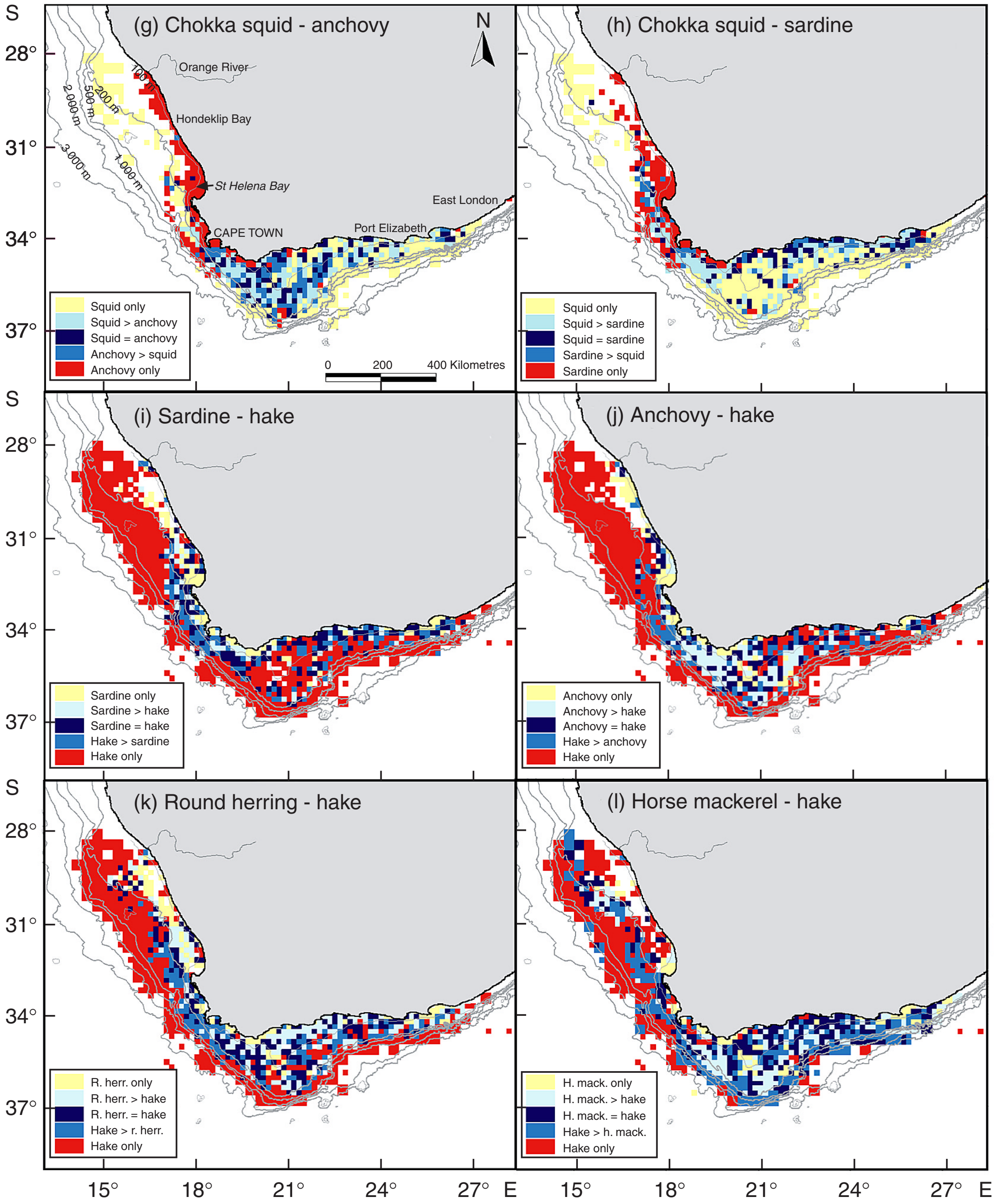

Fig. 3: (*continued*)

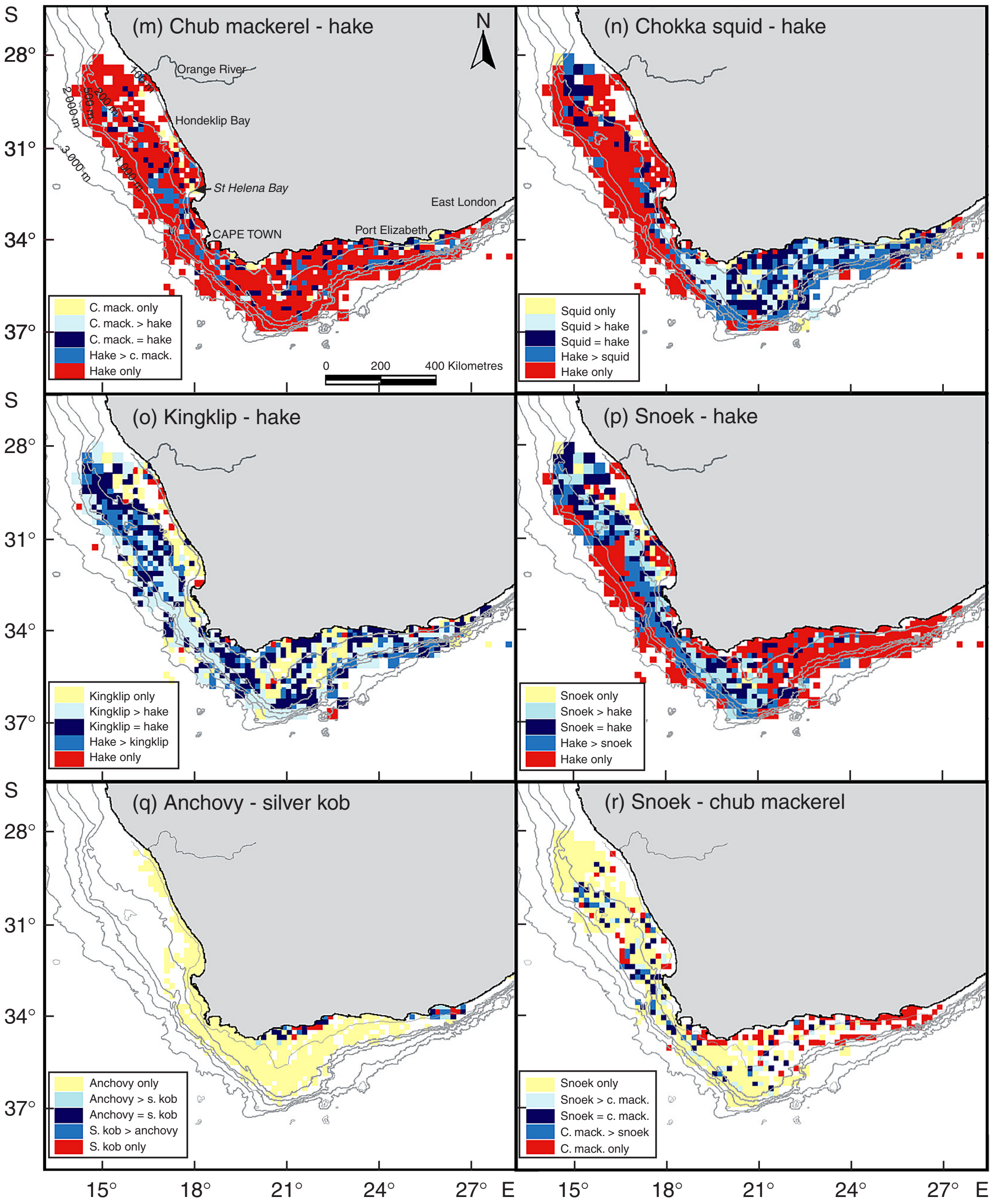

Fig. 3: (*continued*)

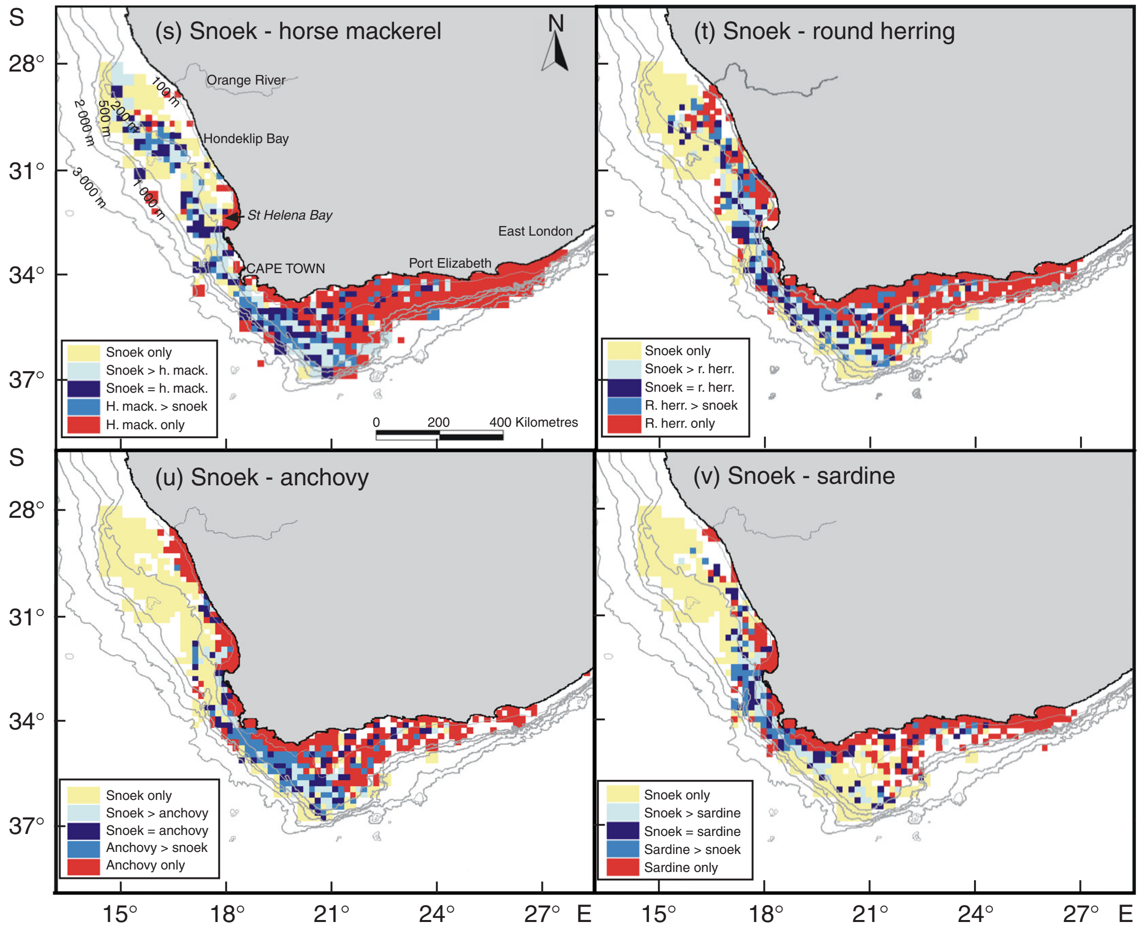

Fig. 3: (*continued*)

Snoek and other species

Apart from its overlap with hake, the spatial distribution of snoek overlapped with those of other predators such as kingklip and chokka squid (maps not shown) and, to a lesser extent, with chub mackerel in small patches along the West Coast and part of the South Coast (Fig. 3r). Overlaps between snoek and tuna species were restricted to a small offshore band on the South Coast, as illustrated in Figure 3z for yellowfin tuna.

Snoek distribution areas overlapped considerably with all pelagic species. For sardine and anchovy, overlaps were mainly from St Helena Bay to west of Port Elizabeth and between 100 and 500 m deep (Figs 3u, v), whereas snoek distributions overlapped with those of horse mackerel and round herring along the same northwest–southeast orientation as was the case for snoek and hake distribution overlap (Figs. 3s, t, p).

Tunas and other species

Apart from their overlap with chokka squid and snoek (Figs 3x, y, z), albacore and yellowfin tuna distributions also overlapped to a limited extent with those of certain pelagic species (Figs 1k, m) along a narrow offshore band, as shown for albacore and sardine (Fig. 3w). Bigeye tuna had a more offshore distribution (Fig. 3β) and there was little overlap with small pelagic

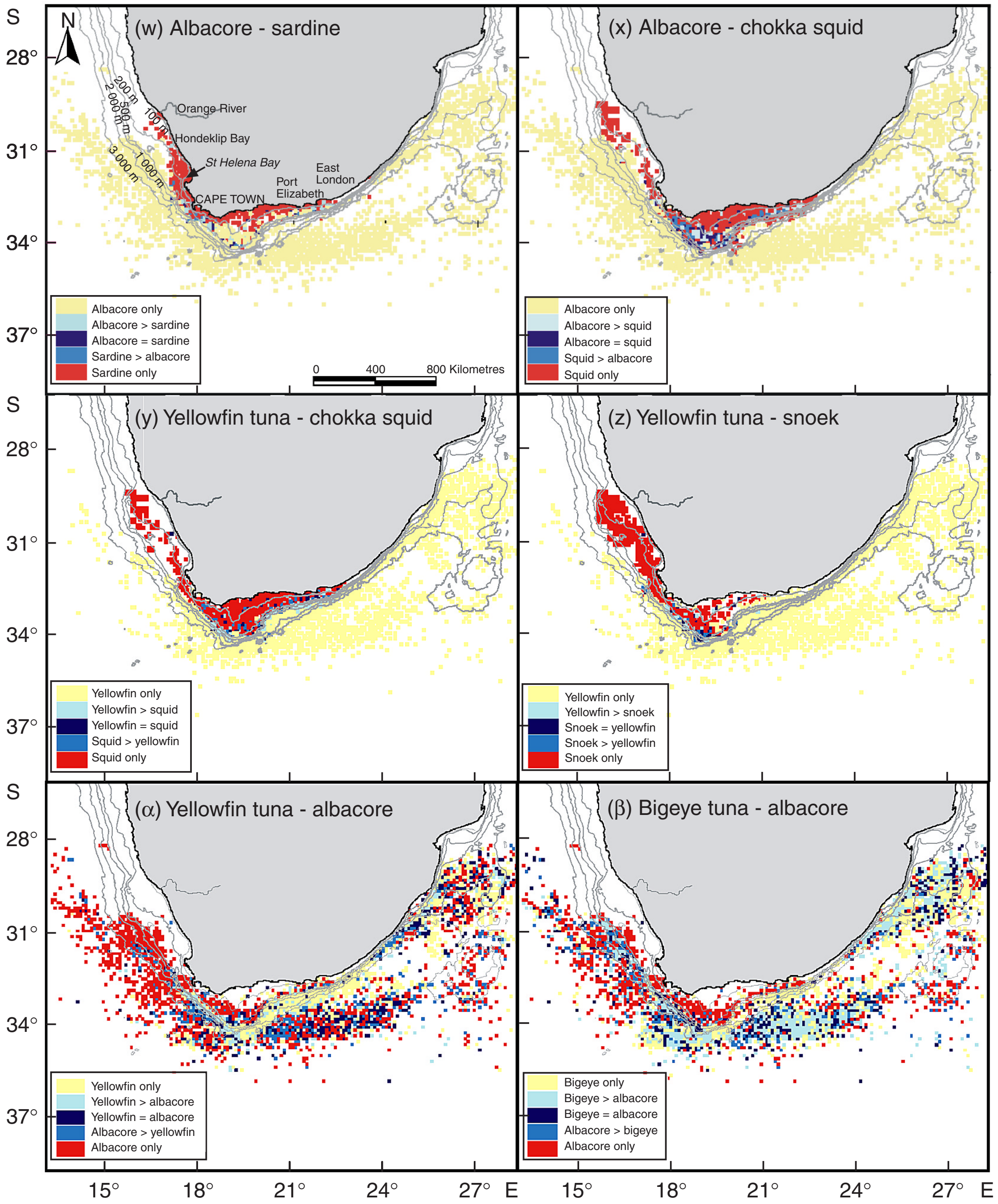

Fig. 3: (*continued*)

species (Fig. 1), contrasting with their high overlaps with albacore and yellowfin tuna. Nonetheless, the overlap of yellowfin tuna and albacore was relatively small (Fig. 3α).

DISCUSSION

Indices of spatial overlap

A FUNCTION OF SPATIAL SCALE AND RESOLUTION

The overlap in area (*AO*), biomass (*OB*) and the weighted kappa indices (*WKI*) were used to quantify spatial overlaps between pairs of species. Because the intensity of spatial overlaps depends on the spatial resolution, the choice of spatial scale is crucial (Schneider 1998, Smith *et al.* 2001, Pecquerie *et al.* 2004, Meaden in press). Ideally, the selected spatial resolution should vary according to the pair of species selected and the time scale: the appropriate spatial resolution should match the mean area covered by the movements of an individual of the most mobile of the two species during a given unit of time, that unit of time itself depending on the temporal scale and on data availability. This was not possible for practical reasons and because individual behaviour for most of the species was largely ignored. Despite these constraints, it might be interesting to make use of the method used by Portilla *et al.* (2002) to determine the "critical scale" of interaction. This method is based on the assumption that, as the size of a grid cell increases, so does the proportion of co-occurrence of species. The scale at which interaction has reached its maximum is termed the "critical scale of interaction".

There was no substantial difference between the indices of overlap based on area or biomass. This might be because of the high spatial resolution chosen for the study. There may have been a difference if the spatial resolution had been lower, because there would have been greater differences in relative biomass between cells. This relatively high spatial resolution, compared with the mobility of the species, may also explain the low values of the weighted kappa index (low level of similarity) estimated. Decreasing the spatial resolution would decrease the patchiness of the density distributions and therefore would result in higher similarity between the distributions.

SYMMETRY/ASSYMETRY

The merit of the *WKI* is its symmetry, i.e. its unique value for a given pair of species. It describes spatial overlap in abundance simultaneously for both species, whereas the other asymmetric indices (*OA* and *OB*) characterize the overlap of one population relative to another. The latter two indices can vary considerably according to the species used as reference. Cases of extreme discrepancy between the two values of *OB* (or *OA*) for one pair of species are interesting, because they clearly show that the interaction is only an important consideration for one of the species in the pair. For example, adult silver kob prey on a variety of pelagic and demersal fish, including anchovy, round herring and hake, as well as on chokka squid (Smale and Bruton 1985), all of which are found throughout the area of distribution of silver kob (e.g. Fig. 3q), whereas for the same species, silver kob is not a major predator because it can access only a limited part of the overall biomass of the potential prey.

HABITAT SELECTION

Different ecological constraints play a role in habitat selection by marine species. First, spatial distribution of marine species can be related to environmental conditions (temperature, salinity, turbidity, bathymetry, etc.; e.g. Laurs *et al.* 1984, Castillo *et al.* 1996, Paramo *et al.* 2003, Taylor and Rand 2003), because they strive to meet their physiological needs. Second, fish might select their habitat according to the presence/absence of their prey, predators and competitors (review in Kramer *et al*. 1997, Fréon and Misund 1999). Third, annual migration related to the need for ensuring survival of offspring might also play a major role in habitat selection. This last example can be illustrated by the reproductive strategy of sardine and anchovy, which spawn on the Agulhas Bank so that their eggs and larvae can be passively transported to nursery areas of the West Coast, without being affected too much by offshore advection (Hutchings *et al*. 1998, Huggett *et al*. 2003). Overall, the present results indicate a relatively low level of potential interaction between prey and predators and a higher level of potential interaction between the predators themselves or between the prey items themselves (Fig. 1). This raises an interesting ecological question related to habitat selection. The two interpretations presented below are not mutually exclusive. Because factors responsible for habitat selection include the search for prey or avoidance of predators and competitors, there are difficulties in the interpretation of observations: a typical "chicken-and-egg" situation.

An extreme overlap of the spatial distribution of a predator with that of its prey can be interpreted as an advanced evolutionary process through which the predator, in its capacity to adapt to the distribution of its prey, must fulfil its own physiological needs, but also increase the probability of encountering, detecting and catching prey in such a habitat. This seems to be partly the case for hake that can prey on sardine and anchovy in a large part of their habitat (Figs 3i, j), but not for tuna and sardine, because their area of overlap is limited to a narrow band near the shelf break (Fig. 3w). This limted co-occurrence is probably attributable to two constraints faced by tuna on the continental shelf: avoiding cold upwelled water (on the West Coast) and water that is not clear enough for efficient visual detection of the prey (nearly all coastal areas). Tuna feed mainly on species that are not incorporated in this study (mesopelagic fish, pelagic invertebrates, etc).

A limited level of co-occurrence combined with a low similarity in distribution may indicate no trophic interaction between the species considered (e.g. silver kob and tunas, Figs 1i, k, l, m), or that there is avoidance between two competing species (e.g. albacore and yellowfin tuna, Figs 1k, m, 3α). Avoidance may also explain a high degree of co-occurrence (high value of *OA*) and a low level of similarity between species (low value of *WKI*). This may be the case for the interaction between sardine and hake, compared with that between sardine and anchovy (Figs 1a, 3a, i). The sardine area of overlap with hake is comparable with that for sardine and anchovy (80 and 70% respectively), but the *WKI* for anchovy and sardine is twice that for hake and sardine. Over a comparable area, high densities of sardine seem to be more closely associated with high densities of anchovy than with high densities of hake, suggesting that sardine avoid hake. Another interpretation is that predation reduces prey abundance to some extent in the area of co-occurrence of many predator and prey species. Prey might also have selected habitat niches that do not suit their predators or make them less available to them. Finally, fish may select habitats according to the distribution of predators or competing prey species that are not among the 13 considered here: e.g. plankton species, benthic prey, mesopelagic fish and top predators such as marine mammals, sharks and birds, which are essential components of the southern Benguela ecosystem (Payne and Crawford 1995). These species will be considered in further work.

From potential to real interactions

DENSITY MAP IMPROVEMENTS

In this study, interactions were qualified as potential for the following reasons:

(i) There was no distinction between adults and juveniles, despite known age-related distribution of some species (e.g. Barange *et al.* 1998, 1999);
(ii) No consideration of the vertical distribution of the different species was taken into account because of the paucity of data. Nevertheless, because most fish species perform diurnal vertical migration (Punt *et al.* 1992, Armstrong and Thomas 1995, Crawford 1995a, b, Prosch *et al.* 1995), they may come into contact with each other, especially during the night, although exceptions exist with regard to diurnal predators;
(iii) The actual trophic links between species were not considered when the three indices were calculated for the 78 pairs of species. We nonetheless focused on the highest level of trophic interactions (Table I);
(iv) Despite the different distributions of the two species of hake according to bathymetry (Badenhorst and Smale 1991, Payne 1995), and their different diets (Payne *et al*., 1987, Punt *et al.* 1992), data constraints forced us to consider them as a single group. Therefore, indices of potential interactions between hake and other species need refinement;
(v) Despite differences in the abundance of pelagic fish in the 1980s and 1990s (Shannon *et al.* 2003, Pecquerie *et al.* 2004), no distinction between periods was made;
(vi) Spatial scale was not related to species mobility, as mentioned earlier, which probably resulted in an overestimation of species overlaps;
(vii) The maps of relative density that have been used to compute overlaps could still be improved by a better combination of the data (intercalibration) and the use of other datasets (jig fishery, handline fishery), as detailed in Pecquerie *et al.* (2004), although some limitations will remain because of limited spatial coverage (e.g. >500 m depth) or low catchability of some species;
(viii) A number of other improvements could be made in the future, such as an increase in the percentage of biomass represented (98 or 99%) and a higher spatial resolution (see also Pecquerie *et al.* 2004).

IDENTIFICATION OF AREAS OF TROPHIC INTERACTION BY CONSIDERING PAIRS OF SPECIES

The maps presented can be used to identify areas of trophic interaction between species, provided that one takes into account the diet of the species as known from stomach content analysis and incorporated in trophic models (Table I). For instance, it is clear that the potential interaction between Cape hake and sardine (Fig. 3i) is less extensive than that between hake and horse mackerel (Fig. 3l), although during the recent period of abundance of sardine, this species likely constituted a substantial prey of both shallow- and deep-water Cape hake, whereas horse mackerel are only important prey for larger, shallow-water Cape hake (Shannon *et al.* 2003). Trophic interactions between hake and kingklip may potentially take place over an extensive area in which both species co-occur. Kingklip prey on hake, although hake rarely consume kingklip (Payne and Badenhorst 1995). In addition, adult hake and bottom-dwelling kingklip may compete for prey in an area. The distribution of round herring lies largely within that of anchovy, the latter species also being distributed offshore along the West Coast where round herring is not as abundant (Fig. 3b). Anchovy and round herring exhibit strong niche overlaps in terms of both their prey and their predators (Shannon *et al.* 2003), and are trophically similar/replaceable (Shannon 2001, Shannon and Cury 2003). By contrast, horse mackerel and chub mackerel, which have only small net trophic impacts on each another (through limited competition for food; Shannon *et al.* 2003), had limited overlap in their distributions (Fig. 3d). Chokka squid are largely restricted to the South Coast and Agulhas Bank, so limiting the extent over which they interact trophically with their predators (e.g. hake), prey (e.g. small pelagic fish) and competitors (e.g. small pelagic fish with respect to zooplankton prey, hake and snoek). Predation on anchovy by chokka squid has been reported (Lipiński 1992, Sauer and Lipiński 1991). Therefore, chokka squid may have the potential to cause substantial mortality on early-stage small pelagic fish spawned on the Agulhas Bank. On the other hand, the predator-prey interaction between snoek and small pelagic fish, such as anchovy, is strong (Shannon 2001, Shannon *et al.* 2003). Considering that snoek are found mainly on the West Coast and the eastern Agulhas Bank, these are the areas where snoek will prey on small pelagic fish (Figs 3t, u, v).

Further applications and perspectives

SPATIAL MODELS

Conventional trophic models are not spatially resolved and may provide biased estimates of interdependence and competition between species if based on trophic data from a limited area of a species' distributional range. Likewise, quantification of overlapping distribution, as presented here, could yield biased estimates of species interactions where there is substantial geographical overlap, but limited trophic interaction. This study highlights the need to combine spatial and trophic data to obtain a clearer understanding of the interactions among species. This approach is used in the OSMOSE (Object-orientated Simulation of Marine ecOSystems Exploitation) ecosystem model that deals with fish species only (Shin *et al.* 2004). Further work is in progress to resolve at a spatial scale models that take into account other components of the ecosystems, such as lower (plankton) and higher (birds, mammals, sharks) trophic levels.

IDENTIFICATION OF FISH ASSEMBLAGES

The next step for trophic interaction studies of the southern Benguela ecosystem with a spatial dimension could be the identification of spatial patterns of fish assemblages related to environmental conditions (Overholtz and Tyler 1985, Roel 1987, Smale 1992, Jacob *et al.* 1998, Gomes *et al.* 2001). There are similarities between the trophic and the spatial organization of marine communities in coastal upwelling ecosystems, with species at lower trophic levels located closer to the coastal upwelling sources than those at higher trophic levels, as found in this study. Furthermore, these fish assemblages are persistent; they retain their species composition for periods that are at least comparable to the average life span of their component species (see review in Gomes *et al.* 2001). The last spatially resolved study of demersal fish assemblages in the southern Benguela was that of Roel (1987), and it could be of value to look at the subsequent 18 years of available data to improve understanding of the effects of fisheries exploitation on the marine community as a whole.

APPLICATION OF SPATIAL INTERACTION INDICES TO THE ECOSYSTEM APPROACH TO FISHERY MANAGEMENT

Interactions between species that are trophically linked (by means of competition or predation; Jarre-Teichmann *et al.* 1998) can be quantified by means of trophic ecosystem indicators (e.g. Shannon and Cury 2003). These can contribute to an ecosystem approach to fisheries management by helping to identify sensitive interactions (direct and indirect) and to assess the local effects of one species on others that share part of the same ecosystem. Information of this nature may be important when trying to manage a number of "interacting" fisheries and exploited or non-exploited species simultaneously.

The identification of areas of potential interaction of pairs of species could serve as an ecological basis for differential management (such as time area closures) of species in mixed species fisheries and reduction of incidental bycatch of some species. If an overexploited species is regularly caught (e.g. as bycatch) in a fishery targeting a species that is not overexploited, a preferred option may be to close areas where the two species co-occur, and to redirect fishing effort on the non-overexploited species to the area where the overexploited species does not co-occur or at least is not abundant. This approach may well be helpful in co-managing the South African demersal trawl fishery and the linefishery. For example, silver kob is a target species in the linefishery and a bycatch species in the inshore sole trawl fishery (R. W. Leslie, MCM, pers. comm.). Another case for seasonal/spatial closures arises when the level of mortality of a species caught as incidental bycatch is not sustainable, e.g. kingklip caught in the hake trawl and longline fisheries (R. W. Leslie, pers. comm.). For species exhibiting a high degree of seasonal segregation, an ability to harvest one species selectively based on seasonal separation of the stocks could be envisaged by seasonal closure or a combination of seasonal and spatial closure of the fisheries (e.g. Murawski and Finn 1988, Caddy 1999). This would require the collection of additional data to improve the spatial and temporal coverage in some databases, especially in surveys that ideally should cover the whole South African continental shelf during each of the two seasons.

Another application of these maps could be to provide information to assist in determining the location and extent of marine protected areas or no-take zones, which ideally should achieve as many objectives as possible, such as providing sanctuary for endangered species, protection of nursery/reproductive areas, rebuilding of overexploited stocks, provision of areas favourable for tourism and recreational activities (Attwood *et al.* 1997, Roberts 1997, Hyrenbach *et al.* 2000, Côté *et al.*, 2001). Marine protected areas and reserves are more than simple regulatory mechanisms; they represent a new trend towards a habitat-based ecosystem approach (Bax *et al.* 1999). Finally, by extending the overlapping distribution maps to top predators breeding in colonies (seals, seabirds), this approach could be used to limit the competition between fisheries and natural predators, especially during their breeding seasons.

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LITERATURE CITED

AGRESTI, A. 1990 — *Categorical Data Analysis*. New York; Wiley-Interscience: 558 pp.

ARMSTRONG, M. J. and R. M. THOMAS 1995 — Clupeoids. In *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 105–121.

ATTWOOD, C. G., HARRIS, J. M. and A. J. WILLIAMS 1997 — International experience of marine protected areas and their relevance to South Africa. *S. Afr. J. mar. Sci.* **18**: 311–332.

BADENHORST, A. and M. J. SMALE 1991 — The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. *S. Afr. J. mar. Sci.* **11**: 377–393.

BAIRD, D., McGLADE, J. M. and R. E. ULANOWICZ 1991 — The comparative ecology of six marine ecosystems. *Phil. Trans. R. Soc. Lond.* **B333**: 15–29.

BARANGE, M., PILLAR, S. C. and I. HAMPTON 1998— Distribution patterns, stock size and life-history strategies of Cape horse mackerel *Trachurus trachurus capensis*, based on bottom trawl and acoustic surveys. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* **19**: 433–447.

BARANGE, M., HAMPTON, I. and B. A. ROEL 1999 — Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. *S. Afr. J. mar. Sci.* **21**: 367–391.

BAX, N., WILLIAMS, A., DAVENPORT, S. and C. BULMAN 1999 — Managing the ecosystem by leverage points: a model for multispecies fishery. In *Ecosystem Approaches for Fishery Management*. Fairbanks; University of Alaska Sea Grant **AK-SG-99-01**: 283–303.

BOLLINGER, J., KIENEST, F. and H. BUGMANN 2000 — Comparing models for tree distribution: concept, structures and behavior. *Ecol. Model.* **134**: 89–102.

BOYCE, M. S., VERNIE, P. R., NIELSEN, S. E. and F. K. A. SCHNIEGELOW 2002 — Evaluating resource selection functions. *Ecol. Model.* **157**: 281–300.

CADDY, J. F. 1999 — Fisheries management in the twenty-first century: will new paradigms apply? *Revs Fish Biol. Fish.* **9**: 1–43.

CASTILLO, J., BARBIERI, M. A. and A. GONZALEZ 1996 — Relationships between sea surface temperature, salinity and pelagic fish distribution off northern Chile. *ICES J. mar. Sci.* **53**(2): 139–146.

CHRISTENSEN, V. and C. J. WALTERS 2000 — ECOPATH with ECOSIM: methods, capabilities and limitations. In *Methods for Assessing the Impact of Fisheries on Marine Ecosystems of the North Atlantic*. Pauly, D. and T. J. Pitcher (Eds). *Fish.*

Cent. Res. Rep. **8**: 79–105.

CONGALTON, R. and A. MEAD 1983 — A quantitative method to test for consistency and correctness in photo-interpretation. *Photogram. Engng Remote Sens*. **49**: 69–74.

CÔTÉ, I. M., MOSQUEIRA, I. and J. D. REYNOLDS 2001 — Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J. Fish Biol*. **59** (Suppl. A): 178–189.

COUTO, P. 2003 — Assessing the accuracy of spatial simulation models. *Ecol. Model*. **167**: 181–198.

CRAWFORD, R. J. M. 1995a — Horse mackerels and saury. In *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 122–129.

CRAWFORD, R. J. M. 1995b — Snoek and chub mackerel. In *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 177–187.

CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353–505.

FAO 1997 — Review of the state of world fishery resources: marine fisheries. *FAO Fish. Circ*. **920**: 105 pp.

FRÉON, P. and O. A. MISUND 1999 — *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment*. Oxford; Fishing News Books: 348 pp.

GARCIA, S. M. and I. de LEIVA MORENO 2003 — Global overview of marine fisheries. In *Responsible Fisheries in the Marine Ecosystem*. Sinclair, M. and G. Valdimarsson (Eds). Wallingford; CAB International: 103–123.

GISLASON, H., SINCLAIR, M., SAINSBURY, K. and R. O'BOYLE 2000 — Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES J. mar. Sci*. **57**: 468–475.

GOMES, M. C., SERRAO, E. and M. F. BORGES 2001 — Spatial patterns of groundfish assemblages on the continental shelf of Portugal. *ICES J. mar. Sci*. **58**: 663–647.

GRIFFITHS, M. H. 1997 — The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters. *Fishery Bull., Wash*. **95**(1): 47–67.

GRIFFITHS, M. H. 2002 — Life history of South African snoek *Thyrsites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem. *Fishery Bull., Wash*. **100**: 690–710.

GUISAN, A. and E. ZIMMERMANN 2000 — Predictive habitat distribution models in ecology. *Ecol. Model*. **135**: 147–186.

HALL, S. J. 1999 — *The Effect of Fishing on Marine Ecosystems and Communities*. Oxford; Blackwell: 274 pp.

HUGGETT, J. A., FRÉON, P., MULLON, C. and P. PENVEN 2003 — Modelling the transport success of anchovy (*Engraulis encrasicolus*) eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. *Mar. Ecol. Prog. Ser.* **250**: 247–262.

HUTCHINGS, L., BARANGE, M., BLOOMER, S. F., BOYD, A. J., CRAWFORD, R. J. M., HUGGETT, J. A., KERSTAN, M., KORRÛBEL, J. L., DE OLIVEIRA, J. A. A., PAINTING, S. J., RICHARDSON, A. J., SHANNON, L. J., SCHÜLEIN, F. H., VAN DER LINGEN, C. D. and H. M. VERHEYE 1998 — Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci*. **19**: 211–225.

HYRENBACH, K. D., FORNEY, K. A. and P. K. DAYTON 2000 — Marine protected area and ocean basin management. *Aquat. Conserv. mar. Freshwat. Ecosyst*. **10**: 437–458.

JACOB, W., McCLATCHIE, S., PROBERT, P. K. and R. J. HURST 1998 — Demersal fish assemblages off southern New Zealand in relation to depth and temperature. *Deep-Sea Res. I* **45**: 2119–2155.

JARRE-TEICHMANN, A., SHANNON, L. J., MOLONEY, C. L. and P. A. WICKENS 1998 — Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci*. **19**: 391–414.

JENNINGS, S. and M. J. KAISER 1998 — The effects of fishing on marine ecosystems. *Adv. mar. Biol*. **34**: 201–352.

KRAMER, D. L., RANGELEY, R. W. and L. J. CHAPMAN 1997 — Habitat selection: patterns of spatial distribution from behavioural decisions. In *Behavioural Ecology of Teleost Fishes*. Godin, J-G. J. (Ed.). Oxford; University Press: 37–80.

LARKIN, P. A. 1996 — Concepts and issues in marine ecosystem management. *Revs Fish Biol. Fish*. **6**: 139–164.

LAURS, R. M., FIELDLER, P. C. and D. R. MONTGOMERY 1984 — Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Res*. **31**: 439–453.

LEGENDRE, P. and L. LEGENDRE 1998 — *Numerical Ecology*. Amsterdam; Elsevier: 853 pp.

LIPIŃSKI, M. R. 1992 — Cephalopods and the Benguela ecosystem: trophic relationships and impact. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci*. **12**: 791–802.

MAY, R. M., BEDDINGTON, J. R., CLARK, C. W., HOLT, S. J. and R. M. LAWS 1979 — Management of multispecies fisheries. *Science, N.Y*. **205**(4403): 267–277.

MEADEN, G. J. (in press) — Challenges of using GIS in aquatic environments. In *Geographic Information Systems in Fisheries*. Fisher, W. and F. Rahel (Eds). *Trans. Am. Fish. Soc*.

MOLONEY, C. L., VAN DER LINGEN, C. D., HUTCHINGS, L. and J. G. FIELD 2004 — Contributions of the Benguela Ecology Programme to pelagic fisheries management in South Africa. In *Ecosystem Approaches to Fisheries in the Southern Benguela*. Shannon, L. J., Cochrane, K. L. and S. C. Pillar (Eds). *Afr. J. mar. Sci*. **26**: 37–51.

MURAWSKI, S. A. and J. T. FINN 1988 — Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. *Can. J. Fish. Aquat. Sci*. **45**: 1720–1735.

NAVARRETE, S. A. and B. A. MENGE 1996 — Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecol. Monogr*. **66**: 409–429.

NEPGEN, C. S. DE V. 1979 — The food of the snoek *Thyrsites atun*. *Fish. Bull. S. Afr*. **11**: 39–42.

OVERHOLTZ, W. J. and A. V. TYLER 1985 — Long-term responses of the demersal fish assemblages of Georges Bank. *Fishery Bull., Wash*. **83**: 507–520.

PARAMO, J., QUIÑONES, R. A., RAMIREZ, A. and R. WIFF 2003 — Relationship between abundance of small pelagic fishes and environmental factors in the Colombian Caribbean Sea: an analysis based on hydroacoustic information. *Aquat. Living Resour*. **16**: 239–245.

PAULY, D., CHRISTENSEN, V. and C. WALTERS 2000 — ECOPATH, ECOSIM, and ECOSPACE as tools for evaluating ecosystem impact of fisheries. *ICES J. mar. Sci*. **57**: 697–706.

PAYNE, A. I. L. 1995 — Cape hakes. In. *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 136–147.

PAYNE, A. I. L. and A. BADENHORST 1995 — Other groundfish resources. In *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town;

Vlaeberg: 148–156.

PAYNE, A. I. L. and R. J. M. CRAWFORD (Eds) 1995 — *Oceans of Life off Southern Africa*, 2nd ed. Cape Town; Vlaeberg: 380 pp.

PAYNE, A. I. L. and J. R. E. LUTJEHARMS 1997 — *A Century of Marine Science in South Africa. Trans. R. Soc. S. Afr.* 52(1): 252 pp.

PAYNE, A. I. L., ROSE, B. and R. W. LESLIE 1987 — Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci*. **5**: 471–501.

PEARSON, R. G., DAWSON, T. P., BERRY, P. M. and P. A. HARRISON 2002 — Species: a spatial evaluation of climate impact on the envelope of species. *Ecol. Model*. **154**: 289–300.

PECQUERIE, L., DRAPEAU, L., FRÉON, P., COETZEE, J. C., LESLIE, R. W. and M. H. GRIFFITHS 2004 — Distribution patterns of key fish species of the southern Benguela ecosystem: an approach combining fishery-dependent and fishery-independent data. In *Ecosystem Approaches to Fisheries in the Southern Benguela*. Shannon, L. J., Cochrane, K. L. and S. C. Pillar (Eds). *Afr. J. mar. Sci.* **26**: 115–139.

PORTILLA, E., PLANQUE, B., PETITGAS, P., MASSÉ, J., BEILLOIS, P., BOURRIAU, P. and M. SANTOS 2002 — Measuring critical spatial scales of biological associations in the ocean. An application to sardine and anchovy in the Bay of Biscay. In *Programme and Abstracts of the Globec 2nd Open Science Meeting, Qingdao, P. R. China, October 2002*: p. 131.

PROSCH, R. M., HULLEY, P. A. and R. A. CRUICKSHANK 1995 — Mesopelagic fish and some other forage species. In *Oceans of Life off Southern Africa*, 2nd ed. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 130–135.

PUNT, A. E., LESLIE, R. W. and S. E. DU PLESSIS 1992 — Estimation of the annual consumption of food by Cape hake *Merluccius capensis* and *M. paradoxus* off the South African west coast. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci*. **12**: 611–634.

ROBERTS, C. M. 1997 — Ecological advice for the global fisheries crisis. *Trends Ecol. Evol*. **12**(1): 35–38.

ROEL, B. A. 1987 — Demersal communities off the west coast of South Africa. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 575–584.

SAUER, W. H. H. and M. R. LIPIŃSKI 1991 — Food of squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the Eastern Cape, South Africa. *S. Afr. J. mar. Sci*. **10**: 193–201.

SCHNEIDER, D. C. 1998 — Applied scaling theory. In *Ecological Scale: Theory and Applications*. Peterson D. L. and V. T. Parker (Eds). New York: Columbia University Press: 253–269.

SHANNON, L. J. 2001 — Trophic models of the Benguela upwelling system: towards an ecosystem approach to fisheries management. Ph.D. thesis, University of Cape Town: *Ecol. Ind.* xxxv + 319 pp.

SHANNON, L. J. and P. M. CURY 2004 — Indicators quantifying small pelagic fish interactions: application using a trophic model of the southern Benguela ecosystem. *Ecol. Ind*. **3**: 305–321.

SHANNON, L. J. and A. JARRE-TEICHMANN 1999 — Comparing models of trophic flows in the northern and southern Benguela upwelling systems during the 1980s. In *Ecosystem Approaches for Fisheries Management*. Fairbanks; University of Alaska Sea Grant **AK-SG-99-01**: 527–541.

SHANNON, L. J., MOLONEY, C. L., JARRE, A. and J. G. FIELD 2003 — Trophic flows in the southern Benguela during the 1980s and the 1990s. *J. mar. Syst*. **39**: 83–116.

SHANNON, L. V. and M. J. O'TOOLE 1998 — Integrated overview of the oceanography and environmental variability of the Benguela Current region. Second Regional Workshop on the Benguela Current Large Marine Ecosystem (BCLME). *BCLME Thematic Rep*. **2**: 58 pp.

SHIN, Y. J. 2000 — Interactions trophiques et dynamiques des populations dans les écosystèmes marins exploités. Approche par modélisation individus-centrée. Doctorat en Biomathématiques. Université Denis Diderot – Paris VII, Paris: 245 pp.

SHIN, Y. J. and P. CURY 2001 — Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquat. Living Resour*. **14**: 65–80.

SHIN, Y-J., SHANNON, L. J. and P. M. CURY 2004 — Simulations of fishing effects on the southern Benguela fish community using an individual-based model: learning from a comparison with ECOSIM. In *Ecosystem Approaches to Fisheries in the Southern Benguela*. Shannon, L. J., Cochrane, K. L. and S. C. Pillar (Eds). *Afr. J. mar. Sci.* **26**: 95–114.

SINCLAIR, M., ARNASON, R., CSIRKE, J., KARNICKI, Z., SIGURJONSSON, J., RUNE SKJOLDAL, H. and G. VALDIMARSSON 2002 — Responsible fisheries in the marine ecosystem. *Fish. Res.* **58**: 255–265.

SINCLAIR, M. and G. VALDIMARSSON 2002 — *Responsible Fisheries in the Marine Ecosystem*. Wallingford, UK; CAB International: 426 pp.

SMALE, M. J. 1992 — Predatory fish and their prey – an overview of trophic interactions in the fish communities of the west and south coasts of South Africa. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 803–821.

SMALE, M. J. and M. N. BRUTON 1985 — Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in South-Eastern Cape waters of South Africa. *S. Afr. J. Zool.* **20**(3): 97–108.

SMITH, P. E., HORNE, J. K. and D. C. SCHNEIDER 2001 — Spatial dynamics of anchovy, sardine, and hake pre-recruit stages in the Californian Current. *ICES J. mar. Sci.* **58**: 1063–1071.

TAYLOR, J. C. and P. S. RAND 2003 — Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. *Aquat. Living Resour.* **16**: 191–196.

WARD, J. H. 1963 — Hierarchical grouping to optimize an objective function *J. Am. Statist. Assoc.* **58**: 236–244.