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LONG-TERM TRENDS IN THE ABUNDANCE AND COMMUNITY STRUCTURE OF COASTAL ZOOPLANKTON IN THE SOUTHERN BENGUELA SYSTEM, 1951–1996

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Long-term trends in the abundance and species composition of zooplankton are described. These trends are based on retrospective analysis of zooplankton samples collected in the St Helena Bay area off the South African west coast since the development of the pelagic fishery in the 1950s. Samples were selected from seven sampling programmes (1951–1967, 1974, 1978, 1983, 1984, 1987 and 1988–1996) that monitored the main commercial fishing grounds during peak recruitment (March–June). Abundance data are presented for size-based taxonomic groups, which include cyclopoid and small, medium and large calanoid copepods, cladocerans, euphausiids, amphipods, chaetognaths and pelagic tunicates. Despite discontinuity in the time-series and the use of different samplers, all taxa showed a significant long-term increase in their abundance by at least one order of magnitude between 1951 and 1996. Total zooplankton abundance increased from 4.2×10^3 to 7.2×10^5 ind·m^{-2} over the same period. Multiple regression analysis of the log-transformed data indicates size-based differential rates of increase in population levels among the crustacean size classes, with a maximum rate in cyclopoids (slope = 0.052) and a minimum rate in euphausiids (slope = 0.035). This resulted in a significant shift through time in the crustacean zooplankton community structure, which may reflect differential size-selective predation during periods of anchovy *Engraulis capensis* or sardine *Sardinops sagax* dominance. The observed long-term increase in zooplankton abundance could be a response to a long-term decrease in predation pressure following decreases in stocks of pelagic fish, which in turn could be caused by increased predation by top predators. Another mechanism contributing to the long-term increase in zooplankton is the observed long-term intensification of coastal upwelling, which could enhance primary and secondary production, and increase advective input of zooplankton populations into the study area and augment their retention.

The Canary Current system off the Iberian Peninsula and North-West Africa, the Humboldt Current system off western South America, the California Current system off the western United States, and the Benguela Current system off the west coast of southern Africa are the four major eastern boundary current regions. Each region is characterized by coastal upwelling as a result of equatorward wind stress (Parrish *et al.* 1983), and supports abundant valuable fishery resources (Bakun 1990). Whereas upwelling intensity in these productive regions has increased over the past four decades (Bakun 1990, Shannon *et al.* 1992), the yields of pelagic fish have shown large fluctuations (Lluch-Belda *et al.* 1989), with populations of certain species collapsing and being replaced by others. Whether such alternation of species results from exploitation causing the originally dominant species to decrease following competitive replacement, or from a change in environmental conditions causing a shift in species dominance, is not clear.

In the southern Benguela, the pelagic fishery off the south-west coast of South Africa was small but unrestricted prior to 1950. Thereafter various management measures were imposed, such as catch quotas, closed seasons and areas, minimum mesh sizes and limitations on fleet size, hold and processing capacities (Crawford *et al.* 1987). Yields of all pelagic species combined rose to >500 000 tons in 1967 and stabilized around 380 000 tons between 1968 and 1985 (Fig. 1a). In the 1950s, catches were dominated by adult sardine *Sardinops sagax* (Fig. 1b) and were largely restricted to the St Helena Bay area (Fig. 2), with peak availability between March and July. Adult fish moved to offshore spawning grounds in August/September (Crawford *et al.* 1987). Large fluctuations in the harvests of anchovy *Engraulis capensis* and sardine have subsequently been observed (Fig. 1b). As in other major upwelling systems, both species were never simultaneously abundant. Yields of sardine fell from >400 000 tons in 1961/62 to <100 000 tons after 1977. This collapse of sardine was followed by a rapid increase in the catches of anchovy (mainly

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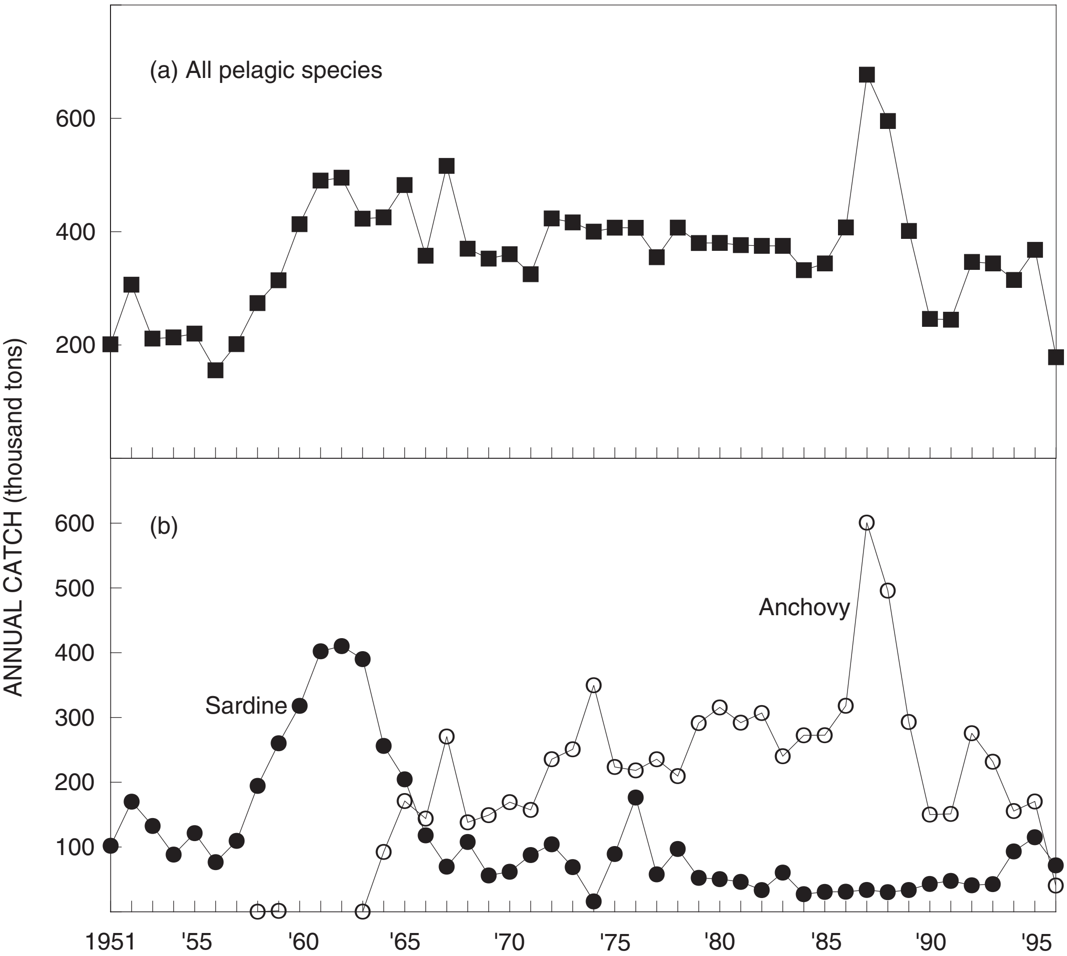

Fig. 1. Annual catches of (a) all pelagic species combined and (b) anchovy and sardine harvested by the South African pelagic fishery in the southern Benguela system between 1951 and 1996 (updated from Schülein *et al.* 1995)

juveniles from negligible levels prior to 1964, when a reduction in the minimum mesh size was introduced, to a peak harvest of 600 000 tons in 1987. Varying proportions (10–20%) of juvenile round herring *Etrumeus whiteheadi* and sardine were also caught during that period (Crawford *et al.* 1987). Thereafter, anchovy catches dropped rapidly to below 300 000 tons in 1989, reaching a minimum of <50 000 tons in 1996. Sardine catches increased steadily during the 1980s and 1990s to >100 000 tons in 1995. The factors responsible for such fluctuations and the shift in species dominance over the past 45 years are unknown (Crawford *et al.* 1987).

Many clupeioids possess two feeding modes, filter- and particulate feeding. Switches between these modes depend on the relative profitability of each mode (Van der Lingen 1994). Besides light intensity and the relative energetic costs associated with each feeding mode, this switch is also influenced by the size and concentration of the food particles, the predator-to-prey size ratio, and the relative densities of large and small prey (Van der Lingen 1994). Therefore, mode shifts to filtering, or conditions favouring filtering, are more common when fish are large relative to their prey, and when prey are small and densely aggregated. Conversely, when fish are

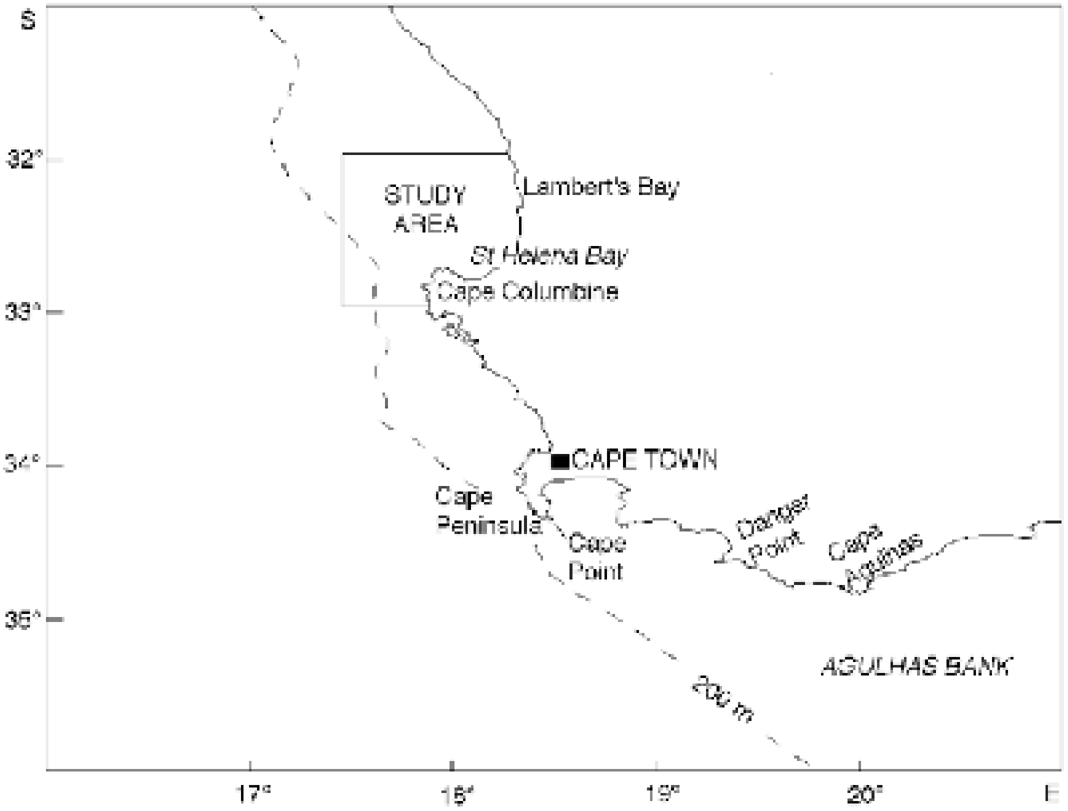

Fig. 2. Map of the south-western coast of South Africa showing the study area (1×1 degree square) where zooplankton samples were collected between 1951 and 1996

small relative to their prey, and prey are large and scarce, the feeding mode is likely to shift towards particulate feeding.

Laboratory feeding studies have shown that *S. sagax* is efficient at removing small particles such as microplankton and small copepods (Van der Lingen 1994), whereas anchovy prefer large particles such as large copepods and euphausiids (James 1987, James and Findlay 1989). This difference in clearance rates over the food size spectrum provides clear evidence of resource partitioning between the two species. Therefore, food environments dominated by small particles would favour sardine, whereas those consisting mainly of large prey items would favour anchovy.

This present paper explores two hypotheses: (i) that the structure of the pelagic foodweb in the southern Benguela has changed over the past 46 years, in terms of zooplankton abundance and species composition, and (ii) that periods of sardine and anchovy dominance coincide respectively with periods of small and large zooplankton-dominated communities off the west coast of South Africa, where these fish recruit to the purse-seine fishery every year between March and September (Crawford *et al.* 1987). These hypotheses are tested by retrospective analysis of zooplankton collections made since 1951 in the nearshore zone of St Helena Bay and Lambert's Bay (Fig. 2), where catch rates of anchovy and sardine are generally greatest (Crawford 1981).

MATERIAL AND METHODS

Data sources

Zooplankton samples selected for this study were collected since 1951, during seven sampling programmes.

Table I: Sampling time, strategy and gear characteristics for each sampling programme between 1951 and 1996. Sources of possible negative methodological bias are indicated with an asterisk (see text). Procedures for the estimation of copepod biomass, and their relevant data sources, are also given

Parameter	1951–1967	1974	1978	1983	1984	1987	1988–1996
Time							
Month	March – June	March and June	March – June	May	April and May	March – April	May or June
Day/night	Both	Both	Night-time	Both	Both (6-hourly)	Daytime *	Both
Strategy							
Grid type	Line of 3 stations	Line of 7–8 stations	3 lines of 6 stations	6 random stations	Box grid	Fixed station	2 lines of 5 stations
Target depth	100–0 m *	Bottom–0 m	100–0 m *	Bottom–0 m	Bottom–0 m	Bottom–0 m	Bottom–0 m
Gear							
Type	N70V	WP-2	Bongo	RMT-1x6	RMT-1x6	Plankton pump	Bongo
Towing mode	Vertical *	Vertical *	Oblique	Oblique	Oblique	Suction *	Vertical *
Mouth area (m^2)	0.384	0.255	0.255	1.000	1.000	0.005 *	0.255
Towing bridles	Present *	Present *	None	None	None	None	None
Mesh size (μm)	6 200/460/200 *	200	300 *	200	200	200 (sieve)	200
Flowmeter	None *	Calibrated N.I.O.	Calibrated digital	Calibrated digital	Calibrated digital	Helical vane water meter	Calibrated electronically
Copepod Biomass Method	Settled volume	Dry mass→Wet mass	Dry mass→Wet mass	Wet mass	Dry mass→Wet mass	Wet mass	Abundance x individual body mass
Source	This study	Hutchings 1988, Verheye *et al*. 1991	Pillar 1986	Verheye and Hutchings 1988	Verheye unpublished data Stuart and Verheye 1991	Verheye 1991	SF unpublished data

These are:

(i) the monthly "Cape Routine" and "Southern Routine" surveys (1951–1967);
(ii) four quarterly "West Coast Monitoring Cruises" between Cape Columbine and the Cape Peninsula (1974);
(iii) monthly surveys of the "Cape Egg and Larva Programme" (CELP), (August 1977–August 1978);
(iv) the first South African hydro-acoustic "Anchovy Recruit Biomass" survey (May 1983);
(v) two pelagic fish "Shoal Ecology" cruises (April and May 1984);
(vi) a 27-day "Anchor Station" time-series study (March–April 1987) and;
(vii) nine annual hydro-acoustic "Pelagic Recruit Biomass" surveys (May or June 1988–1996).

In addition to zooplankton, surface temperature and salinity were measured at each station.

The selection of samples from the above surveys was based on three criteria to minimize bias and allow meaningful comparison between the datasets. First, only samples collected between 31°50′S (north of Lambert's Bay) and 32°50′S (Cape Columbine), the centre of the recruitment and main commercial pelagic fishing grounds on the West Coast, were considered (Fig. 2). This area is where zooplankton has been sampled most intensively since the development of the pelagic fishery in the 1950s. Second, the selected stations were confined to within 52 miles of the coast, representing the most productive region on the continental shelf in the area (Mitchell-Innes and Walker 1991). Third, only samples collected between March and June, the peak recruitment period for anchovy (although sardine recruit over a longer period), were included in the analyses.

The sampling times, strategies and gear used for each individual dataset are summarized in Table I. During the period 1951–1967, zooplankton samples were collected with a vertically towed N70V ring net (internal diameter; 70 cm). Similar to the WP-2 net used in 1974, the N70V net has three towing bridles, whereas the mouths of the other samplers were bridle-free samplers are unobstructed. The 135-cm long, 200-μm nylon mesh filtering section of the N70V net is preceded by a 53-cm section made of 6.2-mm nylon netting material, followed by a 96-cm section of 460-μm nylon mesh. Because no flowmeter was used in the N70V net, the volume of water filtered was calculated from knowledge of the mouth area of the net and the maximum sampling depth. Hauled vertically at a constant speed of 1 m·s^{-1}, the absolute values of tow duration and sampling depth should be equal. If this was not the case, and the absolute value of duration exceeded that of depth, a correction factor, expressed as the ratio of observed:theoretical sampling time, was incorporated into the calculation of volume filtered.

Except for the CELP surveys, when a 300-μm mesh sampler was used, a 200-μm mesh was common to all samplers (Table I). Therefore, to compensate for this larger mesh, a correction factor of ×1.85 (Pillar 1984) was used in the calculation of total copepod biomass and numerical abundances of the smallest zooplankters (cladocerans, cyclopoids and small calanoids), which were undersampled during the CELP surveys.

Because sampling was usually confined to the broad shelf region in the St Helena Bay area (Fig. 2), samples were mostly collected in water of <200 m deep. Whereas target depths were restricted to the upper 100 m during the 1951–1967 and 1978 surveys, the entire water column was sampled on all other cruises (Table I). However, during 1974, when samples were collected off Cape Columbine, where the shelf is comparatively narrow (Fig. 2), sampling depths were sometimes >200 m (max. 265 m).

In most instances, samples collected by day and by night were analysed. However, only night-time samples were analyzed from the 1978 CELP collections (see Pillar 1986), whereas only midday collections were used from the Anchor Station time-series in 1987 (see Verheye 1991).

Sample analysis

The biomass of copepods in the N70V collections of 1951–1967 was determined as the settled volume (mℓ·m^{-2}) of a sample after removal of all large gelatinous zooplankton (including salps) and macrozooplankters (euphausiids and amphipods). It was assumed that 1 mℓ settled volume is equivalent to 1 g wet mass. All other estimates of copepod biomass were extracted from the literature or unpublished data reports (Table I). In these studies, the wet mass of copepods was determined either directly (1983, 1987), or indirectly from either dry mass measurements (1974, 1978, 1984), assuming a wet:dry mass ratio of 10 (Lovegrove 1966, Parsons *et al*. 1977), or from the product of numerical abundance and specific individual body masses (1988–1996). All wet masses were standardized to g·m^{-2} from knowledge of the volume of water filtered and the maximum sampling depth.

The protocol used in the retrospective analysis of samples to determine the numerical abundance of zooplankton taxa was consistent throughout the time-series. Briefly, macrozooplankters (juvenile and adult euphausiids and hyperiid amphipods) and large (>5mm diameter) gelatinous species such as salps,

Table II: List of species identified and enumerated in the samples collected during the 1951–1996 time-series. The species were classified into broad taxonomic groups. Crustacean zooplankton were further categorized into size-classes based on total length (*TL*) of individuals

Species	Taxonomic group (Size-class)
Podon sp. *Penilia* sp. *Evadne* sp.	Cladocerans (900–1 000 µm *TL*)
Oithona spp. *Oncaea* spp.	Cyclopoid copepods (<900 µm *TL*)
Paracalanus parvus *Ctenocalanus vanus* *Clausocalanus scotii* C1–C4 stages of larger calanoids	Small calanoid copepods (900–1 000 µm *TL*)
Centropages brachiatus (™, ¢, C5) *C. chierchiae* (™, ¢, C5) *Pleuromamma* sp. (™, ¢, C5)	Medium calanoid copepods (1 000–2 000 µm *TL*)
Metridia lucens (™, ¢, C5) *Calanoides carinatus* (™, ¢, C5) *Calanus agulhensis* (™, ¢, C5) Other less common species, including *Rhincalanus nasutus* (™, ¢, C5)	Large calanoid copepods (2 000–5 000 µm *TL*)
Euphausia lucens (all stages) *Nyctiphanes capensis* (all stages) Unidentified euphausiids	Euphausiids (>5 000 µm *TL*)
Themisto gaudichaudi (all stages)	Amphipods (>5 000 µm *TL*)
Sagitta friderici *S. minima* Unidentified chaetognaths	Chaetognaths
Doliolids *Oikopleura* sp.	Tunicates

ctenophores and medusae were removed from each sample and counted seperately. The remainder was allowed to settle in a measuring cylinder for 24 h, after which the sample was diluted to ×10 the settled volume of the zooplankton. After gentle agitation of the diluted sample to obtain a homogeneous distribution of the zooplankters in the cylinder, aliquots of 2 ml were drawn bt means of a modified wide-bore Stempel pipette, and all individuals were identified and enumerated under a dissecting microscope. For the purpose of this study, species were classified into broad taxonomic groups (Table II). Among the large copepod species, adult males and females, and subadults (copepodite C5) were counted separately and classified as "large calanoids" or "medium calanoids". Abundances of their young stages (C1–C4) were pooled and classified as "small calanoids", together with a number of small calanoid species of which only the older stages are retained on a 200-µm mesh net (Table II). All counts were standardized to number·m^2 from a knowledge of the volume of water filtered and the maximum sampling depth.

Statistical analysis

All biomass and numerical abundance data were log-transformed ($\text{Log}_{10}[x+1]$) to reduce heteroscedasticity and improve normality. A prior test of parallelism of regression slopes (StatSoft 1996) of the abundance of the various zooplankton taxa against year showed that the slopes were significantly different ($F = 16.83$, $p < 0.001$, $n = 2037$). Therefore, multiple regressions for each taxon were computed with year, month, distance from the coast, surface temperature and surface salinity as the independent variables. Although, theoretically, a time-series approach could have been used, a multiple regression model was considered more appropriate, for the following reasons. First, the objective was to analyse the trend (year effect) and not explicitly to determine the seasonality. Second, the Durbin-Watson statistic, used to assess serial dependency, was non-significant for all of the dependent variables, suggesting that a time-series approach was unnecessary. Third, because of the unbalanced nature of the sample coverage both spatially and temporally, additional descriptor variables such as distance from the coast (catego-rized into three distance intervals: <5, 5–23, and >23 miles) and month (March, April, May and June) were easily included in the regression model as Boolean variables. Fourth, despite the 20-year discontinuity between the 1951–1967 and the 1987–1996 datasets, they could be combined into a single regression if the slopes of the two time-series were not significantly different. To accomplish this, the Boolean variable "period" was included, which assumed a value of 0 for the first time-series and 1 for the second. The year × period interaction was also included. If this interaction was significant, then the two datasets had different slopes, and separate multiple regression analyses were performed on each dataset. No other interactions were included in the model. Non-significant variables ($p > 0.05$) were removed from the full model in a backward stepwise process until the simplest model containing only significant variables was obtained. The final regression equation was used to compute differences in the dependent variable between the beginning and end of the time-series.

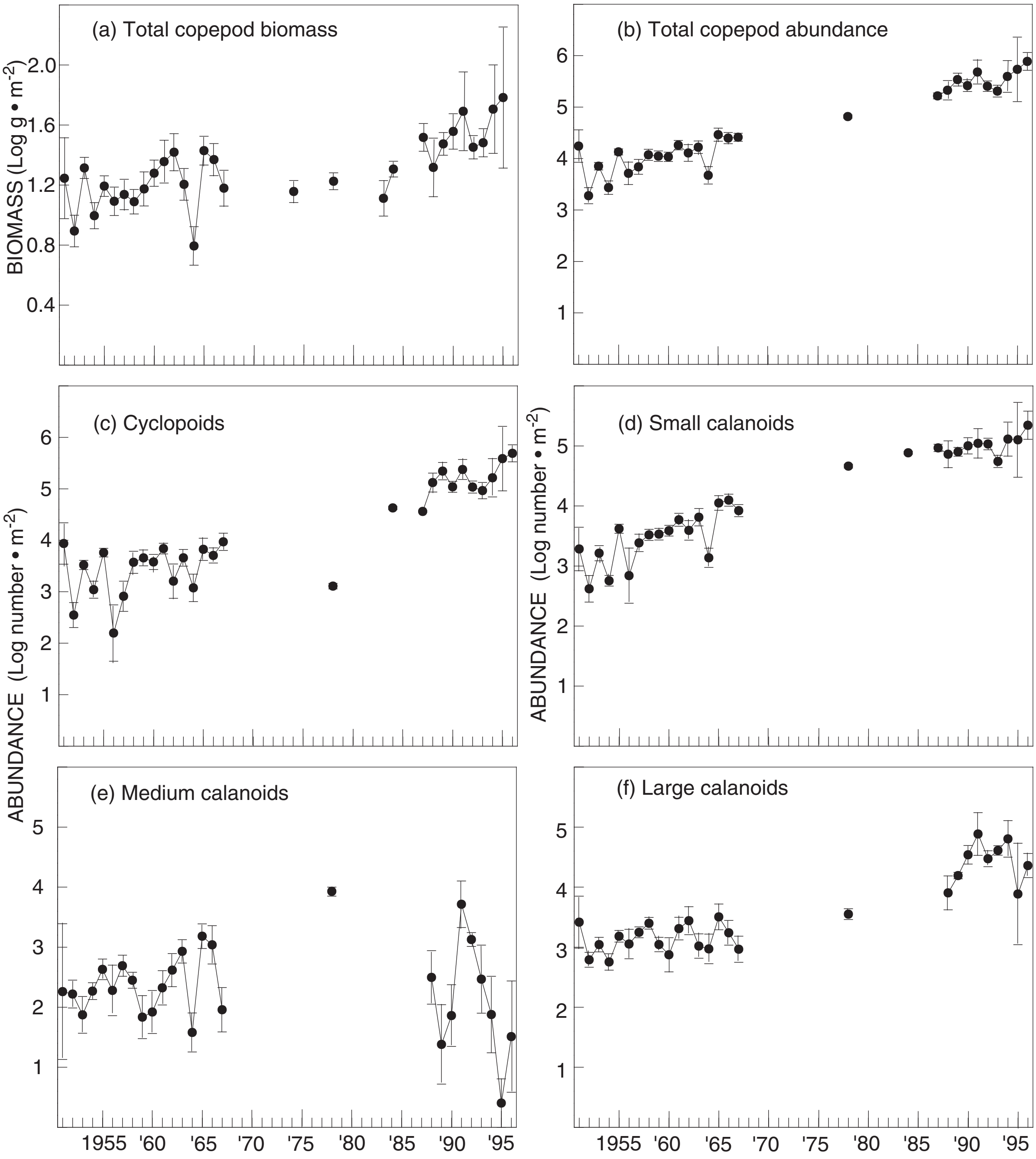

Fig. 3. Time-series of annual means of (a) the wet mass biomass and (b) the abundance of all copepods, and the abundance of (c) cyclopoids and (d) small, (e) medium and (f) large calanoid copepods between 1951 and 1996. All data were log-transformed ($Log_{10}[x+1]$); error bars are ±1 *SE.* Note the position of the data points falling in the 20-year gap between the 1951–1967 and 1987–1996 time-series

Table III: Results of stepwise multiple regression analyses of long-term changes in log-transformed biomass and abundances of zooplankton taxa during the period 1951–1996, with year, month, distance offshore (Dist), surface temperature (Temp) and surface salinity (Sal) as independent variables. Where a significant difference ($p < 0.05$) in slopes (year) between the 1951–1967 and 1987–1996 time-series was detected, multiple regression analyses were performed on these time-series separately. In all cases, only the slope for year is given, whereas for the other independent variables, + and – indicate significant positive and negative slopes respectively. The model was used to compute differences between start and end of the time-series (see text for further details)

Dependent variable	r^2	significance	Y-int.	Slope (Year)	Slope (Month)	Slope (Dist)	Slope (Temp)	Slope (Sal)	*n*	Difference start-end
Biomass: Copepods										
1951–1967	0.21	***	0.740	0.012	–	–	*ns*	*ns*	172	0.200
1987–1996	0.21	***	–3.520	0.051	*ns*	+	*ns*	*ns*	81	0.458
Abundance										
Copepods: all spp.	0.66	***	1.251	0.047	*ns*	*ns*	*ns*	*ns*	244	2.094
– Cyclopoids	0.50	***	0.292	0.052	*ns*	*ns*	*ns*	*ns*	254	2.356
– Small calanoids	0.63	***	0.556	0.049	*ns*	*ns*	*ns*	*ns*	253	2.217
– Medium calanoids										
1951–1967	0.01	*ns*	2.211	*ns*	*ns*	*ns*	*ns*	*ns*	173	–
1987–1996	0.12	**	1.971	*ns*	*ns*	+	*ns*	*ns*	62	–
– Large calanoids	0.39	***	0.862	0.038	*ns*	*ns*	*ns*	*ns*	244	1.711
Cladocerans	0.32	***	25.542	0.037	+	*ns*	*ns*	–	175	1.553
Euphausiids	0.14	***	–0.255	0.035	*ns*	*ns*	*ns*	*ns*	209	1.595
Amphipods										
1951–1967	0.09	***	*ns*	0.041	–	*ns*	–	*ns*	171	0.658
1987–1996	0.16	*	*ns*	0.223	*ns*	*ns*	–	*ns*	28	2.003
Chaetognaths										
1951–1967	0.15	***	–0.186	0.072	*ns*	*ns*	–	*ns*	171	1.200
1987–1996	0.12	*ns*	2.070	*ns*	*ns*	+	*ns*	*ns*	28	–
Tunicates	0.34	***	–2.865	0.049	+	+	*ns*	*ns*	211	2.168
Total zooplankton	0.64	***	1.092	0.050	*ns*	*ns*	*ns*	*ns*	203	2.234
Total crustaceans	0.57	***	0.996	0.051	*ns*	*ns*	*ns*	*ns*	204	2.274

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
ns = not significant ($p > 0.05$)
n = number of samples included in the final model

To analyse changes in the zooplankton community structure, annual mean abundances of the major size-based taxonomic groups (listed in Table II) were computed from the untransformed abundances (number·m^{-2}), irrespective of month or distance from the coast. These means were expressed as percentages of the corresponding annual mean total zooplankton abundance. Because chaetognaths and tunicates generally contributed very little (<3% by number) to total zooplankton abundance and are generally not important in the diet of pelagic fish (James 1987, C. D. Van der Lingen, Sea Fisheries, pers. comm.), only the crustacean fraction of the zooplankton was considered in the analysis. In an attempt to relate changes in the taxonomic composition of the crustacean zooplankton to fluctuations in the abundance of anchovy and sardine (Hypothesis 2), the annual mean percentage proportions were averaged over the periods 1951–1967 (sardine-dominated) and 1988–1996 (anchovy-dominated). Differences in the mean relative abundances between the two periods were tested for each taxon using non-parametric Mann Whitney U-tests (Zar 1984).

RESULTS

Long-term changes in zooplankton abundance

Figures 3 and 4 show long-term trends in the mean (±1 *SE*) copepod biomass and abundance of copepods, cladocerans, euphausiids, amphipods, chaetognaths and pelagic tunicates between 1951 and 1996. Results of the multiple regression analyses are summarized in Table III. Over the past 46 years, the abundance of total zooplankton increased by more than two orders of magnitude, from 4 205·m^{-2} in 1951 to 720 579·m^{-2} in 1996. Copepod biomass (Fig. 3a) shows a significant 10-fold increase from 5.1 g·m^{-2} in 1951 to 55.0 g·m^{-2} in 1996, whereas their total abundance (Fig. 3b) increased significantly by two orders of magnitude

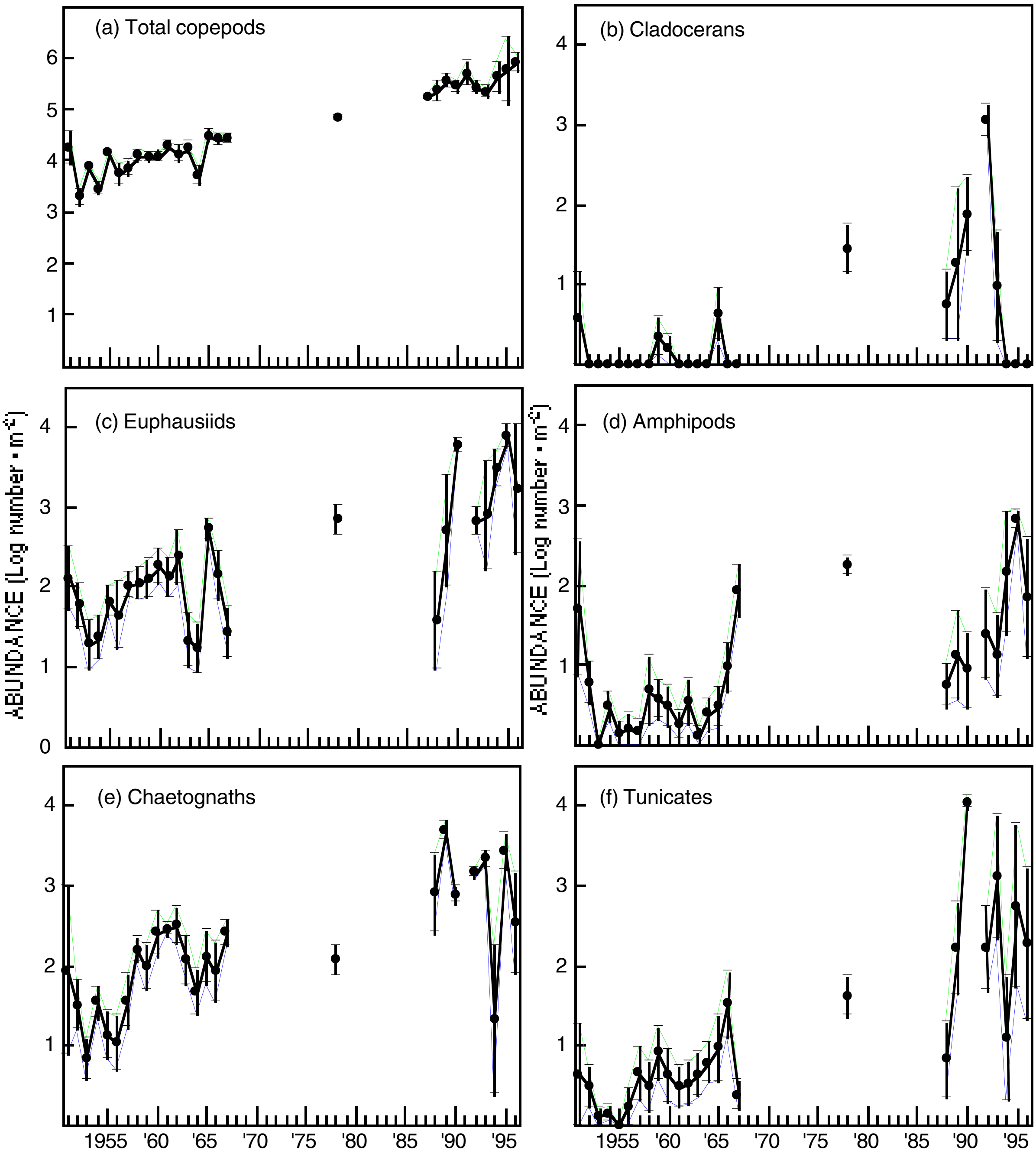

Fig. 4. Time-series of the annual mean abundance of (a) copepods, (b) cladocerans, (c) euphausiids, (d) amphipods, (e) chaetognaths and (f) pelagic tunicates during the period 1951–1996. All data were log-transformed ($Log_{10}[x+1]$); error bars are ±1 *SE*

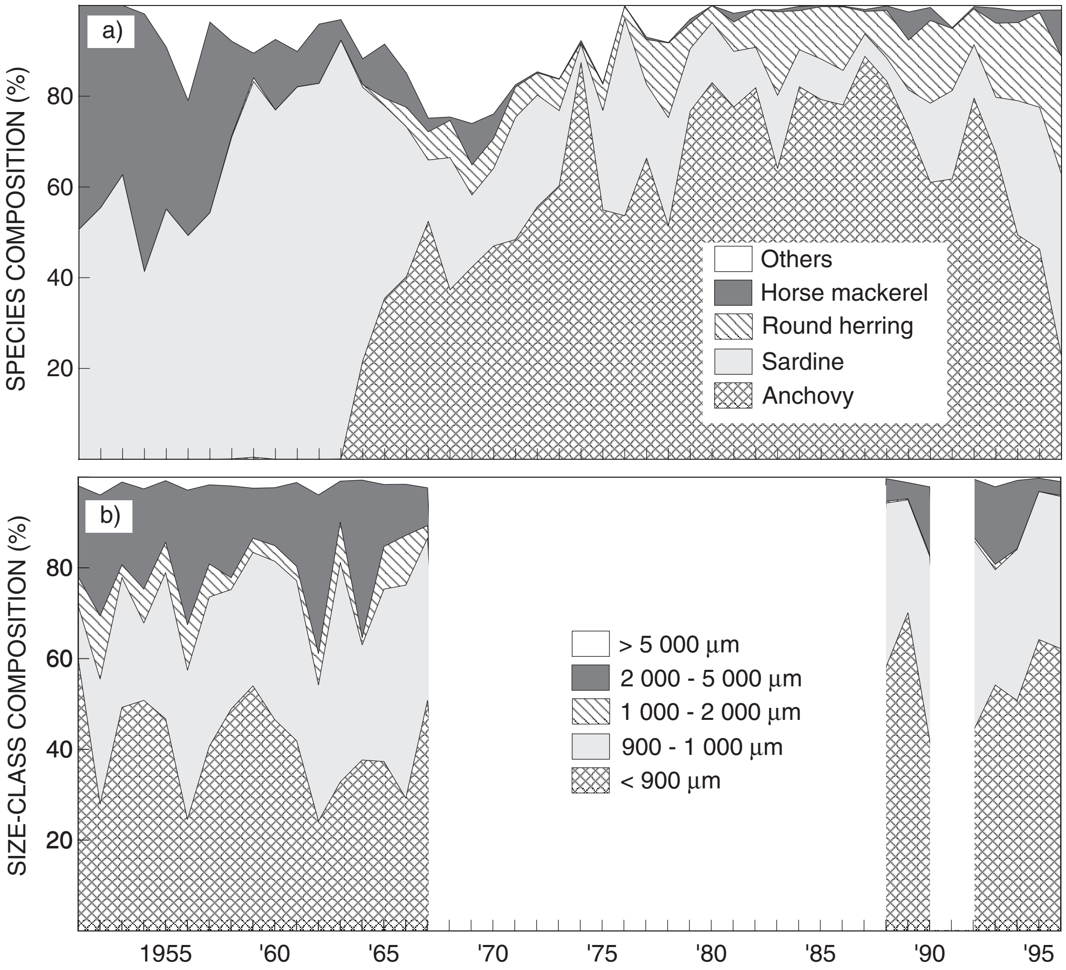

Fig. 5. Time-series of (a) the species composition of pelagic fish catches, expressed as a percentage of the total annual catches shown in Figure 1a, and (b) the percentage size composition of the crustacean zooplankton expressed in terms of numbers, during the period 1951–1996

(Table III). This is a consequence of the smaller copepods such as cyclopoids and small calanoids increasing in numbers at a greater rate (slopes: 0.052 and $0.049\cdot\text{year}^{-1}$ respectively) than large calanoids ($0.038\cdot\text{year}^{-1}$) over the entire time-series (Fig. 3c–f, Table III).

Copepods increased in number at a similar rate (slope = $0.047\cdot\text{year}^{-1}$) during both time periods. However, in terms of biomass, there appears to be a significant acceleration in their rate of increase, from $0.012\cdot\text{year}^{-1}$ during the period 1951–1967 to $0.051\cdot\text{year}^{-1}$ during the years 1987–1996 (Table III). Only medium calanoids showed no significant trend in either period (Fig. 3e, Table III).

The other zooplankton taxa showed similar significant increases in their numbers, 1–2 orders of magnitude between 1951 and 1996 (Table III), despite increased interannual variability. Average year-to-year rates of increase ranged from $0.035–0.039\cdot\text{year}^{-1}$ for cladocerans, euphausiids and amphipods to $0.049\cdot\text{year}^{-1}$ for tunicates and $0.072\cdot\text{year}^{-1}$ for chaetognaths (1951–1967, Table III). Different rates of increase between the 1951–1967 and 1988–1996 periods were evident in the amphipods (Table III), and chaetognaths tended to decrease in number during the second period (Fig. 4).

Table IV: Community structure of the crustacean zooplankton during periods of sardine (1951–1967) and anchovy dominance (1988–1996), expressed as the percentage composition of the taxonomic and size-groups given in Table II. The ranges are derived from Fig. 5b, whereas the means are calculated as the mean of the percentages for each year of each time-series. Differences between means (Δ means) were tested using a non-parametric Mann Whitney U-test

Parameter	Cyclopoids (<900 μm *TL*)	Small calanoids and cladocerans (900–1 000 μm *TL*)	Medium calanoids (1 000–2 000 μm *TL*)	Large calanoids (2 000–5 000 μm *TL*)	Macrocrustaceans (>5 000 μm *TL*)
1951–1967 (n = 17)					
Range	24.2 – 59.8	11.8 – 48.3	1.6 – 13.9	8.4 – 35.0	0.6 – 3.9
Mean	41.4	31.4	6.3	19.0	2.0
SD	10.5	8.8	3.4	8.1	1.0
1988–1996 (n = 8)					
Range	42.0 – 70.1	24.9 – 42.2	0.001 – 0.6	3.0 – 17.1	0.2 – 2.1
Mean	55.7	33.6	0.4	9.3	1.0
SD	9.2	5.8	0.3	5.7	0.7
Δ means	$p < 0.01$	*ns*	$p < 0.001$	$p < 0.05$	$p < 0.05$

n = number of years within each period
ns = not significant ($p > 0,05$)

Zooplankton community structure

Concurrent with a shift in dominance in the catches of anchovy and sardine (Fig. 5a) was a shift in the species composition of crustacean zooplankton (Fig. 5b). During the period 1951–1967, when sardine were dominant (Fig. 5a), cyclopoids of total length (*TL*) <900 μm constituted between 24 and 60% of the crustacean zooplankton (Fig. 5b), with a mean of 41.4% (Table IV); this proportion was significantly less than during the years 1988–1996 (mean = 55.7%, range = 42–70%), when anchovy were dominant. Conversely, the mean proportions of medium (1 000 – 2 000 μm *TL*) and large copepods (2 000 – 5 000 μm *TL*) and macrocrustaceans (>5 000 μm *TL*) were significantly reduced from the early to the late period, from 6.3, 19.0 and 2.0% (total = 27.3%) to 0.4%, 9.3% and 1.0% (total = 10.7%) respectively (Fig. 5b, Table IV). The relative abundance of small calanoids and cladocerans (900–1 000 μm *TL*) remained unchanged at about one-third of the total throughout the time-series (Fig. 5b, Table IV).

DISCUSSION

Validation of the observed long-term trend

Because of methodological differences in the collection of data and the discontinuous nature of the time-series, it is important, from the onset, to establish that the observed trend of increasing zooplankton abundance could not have resulted from sampling artifacts or procedural bias. There were a number of factors that complicated data interpretation. First, to reduce possible seasonal effects, the analysis was restricted to collections made each year during autumn (March–June). Generally, no month effect was evident in the abundance of zooplankton, except in cladocerans and tunicates, which increased between March and June, and in the biomass of copepods, which decreased from March to June during the period 1951–1967 (Table IV). This decrease in copepod biomass is in agreement with observations during the 1970s. Pillar (1986), noted a decrease in the biomass of copepods from summer to winter (1977–1978) in the St Helena Bay/Cape Columbine area. A similar seasonal decline in zooplankton biomass (mainly copepods) was observed off the Cape Peninsula during the period 1970–1973 (Andrews and Hutchings 1980), along the South-Western Cape coast (Hutchings 1988) to Cape Columbine (Verheye *et al.* 1991) in 1974, and on the western Agulhas Bank between Cape Point and Danger Point in 1975 (Hutchings and Nelson 1985). In contrast, there was no evidence of a month effect during 1988–1996 (Table III), perhaps suggesting a shift in the seasonal cycle of zooplankton in the southern Benguela since the 1950s.

Second, the time-series is discontinuous, with a considerable gap in the 1970s. This hiatus is found also in datasets of other upwelling areas (cf. the California Current system: Roemmich and McGowan 1995a) coinciding with the International Decade of Ocean Exploration (see Richards 1981 for reviews), when attention was directed towards studying rate processes associated with coastal upwelling in eastern boundary current systems worldwide, to the detriment of monitoring work. However, the 1974 and 1978 data points in Figures 3 and 4 provide evidence for continuity between the 1951–1967 and 1988–1996 datasets and support the contention of increasing zooplankton abundances.

Third, and probably most important, the use of different gear and sampling strategies during the 46-year time-series has introduced some difficulties with the interpretation of the results, which are listed below.

(i) Using settled volume as a proxy for wet mass has resulted in a positive bias in copepod biomass during the period 1951–1967 owing to the presence of interstitial fluid. Such bias could be as much as 45% (Smith and Kalber 1974). This bias may further have been enhanced by contamination with non-copepod zooplankters (chaetognaths and small tunicates), although these taxa contributed numerically very little (<3%) to the zooplankton. These biases, however, cannot account for the considerable difference between the slopes of the 1951–1967 and 1988–1996 regressions of copepod biomass (Table III). Rather, shifts in species composition (Fig. 5b) contribute largely to this discrepancy.

(ii) The use of multiple meshes in the N70V net could have reduced its effective mouth area from 0.38 m^2 at the mouth to 0.10 m^2 at the 200-µm meshed filtering section, so increasing the per-m^2 biomass and abundance estimates by the same factor. This could have led to a four-fold underestimation of the smallest copepods which could escape through the large meshes (6.2 mm and 460 µm) at the front of the net, but the effect would decrease with increasing body size of zooplankter.

(iii) Restricting sampling to the upper 100 m during the years 1951–1967, as well as in 1978, probably had little effect on the estimates of mean abundance. This is because only a few stations offshore were deeper than >100 m. Furthermore, zooplankton abundance is low deeper than that (Andrews and Hutchings 1980).

(iv) Another negative bias could have resulted from the larger, more-motile zooplankters avoiding the N70V and the WP-2 nets, both of which have towing bridles. Net avoidance would have caused an underestimation only of juvenile and adult euphausiids, amphipods and maybe chaetognaths during the years 1951–1967 and 1974. This underestimation could have been as much as ten-fold (Pillar 1984).

(v) There may be density-dependent limitations associated with the vertically-towed N70V, WP-2 and Bongo nets, compared with the obliquely towed Bongo and RMT-1x6 nets (Currie 1962).

(vi) Avoidance and limited delivery rate and volume filtered are common problems associated with pump sampling (Pillar 1984). However, Verheye (1991) demonstrated that the catchability of 200–500, 500–1 600 and >1 600 µm zooplankton size fractions by a plankton pump and a vertically towed Bongo net did not differ statistically.

(vii) Although the effects of daytime v. night-time sampling have not been investigated in this study, it is considered to be of minor importance because the entire water column was sampled at most stations.

It is difficult, if not impossible, to assess the systematic effects of each of these possible biases. Whereas some of the effects may individually offset one another, or may be negligible relative to natural sources of variability (including species-specific differences), their combined effects could bring into question the observed long-term trends. This would be particularly so for the 1951–1967 time-series, where most of the above-mentioned biases would lead to an unknown net negative bias. However, because the N70V was the only net used during that period and the vertical Bongo net was consistently used during the second period (1988–1996), no methodological changes occurred within each individual time-series, and both increasing trends are real. It is also evident that most taxa increased in abundance during the 20-year hiatus in the time-series. Whereas this may be inferred from the total copepod biomass for the years 1974, 1978, 1983, 1984 and 1987 in Figures 3a and 4a, the period effect was never significant in any of the models. This implies that there was no discontinuous, stepwise increase in abundance over the intermediate period over and above that which was attributable to year. Moreover, most zooplankton taxa showed a continuous increase in abundance of about the same magnitude for the two time-series (Figs. 3 and 4, Table III).

Possible mechanisms underlying a long-term increase in zooplankton

The increase in the abundance of zooplankton in the Cape Columbine/Lambert's Bay area between 1951 and 1996 appears to reflect true long-term changes in the nearshore community rather than methodological bias. Further, there was a significant shift in the relative abundances of crustacean zooplankton taxa with time (Fig. 5). Such species displacement could be attributed to differential size-selective predation by anchovy and sardine, as previously identified in laboratory studies (James and Findlay 1989, Van der Lingen 1994). Indeed, there were proportionately few small copepods (cyclopoids) during the period of sardine dominance (1951–1967), whereas during anchovy dominance (1988–1996) the relative abundance of large crustaceans (>1 000 µm *TL*) had decreased (Table IV). A recent study of the stomach contents of anchovy and sardine recruits of similar size caught in the same trawls along the west coast of South Africa shows that sardine ingested mainly copepods <600 µm prosome length (*PL*), whereas anchovy preferentially ingested larger copepods >600 µm *PL* (Louw *et al.* 1998). These size-classes are roughly equivalent to copepods <900 and >900 µm *TL* respectively in the present study.

These findings suggest that the increase in zooplankton abundance may be a direct response to a long-term overall reduction in predation pressure. Along the West Coast, total catches of pelagic fish which are predominantly planktivorous (James 1987, Wallace-Fincham 1987, Van der Lingen 1994, Pillar and Barange 1998), increased rapidly through the 1950s and subsequently stabilized (Crawford *et al.* 1987). However, exceptionally large catches of anchovy (in excess of 500 000 tons) were made during 1987 and 1988 (Fig. 1). If these two outliers (>2 *SD* from the mean) are removed from the post-1960 time-series, a significant decrease in total pelagic catch is evident (linear regression: $r^2 = 0.47$, $p < 0.001$, $n = 35$). If this decrease reflects a decrease in stock size, such stock reduction may not only be caused by exploitation (Crawford *et al.* 1987), but may in part be attributable to increased predation by top predators. Indeed, a considerable increase in the South African handline catches of snoek *Thyrsites atun*, one of the major predators of anchovy and sardine (Boyd *et al.* 1985, Wickens *et al.* 1992), has been noted since the 1960s, following extensive southward migrations of snoek from Namibian waters (Crawford *et al.* 1995). Also, the population of the Cape fur seal *Arctocephalus pusillus pusillus*, another major predator on pelagic fish, has increased considerably over the past few decades, and its annual food consumption has doubled over the past 20 years (Butterworth *et al.* 1995).

Another plausible mechanism explaining the long-term increase in zooplankton abundance is a response to increased primary productivity following a long-term intensification of coastal upwelling. Evidence in the literature of long-term (decadal-scale) responses of phytoplankton and zooplankton to intensified coastal upwelling is sparse and often contradictory or misleading because of different operating or controlling parameters. Data from Continuous Plankton Recorder collections in the North-East Atlantic and the North Sea since 1948 indicate an initial 30-year decline in the abundance of zooplankton, followed by a recovery after 1980 (CPR Survey Team 1992). This pattern was also observed in the abundance of phytoplankton, as well as in the stocks of herring *Clupea harengus* and the breeding performance of seabirds (Aebischer *et al.* 1990). The last authors speculated that climate is the driving force behind the similarity in the observed trends across all four trophic levels in the North Sea, and Dickson *et al.* (1988) argued that the decline in zooplankton is correlated with a long-term increase in upwelling intensity during spring in the relatively weak upwelling zone along the Iberian west coast.

In the central North Pacific, Venrick *et al.* (1987) noted a sigificant twofold increase in the amount of chlorophyll *a* in the water column during summer over the period 1968–1985, possibly in response to increased nutrient input as a combined result of increased surface cooling and increased winter wind stress and vertical mixing. In the coastal zone along the west coast of South Africa, Shannon *et al.* (1992) documented an increasing trend in upwelling-favourable winds over the years 1950–1989. Unfortunately, data on chlorophyll *a* concentration, which are available for the period 1971–1989 (Brown and Cochrane 1991), are too irregularly distributed in space and time to determine any trend.

Data on long-term changes of zooplankton abundance in eastern boundary current ecosystems, where large-scale intensification of coastal upwelling is a global phenomenon (Bakun 1990), are available for the Humboldt and California Current systems. Carrasco and Lozano (1989; cited in Alheit and Bernal 1993) noted a marked decrease in zooplankton volume off Peru between 1964 and 1986. A similar pattern was evident in the 1964–1973 time-series off Chile (Bernal *et al.* 1983), where a change in ocean circulation, driven by atmospheric forces, was thought to be responsible for the observed change in zooplankton abundance (Loeb and Rojas 1988). Roemmich and McGowan (1995a, b) also documented a decrease, of around 70%, in the biomass of total macrozooplankton (retained by a mesh of 505µm) in the California Current between 1951 and 1993. Those authors suggested that this decrease was linked to a long-term warming of the sea surface by >1.5°C, which could offset or even reverse the effect of increased wind stress. As a result, nutrient supply was greatly reduced, eventually leading to less new production and ultimately resulting in the observed decrease in zooplankton.

In the present study, mean sea surface temperature data collected concomitantly with the zooplankton samples suggest a significant, though minor, long-term warming of the shelf surface waters by 0.48°C between 1951 (13.87°C) and 1996 (14.35°C) $r^2 = 0.29$,

$p < 0.05$, $n = 358$, HMV, unpublished data). Warming of such a small magnitude would impact only marginally on the increased upwelling-induced nutrient supply along the West Coast. The study area is situated downstream of the Cape Columbine upwelling centre, where upwelling may take place throughout the year, with a maximum during summer (Hutchings 1981, Nelson and Hutchings 1983). The upwelled water, of South Atlantic Central Water origin, is highly enriched in nutrients through local recycling (Bailey and Chapman 1991, Waldron and Probyn 1991), and a semi-closed circulation system (Holden 1985) further maintains high levels of nutrients. As a result, enhanced primary production (Henry 1979, Bailey and Chapman 1985, Mitchell-Innes and Walker 1991) and sluggish currents favour high sedimentation of POC (Bailey 1985, 1987) and high organic concentrations in the sediments (Birch 1975). Moreover, this semi-closed circulation system operates as a retention mechanism for plankton populations (Verheye *et al.* 1991, 1992). Combined with the large-scale, long-term intensification of upwelling documented by Shannon *et al.* (1992), this circulation could lead to a long-term increase in primary production in this region. The above processes, together with upwelling-associated advection of zooplankton populations from the Cape Peninsula upwelling centre farther south (Verheye 1991, Verheye *et al.* 1991) could result ultimately in the long-term increase in zooplankton abundance observed over the past 46 years. With these processes peaking in late summer/autumn (Chapman and Bailey 1991), they could provide a regional mechanism for increasing the carrying capacity of this area during peak recruitment of pelagic fish.

CONCLUSIONS

Despite the discontinuity in the zooplankton time-series and notwithstanding possible biases as a result of methodological differences between the various datasets, the data reflect a long-term change in the potential food environment of planktivorous pelagic fish. There has been a significant increase by at least one order of magnitude in the abundance of zooplankton on the recruitment grounds and during peak recruitment of pelagic fish over the past 46 years. This long-term increase was accompanied by a significant shift in the community structure of the nearshore zooplankton community.

Possible causative mechanisms for the observed long-term increase in zooplankton abundance are proposed from both bottom-up and top-down perspectives, which are likely to operate in concert rather than singly. The semi-closed circulation system characteristic of St Helena Bay provides a mechanism for maintaining high production of phytoplankton and zooplankton and for the retention of plankton populations. The long-term intensification of upwelling is the underlying mechanism by which this bottom-up process operates. The resultant increase in zooplankton can be enhanced by a reduction in the predation pressure by primary predators (e.g. anchovy and sardine), which itself may result from increased predation by top predators (e.g. snoek, seals). However, it is not possible to distinguish the relative contributions of altered environmental conditions and predator abundance as mechanisms responsible for the long-term increase in zooplankton.

Because of the spatial and temporal limitations of this study, and owing to the circulation system which characterizes the study area, caution should be exercised in extrapolating the findings of the present study to broader space-scales (e.g. the southern Benguela) or longer time-scales (e.g. covering the entire life cycle of pelagic fish). Further investigation, by retrospective analysis of data collected over wider spatial and temporal scales (e.g. by including the western Agulhas Bank, where anchovy and sardine predominantly spawn during late spring and summer), is necessary.

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