Temporal and spatial changes in the abundance and size structure of copepods in the southern Benguela: 1988 to 2000

DEPARTMENT OF ZOOLOGY
FACULTY OF SCIENCE
UNIVERSITY OF CAPE TOWN

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MUSSIE G. SEBHATU

Supervised by:

Dr Hans M. Verheye and Dr Coleen L. Moloney

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ABSTRACT

Copepod abundance data were collected during the annual pelagic fish spawner and recruit stock assessment surveys, in summer and winter from 1988 to 2000. These data were used to examine temporal and spatial variability in abundance and community structure of copepods in the southern Benguela, by estimating changes in abundance (No. m^{-3}) of individual species and size-classes. The relative abundance of *Calanus agulhensis, Calanoides carinatus, Centropages brachiatus, Metridia lucens, Oithona* spp., *Oncaea* spp., copepod nauplii and other small copepods show that these taxa were important in driving total copepod abundance changes in the region. A general linear model (GLM) was used to help control for different factors that might affect interannual variability in copepod abundance: season, area, chlorophyll concentrations and sea surface temperature. The southern Benguela was divided into six sub-areas. Results of the GLMs show the largest abundances of copepods on the northern and central West Coast, fewer copepods on the central and eastern Agulhas Bank and fewest copepods on the south West Coast and western Agulhas Bank. Relative abundance time-series of four copepod size-classes (cyclopoid copepods (<900 µm total length (TL)), small calanoid copepods (900-1000 µm TL), medium calanoid copepods (1000-2000 µm TL) and large calanoid copepods (2000-5000 µm TL)) show that there was a possible change in control mechanism of copepods in 1996 from bottom-up to top-down. Moreover, in winter 1999 there was a unique event during which the abundance of various species showed a marked decline, but returned to normal levels in 2000. The time series of relative abundance showed reduced numbers of all four size-classes in 1992 – 1994. These findings indicate that factors affecting interannual variability of copepods are complex, but that, similar to previous findings, the southern Benguela system has not undergone a major change over the past two to three decades in terms of total copepod abundance in the different sub-areas.

INTRODUCTION

Copepods form a very important trophic link in the South African pelagic marine environment, playing a key role in transferring energy from phytoplankton to organisms at higher trophic levels, such as anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), round herring (*Etrumeus whiteheadi*), lanternfish (*Lampanyctodes hectoris*) and lightfish (*Maurolicus muelleri*) (Armstrong *et al.*, 1991). Variability in copepod body size provides an important means of apportioning their total biomass to different size-selective pelagic consumers in the region. For instance, Louw *et al.* (1998) analysed the stomach contents of young sardines and anchovies, which co-occurred in the same school on the West Coast. Their results showed that sardine recruits fed preferentially on copepods with a modal length of 300 μm PL (prosome length), whereas those of anchovy fed primarily on copepods of modal lengths between 600 and 900 μm PL.

Verity (1998) indicated that the factors determining the occurrence and abundance of species are not yet well known. In the pelagic environment, this is probably because scientists have afforded more attention to the effect of environmental factors on abundance, than to interactions among species (Cury *et al.*, 2000). Verity (1998) also stated that environmental forces (temperature, nutrients, etc.) were considered to be the main driving factors for the development of phytoplankton blooms. However, in a study conducted in the subarctic North Pacific, Shiomoto *et al.* (1997) found that fluctuations in the grazing intensity of macrozooplankton were responsible for changes in phytoplankton biomass. In Denmark, a jellyfish (*Aurelia aurita*) was found to control community structure of zooplankton in shallow caves (Oleson, 1995). Hence, it is evident that it is not exclusively environmental factors that determine abundance, biomass and community structure of plankton communities.

Marine community structure is hypothesized to be controlled through several mechanisms, including bottom-up, top-down and mixed (e.g. wasp-waist) control mechanisms. In a bottom-up controlled system, resource availability restricts higher trophic levels (Micheli, 1999; Cury *et al.*, 2000). This can result in a regime shift in an ecosystem; this shift in ecosystem function persists if the effect is a long-term climatic regime shift (Cury and Shannon, 2004). In a top-down controlled system, consumer biomass is altered through fishing (Micheli, 1999), allowing the ecosystem to be dominated by small pelagic fish rather than big predators (Cury and Shannon, 2004). Wasp-waist control is a mechanism by which a trophic level exerts top-down control on a lower trophic level and bottom-up control on a higher trophic level simultaneously (Rice, 1995). It is not easy to determine if a community is structured by environmental variables and food availability (bottom-up control) or through predation (top-down control). This is because we usually find both community-controlling mechanisms operating at the same time, and it becomes difficult to assess the intensity of their respective effects on the community (Verheye *et al.*, 1998).

Changes in environmental factors (temperature and nutrients) and food availability can affect copepod abundance and community structure. In a study conducted by Shreeve *et al.* (2002) in South Georgia, it was found that the egg production rate of two copepod species (*Rhincalanus gigas* and *Calanoides acutus*) increased with increased chlorophyll concentration. The authors also found that the carbon mass of the juveniles was food dependent. In the Baltic Sea, increased freshwater run-off (due to meteorological changes) and the absence of saline water input through the Danish Strait led to reduced salinity, which imposed stress and reduced the copepod biomass there (Vuorinen *et al.*, 1998). In European waters, Planque and Taylor (1998) noted a link between changes in zooplankton community structure and Gulf Stream signals (a North Atlantic current system) and the North Atlantic Oscillation (a climatic variability in the North Atlantic). In the 1990s, environmental anomalies in the northern Benguela (off Namibia) probably played a role in the decline of the pelagic fishery (Cury and Shannon, 2004). Bottom-up control over the ecosystem resulted in a regime shift, and favoured the flourishing of jellyfish in the region.

Top-down control can also have marked effects in aquatic ecosystems. In the Subarctic North Pacific, Shiomoto *et al.* (1997) found that before 1989, the abundance of pink salmon was low, that of macrozooplankton was high and that of phytoplankton was low, but after 1989, the abundance of pink salmon increased while the abundance of macrozooplankton decreased and that of phytoplankton increased, indicating a top-down control on both macrozooplankton and phytoplankton. However, Shiomoto *et al.* (1997) did not mention why the abundance of pink salmon increased after 1989. Another example of top-down control is documented for the North Sea from 1978 to 1982 where severe overexploitation of herring and an increase in small pelagic fish were seen together with a decrease in small zooplankton and an increase in euphausiids and large copepods. Preferential feeding on the small zooplankton by the small pelagic fish was assumed to be the reason for this occurrence (Reid *et al.*, 2000).

In this study, the zooplankton communities from a coastal upwelling environment off South Africa are examined in relation to possible trophic controls. The southern Benguela (Fig. 1) extends from 29°S (Orange River) on the West Coast of South Africa, to approximately 28°E (East London) on the South Coast (Shannon, 2001). The region is characterized by a complex and irregular coastline including bays, capes, mountain ranges and upwelling systems (Shannon, 1985). Upwelling in the southern Benguela is mostly wind-driven (Kamstra, 1985) and plays a major role in supporting large stocks of pelagic fish in the region (Shannon *et al.*, 2003). The continental shelf off the southern part of South Africa is a favourable spawning area (mean currents in that area are not strong, reducing the risk of advection to the open ocean (Shannon *et al.*, (1996)), whereas the productive West Coast serves as a nursery ground for the juveniles of various pelagic fish (Hutchings, 1992).

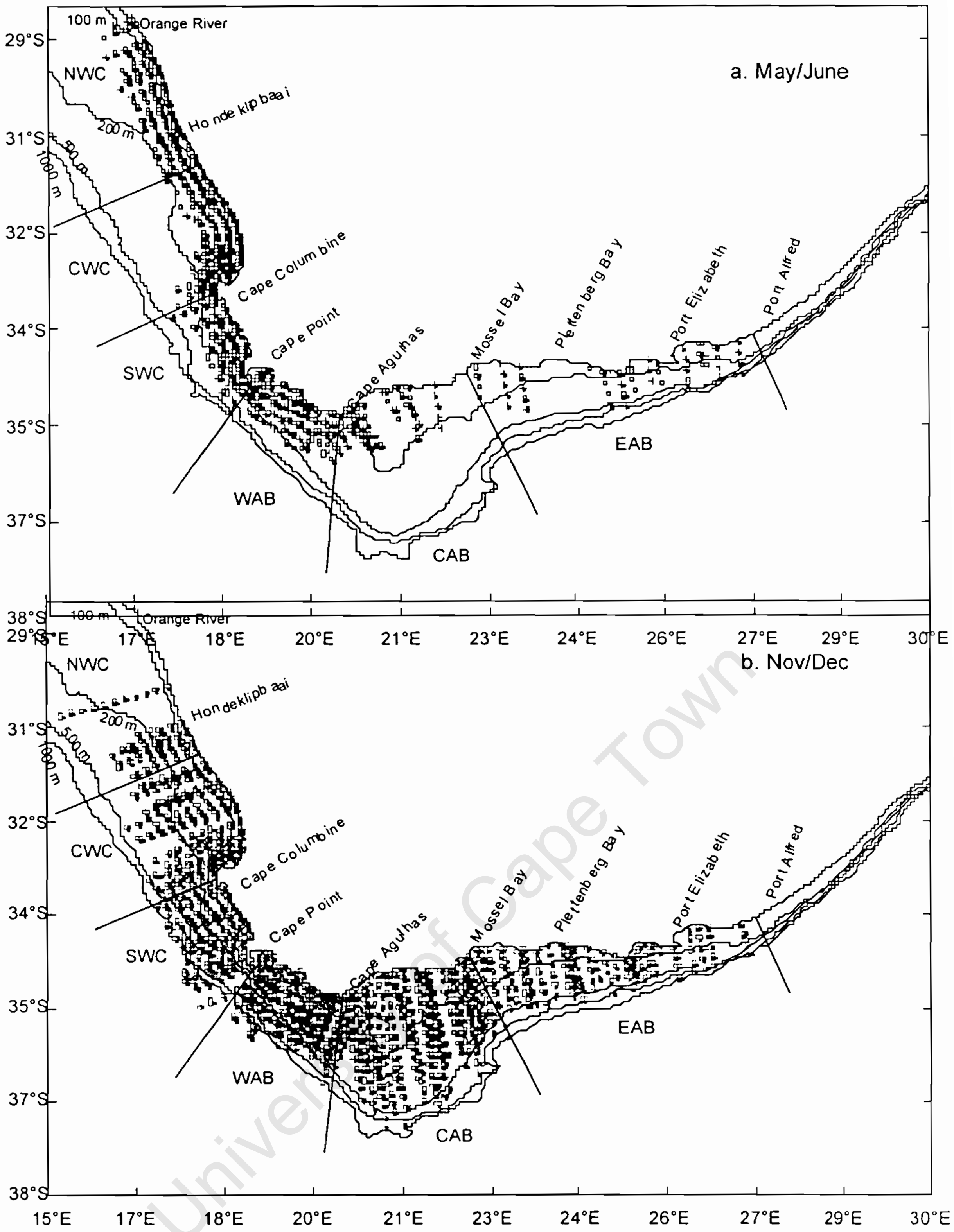

Figure 1. Map of the west and south coasts of South Africa, showing all the sampling sites from the cruises conducted in (a) winter (May/June) and (b) summer (November/December), 1988-2000. The study area is subdivided into six sub-areas: northern west coast (NWC), central west coast (CWC), southern west coast (SWC), western Agulhas Bank (WAB), central Agulhas Bank (CAB) and eastern Agulhas Bank (EAB) (modified from Huggett, 2003).

Shannon and Field (1985) indicated that pelagic fish (sardine and anchovy) could be limited by food. They suggested that the southern Benguela cannot support more than two million tons (wet weight) of fish per year during average environmental conditions. Armstrong *et al.* (1991), however, estimated that the continental shelf of South Africa supported four million tons (wet weight) of pelagic and mesopelagic fish, which needed about 3.6 million tons of carbon annually, 90% of which is supplied by meso- and macrozooplankton.

Hutchings *et al.* (1991) estimated the mean standing stock of mesozooplankton in the southern Benguela shelf region to be 0.8 $gC.m^{-2}$, within the range 0.2 – 2.0 $gC.m^{-2}$. Pillar (1986) showed that from 1977 to 1978 the copepod biomass was higher on the northern and central West Coast than on the southern West Coast and western Agulhas Bank. Verheye *et al.* (1992) also showed that mesozooplankton standing stock increased from south to north along the West Coast (0.5 – 1.0 $gC.m^{-2}$ south of Cape Columbine and 0.5 – 2.5 $gC.m^{-2}$ north of Cape Columbine) and decreased from east to west along the South Coast (1.0 – 2.0 $gC.m^{-2}$ on the eastern side and 0.5 – 1.0 $gC.m^{-2}$ on the western side).

Cury and Shannon (2004) suggested that the southern Benguela has not undergone a major change in its functioning in the past two decades. They further suggested that the increase in abundance of fish that recently took place is a species replacement rather than a regime shift. It is, however, believed that in the past decade there has been a shift in spawning habitat of pelagic fish. Van der Lingen *et al.* (2001) used egg counts and temperature data from 1984 to 1998 to determine the spawning habitat and the relationship of spawning with temperature of anchovy and sardine in the southern Benguela upwelling ecosystem. They found that anchovy spawned at warmer temperatures (17.4 – 21.1 °C) than sardine (15.2 – 20.5 °C). Moreover, the egg counts showed that the spawning grounds of anchovy and sardine have changed since 1994. Prior to 1994, both species shared their spawning grounds east and south of Cape Point; after 1994, however, van der Lingen *et al.* (2001) found that there was a shift in the spawning grounds to the east of Cape Point for anchovy and westward of Cape Point for sardine. Barange *et al.* (1999) also used data from the recruit and spawner acoustic surveys of pelagic fish from 1984 to 1996 to describe abundance and distribution patterns of anchovy and sardine in the southern Benguela. They found that anchovy move eastward as they grow older, whereas sardines move to the east during their growth to adulthood, but disperse both to the South and West coasts afterwards.

Over the past three to five decades, zooplankton abundance in large parts of the world (the California Current system, the Guinea Current system, the Oyashio system off Japan, the Black Sea, and the Humboldt Current system) have shown long-term declining trends, whereas in the South African Benguela region, total zooplankton has been increasing (Cury *et al.*, 2000; Verheye, 2000). Verheye *et al.* (1998) used data from seven consecutive sampling programs between the 1950s and 1990s to examine long-term changes in abundance and community structure of zooplankton in the southern Benguela. They found that total zooplankton abundance had increased by more than two orders of magnitude over the 45-year period (from 4 205 $ind.m^{-2}$ in 1951 to 720 579 $ind.m^{-2}$ in 1996). When considering the copepods separately, they found that their biomass had increased ten-fold (from 5.1 g m^{-2} in 1951 to 55.0 g m^{-2} in 1996). Along with this increase, there were also changes in size-class composition of the copepod community. The proportion of copepods smaller than 0.9 mm TL increased, whereas those larger than 1.0 mm TL decreased over the period 1951 to 1996 (Verheye and Richardson, 1998). The long-term increase in the abundance of zooplankton observed in the southern Benguela is thought to be due to a decadal-scale increase in wind stress (favouring upwelling), whereas the change in size structure of the community, from predominantly larger zooplankton to the smaller cyclopoid copepods, is believed to be due to an alteration of the predator community in the region (shifting from a dominance of sardine which prefer small plankton, to a dominance of anchovy which prefer large zooplankton) (Verheye and Richardson, 1998).

Because of the importance of copepods in the Benguela food web dynamics, detailed investigations of their distribution, abundance, species composition, fecundity and growth rate were initiated in 1988, during the annual hydroacoustic pelagic fish stock assessment surveys (Huggett, 2003; Hutchings *et al.*, 1995; Richardson, 1998; Verheye *et al.*, 1992). The present study examines temporal and spatial changes in the abundance of copepods and size-based structure of their assemblages in the southern Benguela off South Africa from 1988 to 2000. The aim is to assess whether top-down effects (caused by changes in feeding strategies, shifts in distribution and spawning behaviour of pelagic predator species) or bottom-up effects (caused by changes in environmental factors such as temperature and chlorophyll concentration) are likely to control the structure of the copepod community. Both top-down and bottom-up controlling mechanisms may operate at the same time (Verheye *et al.*, 1998), however the one may have a stronger effect than the other. A strong influence of top-down control in the region is expected to produce low abundance of copepods under high abundance of pelagic fish, or high abundance of copepods under low abundance of pelagic fish. In contrast, the influence of strong bottom-up control in the region is likely to result in a high abundance of copepods under enhanced primary production, or low abundance of copepods under poor conditions of primary production.

MATERIALS AND METHODS

Field and laboratory sampling

Personnel from Marine and Coastal Management (MCM), a branch of the South African Department of Environmental Affairs and Tourism, collected the data for this study, from both the south and the west coasts of South Africa during the annual pelagic fish recruit (Fig. 1a) and spawner biomass (Fig. 1b) surveys between 1988 and 2000. The cruises were conducted in winter (May or June) for the assessment of recruitment, and in summer (November or December) for the estimation of spawner biomass. Field collection and laboratory analysis of zooplankton samples performed by MCM personnel are briefly described below.

Zooplankton samples were collected at stations 10 nautical miles apart, along transects perpendicular to the coast. Transects extended up to 40 nautical miles offshore in winter and up to 200 nautical miles offshore during summer (Fig. 1). Sample collection was conducted using a vertically-towed Bongo net with a mouth area of 0.255 m^2 and a mesh size of 200 μm. It was equipped with a depth sensor, temperature sensor and a flow-meter. Maximum depth of sampling was 200 m, but in shallow areas sampling was done from 5 m above the bottom to the surface. The samples were preserved in a 4% formalin-sea water solution. In the laboratory, each sample was poured into a measuring cylinder and left to settle overnight. Samples were then diluted to ten times their settled volume. Subsamples of 2 ml of the diluted sample were taken for analysis, and the number of copepods was counted using a dissecting microscope on the basis of species type and developmental stages.

For each station the number of individuals per m^3 was calculated using the formula:

$$\text{No. of copepods.m}^{-3} = \frac{\text{No. of copepods counted} \times \text{Diluted volume (ml)}}{\text{Volume of sample counted (ml)} \times \text{Total volume filtered (m}^{3}\text{)}}$$

The biomass for each species was calculated using the formula:

$$\text{Biomass of species/group } (\mu\text{g C.m}^{-3}) = \text{abundance } (\text{m}^{-3}) \times \text{individual body mass } (\mu\text{g dry wt}) \times 0.4$$

where 0.4 is a conversion factor from dry weight to carbon mass (Parsons *et al.*, 1984, cited in Verheye *et al.*, 1992).

To help investigate spatial variations in abundance and consider effects of factors controlling the local copepod community, the study area was subdivided into six sub-areas, three on the west coast and three on the south coast of South Africa (Table 1 and Fig.1).

Table 1. Geographical limits of the six sub-areas (after Huggett, 2003)

Coast	Geographical area	Limits of area	Acronym
West	Northern West Coast	Orange River – Hondeklipbaai	NWC
	Central West Coast	Hondeklipbaai - Cape Columbine	CWC
	Southern West Coast	Cape Columbine - Cape Point	SWC
South	Western Agulhas Bank	Cape Point - Cape Agulhas	WAB
	Central Agulhas Bank	Cape Agulhas - Mossel Bay	CAB
	Southern Agulhas Bank	Mossel Bay - Port Alfred	EAB

Data analysis

Changes in community structure were investigated in two ways:

a) By species:

   To assess whether there were any changes in the abundance of individual species over the years, the abundances of males, females and all the juvenile stages of a single species were combined to give a number representing that particular species.

b) By size:

   To assess whether the size structure of the community had changed over time, the abundance of various adult copepods, juvenile stages and nauplii in a particular size range were combined to give four distinct size-classes (Table 2) (based on Verheye *et al.*, 1998). The categorization of Verheye *et al.* (1998) is used here for consistency, although it includes some allocations that might be contentious. For example, C3 and C4 stages of *Calanus agulhensis* and *Calanoides carinatus* were placed into the small calanoid copepod category (900-1000 μm), whereas they are between 1000-2000 μm and might be better placed in the medium calanoid copepod category (Peterson et al. 1990).

To extract the main species/groups that contribute to the total abundance and biomass, the percentage contribution of each species/group to the total abundance and biomass was calculated (Table 3). Species/groups that contributed more than one percent to the total abundance and/or biomass were considered in this study as important enough to warrant examination of temporal variations in their abundance.

Statistical Analysis

A general linear model (GLM) was used to investigate factors influencing year-to-year changes in abundance of four different size classes. All abundance data were log-transformed. In the GLM analysis, *year*, *season* and *area* were investigated as categorical variables, and *sea surface temperature (SST)* and *chlorophyll a concentration* (integrated in the upper 30 m) were investigated as continuous variables. The GLM analysis considers each effect separately and allocates reference points for each categorical variable. The year 2000, summer and EAB were therefore used as reference points for the *year*, *season* and *area* variables respectively. Effects that were not significant (p>0.05) were removed from the model in a backward stepwise process. Interactions between categorical variables were not investigated because of data unavailability during some of the study periods.

Table 2. The main groups and species of copepods found in the southern Benguela, collected during pelagic fish surveys from 1988 to 2000. Groups/species are categorized into four size-classes on the basis of total length (based on Verheye *et al.*, 1998).

Groups	Species and developmental stages	Size class based on total length (TL)
Cyclopoid & Harpacticoid copepods	Copepod nauplii *Corycella* sp. *Oithona* spp. *Oncaea* spp.	<900 µm TL
Small calanoid copepods	Juveniles (C1-C4 of *Calanus agulhensis, Calanoides carinatus, Centropages brachiatus, Metridia lucens* and *Pleuromamma* spp.) *Ctenocalanus vanus Clausocalanus scottii* *Paracalanus parvus Paracalanus scottii* Other small copepods.	900 – 1000 µm TL
Medium calanoid copepods	Adults and C5 of *Centropages brachiatus* and *Pleuromamma* spp. Juveniles of *Rhincalanus nasutus*	1000 – 2000 µm TL
Large calanoid copepods	Adults and C5 of *Calanus agulhensis, Calanoides carinatus* and *Metridia lucens* Other large copepods	2000 – 5000 µm TL

RESULTS

The community structure, averaged over the entire study area and period both in winter and summer, is shown in Table 3. Ten species contributed more than one percent to the total abundance and/or biomass (*Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus,* copepod nauplii, *Metridia lucens*, *Oithona* spp., *Oncaea* spp., *Rhincalanus nasutus, Paracalanus scottii* and other small copepods) and are considered the main constituents of the copepod community.

Calanus agulhensis, *Calanoides carinatus*, *Centropages brachiatus*, copepod nauplii, and *Oncaea* spp. did not contribute as much to the total abundance and biomass during winter as did *Oithona* spp., *Metridia lucens* and other small copepods, which together accounted for >90% of winter abundance and >80% of winter biomass. *Metridia lucens,* however, contributed much less to abundance (~5%) than to biomass (~30%). During summer, the contributions of *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus* and copepod nauplii to the copepod community were greater than those in winter, both in terms of abundance and biomass, whereas *Metridia lucens* and *Oithona* spp. contributed less. Other small copepods contributed about ten percent more to the total abundance in summer than winter, but about three percent less to the biomass. The higher contribution level of *Paracalanus scottii* in summer was only due to a sudden increase in abundance of that species in 1998.

During winter, cyclopoid copepods were the largest contributors in terms of abundance (~63%), whereas small calanoid copepods were the largest contributors in terms of biomass (~43%). Medium calanoid copepods and large calanoid copepods contributed little to the total abundance (<1% and <3% respectively). However, large calanoid copepods contributed as much as cyclopoid copepods to the total biomass (~27%). Small calanoid copepods had the largest contributions to biomass (~50%) and abundance (~60%) during summer, whereas cyclopoid copepods had a much reduced contribution level (by ~50%) in summer. Medium and large calanoid copepods increased their respective contributions to the abundance (~2 and ~4%) and biomass (~4% and ~34%) in summer, but medium calanoid copepods contributed very little overall, and were generally small (<5%) components of the community, both in terms of abundance and biomass.

Changes in species abundance over time

Year-to-year changes in mean species abundance over the whole study area showed some interesting patterns (Fig. 2). *Calanus agulhensis* and *Oncaea* spp. were consistently more abundant in summer than in winter in all years, whereas *Calanoides carinatus, Centropages brachiatus, Metridia lucens, Oithona* spp. and other small copepods were usually less abundant in summer than in winter (Fig. 2).

Calanus agulhensis (Fig. 2a) showed a general declining pattern from 1988 during both winter and summer. *Calanoides carinatus* (Fig. 2b) had a fluctuating pattern, but it declined in the winters of 1998 – 2000. *Centropages brachiatus, Metridia lucens* and *Oithona* spp. (Fig. 2 c,d,e) showed a general increasing pattern and had high abundances in the winters of 1996, 1997 and 1998. The abundance of these three copepods sharply declined in winter of 1999 but increased again dramatically the following year. Copepod nauplii (Fig. 2g) showed a continuous winter increase until 1997. They had their lowest abundance in 1999, but increased to a higher abundance in 2000. The summer trend of copepod nauplii fluctuated, but showed the highest abundance in 1988 and 1996 and the lowest abundance in 1998. The winter trend in the abundance of other small copepods (Fig. 2h) generally increased until 1998, and reached their lowest abundance in 1999. Their summer trend, however, did not show much fluctuation.

Table 3. Mean abundance and biomass, the associated standard error (SE) and the percentage contribution (%) of each copepod species and size-class to the total abundance and biomass, in summer and in winter, combined over all stations and years.

SPECIES	WINTER						SUMMER					
	ABUNDANCE			BIOMASS			ABUNDANCE			BIOMASS		
	MEAN	SE	%	MEAN	SE	%	MEAN	SE	%	MEAN	SE	%
Calanus agulhensis	71.41	4.96	0.99	1322.38	124.64	4.74	289.93	20.65	7.54	5782.84	321.44	24.48
Calanoides carinatus	102.90	9.75	1.42	1864.95	200.23	6.69	188.86	34.48	4.91	3249.29	842.42	13.76
Centropages brachiatus	286.65	16.37	3.96	1221.02	65.32	4.38	434.08	57.61	11.28	1938.44	241.24	8.21
Copepod nauplii	92.35	6.86	1.27	36.94	2.74	0.13	200.28	17.97	5.21	80.19	7.21	0.34
Corycella sp.	3.34	0.33	0.05	40.03	3.92	0.14	9.70	0.48	0.25	116.72	5.79	0.49
Harpacticoid sp.	3.75	0.38	0.05	45.01	4.60	0.16	3.60	0.95	0.09	43.28	11.41	0.18
Metridia lucens	376.47	28.98	5.20	8149.14	612.28	29.22	156.93	54.87	4.08	3228.62	1406.17	13.67
Oithonia spp.	4422.61	618.43	61.03	7076.18	989.49	25.38	952.64	83.08	24.76	1503.36	132.45	6.36
Oncaea spp.	24.87	1.80	0.34	298.39	21.56	1.07	88.68	14.63	2.30	1065.75	176.02	4.51
Other calanoids	12.30	2.05	0.17	147.56	24.62	0.53	12.15	0.83	0.32	146.14	9.97	0.62
Pleuromamma sp.	2.91	0.73	0.04	89.42	26.50	0.32	5.56	1.02	0.14	182.56	60.12	0.77
Rhincalanus nasutus	2.83	0.29	0.04	219.70	22.33	0.79	4.06	0.64	0.11	281.71	49.65	1.19
Ctenocalanus vanus	4.59	1.56	0.06	18.35	6.25	0.07	1.33	0.86	0.03	5.32	3.47	0.02
Clausocalanus scottii	3.06	0.87	0.04	12.23	3.49	0.04	0.19	0.13	0.00	0.77	0.53	0.00
Paracalanus parvus	6.74	1.81	0.09	26.95	7.24	0.10	0.10	0.07	0.00	0.40	0.30	0.00
Paracalanus scottii	8.01	3.35	0.11	32.06	13.38	0.11	126.42	32.07	3.29	507.08	128.64	2.15
Other small copepods	1821.43	160.53	25.14	7285.73	642.12	26.13	1372.93	194.05	35.68	5487.62	778.30	23.23
SIZE-CLASS GROUPS												
Cyclopoid copepods	4546.92	618.68	62.88	7496.55	988.85	27.12	1254.89	91.13	33.20	2809.30	241.84	12.01
Small calanoid copepods	2442.74	180.98	33.78	11967.74	856.95	43.30	2300.68	262.44	60.87	11611.32	1257.90	49.63
Medium calanoid copepods	39.09	2.27	0.54	507.56	34.11	1.84	77.49	8.54	2.05	981.62	104.41	4.20
Large calanoid copepods	202.69	13.86	2.80	7665.56	506.32	27.74	146.58	43.08	3.88	7993.69	1541.07	34.17

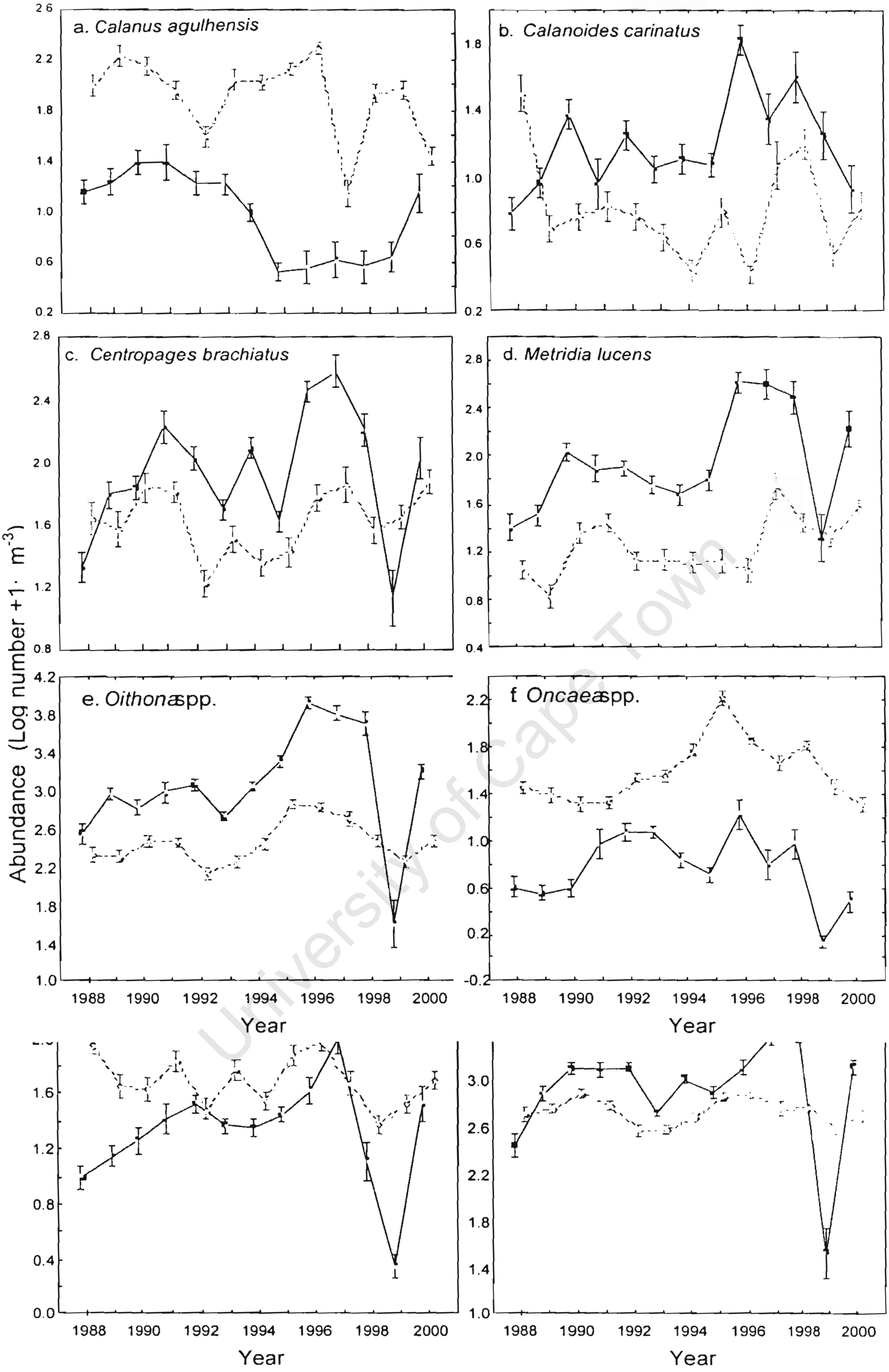

Figure 2. Time-series of mean (± Std. Err) copepod abundance, along the south and west coasts of South Africa from 1988 to 2000. Broken lines represent summer data whereas solid lines represent winter. All data are log (x+1)-transformed. (a) *Calanus agulhensis*, (b). *Calanoides carinatus*, (c) *Centropages brachiatus*, (d) *Metridia lucens* (e) *Oithona* spp., (f) *Oncaea* spp, (g) copepod nauplii and (h) other small copepods

Factors affecting the abundance of size-classes

The five independent variables in the GLM (year, season, area, chlorophyll a and SST) were all found to have significant effects. The final GLM used was of the form:

$$\ln[\text{Copepod abundance } (\text{m}^{-3}) + 1] = \beta_0 + \beta_{year} + \beta_{area} + \beta_{season} + \beta_1 \times chl + \beta_2 \times SST$$

where β_0 is the model intercept, β_1 and β_2 are model coefficients for the continuous variables, and β_{year}, β_{area} and β_{season} are model parameters for categorical variables. The estimated values for the model parameters are given in Table 4.

Relative to their abundance on the eastern Agulhas Bank, all four size classes of copepods tended to have greatest abundance on the north and central West Coast, reduced abundance on the south West Coast and western Agulhas Bank, and similar abundance on the central Agulhas Bank (Fig. 3). The only exceptions were for small calanoid copepods (Fig. 3b), which had slightly greater abundance on the central Agulhas Bank than the eastern Agulhas Bank, and for medium calanoid copepods (Fig. 3c), which had greater abundance on the south West Coast than the eastern Agulhas Bank. The fact that all the size-classes (except for small calanoid copepods) showed a non-significant change ($p>0.05$) in abundance on the central Agulhas Bank (Table 4) indicates that the central and eastern Agulhas Bank had similar abundances. The greatest relative variability was shown by the cyclopoid (Fig. 3a) and large calanoid (Fig. 3d) copepods on the north West Coast, where abundances were much enhanced.

The GLM parameter estimates for cyclopoid copepods and small calanoid copepods showed that these size-classes had greater abundance in winter than in summer (parameter values of winter: 0.11, $p<0.01$; 0.04, $p < 0.01$ respectively), whereas abundance of medium and large calanoid copepods did not show significant seasonal differences (Table 4). In addition, Table 4 shows that the small copepods (cyclopoid copepods and small calanoid copepods) have a positive linear relationship with chlorophyll *a* and a negative relationship with temperature, whereas the medium and large calanoid copepods did not show a relationship with these two environmental variables.

Changes in abundance of size-classes over time

When copepod size-class abundance is corrected for other factors using the GLM results, the four size classes show some similar trends over time in relative abundance (Fig. 4). Relative to their abundance in 2000, all the size classes had enhanced abundance from 1996-1998. Cyclopoid and small calanoid copepods had mostly reduced abundance from 1988-1993, whereas medium and large calanoid copepods tended to have enhanced abundance from 1988-1992. Medium and large calanoid copepods had very reduced abundance in 1995.

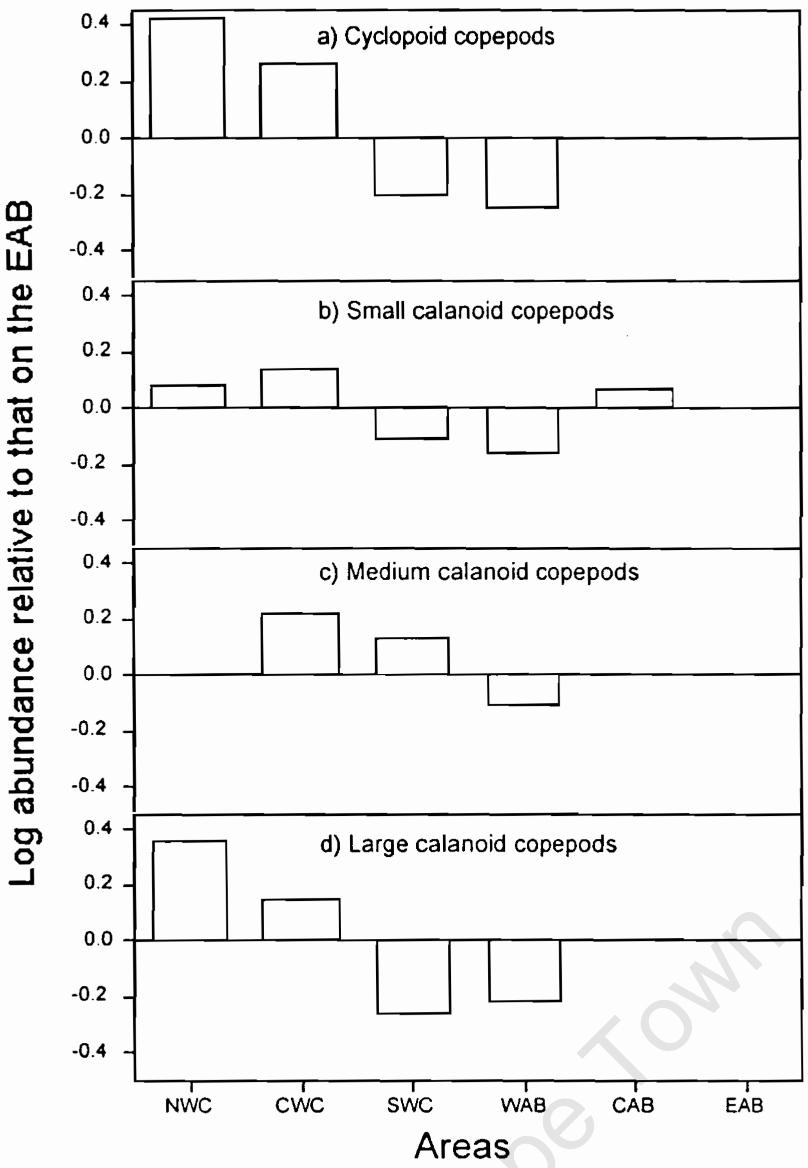

Figure 3. Results of the GLM showing the relative abundance of different size classes of copepods in different areas, after taking into account the effects of inter-annual differences, season, chlorophyll and SST. Note that the EAB is the reference point in all cases (relative abundance = 0). a) cyclopoid copepods, b) small calanoid copepods, c) medium calanoid copepods, d) large calanoid copepods.

Table 4. Results of the GLM analysis investigating the variables influencing the abundance of copepod size-classes (cyclopoid copepods, small calanoid copepods, medium calanoid copepods and large calanoid copepods) using sigma-restricted parameterization. Grouping variables are *year, season* and *area*, continuous variables are *SST* and *Chlorophyll a*. All of the variables were statistically significant in the model. For each variable the appropriate parameter estimate (Par. Est.) is given together with its standard error (SE) and probability value (p). The reference points (i.e. value=0) for each of the categorical variables were: *year* 2000, *season* summer, and *area* EAB. R^2 of cyclopoid copepods = 0.40, R^2 of small cal. cop. = 0.17, R^2 of medium cal. cop. = 0.06 and R^2 of large cal. cop. = 0.13.

Level of Effect	N	Cyclopoid copepods			Small cal. Cop			Medium cal. Cop			Large cal. Cop.		
		Par. Est.	Std Err.	p	Par. Est.	Std Err.	p	Par. Est.	Std Err.	p	Par. Est.	Std Err.	p
Intercept	2051	4.39	0.39	**	4.49	0.37	**	1.02	0.02	**	1.82	0.01	**
1988	127	-0.19	0.04	**	-0.11	0.04	*	ns	ns	ns	0.11	0.04	*
1989	153	-0.16	0.04	**	ns	ns	ns	ns	ns	ns	0.10	0.05	*
1990	182	ns	ns	ns	0.13	0.04	**	0.12	0.05	*	0.09	0.05	*
1991	159	ns	ns	ns	0.08	0.04	*	0.17	0.06	**	ns	ns	ns
1992	215	-0.08	0.03	*	ns	ns	ns	ns	ns	ns	-0.26	0.04	**
1993	239	-0.17	0.03	**	-0.12	0.03	**	-0.11	0.05	0.02	ns	ns	ns
1994	271	ns	ns	ns	ns	ns	ns	0.09	0.04	0.04	ns	ns	ns
1995	146	0.11	0.04	*	-0.17	0.04	**	-0.38	0.05	**	-0.23	0.04	**
1996	136	0.44	0.04	**	0.12	0.04	**	0.32	0.06	**	0.19	0.05	**
1997	72	0.30	0.06	**	0.16	0.06	**	ns	ns	ns	ns	ns	ns
1998	149	0.12	0.04	**	0.19	0.04	**	ns	ns	ns	0.23	0.05	**
1999	78	-0.29	0.06	**	-0.14	0.05	*	ns	ns	ns	ns	ns	ns
Winter	938	0.11	0.01	**	0.04	0.01	**	ns	ns	ns	ns	ns	ns
NWC	250	0.42	0.04	**	0.08	0.04	*	ns	ns	ns	0.36	0.03	**
CWC	516	0.26	0.03	**	0.14	0.03	**	0.22	0.03	**	0.15	0.03	**
SWC	304	-0.20	0.03	**	-0.11	0.03	**	0.13	0.04	**	-0.26	0.03	**
WAB	468	-0.25	0.02	**	-0.16	0.02	**	-0.11	0.03	**	-0.22	0.03	**
CAB	339	ns	ns	ns	0.07	0.03	*	ns	ns	ns	ns	ns	ns
SST.		-1.24	0.31	**	-1.22	0.29	**	ns	ns	ns	ns	ns	ns
Chl. *a*.		0.11	0.04	*	0.10	0.04	*	ns	ns	ns	ns	ns	ns

* p<0.05, ** p<0.01, ns = not significant, N = number of samples

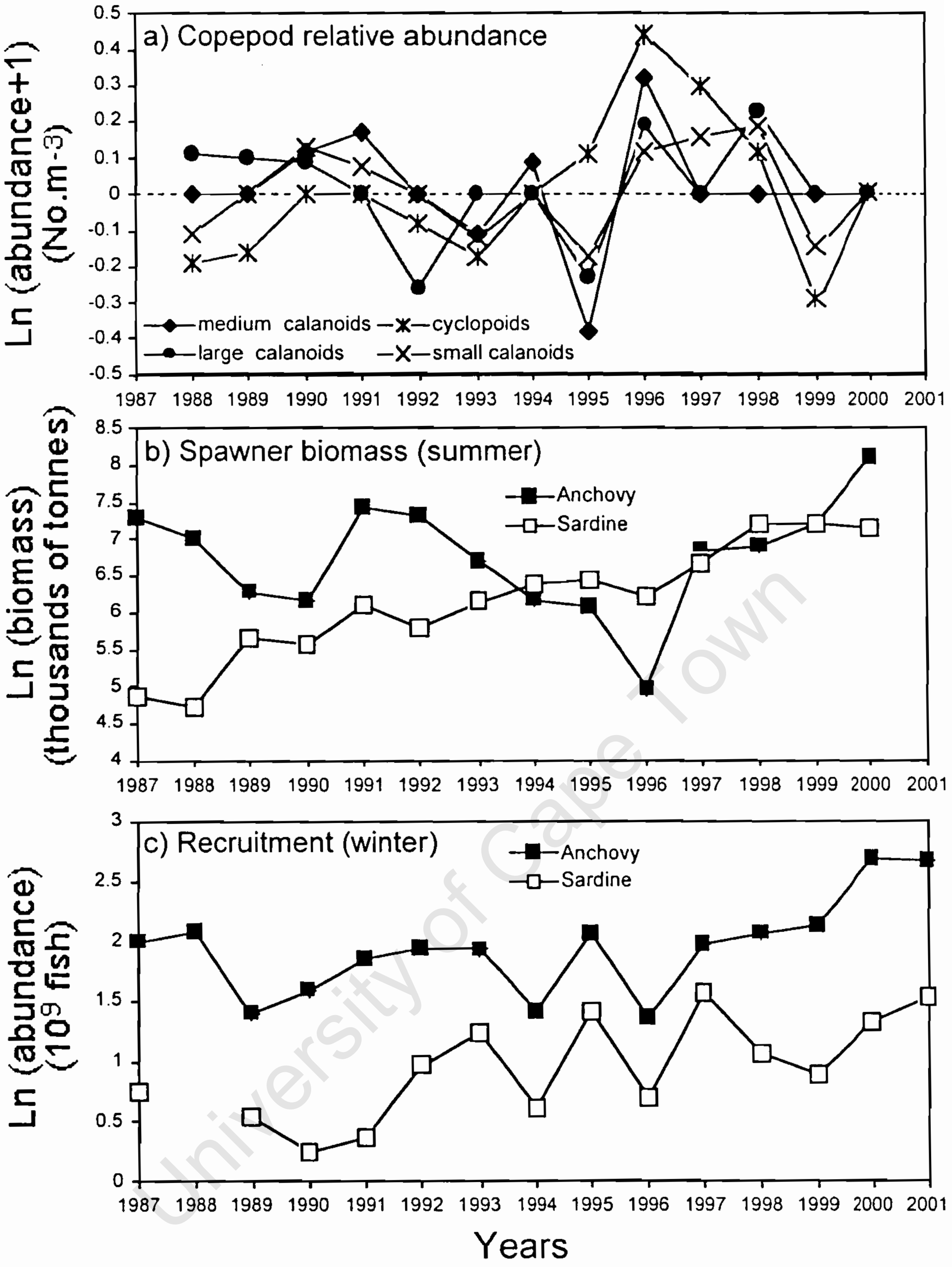

Figure 4. Results of the GLM showing the relative log abundance of different size classes of copepods over time, after taking into account the effects of area, season, chlorophyll and SST. Note that 2000 is the reference year in all cases (relative abundance = 0). a) Copepod relative abundance, b) estimates of spawner biomass of sardine and anchovy, and c) estimates of recruitment for sardine and anchovy.

DISCUSSION

Sample collection and analysis of copepod abundance and species composition were carried out in the same way throughout the study period (1988 – 2000). Therefore it is important to note that the observed changes in copepod abundance and community structure were not due to any sampling or processing artifacts. However, it should also be noted that the time series was relatively short (13 years), and the frequency of sampling (twice per year) was relatively low, because of necessary financial and logistic constraints.

Species change in abundance

The general declining pattern of *Calanus agulhensis* both in winter and summer (Fig. 2) could be attributed to a top-down effect of cumulative predation pressure by sardine and anchovy. This species is most abundantly found on the central Agulhas Bank (Huggett and Richardson, 2000), meaning that the changes of *Calanus agulhensis* in Fig. 2. could be due to fluctuations observed in that sub-area. Van der Lingen *et al.* (2001) indicated that there has been a shift in spawning ground for anchovy east of Cape Point since 1994, and Barange *et al.* (1999) found that anchovies move eastward to the Agulhas Bank as they grow older. Therefore, the accumulation of older anchovies on the Agulhas Bank, which is the core residence area of *Calanus agulhensis* (Huggett, 2003), could be the reason for its decline after the mid 1990s.

Calanoides carinatus, whose core is the West Coast (Huggett, 2003), fluctuates greatly in abundance from year to year. However its continued decline in winter over the last three years of the study period (1998 – 2000) is likely due to a markedly increasing predation pressure by exceptionally high densities of anchovy recruits during these years, primarily on the West Coast. *Centropages brachiatus, Metridia lucens* and *Oithona* spp. show generally increasing patterns in both winter and summer throughout the study period, except in 1999 (Fig. 2), when their abundance was very low. *Oncaea* spp. increases till the mid 1990s, but decreases in abundance thereafter, and also showed a sudden decline in winter 1999. There was no substantial change in abundance or biomass of either sardine or anchovy in 1999, indicating that the sudden decline in abundance of all these copepods that year is probably not due to a top-down effect. Demarcq *et al.* (2002) showed that the monthly average of chlorophyll *a* (using SeaWiFS Global Area Coverage data) was considerably reduced in June 1999 in the southern Benguela (Fig. 5). This event could have had a direct or indirect negative effect on the abundance of these copepod species through the lack of food, indicating a bottom-up control in that particular year.

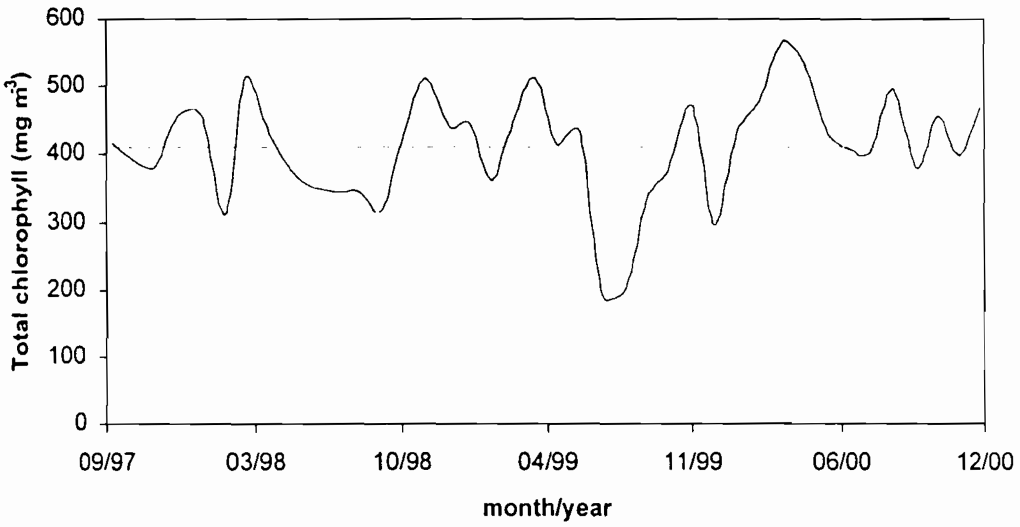

Figure 5. Total chlorophyll *a* concentration in the southern Benguela 1997-2000, from SeaWiFS data (after Demarcq *et al.*, 2002).

Size-class change in abundance

The most noticeable features of the trend in abundance of all size-classes are the relatively constant values till 1994, the small values in 1995, the relatively large values from 1996 to 1998, and the reduction in the two small size classes in 1999 (Fig. 4). Anchovy and sardine recruits (in winter) generally increased from 1988 to 2000 (Fig. 4c), but do not appear to have affected the total copepods during the early part of this period. The decrease in copepods in 1995 is unexplained here, but it occurred when sardine and anchovy recruitment was relatively high, and was followed in 1996 by very reduced anchovy spawning biomass, implying a possible bottom-up effect. Both copepods and fish increased in abundance after 1996. Continuous predation by an increasing fish population on copepods can eventually inflict a top-down control (Cury *et al.*, 2003), and after 1998 intensified predation pressure by sardine and anchovy recruits and other fish on copepods could have lead to their reduction in abundance from 1998 – 1999, possibly reversing the primary controlling mechanism from bottom-up to top-down.

It is possible that a long-term bottom-up effect influenced the increased abundance of small copepods till 1996, because increased nutrient concentrations in the St Helena Bay region have been observed from the 1950s till 1996 (Verheye, 2000). This increase in nutrient concentration would favour primary production and thereby enhance copepod production in the region. The abundances of the two small copepod size classes were positively related to cholorophyll concentrations, supporting this hypothesis of bottom-up control. Figure 4 shows that elevated abundance occurred in 1996 in all copepod size-classes. Barange *et al.* (1999) showed that in June 1997 there was an increase in biomass of both sardine and anchovy in the southern Benguela. This increase could have initiated the reduction of the copepod abundance via a top-down controlling mechanism, leading to the hypothesis that there was a change in the primary control mechanism of copepods in the southern Benguela in 1996-1997 from bottom-up to top-down.

Cyclopoid copepods had their lowest relative abundance in 1999. The continuous increase in the biomass of sardines (Fig. 4b) (which mainly feed on small copepods (van der Lingen, 1994)) could be an important factor in reducing the abundance of cyclopoid copepods (Verheye, 2000) after the mid 1990s. However, there is no consistent, simple relationship between the abundance of copepods and the abundance of pelagic fish (Fig. 6), indicating that many factors probably operate at different times to influence copepod abundance.

The season and environmental parameters (sea surface temperature and chlorophyll *a*) did not have significant effects on the abundance of large and medium calanoid copepods, whereas these variables significantly affected cyclopoid and small calanoid copepods. This similarity in trends and responses to the environmental variables between cyclopoid copepods and small calanoid copepods, and between medium calanoid copepods and large calanoid copepods, is probably due to their respective size similarities, causing them to respond (e.g. in terms of growth in respect of their susceptibility to size-selective predation) in a similar way to the prevailing control mechanisms.

Spatial change in size-class abundance

The abundance of most copepods was greatest on the north and central West Coast, reduced on the central and eastern Agulhas Bank and lowest on the south West Coast and western Agulhas Bank (Fig. 3). The northern part of the West Coast usually has low abundances of pelagic fish, especially during summer when pelagic fish move to the Agulhas Bank to spawn (Barange *et al*., 1999; C. D. van der Lingen, MCM, pers. comm.). These fish are important predators of copepods. Therefore, the absence of predators in the north could have created a favorable environment to support large abundances of copepods there. Upwelling activity on the West Coast could have also increased the production of copepods there, because of enhanced primary production. In addition, abundances on the north and central West Coast could be supplemented by the introduction (by advection) of copepods to that area from further south around Cape Columbine. During the upwelling season, currents usually move northwards from Cape Columbine (Shillington 1990). The main reason for the low abundance of copepods on the south West Coast and western Agulhas Bank seems to be increased predation pressure by recruiting and spawning pelagic fish in those areas. Hutchings *et al*. (1991) found similar results in that the abundance of mesozooplankton decreased towards the western part of the Agulhas Bank in November, and they suggested that this was caused by predation pressure by spawning anchovy on calanoid copepods.

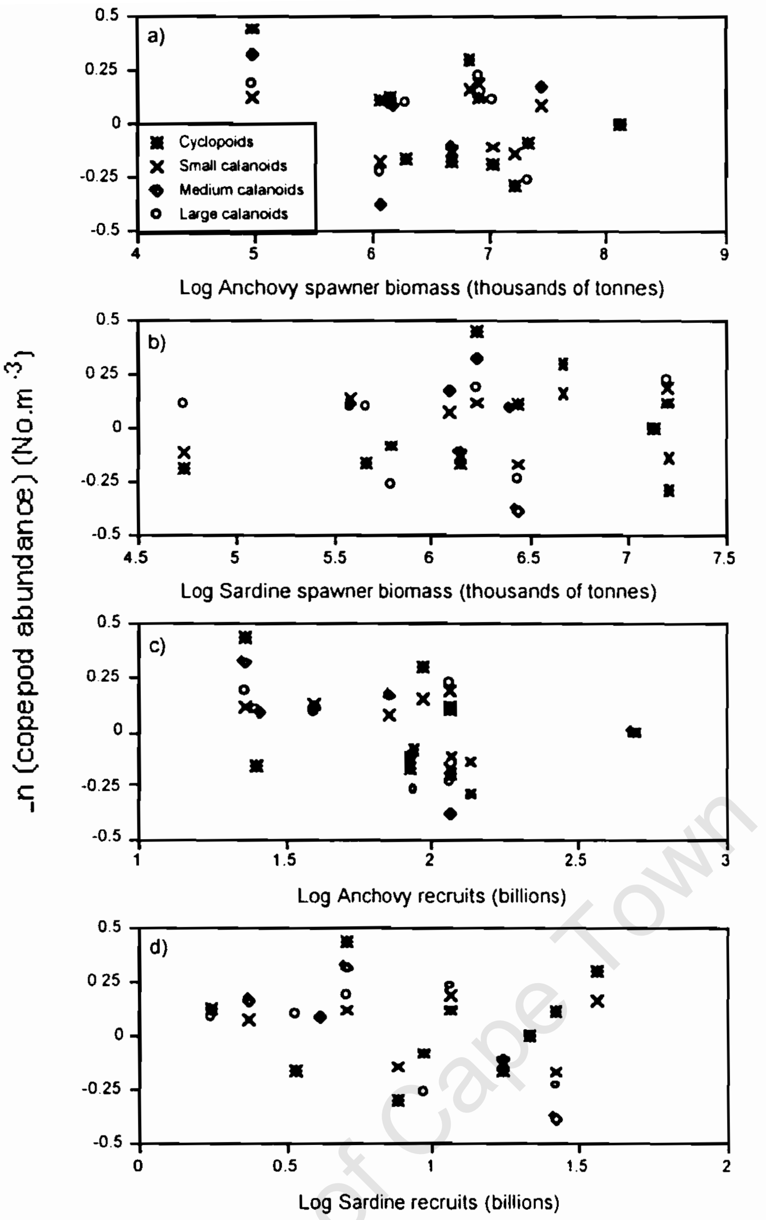

Figure 6. Relationships between the GLM-standardized log abundance of four different size classes of copepods and the log-transformed spawner biomass and numbers of recruits of pelagic fish. a) Copepods versus anchovy spawner biomass, b) copepods versus sardine spawner biomass, c) Copepods versus anchovy recruits, d) Copepods versus sardine recruits

The GLM results in Table 4 are based on assumptions that there are linear relationships between the log-abundance of copepods and the continuous predictor variables, although it is possible to accommodate non-linearities through the careful choice of categorical variables. However, the relationship between copepod abundance and environmental variables can be more complex. Richardson and Verheye (1998) constructed a hypothetical relationship between the growth rate of copepods and chlorophyll *a* concentrations. They graphically showed that the relationship between chlorophyll *a* and copepod growth could vary from a perfectly linear, positive relationship to a perfectly linear, negative relationship depending on the time lag of the growth. Different types of these relationships might describe the relationship between the abundance of different copepod size-classes and chlorophyll *a* concentrations. In their study, Hirst and Sheader (1997) found that the generation time of copepods was positively related to their body weight. Therefore, it could mean that small copepods, with short generation times, have short time-lags for population growth in respect to feeding, whereas large copepods, with long generation times, have longer time-lags. Table 4 shows that the small copepods have a positive linear relationship with chlorophyll *a*, whereas the large copepods have no relationship with chlorophyll *a*. One reason for this could thus be the faster generation time of the small copepods, allowing them to respond faster than the large copepods to improved food conditions.

CONCLUSIONS

In this study, observed changes in abundance of copepods were discussed relative to top-down and bottom-up control mechanisms. Although the copepod data set that was used is more comprehensive than many that exist today, it is still insufficient to resolve issues around the complex factors affecting copepod abundance and distribution. There was no consistent, clear evidence for either bottom-up or top-down control of copepod populations. It was found that small copepods are positively related to chlorophyll concentrations, indicating that bottom-up control might occur. This was further supported by anomalously low chlorophyll concentrations in 1999, when small copepod abundance was much lower than average. However, small copepods tended to be more abundant in winter than summer, implying that some predation mechanisms might operate during different times of the year. Greater than average abundance of medium and large copepods can be interpreted as reduced predation pressure by pelagic fish and/or enhanced copepod production, but these hypotheses require further investigation and validation. Based on the time series observed here, it is hypothesized that there has been a change in the primary control mechanism on the copepod community in 1996/97 from bottom-up to top-down control, following increased predation pressure by pelagic fish recruits.

The findings of this study show that the north and central West Coast had the highest abundances of copepods, the central and eastern Agulhas Bank had lower abundances and the south West Coast and western Agulhas Bank had the lowest abundances of copepods. Therefore, it can be concluded, in conjunction with other studies such us that of Hutchings *et al.* (1991), that the overall spatial distribution of copepods has not changed over the past two to three decades in the southern Benguela.

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