Ecosystem Approaches to Fisheries in the Southern Benguela
Afr. J. mar. Sci. 26: 161–177
2004

EFFECTS OF FISHING ON THE SIZE AND DOMINANCE STRUCTURE OF LINEFISH OF THE CAPE REGION, SOUTH AFRICA

D. YEMANE, J. G. FIELD* and M. H. GRIFFITHS†*

A dataset of linefish catch, effort and fish size distribution records has been assembled from archives to cover three short periods over the 100 years from 1897 to 1998 in four regions of the former Cape Colony, South Africa. Linefish catch and effort have increased several-fold over the period. Aggregate catch per unit effort (*cpue*) declined by more than 80% from values in the 1890s, but the *cpue* of several species within that aggregate have declined much more. Analysis of historical mean size and modern length frequency data shows that in seven of 12 species considered, the mean length of fish declined substantially along with the increased fishing pressure. Multivariate analysis of *cpue* shows that the years 1897–1906 cluster quite close to the years 1927–1931, but a major change by the years 1986–1998, revealing a large change in abundances of linefish between the 1930s and the 1990s, which is also the period when fishing effort increased most. A related dataset was used to calculate the combined distribution of fish sizes of the 12 species in logarithmic size-classes in the same years. The negative slope of that size spectrum indicates the decline in numbers of large size-classes compared with small ones; the more negative the slope, the greater the relative decline in numbers of large fish. Slopes become significantly more negative in the modern period, showing that the modern linefish catch has fewer large fish and relatively more small ones than previously. Changes in linefish assemblages, implied by changes in catch composition, are different in the four regions studied. The cool-temperate upwelling regions differ from the warm-temperate ones, particularly with regard to the influence of the fast-growing, nomadic, pelagic snoek *Thyrsites atun*. Inclusion of snoek gives the size spectrum of the cool-temperate regions a shallower slope than the warm-temperate ones. A new method of plotting the size spectrum is believed to free the intercept (height) from dependence on the slope and simplifies interpretation of the relative values of height, which reflect overall fish abundance. Dominance curves reflect the distribution of biomass among species. The cool waters of the Western Cape show a trend towards increasing dominance with increased effort, whereas the warm-temperate regions show decreased dominance with increased fishing pressure. These findings have important consequences for fisheries management, because not only are several stocks badly overfished, but the linefish considered are predators at different trophic levels that influence the tropho-dynamic functioning of whole ecosystems.

Key words: community structure, dominance curves, linefish, size spectrum, South Africa

The effects of fishing extend well beyond the direct impact on the target species in the forms of reduction in abundance, decrease in mean size (Haedrich and Barnes 1997) and habitat destruction. Currently, much effort is directed at understanding the previously overlooked effects of fishing on the interacting species (community level) that cascade to the whole ecosystem (Greenstreet and Hall 1996, Jennings and Kaiser 1998, Fogarty and Murawski 1998, Daan *et al*. 2003). It is difficult to predict indirect effects of fishing on the ecosystem and to quantify their long-term consequences (Gulland 1987, Gislason *et al*. 2000). Changes in the structure of fish communities have been documented for several heavily exploited fisheries. Fogarty and Murawski (1998) reported changes in the community structure of Georges Bank, where the community is seemingly dominated by skates and dogfish following a substantial reduction in the biomass of gadoid fishes. This reduction, mainly as a result of overfishing, is believed to have relieved competitive pressure in favour of the elasmobranchs (skates and dogfish). Similarly, changes have been reported in the composition and distribution of the demersal fish communities of the Adriatic Sea between 1948 and 1998 (Jukick-Peladic *et al*. 2001). During that 50-year period, larger species of sharks and rays tended to disappear whereas small-sized species of sharks, rays and bony fish appeared more frequently. Jennings *et al*. (1999) assessed the long-term trend in the abundance of North Sea demersal fish communities and related this to the life-history characteristics of individual species. They found, for the period 1925–1996, an increase in mean growth rate, whereas the mean maximum size, age and size-at-maturity decreased towards

* Marine Biology Research Institute, Zoology Department, University of Cape Town, Rondebosch, South Africa.
E-mail: dghebreh@botzoo.uct.ac.za
† Formerly Marine & Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa; now Ministry of Fisheries, P.O. Box 1020, Wellington, New Zealand

Manuscript received July 2003; accepted November 2003

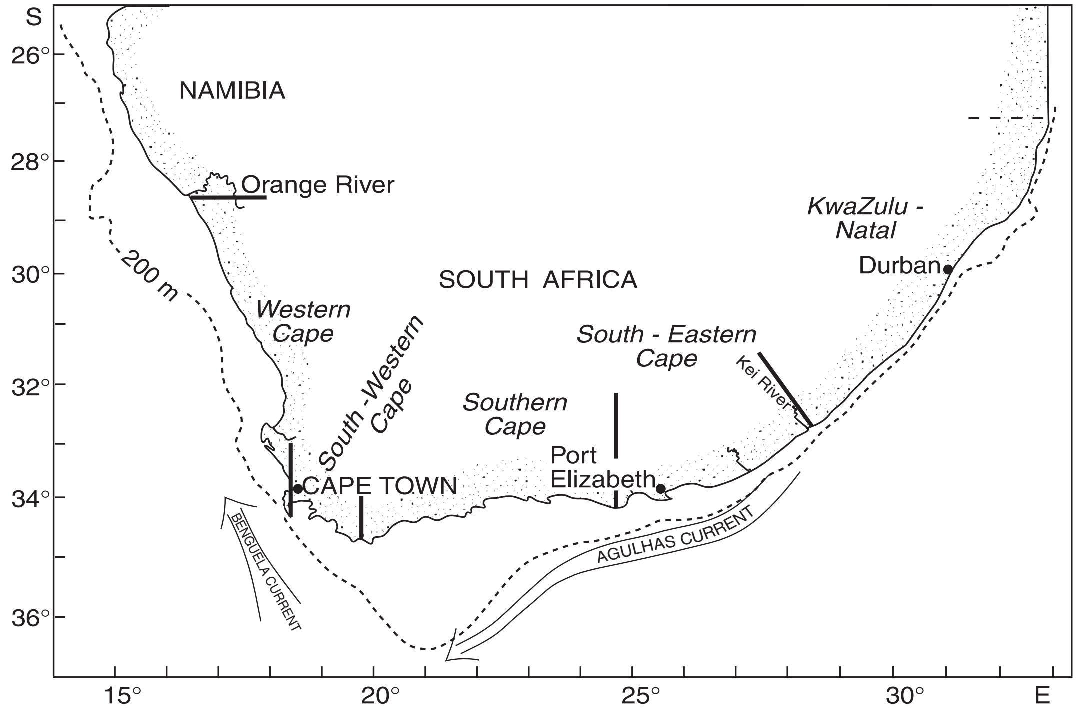

Fig. 1: Map of South Africa showing the four regions of the Cape Province

the 1990s, a period characterized by heavy fishing. Furthermore, the response of species to fishing pressure was related to life-history traits, larger, slow-growing, late-maturing species tending to decline in abundance more quickly than smaller, fast-growing, early-maturing species (Jennings *et al*. 1999), as noted also for other assemblages by Griffiths (2000) and Fromentin and Fonteneau (2001).

A number of community metrics can be used to assess ecosystem effects: diversity indices, ordination techniques, size spectra (either abundance or biomass), dominance curves (K-dominance and ABC curves) and metrics derived from ecosystem mass-balance models. A review of the performance of these metrics as used in evaluating the ecosystem effects of fishing is given by Rice (2000). Relative to other community metrics, size spectra, K-dominance curves and non-metric multidimensional scaling appear most promising for assessing the ecosystem effects of fishing (Rice 2000). The use of size spectra in assessing the effects of fishing has a solid theoretical and empirical basis. Rice and Gislason (1996) observed a decline in the slopes and an increase in the heights of the size spectra of the North Sea demersal fish community between 1973 and 1993. The steeper negative slope of log numbers plotted against log size-classes was attributed to the selective removal of large fish from the community. Subsequently, Gislason and Rice (1998) modelled the response of the slope and height of the size spectrum to changes in fishing effort and found that the slope and height of the size spectrum changed proportionally to the changes in fishing intensity. With an increase in fishing pressure, slopes steepened and heights increased. Shin and Cury (2004) developed the individual based and spatially explicit model OSMOSE (Object-orientated Simulator of Marine EcOSystems Exploitation), founded on opportunistic size-based predation as a main structuring process in fish communities. They found that the slope of the size spectrum steepens quasi-linearly with increasing fishing pressure. Similar trends in the slopes and heights of the size spectrum are reported for different systems around the world (Bianchi *et al*. 2000). The height of the size spectrum has been suggested to reflect overall abundance or system productivity (Borgmann 1987, Boudreau and Dickie 1992, Bianchi *et al*. 2001).

K-dominance curves help to capture the differential effects of disturbance on the abundance of component species, which result in changes in the dominance structure of a community. Bianchi *et al*. (2000) found an increased dominance over time in the temperate systems of the Canadian Scotian shelf and off Portugal, and a similar trend of increasing dominance was noticed in the north-western North Sea by Greenstreet and Hall (1996). However, the opposite trend was observed with time for tropical systems off Ghana, in Campeche Bay and on the Sofala Bank (Bianchi *et al.* 2000).

The linefishery of the present Western and Eastern Cape Provinces (the former Cape Province) has a long history that dates back to the turn of the 19th century. It is the biggest linefishery in South Africa, comprising some 2 500 commercial vessels that land around 15 500 tons annually, or 95% of the nation's linefish landings (Griffiths 2000). It has commercial and recreational sectors, which target around 40 teleosts, of which 20 are economically important (Griffiths and Lamberth 2002). Competition for the same resource among user-groups, a large number of species with contrasting life histories, diverse behaviour patterns and different habitat preferences make the management of the linefishery complex. Owing to its long history of fishing and the failure of regulatory schemes (Attwood and Bennett 1995, Brouwer *et al*. 1997), many Cape linefish species are overexploited (Griffiths 1997a, b). Work by Attwood and Farquhar (1999), which assessed the state of the linefishery between Cape Hangklip and Walker Bay in the South-Western Cape (see Fig. 1), have demonstrated the long-term overexploitation of most species. Some have even disappeared from catches completely (e.g. seventyfour *Polysteganus undulosus*), a trend Griffiths (2000) stated applied to the whole Cape region. Griffiths (2000) showed that, according to long-term catch per unit effort (*cpue*) and effort data, most linefish species are overfished, especially the large, warm-temperate reef (demersal) fish (e.g. silver kob *Argyrosomus japonicus*, geelbek *Atractoscion aequidens* and seventyfour).

Long-term historical fisheries data (e.g. abundance and number of species, size composition, fishing ground, gear used and fishing effort) give insight into the status and structure and/or functioning of the fish community prior to heavy fishing pressure and are indispensible in evaluating the effects of fishing on the fish community. The aim of the present study was to confirm the changes in catch rate over time, using multivariate analysis, as well as to assess the long-term changes in the size composition (size spectra and changes in mean size), and dominance structure (K-dominance curves) of the linefish catch of the whole Cape region over the 100-year period 1897–1998.

MATERIAL AND METHODS

Spatial and temporal coverage

The present study covers the entire Cape region, previously known as the Cape Province. It extends from the Orange River on South Africa's West Coast to the Kei River on its East Coast (Fig. 1). The region is subdivided here into four coastal regions (Western Cape, South-Western Cape, Southern Cape, South-Eastern Cape), each characterized by a different history of fishing (Griffiths 2000). The overall region covers two biogeographic zones (Branch and Branch 1981), the cool-temperate Western Cape and the warm-temperate Southern and South-Eastern Capes. The South-Western Cape is a transition region where species common to both biogeographic regions are present. The Western and Eastern Capes are distinct in terms of prevailing oceanographic conditions. The former is characterized by the cool Benguela Current and coastal upwelling, which result in high productivity (Shannon and Nelson 1996). And the latter by the warm, south-flowing Agulhas Current, which has limited inshore dynamic upwelling (Schumann 1987). Differences among the four regions are also highlighted by the presence of some linefish species as discrete stocks. For example, white stumpnose *Rhabdosargus globiceps* occurs as four discrete stocks in the four regions (Griffiths *et al.* 2002) and silver kob as three (Griffiths 1997b). On the other hand, geelbek exist as three age-structured subpopulations in three regions, but comprise a single stock (Griffiths and Hecht 1995). The study covers three periods over the past 100 years, two historical ones (1897–1906, 1927–1931) and one recent one (1986–1998).

The Cape linefishery has always used a range of hook sizes, depending upon the target species and their sizes. Simple J-hooks are used, and neither hook design nor hook size has changed much over the past 100 years. When hook size decreases in a particular sector, it is usually done to compensate for declining catch rates resulting from the removal of larger fish. Therefore, there is no reason to believe that hook size has caused the patterns reported here; on the contrary, fishers may have continued to use larger hooks because of minimum size regulations for the targeted species first introduced in 1940 and strengthened in 1985. The continued use of large hooks and the imposition of minimum size regulations would have maintained relatively low selectivity for smaller size-classes in the fishery, tending to prevent or reduce any progressive fishing down of the size-classes of the target species.

The study is based on 12 linefish species (Table I), with fish ranging in mean length from 25 to 90 cm. Species whose linefishery records have historically been confounded with trawl and other fishery records have been omitted from the study. The species together represent assemblages of predatory fish at different trophic levels, constituting important parts of regional marine communities and ecosystems. The size spectra derived from them therefore represent parts of whole community size spectra.

Data sources

Data were obtained from commercial linefisheries and consist of two historical and one modern data set. For the period 1897–1906, data were obtained from the reports of John D. F. Gilchrist, who was then Government Marine Biologist (Gilchrist 1898, 1899, 1900, 1901, 1902, 1903, 1904, 1906, 1907). Those data were collected by observers at all major harbours in the four coastal regions of the Cape, and include information on the catch of each linefish species and the number of boats operating in each region. For the period 1927–1931, catch data were obtained from unpublished monthly catch records collected by the Cape Provincial Administration. The number of boats operating at each fishing site were obtained from Fishing Harbour Reports of the Department of Mines and Industries (Mansergh *et al.* 1926, 1927, 1928) and from Report 180 of the Board of Trade and Industries (Fahey *et al.* 1934). Finally, for the recent period, 1986–1998, data were obtained from compulsory daily catch and effort returns submitted by owners of boats involved in commercial linefishing.

Information on size composition for the period 1897–1906 was in the form of mean weight of each species caught. The mean sizes for the period 1927–1931 are not available, so those available for the closest period (1917–1919) were used instead. They were estimated from monthly number and catch weight for each species obtained from the linefish section of Marine and Coastal Management (MCM). However, because the data were not available for all sites in each region, they were not used in the *cpue* analysis, though the mean sizes of each species in the period 1917–1919 were used directly in comparing mean sizes over the three periods. In addition, they were used as close approximates of mean sizes of each species in the construction of size spectra for the period 1927–1931. For the most recent period, length frequencies of the linefish were obtained from official observers at fishing harbours in the four regions of the Cape.

Table I: Mean lengths of main linefish species in the Cape region in the three different periods under study. The mean lengths in the 1917–1919 and 1986–1998 periods are weighted by the average *cpue* of each species in each region

Species	Period	Mean length (cm)
Panga	1897–1906	27.13
Pterogymnus laniarius	1917–1919	31.91
	1986–1998	29.69
White stumpnose	1897–1906	27.70
Rhabdosargus globiceps	1917–1919	25.33
	1986–1998	32.62
Hottentot	1897–1906	29.95
Pachymetopon blochii	1917–1919	26.62
	1986–1998	29.71
Chub mackerel	1897–1906	33.90
Scomber japonicus	1917–1919	35.73
	1986–1998	37.56
Roman	1897–1906	35.81
Chrysobelphus laticeps	1917–1919	30.50
	1986–1998	32.40
Red stumpnose	1897–1906	36.04
Chrysoblephus gibbiceps	1917–1919	38.98
	1986–1998	40.67
Carpenter	1897–1906	39.17
Argyrozona argyrozona	1917–1919	31.76
	1986–1998	33.03
Seventyfour	1897–1906	56.09
Polysteganus undulosus	1917–1919	49.73
	1986–1998	27.66
Silver kob	1897–1906	61.33
Argyrosomus inodorus	1917–1919	58.95
	1986–1998	52.44
Yellowtail	1897–1906	70.35
Seriola lalandi	1917–1919	57.89
	1986–1998	61.51
Snoek	1897–1906	83.48
Thyrsites atun	1917–1919	83.34
	1986–1998	75.93
Geelbek	1897–1906	84.60
Atractoscion aequidens	1917–1919	78.61
	1986–1998	68.48

Analysis of catch and effort

The aggregate total catch (tons) for each region was calculated as the sum of the catches of each linefish species included in the study, and the annual aggregate *cpue* (tons boat-year^{-1}) was calculated by dividing the total catch by the effort (boats year^{-1}). In the analysis of catch-and-effort data, shallow-water Cape hake *Merluccius capensis*, panga *Pterogymnus laniarius* and chub mackerel *Scomber japonicus* were not included, because the majority of the catches of these species is made by fisheries other than the linefishery. Details of possible sources of bias in available handline *cpue* as indices of linefish abundance for each period are given in Griffiths (2000).

Cluster analysis and ordination

Multivariate analysis of the annual *cpue* (tons boat-year^{-1}) of each species was carried out, using cluster analysis and ordination techniques, to assess overall changes in catch composition with time (Clarke and Warwick 1994). The *cpue* data of each species in each year for the whole Cape was first root-root transformed, because the range of values was wide. This was done to prevent abundant species from swamping the others, affecting the similarity matrix and in turn the classification and ordination. The Bray-Curtis measure of similarity was used because it avoids the problem of joint absences and attributes more weight to abundant species than to rare ones (Field *et al.* 1982). Finally group-average linkage was used to produce a dendrogram of the time-series. Field *et al.* (1982) and Clarke and Warwick (1994) suggested that cluster analysis and ordination techniques give better information when used together. Non-metric multidimensional scaling (NMDS) was used to create the ordination plot. The ordination of the time-series using *cpue* of each species was computed from the Bray-Curtis similarity matrix. Details of clustering and ordination techniques, their advantages and drawbacks are given in Clarke and Warwick (1994).

Changes in mean length

The average length of each species in the historical period was calculated from the mean weight using the length-weight relationship for each species (Mann 2000). Use of individual length-weight relationships for each species reduces the error that may be introduced by applying a single theoretical one ($W = 0.01 \times L^3$) for all species, as used by Bianchi *et al.* (2000, 2001).

For the period 1897–1906, mean sizes (weight or length) of each species were considered to be consistent among the four coastal regions, though such an assumption may bias the estimates of the size spectrum. Nevertheless, comparison with the modern data was expected to capture changes in size composition over the long term. Changes in mean length of each species were assessed by comparing weighted mean lengths in the three periods. The average lengths of each species in each period were weighted by the *cpue* of each species in each region to obtain weighted mean lengths for the whole Cape region.

The mean length of fish in the catch was calculated by weighting the length of each species by its corresponding *cpue* in each year:

$$\overline{\text{catch}\,L} = \frac{\sum Lij \times Cij}{\sum Cij}$$

where catch$\overline{L}$ is mean catch length and L_{ij} and C_{ij} are the length and *cpue* of species *i* in the j^{th} year respectively. In this way, the mean catch length of each region is calculated, then weighted by the aggregate *cpue* of each region to obtain the mean catch length for the whole Cape region.

Size spectra and K-dominance

An index of abundance for each species was estimated by dividing the catch (total number of fish) in each year by the effort (boat-years), expressed as number per boat-year. Length frequencies of each species were used to estimate the mean length of each species for the more recent period. The length frequency data for each species were not directly used for the comparative size spectra reported here, because such data were not available for the historical periods. A separate study (Yemane *et al.* in press) has shown that slightly biased size-spectrum statistics (slopes and heights) are obtained from mean size data for each species when compared with size frequency data for all species.

A fish size range of 25–89 cm was used in the size spectra. The size spectrum for each region and period was constructed by distributing the number of individuals of each species into the appropriate 5-cm size-classes (based on the mean length of that species), then plotting the logarithm of overall abundance per size-class against the logarithm of the class-mark, as done by Bianchi *et al.* (2000, 2001). Slopes and intercepts (heights) were estimated by linear regression. Because slopes and heights are highly correlated, the trend in the height is partly the result of its correlation with the slope (Rice and Gislason 1996). Therefore, to make the slope and height of the size spectrum independent and thus to provide different information, the correlation should be removed. Daan *et al.* (2003) suggested a way of removing the correlation between the slope and height by estimating the height at the mean value of the independent variable ($\log_e$ class-mark). By standardizing the independent variable to

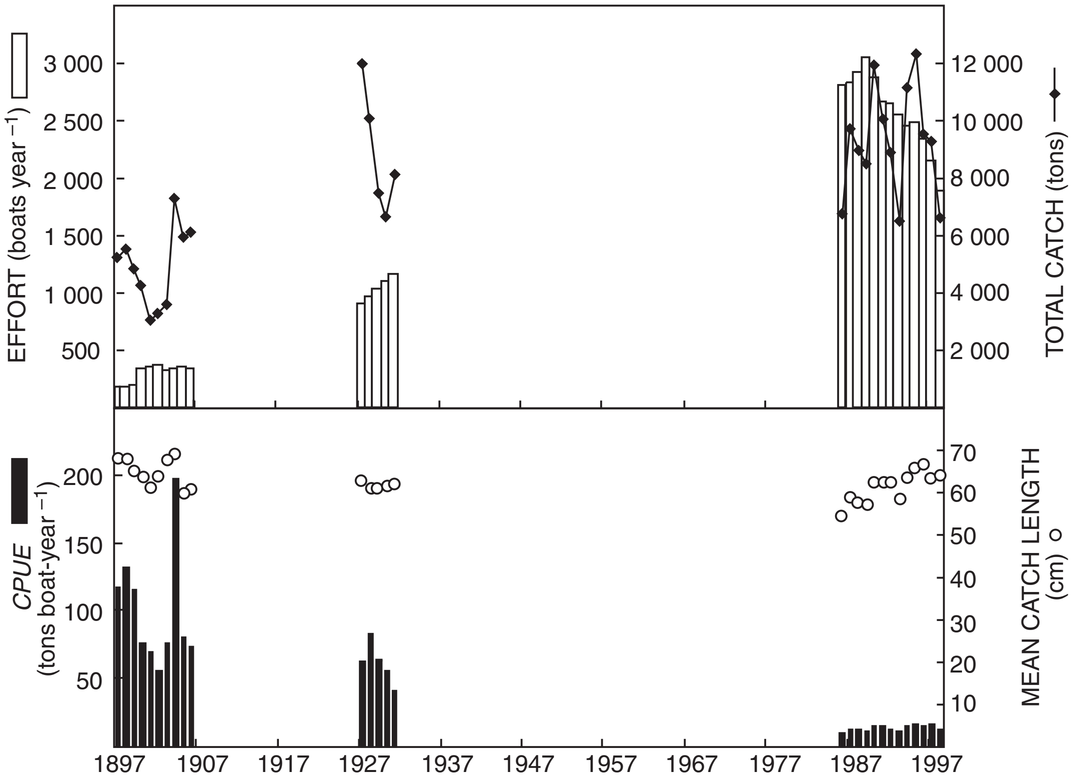

Fig. 2: Long-term trend in catch, effort, *cpue* and weighted mean length in the catch for the whole Cape region

a mean of zero, the ordinate is moved systematically to the midpoint of the size-class, giving the height at the mean size-class. Therefore, the height represents the (log) abundance of the mean size-class. Slope and height are then estimated by log-linear regression. The x-axis is expressed as log size-classes above and below a mean of zero. The significance of the trend in the slopes and heights of the size spectra over the period 1897–1998 was tested using a Students *t*-test (Zar 1999).

The change with time in the dominance structure of the linefish catch was assessed graphically using K-dominance curves, whereby cumulative dominance in biomass is plotted against species rank, or log species rank (Clarke 1990, Clarke and Gorley 2001). This approach is useful in that it picks up patterns of relative species abundance without reducing the information to a single summary statistic, such as a diversity index (Clarke and Warwick 1994).

RESULTS AND DISCUSSION

Trends in catch, effort and *cpue*

Trends in the aggregate total catch, effort and *cpue* of the Cape linefishery are presented in Figures 2 and 3. The total catch for the whole Cape region increased over time along with effort, but *cpue* declined substantially from around 93.94 tons boat-year^{-1} in the 1890s to 12.25 tons boat-year^{-1} in the 1990s (Fig. 2). The peak in *cpue* in 1904 was caused by an exceptionally large catch of geelbek in the South-Eastern Cape then. Most of the region's landings came from the Western Cape. The total catch does not reflect the overall biomass removed by the linefishery, because catches from several sites were excluded if they lacked observers; also it should be remembered that linefish catches were lumped with trawl catches, so the

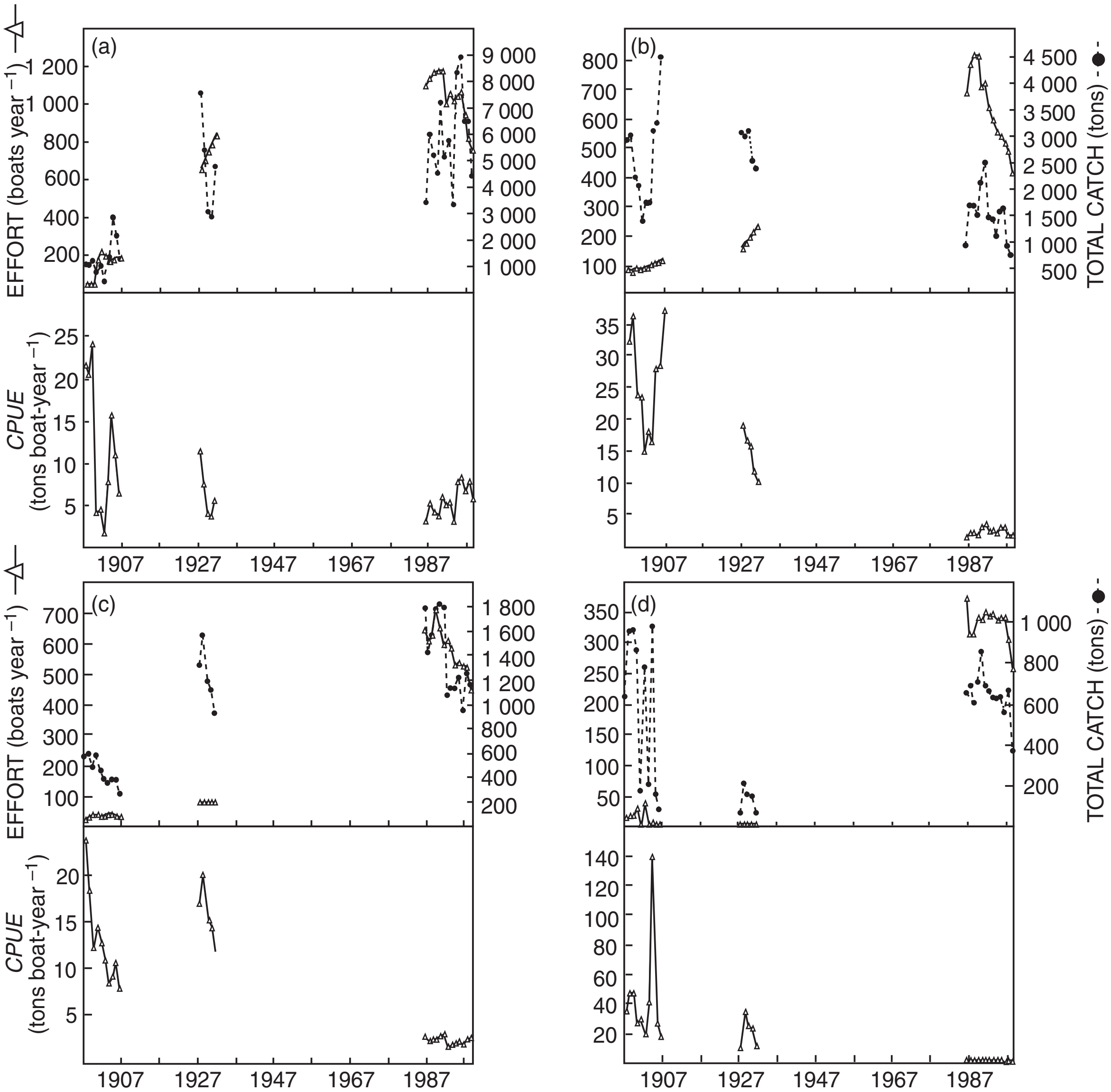

Fig. 3: Long-term trend in the catch, effort and *cpue* for (a) the Western Cape, (b) the South-Western Cape, (c) the Southern Cape and (d) the South-Eastern Cape

catches reflected in Figure 2 are similarly not representative of total biomass removed. Abundance trends are mainly inferred from the trend in *cpue*. Similar trends of an increase in the total catch and a decline in *cpue* were found for the Western Cape (from 11.8 tons boat-year^{-1} at the turn of the century to 5.63 tons boat-year^{-1} in the 1990s; Fig. 3a). The increase in the total catch in the Western Cape is mainly attributed to catches of the dominant pelagic, migratory snoek *Thyrsites atun*, which constitute 78–96% of the

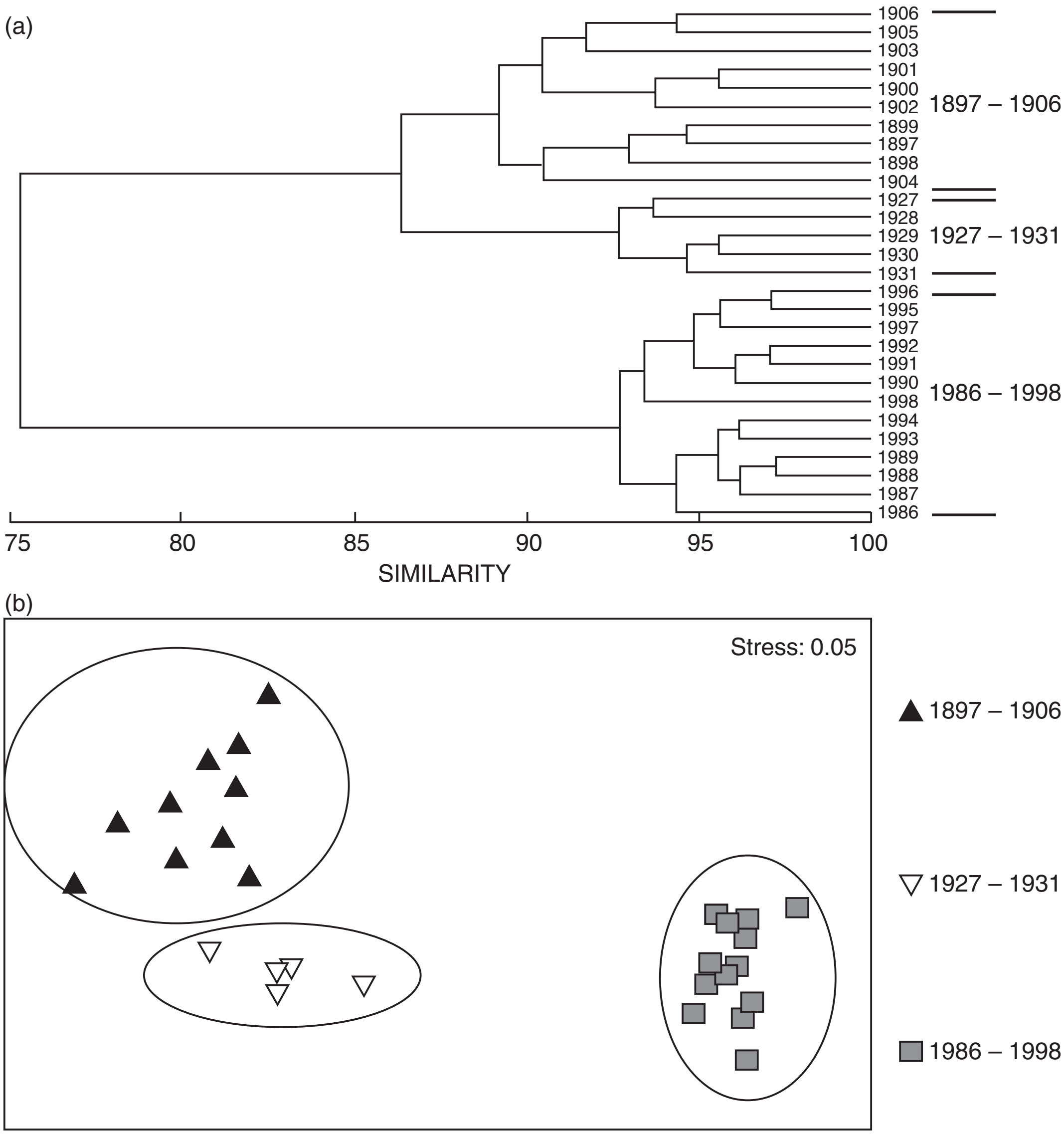

Fig. 4: (a) Dendrogram and (b) non-metric multidimensional scaling (MDS) ordination plot of the time-series using *cpue* of the 12 linefish species under study. Both are based on root-root transformed data and the Bray-Curtis measure of similarity

catch. Off the South-Western Cape, *cpue* dropped from 25.8 to 2.31 tons boat-year^{-1} between the 1890s and 1990s (Fig. 3b). Snoek again contributed the largest proportion to the total catch there. Off the Southern Cape, *cpue* decreased from 12.8 tons boat-year^{-1} in the 1890s to 2.36 tons boat-year^{-1} in the 1990s (Fig. 3c) and, off the South-Eastern Cape, it dropped from 43.4 to 1.94 tons boat-year^{-1} over the same period (Fig. 3d). Carpenter *Argyrozona argyrozona* and silver kob made up the biggest proportion of the catch off the Southern and South-Eastern Capes.

The dramatic declines in *cpue* reflect the heavy commercial exploitation of the linefishery. This is attributed to unregulated commercial effort on species whose life histories do not support massive exploitation (Griffiths 2000). The depletion of most species is mainly attributable to overfishing (Attwood and Farquhar 1999, Griffiths 2000). Although misreporting could theoretically have influenced the observed trends, the commercial handline trends were verified by similar trends in commercial trawl datasets (silver kob and carpenter), fishery independent linefish surveys (Southern Cape) and stock assessment (silver kob, geelbek, carpenter and yellowtail; Griffiths 2000).

Multivariate analysis of *cpue*

The classification and ordination (using non-metric MDS) plot of years in the three periods are shown in Figure 4, based on the *cpue* of each species included in the study. The three periods clustered separately; ordination of the same data further confirms this. The two historical periods, which were characterized by high *cpue* for most linefish species and lower effort, tended to be grouped close to each other, whereas the years in the more recent period were characterized by high effort, when most species were overexploited (Griffiths 2000), so were grouped together away from the other periods. This corroborates the observed trend in aggregate *cpue* and effort over the 100 years. It also implies that there were differences in species abundances among the three periods. Catch composition data indicated that the biggest change in catch composition was between 1931 and 1986, confirming the concept that many linefish species were heavily depleted during that period, primarily as a result of developing technology and unregulated effort (Griffiths 2000).

Size composition

MEAN LENGTH

The mean lengths of the species considered are given in Table I. The mean lengths of >50% decreased between the periods 1897–1906 and 1986–1998. The mean lengths of chub mackerel, red stumpnose *Chrysoblephus laticeps* and white stumpnose *Rhabdosargus globiceps* increased towards the present, whereas that of hottentot *Pachymetopon blochii* showed no clear trend. Mean size of larger species (snoek, geelbek, silver kob, seventyfour and yellowtail *Seriola lalandi*) decreased substantially, but they are preferred species of the linefishery. The decrease in the mean length of seventyfour appeared extreme, but it may to some extent have been exaggerated by a shortage of samples and the scarcity of the species in recent catches. This shoaling species has shown the greatest decline in abundance (>99%; Griffiths 2000), so a large decline in its mean size is not surprising. Seventyfour had essentially become commercially extinct prior to the moratorium imposed in 1998.

The average size of species may decrease with changes in growth rate in response to environmental changes (e.g. change in the ambient temperature). However, there is no evidence of a long-term trend in coastal ocean temperature off the Western or Southern Capes. If data are from just a short period, size change may be the result of interannual dynamics in the recruitment of individual species (Haedrich and Barnes 1997), but if the measured decreases in the mean length are assessed in conjunction with the trend in *cpue* of individual species reported in Griffiths (2000), the conclusion can only be that heavy exploitation is the most likely cause of the reduction in mean length. The average length in the recent catches would have been strongly influenced by the minimum size limit regulations introduced in 1940 and 1985 and the selectivity of the hooks used, the sizes of which have seemingly remained largely constant over time. These factors would have tended to limit fishing mortality to the larger size-classes and prevented progressive fishing down the size-classes. Therefore, a substantial reduction in mean length would not be expected in the fishery, and this measure alone would therefore not provide a reliable index of the impact of fishing on target stocks.

The weighted mean catch length of the whole Cape region is shown alongside the catch, *cpue* and effort statistics in Figure 2. The trend in mean overall catch length over time was marginally not significant when all species were included in the analysis (slope = –0.031, $t = -2.04$, $p = 0.052$). This slight trend may be the influence of the dominance of snoek and a switch towards a species that was not targeted in the historical period, i.e. yellowtail (Griffiths 2000). Based on trends in *cpue* and stock assessment, these fast-growing pelagic nomads are the only two species targeted by the linefishery that do not appear to have been overexploited (Griffiths 2000).

SIZE SPECTRA

Examples of the size spectra for selected years for each region are depicted in Figure 5. The intension was to show how an abundant species like snoek can

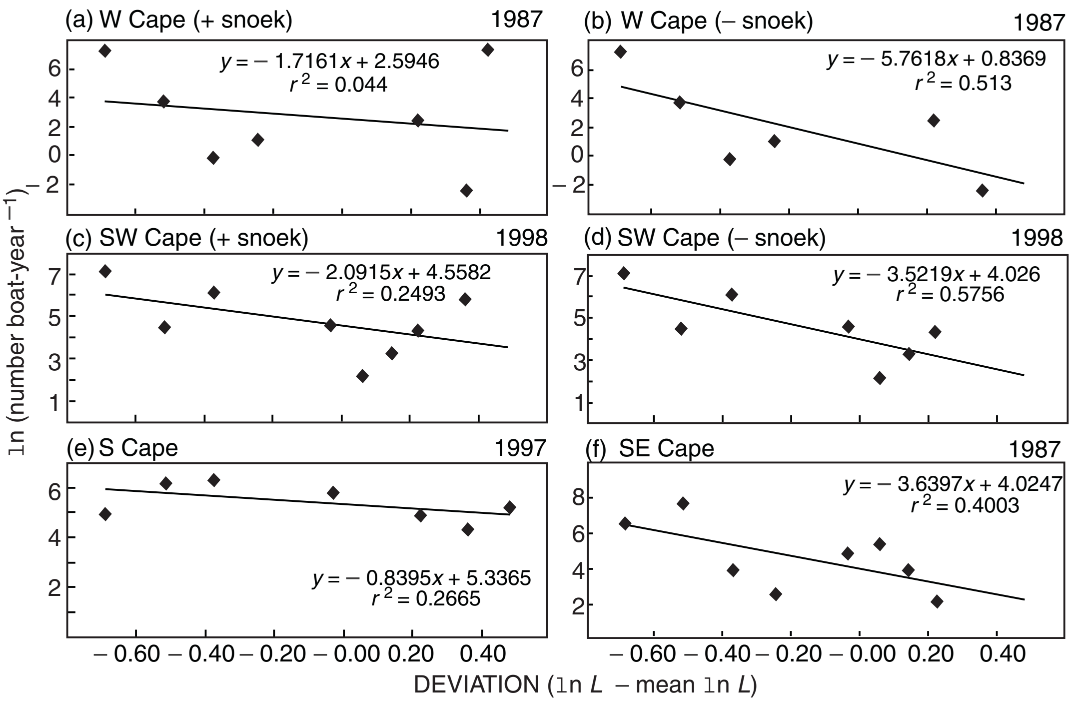

Fig. 5: Sample size spectra of the four regions in the Cape for selected years; (a) Western Cape with snoek, (b) Western Cape without snoek, (c) South-Western Cape with snoek, (d) South-Western Cape without snoek, (e) Southern Cape and (f) South-Eastern Cape

affect the size spectra and in turn the spectrum statistics (slope and height). For example, in the size spectra for the Western Cape, snoek appeared towards the tail of the size distribution; in the case of the historical data snoek contributed largely to size-class 80–84 cm and in the modern data to size-class 75–85 cm. Similarly for the South-Western Cape, the size spectrum was affected by snoek, making the negative slope

Table II: Significance tests of the long-term trends in the slopes and heights of the size spectrum over the three periods from 1897 to 1998 (see Figs 6 and 7)

Region	Parameter	Estimate (*b*)	*SE*	*t*-value	*P*-value
Whole Cape	Slope	−0.010	0.005	−2.029	0.053
	Height	−0.027	0.002	−16.150	0.000
Western Cape with snoek	Slope	0.006	0.007	0.807	0.427
	Height	−0.022	0.005	−4.619	0.000
Western Cape without snoek	Slope	−0.050	0.012	−4.326	0.000
	Height	−0.044	0.007	−6.085	0.000
South-Western Cape	Slope	0.016	0.004	3.644	0.001
	Height	−0.048	0.003	−16.038	0.000
Southern Cape	Slope	0.016	0.004	3.644	0.001
	Height	−0.002	0.003	−0.617	0.542
South-Eastern	Slope	−0.035	0.010	−3.477	0.002
	Height	−0.019	0.004	−4.806	0.000

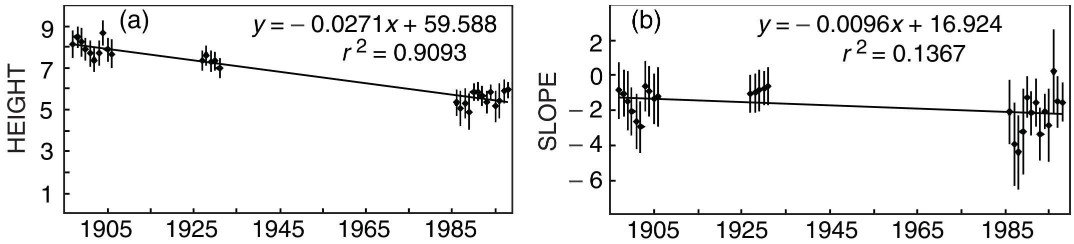

Fig. 6: Long-term trends of the (a) heights and (b) slopes of the size spectra of the pooled data for the whole Cape region, including snoek. Error bars denote ± 2 *SE* (*n* = 28)

shallower.

Figure 6 shows the long-term trend in estimates of the size spectra of the whole Cape plotted against time. Heights decreased significantly between the 1890s and 1990s (Table II, Fig. 7e), although they fluctuated annually within each period. The slopes did not decline significantly.

For the Western Cape, the trends in the slopes of the size spectra did not show significant change over time when snoek were included, but the heights of the size spectra consistently declined with and without snoek over the 100 years (Fig. 7a, b). This suggests a decline in overall abundance of linefish. The insignificant change in the slopes of the size spectra can be explained by species composition in the Western Cape between 1897 and 1998, where snoek was the dominant species, followed by hottentot, with other species contributing little to overall abundance (Griffiths 2000). When snoek were included in the size spectra, the slopes tended to be shallower in both historical and recent periods. When the size spectrum was constructed without snoek, the slopes became steeper (more negative) in the recent period. For the South-Western Cape, the slopes of the size spectra became significantly shallower with time, again attributable to the dominance of snoek (Fig. 7c), whereas height declined over time. The slopes for the Southern Cape data also shallowed over time (Fig. 7d). This may have been influenced by the larger catches of yellowtail in the recent period relative to the earlier ones. Surprisingly, the height did not show any trend over time. This would have been mainly because of yellowtail and silver kob occupying the mean size-classes (50–60 cm) occupied by seventyfour in the 1890s. For the South-Eastern Cape, the slopes and heights of the size spectra declined significantly over time (Fig. 7e), suggesting both shifts in size composition and reduction in overall linefish abundance.

The significant decline in the slopes for the South-Eastern Cape indicates a long-term shift in the size composition towards smaller fish (Table II). This could be both the result of decreasing abundance of larger fish of all species and the differential overexploitation of larger, long-lived species. For the whole Cape linefishery, both reasons for the decline seem to be appropriate, because the mean size (Table I) and abundance of smaller species such as carpenter and Roman *Chrysobelphus laticeps* was substantially reduced at the same time as larger species such as seventyfour, kob and geelbek were being overexploited (Griffiths 2000). On the other hand, the significant decline in the heights of the size spectra over time indicates an overall reduction in the abundance of all linefish in the landings. The negative slope of the size spectrum was directly proportional to the level of exploitation (Gislason and Rice 1998, Shin and Cury in press). The work of Bianchi *et al.* (2000, 2001), which synthesizes size spectra and dominance structures of different marine ecosystems, adds further support to the findings of Gislason and Rice (1998).

For the cool-temperate Western Cape, the size spectrum was strongly influenced by the abundant snoek, and the slope did not change with time. Snoek are important socio-economically and, as a pelagic predator, are also ecologically important (Griffiths 2002) in the Cape. Owing to their unpredictable longshore and offshore migrations and their *r*-selected life-history traits, such as fast growth, early maturity and relatively short life (Attwood and Farquhar 1999, Griffiths 2002), as a population they are less vulnerable to overexploitation than other linefish species. The trend for the Western Cape provides a good example of how the size spectrum can easily be influenced by a dominant species. If the dominant species is large, the slope of the size spectrum will tend to be shallower and may even become positive. This can mask changes in the size composition of the other species with changes in fishing effort.

The heights of the spectra reflect overall abundance; heights for the whole Cape and for all regions except

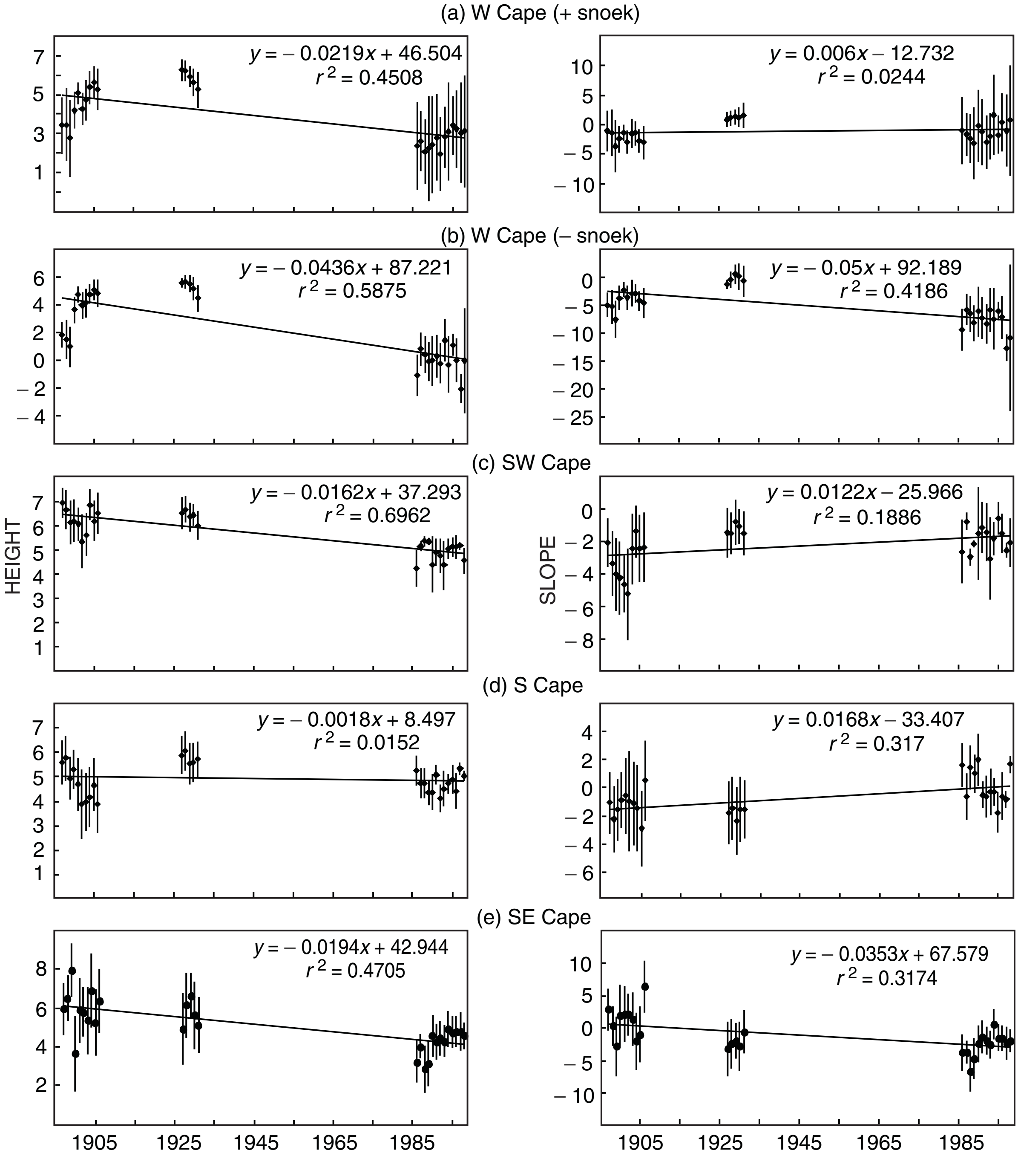

Fig. 7: Long-term trends in the heights and slopes of size spectra in the four regions of the Cape: (a) Western Cape with snoek, (b) Western Cape without snoek, (c) South-Western Cape, (d) Southern Cape and (e) South-Eastern Cape. Error bars denote ± 2 *SE* ($n = 28$)

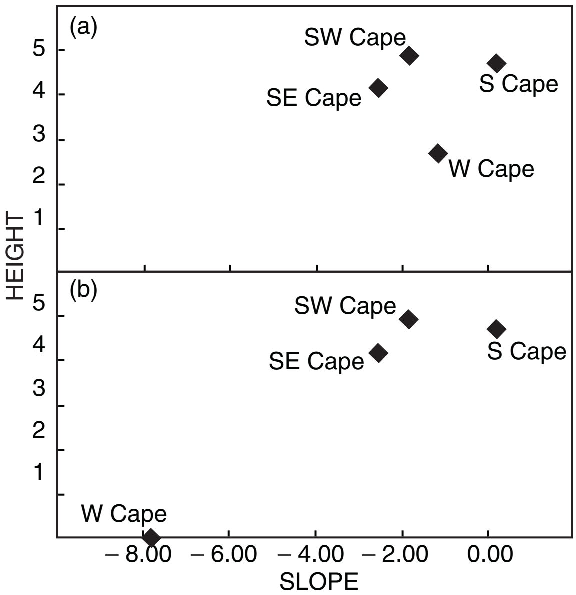

Fig. 8: Regional comparison of size spectra using the slope and height in the modern period (1986–1998), (a) including snoek and (b) excluding snoek

the Southern Cape, decreased significantly over the 100 years, suggesting an overall reduction in abundance of all size-classes. The substantial steepening of the slope of the South-Eastern and Western Cape (excluding snoek) was accompanied by a significant decrease in the height. Therefore, both size structure and overall abundance of linefish have been negatively impacted by heavy fishing, as suggested by Griffiths (2000).

Regional comparison

The mean heights of the modern size spectra of the four regions are plotted against the corresponding slopes in Figure 8. There were distinct differences in the size spectra of the four regions, and the position of the Western Cape on the plot appeared to depend on the inclusion or exclusion of snoek for the analysis. If snoek was included, all four regions grouped together, but its exclusion resulted in a dramatic shift of the position of the Western Cape; the other regions remained in their original positions (Fig. 8).

The pattern in the average slopes and heights for the regions reflected the size composition and overall abundance of linefish. The shallow slope for the Southern Cape suggests relatively abundant larger fish, likely the dominant species (carpenter, silver kob, yellowtail, snoek and geelbek) because all except carpenter are large (see Table I). The Western Cape had the second shallowest slope, mainly because of snoek. There was a relatively steep slope for the South-Western Cape, indicating that smaller fish dominated the catch there. The South-Eastern Cape had the steepest slope, which implies a shift from large to small fish. Catches there are dominated mainly by small carpenter and panga and, to a lesser extent, by silver kob.

Slopes and heights of the fish size spectra of different ecosystems worldwide were compared by Bianchi *et al*. (2000, 2001). Both studies showed distinct differences in size composition among the different ecosystems and between the shelf and slope assemblages; they were aligned almost linearly on the plot of the slope against height. Bianchi and her co-authors pointed out that this trend was partly a reflection of the correlation between slope and height, steeper slopes corresponding to larger heights. In the present study, the four regions were not aligned linearly, possibly because of the removal of the correlation between slopes and heights.

Dominance

The K-dominance curves for the four regions are depicted in Figure 9. There were considerable changes in dominance between the 1890s and 1990s, but the responses of the cool-temperate and warm-temperate regions were opposite. Catches from the cool-temperate Western Cape have tended to shift with time towards the catch being dominated by a few species; snoek contributed nearly 90% of the catch, followed by hottentot. The region also had a low species diversity historically compared with the other regions; whereas the other species were depleted, there was a tendency for the system to be dominated by a single (fast-growing) species. Similar patterns of increasing dominance in temperate regions have been reported for the north-western North Sea (Greenstreet and Hall 1996), southern North Sea (Rijnsdorp *et al*. 1996) and the Scotian Shelf and off Portugal (Bianchi *et al*. 2000). For the South-Western Cape, there has not been much change in the dominance plot between the historical and recent periods, but there has been a change in the dominant species from geelbek to snoek recently (Griffiths 2000). The more species-diverse, warm-temperate regions (Southern and South-Eastern Cape) demonstrated a reversal of the trend from the catch being historically dominated by few species towards a more evenly spread modern catch (1986–1998). This is because the preferred stocks in the regions,

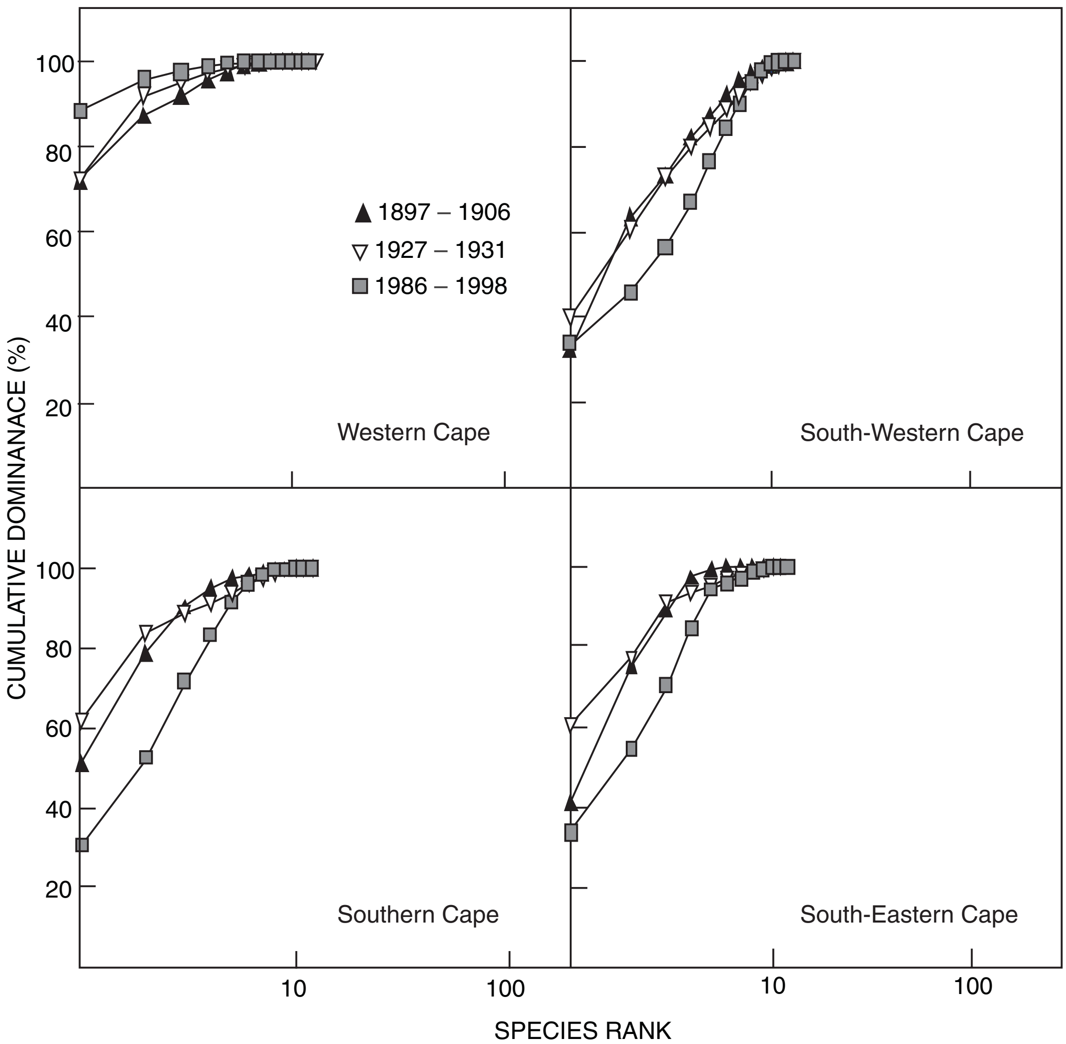

Fig. 9: K-dominance plots of species biomasses for all four regions for the three periods analysed

geelbek and silver kob, were depleted, resulting in fishers tending to target other, less-preferred species (Griffiths 2000). Bianchi *et al.* (2000) found the same pattern of decreasing dominance in tropical regions (Ghana, Campeche Bank and Sofala Bank). This may be explained by life-history traits, a relatively higher diversity, and the fact that most species are associated with rocky reefs. Such species are usually relatively long-lived, k-selected species with restricted ranges. When a fish community dominated by k-selected species is heavily fished, abundance and productivity will be too low to cope with fishing pressure, so dominance will tend to decrease. For the South-Eastern Cape, Griffiths (2000) showed that the linefishery was historically dominated by geelbek, followed by silver kob and seventyfour, all of which are k-selected and slow-growing. The formerly dominant species have now been overexploited, so the catch tends to be dominated now by the smaller carpenter, and the level of overall dominance has decreased.

CONCLUSIONS

Catch and effort in the linefishery have increased several-fold over the past 100 years off the Cape. The aggregate *cpue* declined to <20% of its level in the 1890s. However, this is a very conservative estimate, because the estimates of the effort presented here do not take cognizance of major technological improvement in the fishery (e.g. motorization, echo-sounding, satellite positioning). This aggregate analysis also fails to take into account changes in catch composition and size.

Multivariate analysis showed the combined effect of the changes in *cpue* for all 12 linefish species considered, confirming the conventional catch-and-effort analysis and showing that there was relatively little change in catch rate and catch composition from 1900 to the 1930s. However, there was a major change between 1930 and 1980, demonstrating a substantial change in abundance of most species, and corresponding with the large increase in fishing effort up to the 1980s. Previous studies on the effects of heavy fishing on fish assemblages have shown that changes in the catch composition often reflect changes in the assemblage considered (Gulland 1987, Pinnegar *et al.* 2002).

There was a minor (marginally non-significant) change in the overall mean length of the pooled catch in all four regions and species. The gentle trend in declining overall mean length is attributed to the masking effects of the dominant snoek and to a switch in target towards yellowtail more recently. When snoek were excluded from the analysis or when regions were analysed separately (both not shown), the declines in overall mean length over the 100 year period are significant. Table I demonstrates the responses to heavy fishing pressure that would be expected: in seven of the 12 species considered, the mean length of fish declined substantially.

Analysis of the combined distribution of fish sizes of the 12 species in logarithmic size-classes was depicted in size spectra, summarized by the twin statistics of slope and height of the log-linear regression (Table II). Slopes of the spectra of some regions became significantly more negative recently, showing that the modern linefish catch has fewer large fish and relatively more small ones than there used to be, in spite of present-day minimum size regulations. Furthermore, the linefish assemblage changes that are implied by changes in catch composition were different in the four regions. The cool-temperate regions differed from the warm-temperate ones, particularly with regard to the inclusion or exclusion of snoek. Inclusion of snoek gave the size spectrum of the cool-temperate regions a shallower slope. The height of the size spectrum reflects overall fish abundance (Daan *et al.* 2003). This showed declines in overall abundance of the fish assemblages over the past 100 years in all four regions, with statistically significant declines in all but one region (Table II).

Dominance curves reflected the distribution of biomasses among species. These were also affected by the inclusion or exclusion of dominant species such as snoek. The cool, upwelling-influenced Western Cape showed a trend towards increasing dominance in the recent period, but the warm-temperate regions showed decreased dominance with increasing fishing pressure. This accords with the work of Bianchi *et al.* (2000) for warm-tropical regions with increased fishing pressure. The use of K-dominance curves in assessing the effects of fishing may still need some refinement to analyse the direction of responses of the fish communities to disturbance.

The present study shows that traditional analyses of overall catch rates are enhanced by multivariate analysis of the combined effects of fishing on all species, analysis of mean size, the slope and height of the size spectrum and dominance curves. These analyses are complementary and need to be assessed together with information on the life-history traits of the species, changes in target species and other related aspects such as spatial considerations (Pequerie *et al*. 2004, Drapeau *et al*. 2004). Taking into account the fact that most linefish considered in this study are predators at different trophic levels, overexploitation and decreases in the abundance of larger fish are likely to have trophodynamic implications for the functioning of the whole ecosystem.

ACKNOWLEDGEMENTS

We thank Yunne Shin and Gabriella Bianchi for constructive comments on an early version of the manuscript. Henrik Gislason and other members of SCOR Working Group 119 on Quantitative Ecosystem Indicators for Fisheries Management are thanked for constructive discussion of the original version presented at the first meeting of the Working Group. Tony van Dalsen is thanked for his help with the artwork. We also thank the Eritrean Human Resource Development Programme of the World Bank for funding for DY.

LITERATURE CITED

ATTWOOD, C. G. and B. A. BENNETT 1995 — A procedure for setting daily bag limits on the recreational shore-fishery of the South-Western Cape, South Africa. *S. Afr. J. mar. Sci.* **15**: 241–251.

ATTWOOD, C. D. and M. FARQUHAR 1999 — Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. *S. Afr. J. mar. Sci*. **21**: 415–432.

BIANCHI, G., GISLASON, H., GRAHAM, K., HILL, L., JIN, X., KORANTENG, K., MANICKCHAND-HEILEMAN, S., PAYA, I., SAINSBURY, K., SANCHEZ, F. and K. ZWANENBURG 2000 — Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. mar. Sci.* **57**: 558–571.

BIANCHI, G., HAMUKUAYA, H. and O. ALVHEIM 2001 — On the dynamics of demersal fish assemblages off Namibia in the 1990s. *S. Afr. J. mar. Sci.* **23**: 419–428.

BORGMANN, U. 1987 — Models on the slope of, and biomass flow up, the biomass size spectrum. *Can. J. Fish. aquat. Sci.* **44**: 136–140.

BOUDREAU, P. R. and L. E. DICKIE 1992 — Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. aquat. Sci.* **49**: 1528–1538.

BRANCH, G. [M.] and M. [L.] BRANCH 1981 — *The Living Shores of Southern Africa*. Cape Town; Struik: 272 pp. + 60 pp. Plates.

BROUWER, S. L., MANN, B. Q., LAMBERTH, S. J., SAUER, W. H. H. and C. ERASMUS 1997 — A survey of the South African shore-angling fishery. *S. Afr. J. mar. Sci.* **18**: 165–177.

CLARKE, K. R. 1990 — Comparisons of dominance curves. *J. expl mar. Biol. Ecol.* **138**: 143–157.

CLARKE, K. R. and R. N. GORLEY 2001 — *PRIMER v5: User Manual/Tutorial*. PRIMER-E Ltd: 91 pp.

CLARKE, K. R. and R. M. WARWICK 1994 — *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Plymouth; Plymouth Marine Laboratory: 144 pp.

DAAN, N., GISLASON, H., POPE, J. G. and J. RICE 2003 — Changes in the North Sea fish community: evidence of indirect effects of fishing. *ICES Doc.* **CM 2003/N 10**: 12 pp.

DRAPEAU, L., PECQUERIE, L., FRÉON, P. and L. J. SHANNON 2004 — Quantification and representation of potential spatial interactions in the southern Benguela ecosystem. 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**: 141–159.

FAHEY, F. J., RUSSOUW, G. S. H., STALS, A. J. and D. H. STEYN 1934 — The fishing industry, board of trade and industries **180**: Pretoria; Government Printer: 90 pp + 1 chart.

FIELD, J. G., CLARKE, K. R. and R. M. WARWICK 1982 — A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* **8**(1): 37–52.

FOGARTY, M. J. and S. A. MURAWSKI 1998 — Large scale disturbance and structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* **8**: s6–s22.

FROMENTIN, J-M. and A. FONTENEAU 2001 — Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fish. Res.* **53**: 133–150.

GILCHRIST, J. D. F. 1898 — *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1897*. Cape Town; Government Printer: 148 pp. + 1 Chart.

GILCHRIST, J. D. F. 1899 — *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1898*. Cape Town; Government Printer: 362 pp. + 21 Charts.

GILCHRIST, J. D. F. 1900 — *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1899*. Cape Town; Government Printer: 124 pp.

GILCHRIST, J. D. F. 1901 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1900*. Cape Town; Government Printer: 180 pp. + 3 Charts.

GILCHRIST, J. D. F. 1902 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1901*. Cape Town; Government Printer: 104 pp. + 2 Charts.

GILCHRIST, J. D. F. 1903 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1902*. Cape Town; Government Printer: 283 pp. + 3 Charts.

GILCHRIST, J. D. F. 1904 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1903*. Cape Town; Government Printer: 194 pp.

GILCHRIST, J. D. F. 1906 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1904*. Cape Town; Government Printer: 40 pp.

GILCHRIST, J. D. F. 1907 — *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1906*. Cape Town; Government Printer: 44 pp.

GISLASON, H. and J. C. RICE 1998 — Modeling the response of size and diversity spectra of fish assemblages to changes in exploitation. *ICES J. mar. Sci.* **55**: 362–370.

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.

GREENSTREET, S. P. R. and S. J. HALL 1996 — Fishing and the ground-fish assemblage structure in the Northwestern North Sea: an analysis of long-term and spatial trends. *J. Anim. Ecol.* **65**: 577–598.

GRIFFITHS, M. H. 1997a — Management of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on per-recruit models. *S. Afr. J. mar. Sci.* **18**: 213–228.

GRIFFITHS, M. H. 1997b — The application of per-recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. *Fish. Res.* **30**: 103–115.

GRIFFITHS, M. H. 2000 — Long-trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *S. Afr. J. mar. Sci.* **22**: 81–110.

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.

GRIFFITHS, M. H. and T. HECHT 1995 — On the life-history of *Atractoscion aequidens*, a migratory sciaenid off the east coast of southern Africa. *J. Fish Biol.* **47**: 962–985.

GRIFFITHS, M. H. and S. J. LAMBERTH 2002 — Evaluating the marine recreational fishery in South Africa. In *Recreational Fisheries: Ecological, Economic and Social Evaluation*. Pitcher, T. J. and C. E. Hollingworth (Eds). London; Blackwell: 227–251.

GRIFFITHS, M. H., WILKE, C., PENNEY, A. J. and Y. MELO 2002 — Life history of white stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) off South Africa. *S. Afr. J. mar. Sci.* **24**: 281–300.

GULLAND, J. A. 1987 — The effect of fishing on community structure. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 839–849.

HAEDRICH, R. L. and S. M. BARNES 1997 — Changes over time of the size structure in an exploited shelf fish community. *Fish. Res.* **31**: 229–239.

JENNINGS, S. and M. J. KAISER 1998 — The effects of fishing on marine ecosystems. *Adv. mar. Biol.* **34**: 201–251.

JENNINGS, S., GREENSTREET, S. P. R. and J. D. REYNOLDS 1999 — Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**: 617–627.

JUKIC-PELADIC, S., VRGOC, N., KRSTULOVIC-SIFNER, S., PICCINETTI, C., PICCINETTI-MANFRIN, G., MARANO, G. and N. UNGARO 2001 — Long-term changes in demersal resources of the Adriatic Sea: comparison between trawl surveys carried out in 1948 and 1998. *Fish. Res.* **53**: 95–104.

MANN, B. Q. (Ed.) 2000 — *Southern African Marine Linefish Status Reports. Spec. Publ. oceanogr. Res. Inst. S. Afr.* **7**: 257 pp.

MANSERGH, L., NICHOLSON, G. T. and R. A. LEIGH 1926 — Fishing Harbours Report (Parts 1–3), Department of Mines and Industries. Cape Town; Government Printer: 70 pp. + 36 Plates and 10 Charts.

MANSERGH, L., NICHOLSON, G. T. and R. A. LEIGH 1927 —

Fishing Harbours Report (Parts 4 and 5), Department of Mines and Industries. Cape Town; Government Printer: 85 pp. + 19 Plates and 8 Charts.

MANSERGH, L., NICHOLSON, G. T., LEIGH, R. A. and C. VON BONDE 1928 — Fishing Harbours Report (Parts 6 and 7), Department of Mines and Industries. Pretoria; Government Printer: 85 pp. + 19 Plates and 8 Charts.

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.

PINNEGAR, J. K., JENNINGS, S., O'BRIEN, C. M. and N. V. C. POLUNIN 2002 — Long-term changes in the trophic level of the Celtic Sea fish community and fish market distribution. *J. appl. Ecol*. **39**: 377–390.

RICE, J. C. 2000 — Evaluating fishery impacts using metrics of community structure. *ICES J. mar. Sci*. **57**: 682–688.

RICE, J. C. and H. GISLASON 1996 — Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J. mar. Sci*. **53**: 1214–1225.

RIJNSDORP, A. D., VAN LEEUWEN, P. I., DAAN. N. and H. J. L. HEESSEN 1996 — Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES J. mar. Sci*. **53**: 1054–1062.

SCHUMANN, E. H. 1987 — The coastal ocean off the east coast of South Africa. *Trans. R. Soc. S. Afr.* **46**(3): 215–228.

SHANNON, L. V. and G. NELSON 1996 — The Benguela: large scale features and processes and system variability. In *The South Atlantic: Present and Past Circulation*. Wefer, G., Berger, W. H., Siedler, G. and D. J. Webb (Eds). Berlin; Springer: 163–210.

SHIN, Y–J. and P. CURY 2004 — Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. aquat. Sci*. **61**: 414–431.

YEMANE, D., GRIFFITHS, M. H. and J. G. FIELD (in press) — Comparison of fish community size spectra and length frequencies and mean length. *Afr. J. mar. Sci.* **27**.

ZAR, J. H. 1999 — *Biostatistical Analysis*, 4th Ed. New Jersey; Prentice-Hall: 663 pp.