Temporal and spatial variability in copepod abundance, distribution and community structure off Walvis Bay in the northern Benguela Current, 1979-1981

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A thesis submitted in fulfilment of the requirements for the degree of Magister Scientiae, in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

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November 2005

DECLARATION

I declare that *Temporal and spatial variability in copepod abundance, distribution and community structure off Walvis Bay in the northern Benguela Current, 1979-81* is my own work, that it has not been previously submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been acknowledged and indicated as complete references.

Sakhile V. Tsotsobe November 2005

Signed: ....

TEMPORAL AND SPATIAL VARIABILITY IN COPEPOD ABUNDANCE, DISTRIBUTION AND COMMUNITY STRUCTURE OFF WALVIS BAY IN THE NORTHERN BENGUELA CURRENT, 1979-1981

KEY WORDS: zooplankton, SWAPELS, Walvis Bay, biomass, total copepod abundance, copepod community structure, *Calanoides carinatus*, *Centropages brachiatus*, *Metridia lucens*, *Rhincalanus nasutus*

ABSTRACT

The zooplankton samples used for retrospective analysis in this study form part of the historical SWAPELS (South West African Pelagic Egg and Larva Survey) collection from January 1972 to December 1989, which covered the entire Namibian shelf. The SWAPELS Programme was initiated following the collapse of the Namibian sardine fishery during the late 1960s and early 1970s. This study investigates variability in the temporal and spatial distribution of total zooplankton (non-gelatinous) biomass, total copepod abundance, as well as copepod community structure off the coast of Walvis Bay along, primarily, transect 70 (23° S), and secondarily, transects 66 (22°67 S) and 74 (23°33 S), over the period 1979-1981. Included in the data set are sea surface temperatures (SSTs) and surface salinities, allowing for spatio-temporal trends in the hydrology of this region to be examined.

Despite extensive variability in SST (11.27-18.15 °C), the most frequently occurring SSTs were in the 15-16 °C range. In 1979 salinities ranged mostly between 35.1 and 35.2, whereas in 1980 and 1981 modal salinities fell within the 35.0-35.1 and 35.2-35.3 ranges, respectively. A clear seasonal pattern in the cross-shelf distribution of SST and salinity was observed in 1979-80, when, generally, warm, high-salinity water covered most of transect 70 (23° S) in summer to early autumn. In spring the cool inshore water extended seaward, to recede again into summer. The existence of cool inshore surface water from mid-winter to mid-spring, warming up into summer and extending offshore, was indicative of a typical upwelling cycle off Walvis Bay.

Cross-shelf distribution of zooplankton biomass exhibited multiple peaks, mostly bimodal, attributable to the effects of coastal upwelling. Similarly, total copepod abundance showed a 'delayed' response to the surge of cool, low-salinity water in late autumn and spring commonly observed during upwelling. However, variability in total copepod abundance was not necessarily reflected in total zooplankton biomass. This pointed to the changes over time in the taxonomic composition of the zooplankton, which, in general, does not remain constant, as the zooplankton comprises other taxa in addition to copepods.

Cluster analyses revealed copepod communities grouped according to both cross-shelf and alongshore distribution. However, no clear seasonal patterns could be discerned, probably due to loss of information caused by shortfalls during sample collection and analysis. From the cluster analysis it emerged that four calanoid copepod species were mainly responsible for the structuring of copepod communities, namely, *Calanoides carinatus*, *Centropages brachiatus*, *Metridia lucens* and *Rhincalanus nasutus*. These species displayed some specific distribution characteristics. *C. carinatus* was associated with cool waters, occurring mainly close to the shore, and was most abundant during the upwelling season. *M. lucens* also increased in numbers after upwelling, but was also present in the absence of upwelling. *C. brachiatus* was abundant during 1979, and was almost absent during 1980-81. *R. nasutus* also increased in numbers during spring and summer, but was not necessarily restricted to the inshore region. The spatio-temporal distribution of these four species is indicative of their respective life history strategies: the herbivorous *C. carinatus* and *R. nasutus* being associated with conditions of upwelling and high phytoplankton biomass; and the omnivorous *C. brachiatus* and *M. lucens* showing a generally uniform spatio-temporal distribution throughout the year.

Finally, biomass and abundance data from this study are discussed in the context of long-term variability – over the period 1959-2004. An increasing trend in both biovolume and total copepod abundance was observed. Moreover, this trend was also reflected in the abundances of *C. carinatus* and *M. lucens*, but not *C. brachiatus* and *R. nasutus*, suggesting long-term changes in community structure.

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1 Introduction

The Benguela Current region, as defined in Shannon and Nelson (1996), is situated between approximately 14° S and 37° S, with the western boundary at the 0° meridian (Fig. 1). The northern boundary of this region is marked by the Angola-Benguela surface frontal zone, between 14 and 17° S (Shannon *et al*. 1987, Meeuwis and Lutjeharms 1990). The Agulhas retroflection area – typically between 36 and 37° S (Lutjeharms and Meeuwis 1987) – is considered to be the southern boundary of the Benguela, which Shannon and Nelson (1996) describe as a product of oceanographic, topographic, meteorological and biological factors acting in synergy. The northern and the southern subsystems of the Benguela are separated by a semi-permanent upwelling cell off Lüderitz (27 °S), which, together with other identified latitudinal and longitudinal pelagic borders, have been reported to act as environmental barriers to fish and planktonic biota (Shannon 1988, Barange *et al*. 1992, Gibbons and Hutchings 1996). The bathymetry of the continental shelf is variable: it is narrow off southern Angola, south of Lüderitz, and off the Cape Peninsula (20, 75 and 40 km, respectively); and it is at its widest off the Orange River and in the southern-most region of the Benguela (Agulhas Bank), at 180 and 230 km, respectively.

Winds in the Benguela system are known to be controlled by three forces: an anticyclonic motion round the South Atlantic high-pressure system; the seasonal low pressure field over the subcontinent; and east-moving cyclones which cross the southern part of the continent (Shannon and Nelson 1996). Although the South Atlantic anticyclone persists throughout the year, it displays some seasonal variations in pressure, to the order of 3-4 mb. For instance, it shifts over 6° of latitude to reach northern and southern extremities in May and February, respectively. It then shifts 13° of longitude, reaching an extreme westward position in August (Tyson 1986, as cited in Shannon and Nelson 1996).

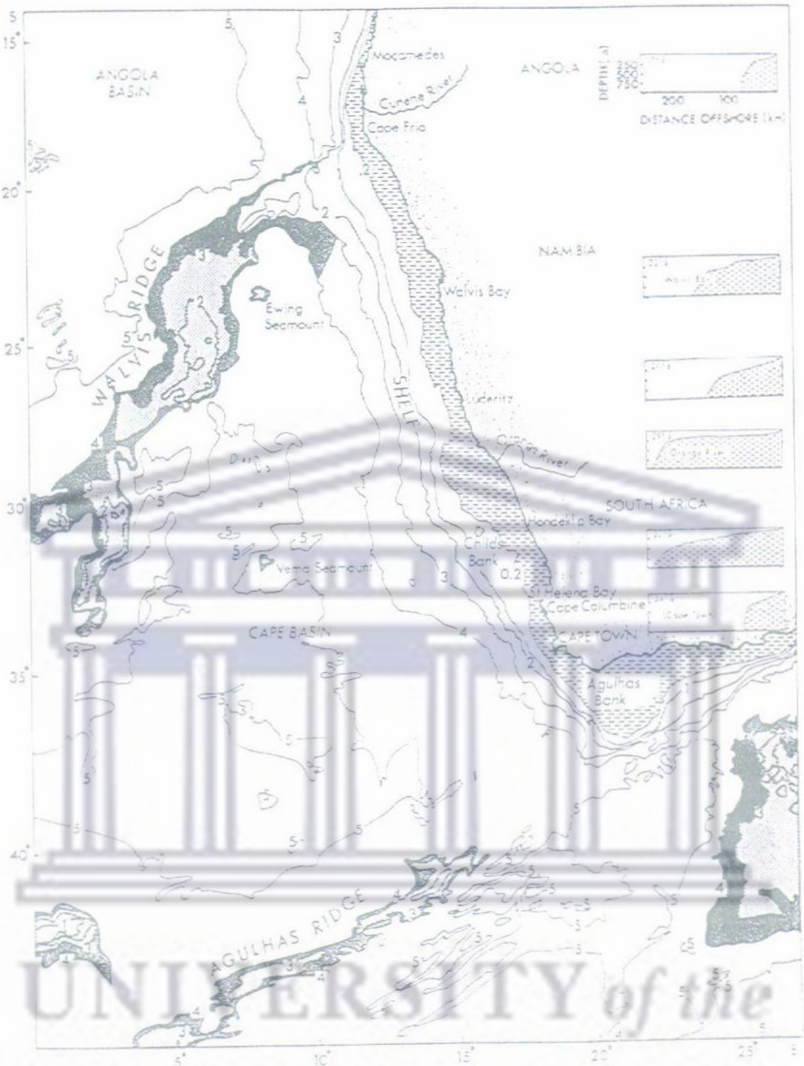

Fig. 1: Map showing the Benguela Current region off the coast of southern Africa (after Shannon and Nelson 1996)

Thus, there is anticyclonic wind-stress curl, which results in strong westerly zonal winds that blow during all seasons, reaching a maximum and minimum in the austral winter and summer, respectively (Shannon and Nelson 1996). The area south of 25 °S is known to be the region of strongest alongshore winds, which prevail in all seasons (Bakun and Nelson 1991).

Bakun and Nelson (1991) identified a coastal wedge-shaped area of strongest cyclonic wind-stress curl (Fig. 2). Just south of this cyclonic wind stress curl lies the principal centre of perennial upwelling-favourable winds, near Lüderitz, and a secondary centre of upwelling-favourable winds near Cape Frio (18 °S). The northward shift of the pressure system in winter (June-July) has an influence in the south, where an increase in the frequency of westerly winds can be observed. These westerly winds do not cause upwelling. In other words, in the southern Benguela, upwelling-favourable winds are most prominent during spring and summer (27 °S), with the upwelling season occurring between September and March. On the other hand, in the southern (as far as 25 °S) part of the northern Benguela, upwelling is perennial, with a spring-summer maximum and an autumn minimum. Off central Namibia, there are lower wind speeds and there is little seasonality in upwelling. Off northern Namibia, near Cape Frio, upwelling occurs during autumn and spring, as the alongshore winds are strongest during this time.

The northern Benguela is characterised by episodic climatic and hydrological events, which are manifest as extreme warming in the tropical eastern Atlantic, as well as the advection of tropical water southwards along the coast of Namibia (Shannon *et al*. 1986, Boyd *et al*. 1987a, and Shannon and Nelson 1996). Even though this southward intrusion of warm (20-24 °C), saline (35.4-35.5) Angolan water has been described previously by Hart and Currie (1960) and Stander (1964), Boyd *et al*. (1987a) gave a more comprehensive account using the events of 1973-1974 and 1979-1986. Furthermore, these intrusions can be extreme, to such an extent that they can be likened to the *El Niño* phenomenon of the southern Pacific Ocean. Stander and De Decker (1969) and Boyd *et al*. (1987a) described such events during 1963 and 1984, respectively, resulting in the coining of the term *Benguela Niño*. This movement of water onto the northern and central Namibian shelf mostly occurs in summer and early autumn – in March extending as far south as 18 °S.

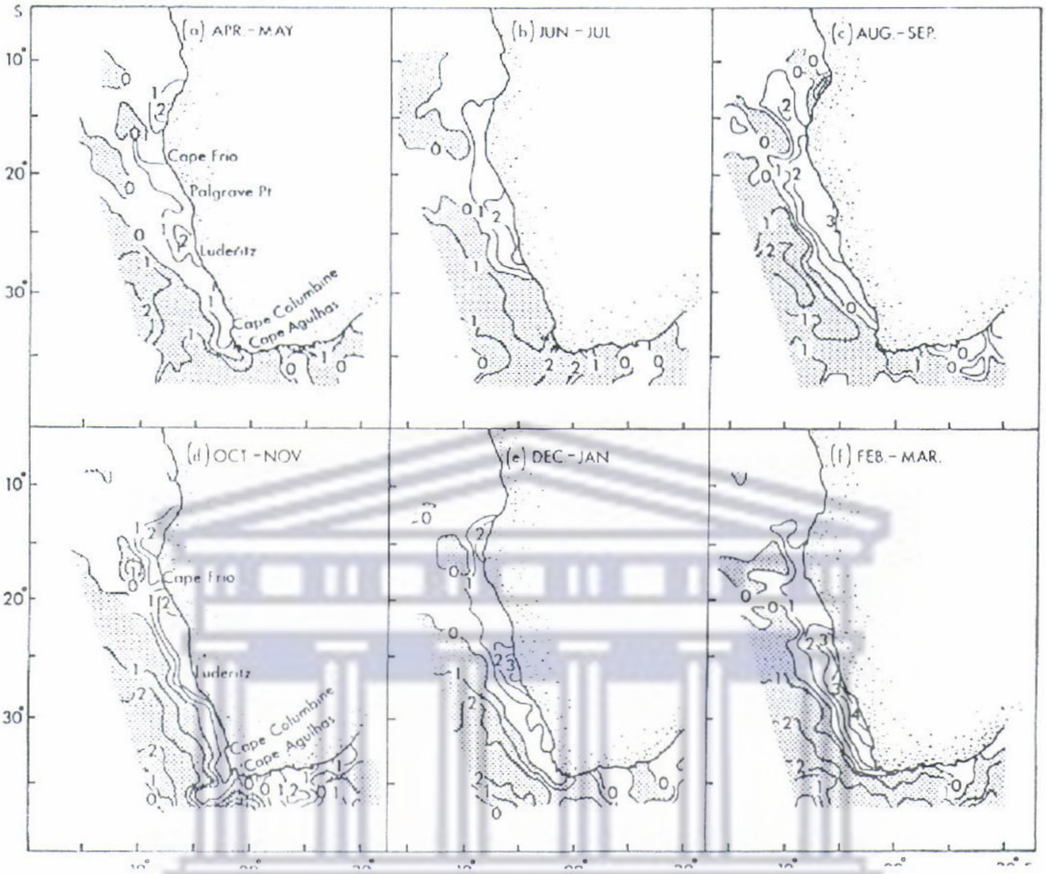

Fig. 2: Wind-stress curl (10^{-8} dyn.cm^{-3}) in the Benguela region (a-f). Regions of anticyclonic wind-stress curl are shaded (modified by Shannon and Nelson 1996, after Bakun and Nelson 1991)

These intrusions appear to negatively affect the fisheries of the region, as they have been observed to have an adverse impact on the spawning areas of sardine *Sardinops sagax* and Cape anchovy *Engraulis encrasicolus*, and on the distribution of juvenile Cape horse mackerel *Trachurus trachurus capensis* (Boyd *et al.* 1987b). The anomalies have also been observed to result in low recruitment of other species, such as the bivalve *Donax serra* (Birkett and Cook 1987).

Although there is variability in chlorophyll *a* concentration throughout the Benguela, Brown *et al.* (1991) reported on highest surface concentrations north of Lüderitz in the northern Benguela. In the southern Benguela, the highest concentrations were observed between Cape Columbine and Cape Point, with lowest values on the south coast. Furthermore, in terms of phytoplankton biomass, there were similar quantities on the west and south coasts of the southern Benguela. The northern Benguela, however, was generally richer in terms of phytoplankton biomass than the southern Benguela. Interestingly, Brown *et al*. (1991) found primary production to be higher in the southern than in the northern Benguela. They subsequently speculated that the reason for this might be the inhibition of production by self-shading of phytoplankton stocks, which otherwise accumulate in the northern Benguela. The overall estimated primary production in the Benguela was between 70 and 80 million tonnes of carbon per year.

Waldron *et al*. (1997a, b) highlighted the interactions and relationships between the physical forcing – in particular upwelling – and potential new production. They regarded new production to be the amount of NO_3-N made available to phytoplankton via upwelling dynamics, as opposed to the amount of NO_3-N actually incorporated in phytoplankton biomass. As a result of their studies in the southern Benguela, they confirmed the "optimal environmental window" hypothesis (Cury and Roy 1989, Roy *et al*. 1992), which suggested that there was an optimal environmental window in which anchovy biomass was maximised by a median range of upwelling. Primary production is an essential component of the marine ecosystem trophic structure.

Jarre-Teichmann *et al*. (1998) described trophic flows in the southern Benguela using network analysis. Plankton and benthic invertebrates formed the link between primary production and the pelagic fish anchovy, sardine, chub mackerel *Scomber japonicus*, and round herring *Etrumeus whiteheadi*; of all the pelagic species, sardine fed lowest in the food web: horse mackerel, chub mackerel and some demersal fish were placed higher but on comparable trophic levels, even though they had different diets; hake and large pelagic fish were the top predators, their trophic positions being exceeded only by sharks, whales, seals and seabirds. Jarre-Teichmann *et al*. (1998) further reported that in the southern Benguela zooplankton was most important with regard to flow of energy in the system, as compared to other systems such as the Humboldt Current, where zooplankton was less limiting for higher trophic levels. Furthermore, in the southern Benguela anchovy was a competitor with horse mackerel, whereas it was prey for horse mackerel in the Humboldt.

The Benguela ecosystem supports several fisheries, with the most exploited species being the shallow-water hake *Merluccius capensis* and deep-water Cape hake *M. paradoxus*, sardine, anchovy, Cape horse mackerel, and the small, yet valuable fishery for West Coast rock lobster *Jasus lalandii* (Schülein *et al.* 1995, Boyer and Hampton 2001). Various studies in the southern Benguela (e.g. Le Clus and Kruger 1982, James 1987, van der Lingen 1994, Richardson *et al.* 2003) revealed that sardine and anchovy are important predators on zooplankton – mainly copepods. It has also been shown that, when these species co-occur, they are never simultaneously abundant (Schülein *et al.* 1995), and this becomes reflected in "regime" shifts in copepod communities (Verheye *et al.* 1998, Cury *et al.* 2000) as these pelagic fish are known to be selective feeders (James 1987, van der Lingen 1994, Louw *et al.* 1998).

James (1987) found that calanoid copepods (0.5-2 mm body length) were the dominant items in the diet of *E. encrasicolus*. Furthermore, his data showed that *E. encrasicolus* filter-fed on particles less than 0.5 mm in maximum dimension, whereas it selectively preyed on organisms greater than 0.7 mm maximum dimension. The author further asserted that anchovy showed a strong preference for larger items even when small prey were more abundant. Also, filter-feeding decreased with increasing fish length. He concluded that in upwelling areas anchovies were secondary rather than primary consumers.

Similarly, van der Lingen (1994) demonstrated how sardine switches its feeding mode from filter-feeding to particulate feeding, depending on size and concentration of available prey. High concentrations of zooplankton elicit a filtering response. Filter feeding is favoured under conditions when prey are small relative to fish, and are present in high concentrations, and light intensity is low. In contrast, particulate feeding is the preferred mode when the prey is large relative to the fish and present in low concentration, and light is sufficient for visual feeding.

In the Benguela ecosystem copepods are the most dominant zooplankton taxon, both numerically and in terms of biomass (Verheye and Hutchings 1988, Timonin 1990, Timonin *et al.* 1992, Verheye *et al.* 1992, Hansen *et al.* 2005). Their horizontal and vertical distributions have been well documented (e.g. Pillar 1984a, Verheye and Hutchings 1988, Verheye 1991, Verheye and Field 1992, Stuart and Verheye 1991). Literature on zooplankton ecology in the Benguela has, throughout the decades, shown that because of their large contribution to total zooplankton biomass, three to five dominant copepod species govern the distribution of total zooplankton biomass on both spatial and temporal scales. In the northern Benguela, in particular, the dominant species are *Calanoides carinatus*, *Rhincalanus nasutus*, *Metridia lucens*, and *Centropages brachiatus* (Unterüberbacher 1964, Timonin *et al.* 1992, Hansen *et al.* 2005).

Stander and De Decker (1969), Visser *et al.* (1973), Kruger (1983), Fearon *et al.* (1986), Olivar and Barange (1990), Barange and Boyd (1992), Timonin *et al.* (1992), Richardson *et al.* (2001), and Verheye *et al.* (2001) reported on the abundance and distribution of zooplankton assemblages off the coast of Namibia, based on staggered and sparse sampling programmes, therefore providing "snapshot" impressions of zooplankton abundance and distribution in this region. However, notwithstanding the fact that these works were limited in temporal coverage, they covered a greater spatial area (both vertically and horizontally) in comparison to data collected during, for instance, the monthly SWAPELS (South West African Pelagic Egg and Larva Survey) surveys off the entire coast of Namibia (see Chapter 2 for a detailed description). The themes which are highlighted in these works include the ecological characteristics of zooplankton in relation to upwelling phases (Timonin *et al.* 1992) and other hydrological conditions (Stander and De Decker 1969, Kruger and Boyd 1984, Fearon *et al.* 1986, Timonin 1991), primary production (Kruger 1983; Kruger and Boyd 1984, Fearon *et al.* 1986), egg and larval distribution of clupeioid fish species (King 1977, Olivar 1990), and zooplankton horizontal and vertical distribution, migration and production (Barange 1989; Timonin 1990, 1991 and 1992, Richardson *et al.* 2001, Verheye *et al.* 2001). To date, there have not been any published seasonal studies on mesozooplankton in the northern Benguela, which cover a full annual cycle, except for works by Kollmer (1963) and Unterüberbacher (1964) in the late 1950s and early 1960s, and the recent work by Hansen *et al.* (2005) based on samples collected along one transect in 2000. However, all these studies are based on samples that cover one annual cycle.

The data presented here are derived from the retrospective analysis of zooplankton samples collected over a period of three consecutive years (1979-81), with up to nine months of sampling each year, and extending to a distance of 65 nautical miles (n. m.) offshore. The availability of the SWAPELS samples thus presents a unique opportunity to describe temporal and spatial variations in the abundance of mesozooplankton of this region over a period of three consecutive years, and to attempt to compare these data with historic data and recent data. A long-term increase in zooplankton abundance has been observed in the southern Benguela, attributed to both top-down and bottom-up control mechanisms (Verheye *et al.* 1998, Verheye and Richardson 1998, Verheye 2000). There are no published time-series data for the northern Benguela. In other eastern boundary current systems (e.g. the Californian, Guinea, and Humboldt Current systems) where there has also been large-scale intensification in coastal upwelling, a long-term decline in zooplankton has been reported (Carrasco and Lozano 1989, Mensah 1995 as cited in Verheye 2000, Roemmich and McGowan 1995). Classically, in all these systems bottom-up control – by way of changes in climate and ocean circulation – has been suggested as being the operating mechanism influencing the decrease in zooplankton.

This project seeks to answer the following key questions:

(a) Are there any seasonal and interannual changes in the abundance and distribution of coastal zooplankton off Walvis Bay?

(b) Are there any changes with time in copepod community structure in this area?

(c) How do these data compare with previous and subsequent data sets collected off Walvis Bay over the past five decades?

2 Material and methods

The zooplankton samples used for retrospective analysis in this study form part of the historical SWAPELS (South West African Pelagic Egg and Larva Survey) collection of monthly sampling from January 1972 to December 1989, which covered the entire Namibian coast. A detailed description of the surveys can be obtained from various sources such as Le Clus and Kruger (1982), Kruger (1983), Kruger and Boyd (1984), Le Clus (1985), Fearon *et al.* (1986), Barange and Boyd (1992), Barange *et al.* (1992), Pagès (1992), and O'Toole (1999). For the purpose of this thesis, samples collected off Walvis Bay (approximately at 23° S) between January 1979 and December 1981 were analysed. Among these SWAPELS samples were zooplankton collections acquired on board various ships-of-opportunity (Kruger 1983, Kruger and Boyd 1984; A. J. Boyd, M&CM, pers. comm.).

2.1 *The research area*

Throughout the past five to six decades, the largest catches of anchovy and sardine off Namibia have been reported off Walvis Bay, making this part of the coast the centre of the Namibian pelagic fisheries (Pieterse and van der Post 1967, Cram and Visser 1972, Boyer *et al.* 2001). This resulted in the pelagic fishery (from landing sites to processing factories) being located in and around the city of Walvis Bay.

This coastal area has a wide and shallow continental shelf, which is seen to play a major role in the hydrological characteristics of the area (Boyd 1983). Winds show diurnal variation (Boyd 1983) and there is a strong seasonal occurrence of thermoclines – with most occurrences in summer, followed by a rapid decline in frequency of occurrence in autumn through winter, to increase again in spring (Du Plessis 1967). It has been suggested that this coast is characterised by a semi-enclosed circulation which, together with moderate wind speeds, has been seen to reduce advective losses of euphausiid assemblages, thereby maintaining high productivity and retaining plankton assemblages in this area (Brown *et al.* 1991, Barange and Boyd 1992). Moreover, the coastal zone off Walvis Bay has been reported by Le Clus (1989) to be an important spawning area for sardine.

2.2 SWAPELS sampling programme

Subsequent to the collapse of the sardine fishery in Namibia – notably in 1969 and 1970 (Cram and Visser 1972, Cram 1978, Boyer *et al.* 2001), an extensive scientific programme, named the Cape Cross Programme, was initiated in 1972 (Cram and Visser 1972). SWAPELS formed part of this umbrella programme with the aim to monitor the distribution and abundance of eggs and larvae of primarily sardine, and subsequently anchovy and Cape horse mackerel.

The SWAPELS surveys were timed to coincide with the spawning of the commercially exploited pelagic fish species (mainly sardine and anchovy), therefore sampling took place only for nine months of the year (Table I gives an example of the timing of sampling). The works by King (1977), O'Toole (1977) and Le Clus (1979) were used as a basis for the timing of sampling eggs and larvae (Le Clus 1985).

The SWAPELS grid extended from the Kunene River (approximately 17° S) in the north to near Lüderitz (approximately 27° S) in the south (Fig. 3). Only on one occasion (1983) did the survey extend south of Lüderitz, as far south as St Helena Bay in South Africa (Kauvee 2005).

Table I: Timing of anchovy egg cruises off Namibia, during SWAPELS 1978-82 (only cruises applicable to this study). Adapted from Le Clus (1985)

Survey	Cruise dates
1978/79	
Aug	21.08.78 - 25.08.78
Oct	13.10.78 - 23.10.78
Nov	08.11.78 - 21.11.78
Dec	30.11.78 - 13.12.78
Jan	12.01.79 - 24.01.79
Feb	06.02.79 - 19.02.79
Mar	10.03.79 - 22.03.79
Apr	13.04.79 - 23.04.79
1979/80	
Oct	15.10.79 - 24.10.79
Nov/Dec	25.11.79 - 07.12.79
Jan	11.01.80 - 21.01.80
Feb	11.02.80 - 22.02.80
Mar	22.03.80 - 01.04.80
1980/81	
Sep	20.09.80 - 30.09.80
Nov/Dec	26.11.80 - 06.12.80
Jan	16.01.81 - 28.01.81
Feb	14.02.81 - 26.02.81
Mar/Apr	24.03.81 - 04.04.81
1981/82	
Sep	13.09.81 - 24.09.81
Nov/Dec	30.11.81 - 12.12.81
Jan	12.01.82 - 24.01.82
Feb	13.02.82 - 24.02.82
Mar	20.03.82 - 29.03.82

The grid consisted of 28 transects positioned 20 n. m. (nautical miles) apart (Fig. 3a) and each comprising four inshore (within 15 n. m. offshore) stations 5 n. m. apart, and five offshore (15-65 n. m. offshore) stations 10 n. m. apart. Starting from the 1981/82 cruises and onwards, the sampling grid was reduced to 20 transects, which were 30 n. m. apart (Fig. 3b). Occasionally, some transects and/or stations were not sampled for various reasons, e.g. bad weather and the capabilities of different ships used (Kruger 1983), loss or breakdown of equipment and limited ships time (Le Clus 1985). This is evidenced by the sometimes-staggered spatial and temporal representation of the samples. Prior to the 1981/82 cruises, sampling commenced south of the Kunene River at 17°20 S (transect 6 in Fig. 3a), whereas sampling started at 17°30 S from the 1981/82 cruises onwards (transect 4 in Fig. 3b). The southern limit of the survey varied between 26 and 27° S.

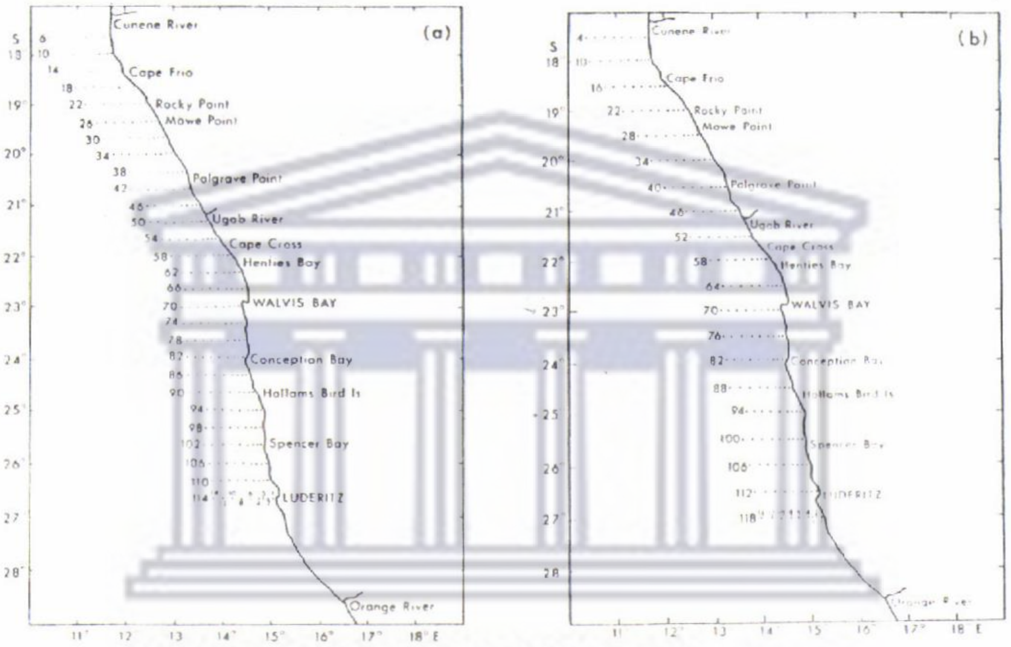

Fig. 3: SWAPELS grid of stations sampled during surveys of (a) 1978/79 to 1980/81, and (b) 1981/82 (after Le Clus 1985)

2.2.1 Collection of samples

The SWAPELS surveys were usually conducted on board the *RS Benguela* or the *RS Sardinops*. Zooplankton was collected using an obliquely towed, paired Bongo net system. One net had a 300-µm mesh while the other net had either a 940-µm or a 500-µm mesh. Only samples from the 300-µm-mesh net were analysed for this thesis in order to assess the abundance and distribution of most copepods. Mouth areas of the Bongo nets were 0.255 m^2 each. At each station the Bongo nets were towed from depths of approximately 50 m at a cable speed of about two knots, while the vessel maintained a near constant speed of 2 knots. At stations where depths were less than 50 m, samples were collected from 5 m above the seabed. Calibrated digital flowmeters, placed in the centre of the net mouths, were used to measure the volume of water flowing through the nets. The flowmeters were connected to an electronic read-out system on the deck of the ship and were coupled to a strip chart recorder. Surface seawater was collected in bottles and sea surface temperature (SST) was measured immediately by means of a mercury thermometer, while salinity was measured in the laboratory ashore using a Beckman inductive salinometer. The acquired data were used in this study to profile the horizontal distribution of SST and salinity of the Walvis Bay area.

During cruises-of-opportunity zooplankton were commonly sampled by means of a 80-µm mesh, 0.196-m^2 mouth area (Kemp *et al.* 1929) N50V net (Table II), vertically hauled from 50 m, or from 5 m off the bottom where depth was shallower than 50 m. The Bongo net (300-µm mesh size) used in June 1979 (Table II) was obliquely towed over the same depth range.

Table II: Months sampled during SWAPELS surveys (period applicable to this study) using ships-of-opportunity, and the type of gear used

1979		1980		1981	
Month	Gear	Month	Gear	Month	Gear
June	Bongo Net	July	N50V Net	August	N50V Net
August	N50V Net	August	N50V Net	October	N50V Net

As can be seen in Fig. 3, transects were assigned numbers. The Walvis Bay (23° S) transect is labelled 70. Altogether 155 samples, covering the period 1979-81, were analysed from this transect. The period 1979-81 was selected for this study because according to an inventory – and thereafter the cataloguing – of the SWAPELS collection done at M&CM, it was during this period that the best temporal (comparatively the most months over consecutive years) and spatial (comparatively the most stations along a transect) coverage of transect 70 was observed. In order to improve spatial resolution samples from transect 66 (22°67) to the north, and from transect 74 (23°33) to the south of transect 70 were analysed. These additional samples covered the months January to March of 1979/80/81 because only these months were consistently sampled successively, and also only three months each year were selected due to time limitations for the completion of the degree. In total, 289 samples were therefore analysed for this study.

On board the vessel, each sample was washed into a 10-litre bucket containing seawater, from which large zooplankters, such as salps and medusae, were removed. The remaining plankton was transferred into storage jars after being concentrated on a 300-μm mesh sieve in the case where a 300-μm mesh Bongo net was used, differing accordingly on occasions when N50V (80-μm) nets were used. Samples were then topped up with seawater, labelled and preserved with borax-buffered formalin.

2.2.2 Processing and analysis of samples

For the retrospective analysis of the samples, any remaining gelatinous organisms in the samples were handpicked and removed; N50V net samples were first washed through a 200-μm mesh sieve, to allow for subsequent standardization with the Bongo net samples (see Section 2.3.1); all samples were then transferred into a measuring cylinder, and 'initial' settled volume was recorded after allowing the sample to settle for a period of at least 24 hours. It was observed that samples that contained large amounts of phytoplankton required a longer time to settle, and were thus allowed 48 hours to settle. The settled volumes were then converted into biovolumes (refer to Section 2.3.1), which were used to examine crude temporal and spatial patterns in the distribution of total zooplankton (excluding gelatinous species) biomass (including a subsequent comparison with earlier and recent data sets to explore trends of long-term variability) off Walvis Bay. Also, it was decided that all biovolumes obtained from samples that were noticeably dominated by phytoplankton were to be eliminated from subsequent analyses, as these biovolumes would have been upwardly biased by the relatively large volumes of phytoplankton in those samples.

Thereafter, crustacean macrozooplankton such as euphausiids (from furcilia to adults), amphipods, mysids, etc, were removed by first filtering the samples through a 1600-μm mesh sieve – which retained most of the "undesired" macrozooplankton – and then by handpicking "undesired" animals (such as furcilia) that managed to pass through the 1600-μm mesh sieve. Only plankton small enough to wash through the sieve was considered for analysis. The samples were then transferred into measuring cylinders and were allowed 24 hours to settle. Settled volumes were then recorded. These 'final' settled volumes were used in the procedure for the estimation of copepod abundance (refer to Section 2.3.2). Abundance data were used to investigate spatio-temporal trends in copepod distribution and community structure.

In order to identify and enumerate copepods, sub-samples were drawn from each sample as follows: each sample in the measuring cylinder was diluted with filtered seawater to a volume ten times that of its 'final' settled volume; the plankton was then resuspended by bubbling air through it until all the plankton was homogeneously distributed in the cylinder. Two sub-samples of 2 ml each were then immediately removed with a modified wide-bore Stempel pipette and transferred into a Bogorov tray. A stereomicroscope was used for the identification and enumeration of copepods. The average of the two sub-samples was taken as the estimate of copepod abundance at that station. Moreover, this average was acceptable only if the variation between the sub-samples with respect to the total number of copepods counted in each sub-sample, was <10%. Whenever this was not the case, the station sample would be sub-sampled and analysed again until the aforementioned condition was satisfied.

2.3 *Estimation of total zooplankton biomass and copepod abundance*

Determining biovolume from settled volume measurements is a crude way of estimating total (non-gelatinous) zooplankton biomass and is based on the assumption that 1 ml settled volume = 1 g wet mass (see Verheye *et al.* 1998). To investigate seasonal and interannual variability, as well as community structure of copepods during the period 1979-81, biomass and abundance estimates were used.

2.3.1 Estimation of zooplankton biomass

Biovolumes (V_b) were standardized to ml m^{-2} from a knowledge of the 'initial' settled volume (V_s) together with the volume of water filtered through the net (V_f), and the maximum sampling depth (d), as follows:

$$V_b\ (\mathrm{ml\ m^{-2}}) = [V_s\ (\mathrm{ml})/V_f\ (\mathrm{m^3})] \times d\ (\mathrm{m}) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Volume filtered was obtained from the product of the length of the haul and the mouth area of the Bongo net. The haul length (m) was calculated by dividing the flowmeter reading (revs) by the calibration factor (revs m^{-1}) of the flowmeter. For the N50V net data, for which samples were collected by means of vertical hauls, volume filtered through the nets was computed from knowledge of the area of the mouth of the net and the maximum depth sampled. This approach is based on the assumption made by Verheye *et al.* (1998) that the absolute values of tow duration and sampling depth could be considered equal, assuming the vertical hauls were taken at a constant speed of 1 m s^{-1}. Biomass (biovolume) data – and abundance data (Section 2.3.2) – acquired from the Bongo net (300-μm) samples were multiplied by a correction factor of 1.85, following Pillar (1984b) (see also Verheye *et al.* 1998), to compensate for the zooplankton not retained by the 300-μm mesh net compared with the 200-μm mesh sieve used during processing of N50V net samples (as described in Section 2.2.2).

2.3.2 Estimation of copepod abundance

Abundance (A) was calculated according to the following formula:

$$A\ (\text{ind. m}^{-2}) = ([N \times V_{10}\ (\text{ml})] / [v\ (\text{ml}) \times V_f\ (\text{m}^3)]) \times d\ (\text{m}) \ldots\ldots..(2)$$

The number counted (N) in this formula represents the average of counts from the two sub-samples analysed. Even though the volume of each sub-sample (v) was 2 ml, it was decided that samples with settled volumes of <6 ml were to be analysed entirely, that is, without sub-sampling. V_{10} denotes the diluted volume, which is 10 x the 'final' settled volume (see section 2.2.2). Even though all copepods were counted, in this study only adults (males and females) were considered for examining trends in the abundance distribution and community structure. The reason for this was that I was confident that the 300-μm mesh of the Bongo net sampled these two adult stages – mainly of calanoid copepods – quantitatively, which cannot be said about the younger stages of copepod species.

2.4 *Numerical analysis*

To depict spatial and temporal distributions of SST, salinity, total zooplankton biomass, and copepod abundance, the software package, SURFER Version 8.01 (Golden Software, Inc. 2002), was used. Kriging was used in the gridding of data, which resulted in a smoothing effect in the contour maps created. To describe changes in species assemblages over time and space, multivariate statistics were employed.

2.4.1 Multivariate analysis

All multivariate analyses were performed using PRIMER Version 5.2.9 (Plymouth Routines in Multivariate Ecological Research; Clarke and Warwick, 1997). All samples in which zero copepod species were present, as well as samples in which less than three species per sample were counted, were excluded from the analysis. Moreover, only abundance data from stations for which temperature and salinity measurements were available, were used. Cluster analysis – using hierarchical agglomerative clustering – among samples was performed on root-root-transformed data, using the Bray-Curtis similarity index. Results were presented as dendrograms based on group average linkage. The SIMPER (similarity percentage breakdown) routine from PRIMER was used to identify indicator species from the different cluster groups, after the data had been root-root transformed. This analysis was based on species contributing at least 75% to the overall similarity between samples. To determine the contributions of the abiotic factors, namely SST, salinity, bottom depth and season, the BIO-ENV procedure – based on Spearman rank correlation – from PRIMER was employed. Again, in this procedure the Bray-Curtis similarity index was used on root-root-transformed abundance data. Species diversity (number of species per sample), and evenness – based on Pielou's index (see Clarke and Warwick 1997) – were also determined using PRIMER.

Multivariate analyses were performed on all three transects: firstly, on a monthly basis, and secondly, on the entire data set (1979-81). In the latter case, seasons were assigned different numerical values based on a four-season cycle, as follows:

1 = summer = December-February
2 = autumn = March-April
4 = spring = September-October

It must be noted that, in the process of performing multivariate analyses, existing winter species abundances were excluded, as there were no corresponding physical data (SST and salinity) for winter months.

2.4.2 Statistical analysis

All statistical analyses were done using the software programme STATISTICA Version 6 (StatSoft, Inc. 2004). In order to determine how the different clusters identified in the cluster analysis were associated with the biotic (abundance, diversity and evenness) and abiotic (SST, salinity, bottom depth and season) parameters, ANOVA (analysis of variance), t-tests and correlations were performed. For both ANOVA and the t-test, normality was tested using frequency histograms, and homoscedascity was tested using the Levene's test for homogeneity of variances (Zar 1999). A Tukey test for unequal sample sizes (Zar 1999) was performed whenever ANOVA indicated significant differences, to determine where the significant differences among the groups lay. Whenever assumptions for ANOVA were not true – after data were log-transformed – the nonparametric Kruskal-Wallis test (Zar 1999) was performed. And, where significant differences occurred, a nonparametric Tukey-type multiple comparison was used (Zar 1999). A nonparametric test, namely, the Mann-Whitney test, was employed where assumptions for the t-test were not met.

3 Results

3.1 The physical environment

Among the three years (1979-1981), 1979 had the lowest annual SST mean of 15.19 °C, with 1981 showing the highest mean of 15.74 °C (Table III). What was common in all three years was the highly frequent occurrence of SSTs ranging between 15 and 16 °C (Fig. 4). The comparatively low SST mean for 1979 seems to be the result of the high frequency of occurrence of cool (13-14 °C) surface water during this year (Fig. 4), as opposed to the dominance of warmer (> 15 °C) water in 1981. In 1980, SSTs were generally moderate, mostly measuring within the 14-17 °C band (Fig. 4). There was also greater variability – as indicated by high standard deviations – of SSTs in 1979 compared to the lower variability – lowest standard deviations – in 1981 (Table III).

There were no significant differences ($p < 0.05$) among the three years (1979, '80 and '81) with respect to salinities. All three years had annual salinity means of 35.18 each (Table III), with 1980 showing the widest range (34.92-35.62). Even though all three years had equal annual means of 35.18 each (Table III), the frequency distribution of the salinities differed (Fig. 4). Salinities ranging between 35.1 and 35.2 occurred the most in 1979 (Fig. 4). The year 1980 had the widest range of salinities – as already mentioned – but most of them were skewed towards the lower end of the scale (mostly 35.0-35.2). Modal salinities in 1981 were between 35.2 and 35.3

Table III: Interannual variability in sea surface temperature (SST) and salinity measured along transect 70 (23° S) from 1979 to 1981

Year (No. of samples)	SST (°C)		Salinity	
	Mean (*SD*)	Range	Mean (*SD*)	Range
1979 (98)	15.19 (*1.73*)	11.27-18.10	35.18 (*0.16*)	34.97-35.50
1980 (76)	15.68 (*1.38*)	12.90-18.15	35.18 (*0.15*)	34.92-35.62
1981 (39)	15.74 (*1.07*)	13.00-17.70	35.18 (*0.12*)	34.96-35.37

SD = Standard deviation

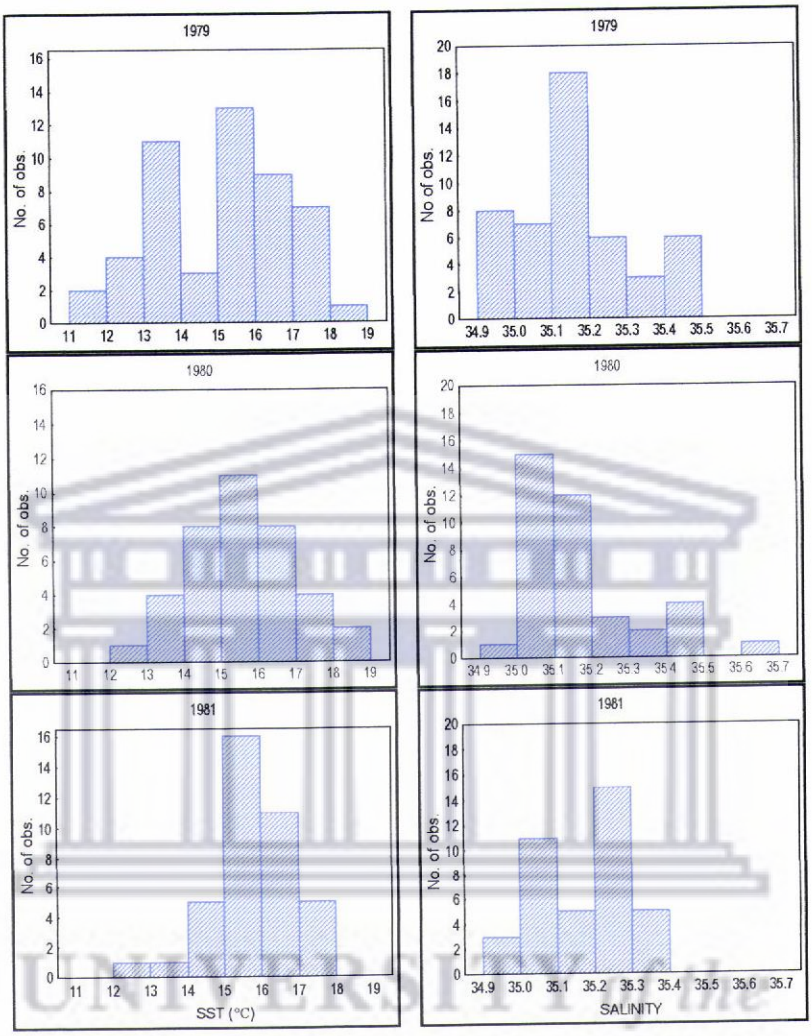

Fig. 4: Frequency distributions of SST (left) and salinity (right) measured along transect 70 (23° S) from 1979 to 1981

As shown in Fig. 5, there was a repeated pattern in the temporal distribution of SST and salinity in the first two years, which showed a dominance of relatively warm (c. 16 °C), high-salinity (c. 35.14) water s from January to February, that became cooler and less saline in March (and April in 1979). In 1981, higher SST and lower salinity values were recorded in March than in January-February. Low mean SST (c. 14.19 °C) and salinity (c. 35.05) was observed in early spring (suggesting recently upwelled water), gradually increasing until early summer (December) in 1979 and 1980. Even though this trend of a spring-to-summer increase in temperature persisted in 1981, the reverse was observed for salinity, when mean values in summer were lower than in spring.

From January through March 1979, warm (16-17 °C) surface water prevailed throughout the offshore stations (Fig. 5a). Meanwhile, from March to April 1979 cool (13-14.5 °C) water started extending offshore (as far as c. 50 n. m. from the coast), to recede inshore by December, when warm water moved shorewards, extending over the entire transect. This warm water persisted until March 1980 over most of the transect, except in January when water of moderate (c. 15 °C) temperature was observed at the first three inshore stations. Again in spring a body of cool water extended up to 45 n. m. offshore. In early summer this cool water was being replaced again with warm surface water. The first quarter of 1981 was characterised by warm (> 16 °C) water, which extended over the entire transect. However, in spring there were cool water masses extending from either ends of the transect. In December of this year SSTs lower than in previous years prevailed inshore, increasing offshore.

High salinities tended to dominate up to 35 n. m. offshore during January through March of the first two years (Fig. 5b), to increase again from c. 55 n. m. offshore. In spring of 1979 relatively low (< 35) salinities were observed extending over most of the transect. Although low salinities were observed in spring of the following year, the values fell within a higher range of 35-35.2. In January and February 1981 the inshore stations were characterised by moderate (c. 35.3) salinities, which decreased midshore (15-40 n. m.), to increase again offshore. The moderate salinities were characteristic of the spring of this year, extending over the entire transect. In December 1981 relatively low (c. 35.05) salinities prevailed over most of the transect.

Looking at alongshore distribution of SST, there was clear variability among the transects (Figs 6-8). In January 1979 and 1980, cool water was observed on transects 70 and 74, within 12 n. m. from the coast (Figs 6a and 7a). In January 1981, this cool (< 13 °C) water was restricted within 5 n. m. from the coast of transect 74. February 1979 and 1980 had the warmest surface water (Figs 6a and 7a), with SSTs reaching levels greater than19.5 °C on transect 66 in the latter year. In January and February of 1981, SSTs were moderate (±15 °C) and were virtually uniformly distributed across the three transects. Warmer SSTs were recorded in March than in the earlier months in 1981, with transect 74 being the coolest of the three transects.

In January and February 1979/80/81 (Figs 6b, 7b and 8b) salinities were uniformly distributed across the three transects, with the exception of February 1980 when the distribution of salinities was variable among the transects. Higher salinities (c. 35.5) were observed during March 1979 and 1980 than in January/February, whereas in 1981 the lowest values were recorded in March. Furthermore, the salinities in March 1980 appear exceptionally high compared to other months and years.

SST and salinity measured on transect 70 over a period of three years (Table IV), were uncorrelated ($r^2 = 0.0024$, $p > 0.05$). There was a significant relationship between SST and bottom depth ($r^2 = 0.065$, $p < 0.05$) – in this study bottom depth was regarded as a proxy for distance offshore – while salinity was unrelated to bottom depth ($r^2 = 0.0008$, $p > 0.05$). Correlations between these three physical variables and some biotic parameters, computed on a monthly basis, will be reported further on in this Chapter.

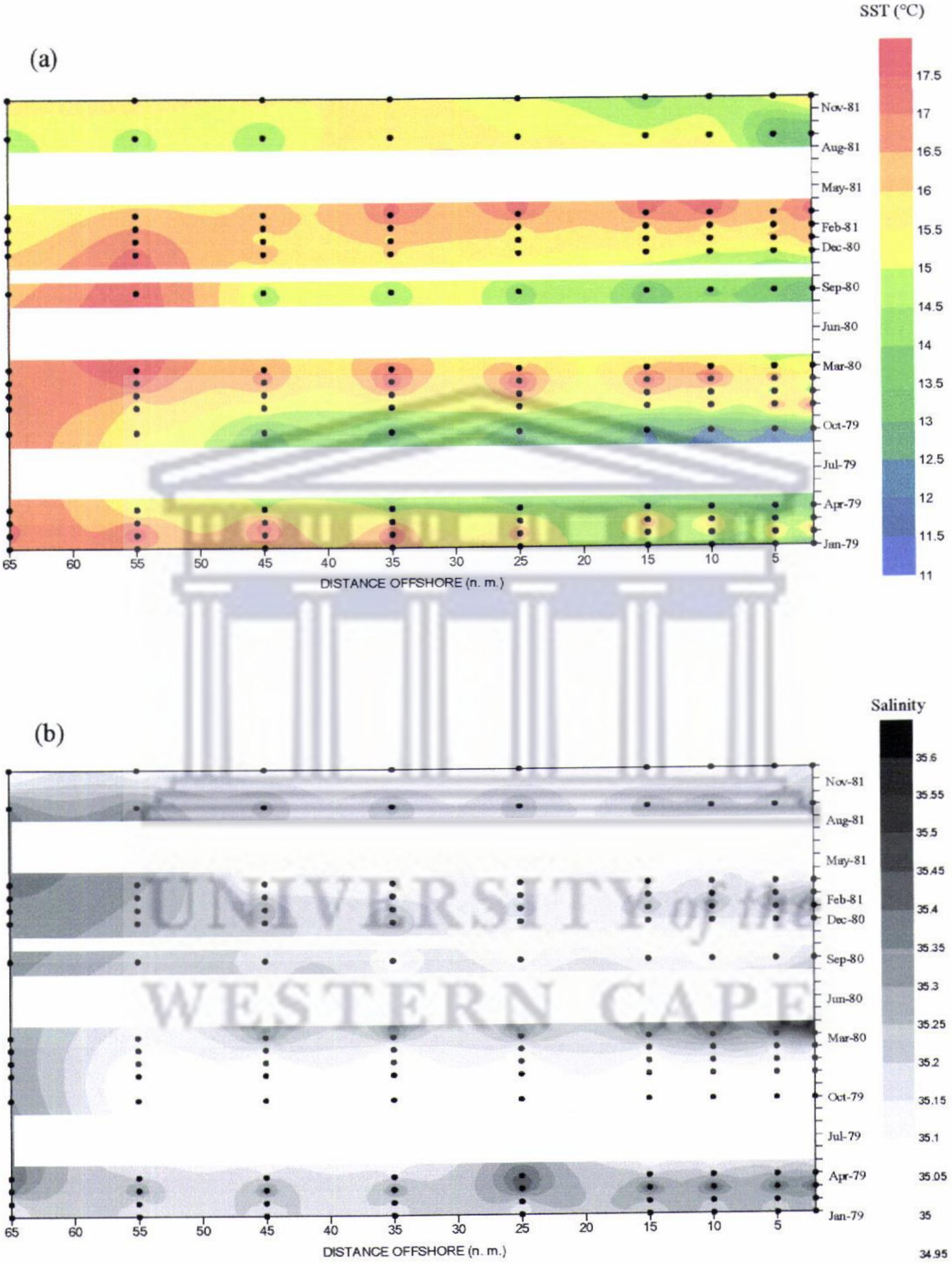

Fig. 5: SST (a) and salinity (b) measured along transect 70 (23° S) from January 1979 to December 1981. Dots indicate positions of sampling stations along the transect. White blank spaces indicate the absence of data

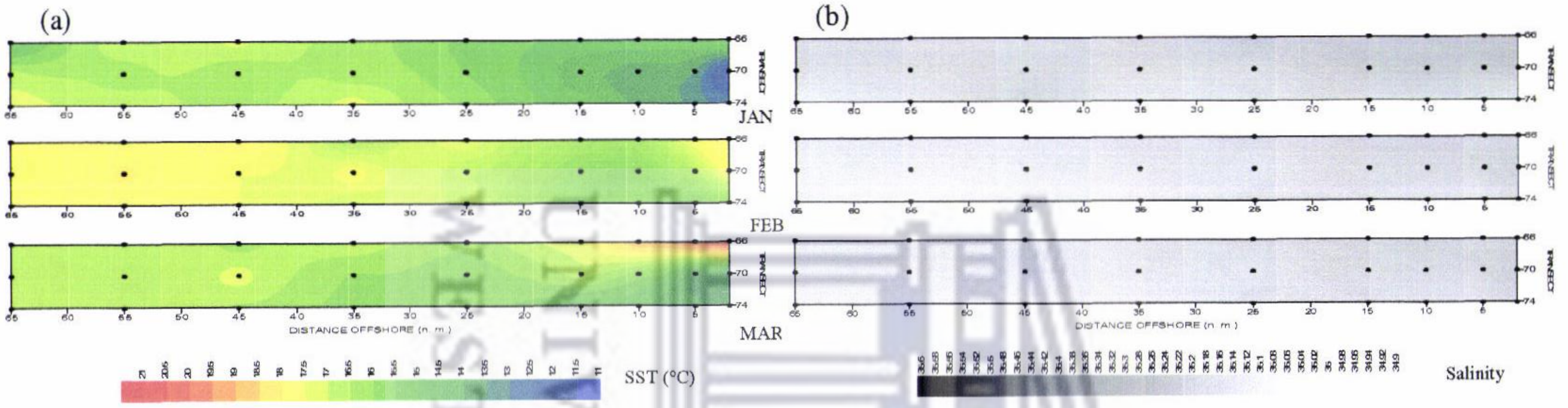

Fig. 6: SST (a) and salinity (b) measured on transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979. Dots indicate positions of sampling stations along the transect

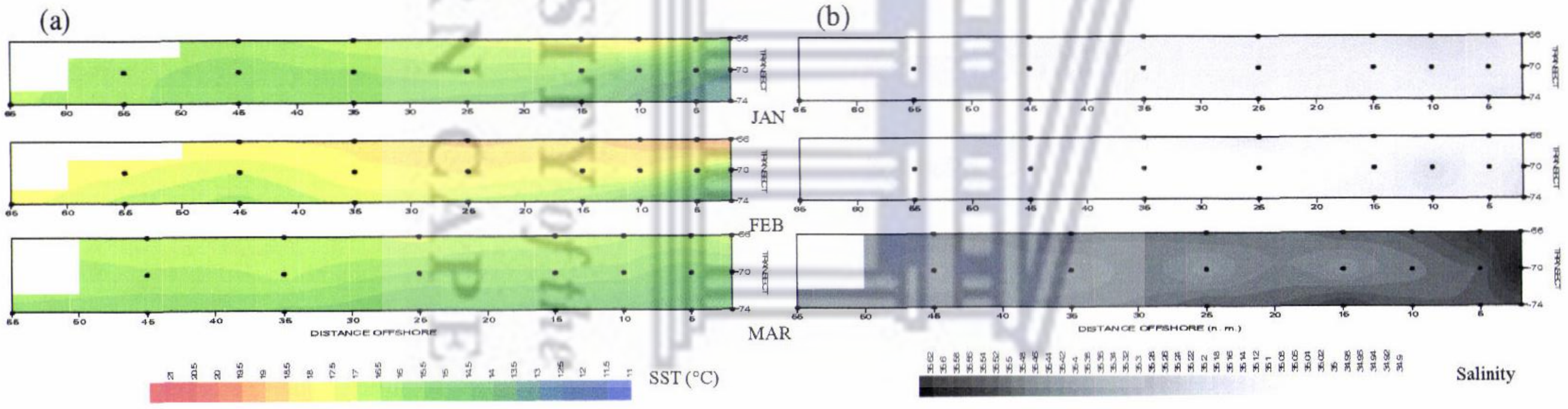

Fig. 7: SST (a) and salinity (b) measured on transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Dots indicate positions of sampling stations along the transect. White blank spaces indicate the absence of data

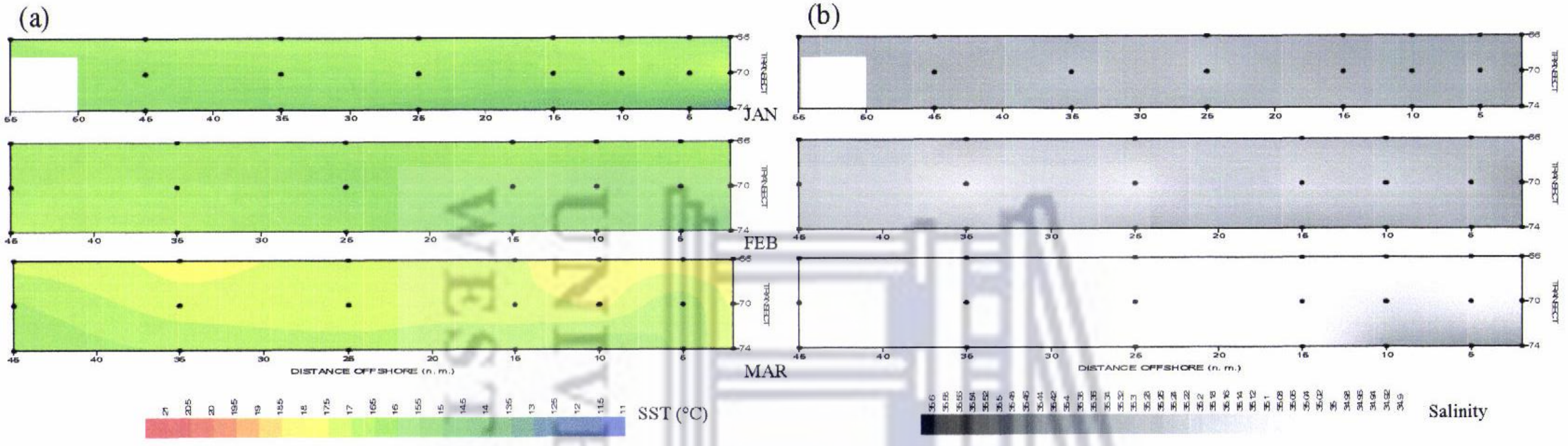

Fig. 8: SST (a) and salinity (b) measured on transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Dots indicate positions of sampling stations along the transect. White blank spaces indicate the absence of data

Table IV: Correlation matrix showing relationships between SST, salinity, and bottom depth measured along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S) from 1979 to 1981

	Salinity	Bottom depth (m)
SST (°C)	N = 142 r^2 = 0.0024 p = 0.57 y = 0.0046x + 35.1	**N = 142** **r^2 = 0.065** **P = 0.002** **y = 0.0049x + 15.2**
Bottom depth (m)	N = 142 r^2 = 0.0008 P = 0.75 y = -0.0001x + 35.19	

3.2 Seasonal variability in total zooplankton biomass distribution

In order to examine seasonal variability in the distribution of total zooplankton biomass over the period 1979-1981, biovolumes computed using the 'initial' settled volumes were used in the analysis (see section 2.2.2). Therefore, these biovolumes exclude all gelatinous organisms, but include crustacean zooplankton, and some non-gelatinous holoplankton and meroplankton.

Zooplankton biomass along transect 70 displayed a bimodal distribution for most months over the three-year period (Fig. 9). In 1979 these peaks occurred in late summer and autumn, at 5-15 and 30-40 n. m. off the coast, and again in late winter to early summer, at 20-30 and 50-60 n. m. from the coast. In 1980 the peaks in biomass were observed in spring and early summer, however both occurring closer inshore (5-10 and around 25 n. m. offshore). In 1981 zooplankton biomass did not exceed 400 ml m^{-2}, and peaked in March (15 n. m. offshore) and in late winter to spring (5-10 and 40-50 n. m. offshore). Apart from spring-summer of 1981, the region between 40-50 n. m. offshore often contained low zooplankton biomass (< 50 ml m^{-2}). From the winter of 1980 to the summer of 1981, zooplankton was concentrated within 35 n. m. from the coast; further offshore biomass fell to levels below 50 ml m^{-2} in biovolume.

From January to March, there were changes in the spatial distribution of zooplankton biomass along the three transects (Figs 10, 11 and 12). Most of the time the bimodal distribution in biomass (as depicted by Fig. 9) was still observed over the three transects, though it was variable for each transect. In January 1979, the greatest biomass was found within the first 5 n. m. of transects 70 and 74, and at 65 n. m. offshore of transect 66 (Fig. 10). In February there was a tendency towards a bimodal distribution, which became pronounced in March. In January 1980 most of the biomass was concentrated in transects 66 and 74, with transect 70 showing relatively low levels over all the stations, barring the farthest station offshore (Fig. 11). From February, the zooplankton appeared to be aggregating inshore and southwards, culminating in a distribution that was mostly concentrated inshore of transect 74. In January 1981, moderate (80-160 ml m^{-2}) biomasses of zooplankton were spread over a distance of 20-45 n. m. offshore, across the three transects, with a patch of high biomass (c. 250 ml m^{-2}) around 25 n. m. offshore of transect 74 (Fig. 12). In February of the same year, zooplankton was mostly aggregated in the south, within 25 n. m. of the coast on transect 74. However, in March 1981, transect 70 saw the largest biomass of zooplankton being concentrated at 15-25 n. m. offshore. Moreover, transect 70 displayed a trimodal distribution of zooplankton biomass.

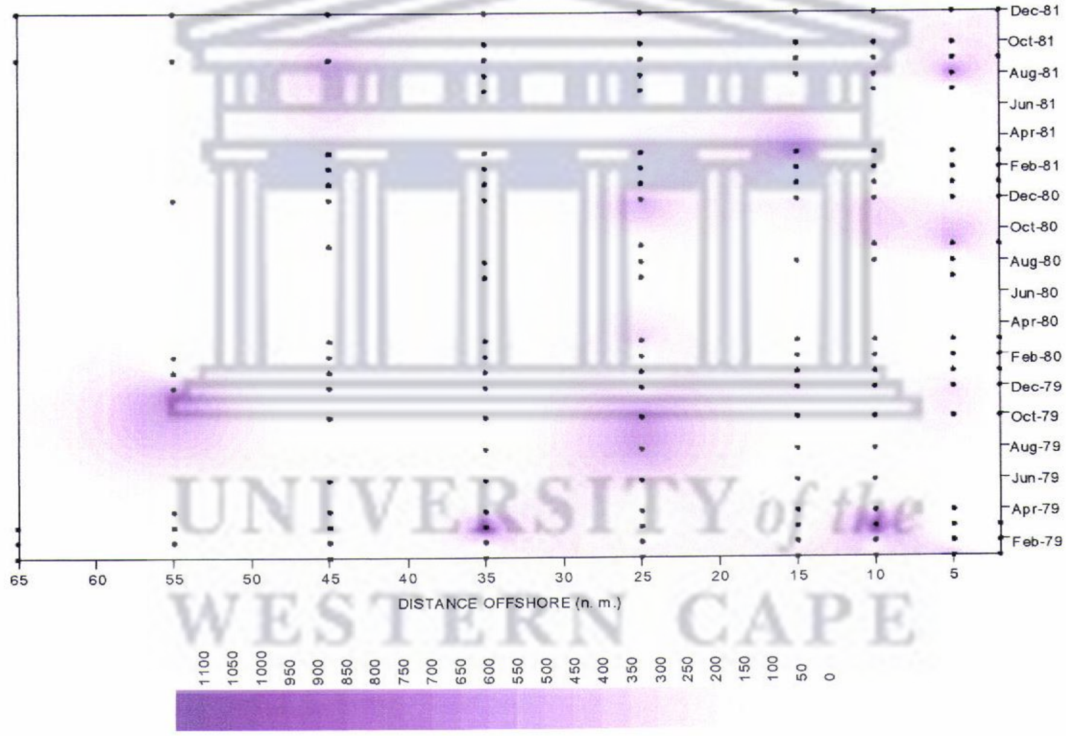

Fig. 9: Spatial and temporal distribution of zooplankton biomass along transect 70 (23° S), over a period of three years (1979-81), estimated using biovolume (ml m^{-2}). Dots indicate positions of sampling stations along the transect

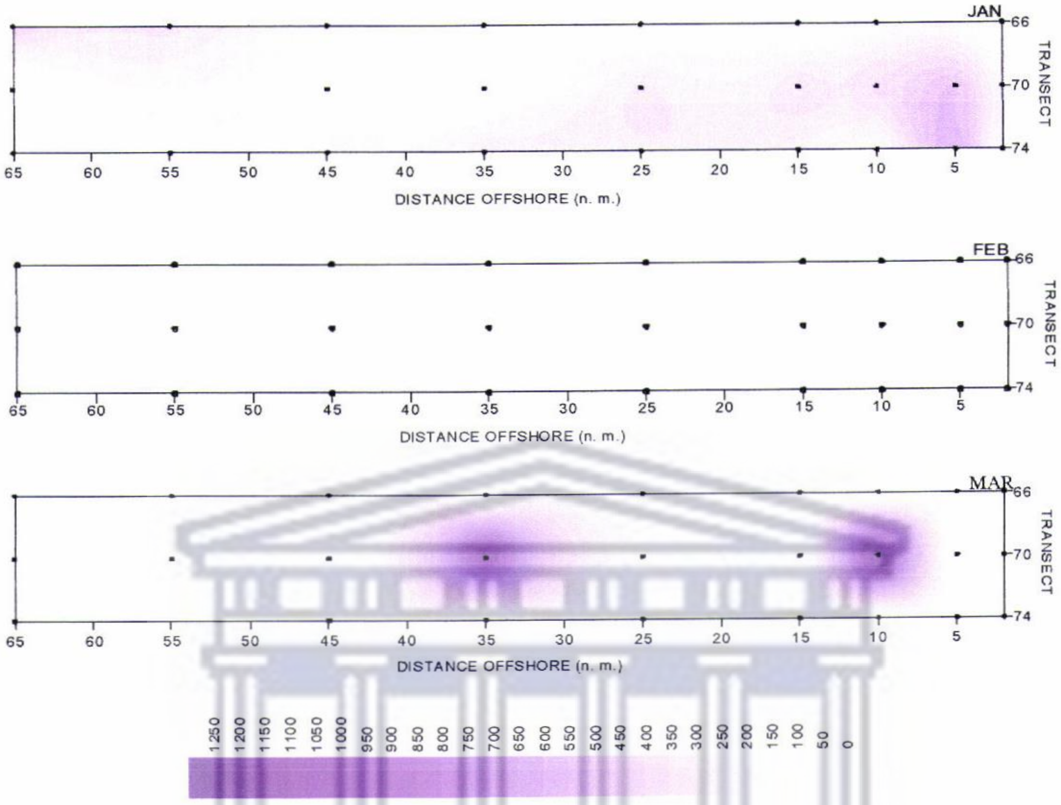

Fig. 10: Zooplankton biomass distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979, estimated using biovolume (ml m^{-2}). Dots indicate positions of sampling stations along the transects

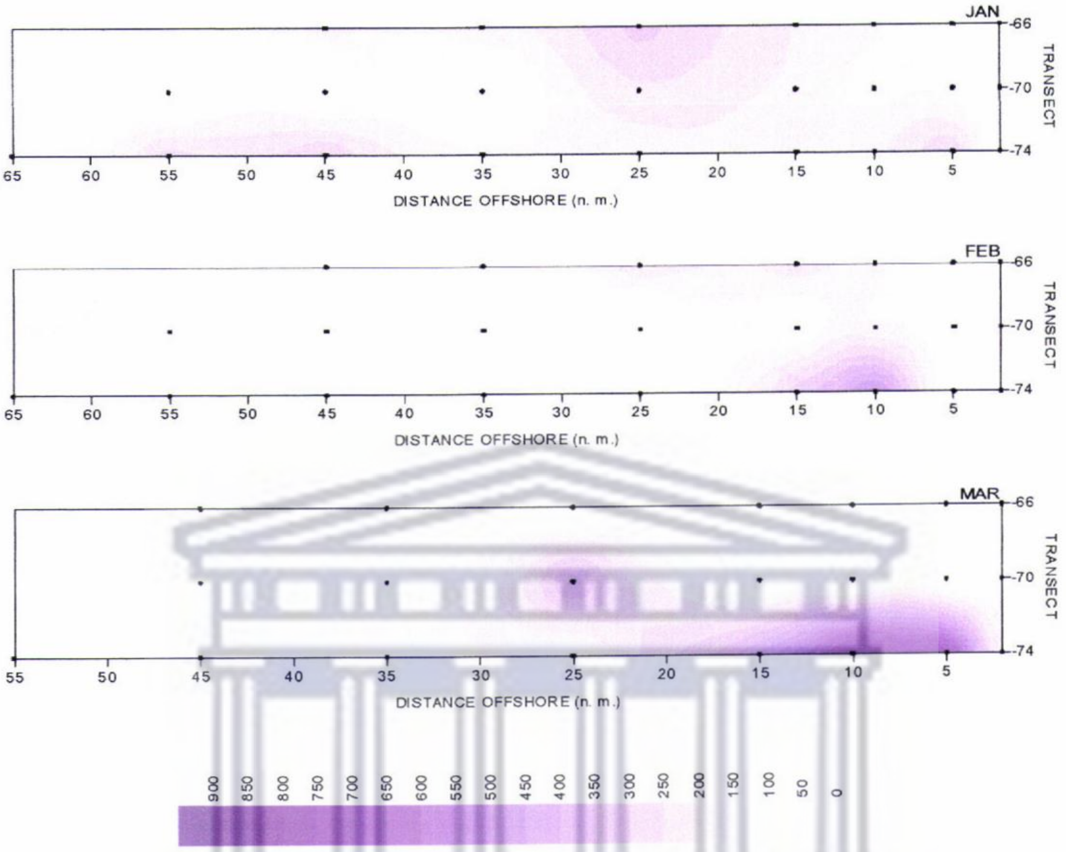

Fig. 11: Zooplankton biomass distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980, estimated using biovolume (ml m^{-2}). Dots indicate positions of sampling stations along the transects

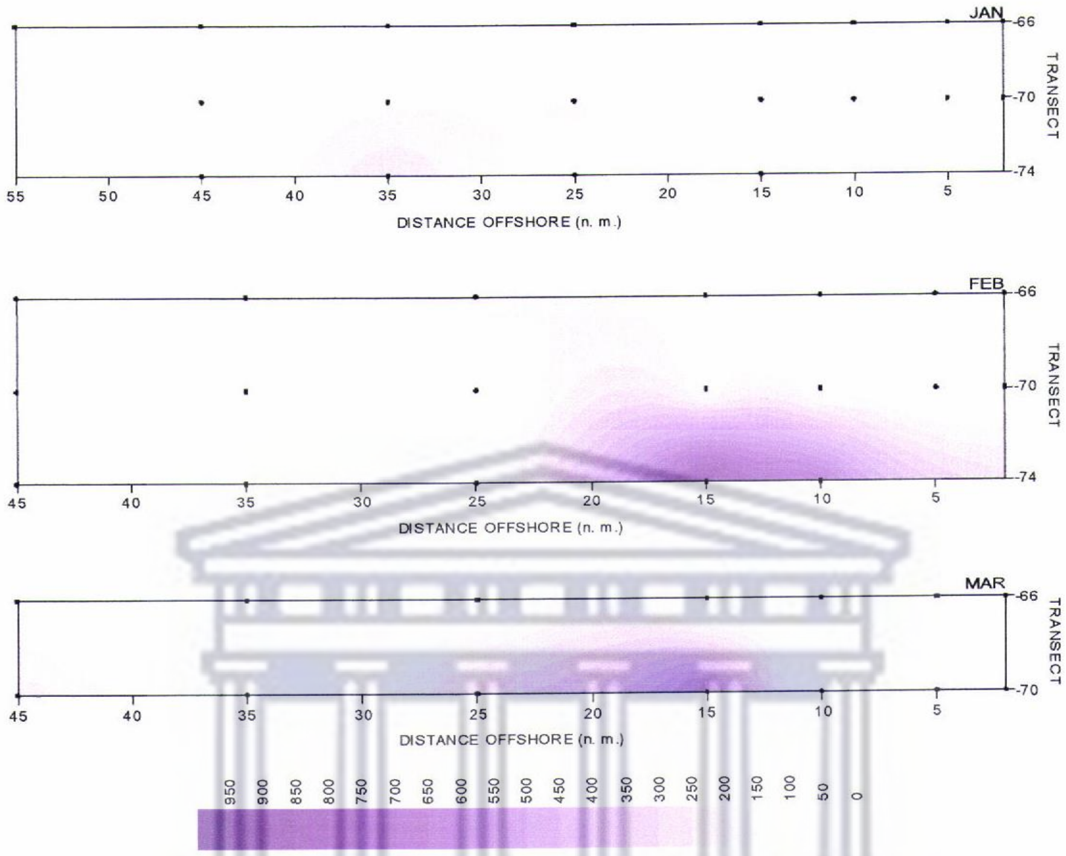

Fig. 12: Zooplankton biomass distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981, estimated using biovolume (ml m^{-2}). Dots indicate positions of sampling stations along the transects

3.3 Seasonal variability in total copepod abundance

As discussed in Chapter 1, studies have shown that copepods are numerically the most dominant zooplankton taxa in the Benguela Current ecosystem. In this section total copepod abundance data acquired after the enumeration of the SWAPELS samples are presented, and spatio-temporal variability is investigated.

Interannual variability in the distribution of total copepod abundance along transect 70 is shown in Fig. 13. Throughout the study period (1979-1981), copepod distribution along the transect appeared to be confined mainly within 45 n. m. offshore, with the exception of December 1981, when copepods could be observed as far offshore as 65 n. m. A seasonal pattern in the distribution of copepod assemblages could be detected. In mid-late summer (January-February), relatively high abundances were observed up to 30 n. m. offshore. Abundances decreased from autumn to winter, increasing in spring (September-November) and aggregating inshore (within 10 n. m. of the coast). This inshore community then moved offshore in early summer (December). However, in 1981 abundances started recovering earlier than in 1979 and 1980, as the inshore 'spring' bloom was observed in late winter (August 1981).

In January of each year, relatively high inshore (within 10 n. m. offshore) copepod abundances were observed spanning across transects 70 and 74 (Figs 14-16). Also, in March of each year there was a tendency for copepods to aggregate southward, i.e. towards transect 74 in 1979-80, and towards transect 70 in 1981. For transect 66, no temporal and/or spatial patterns could be discerned. Overall, there was considerable variability among the transects with respect to total copepod abundance.

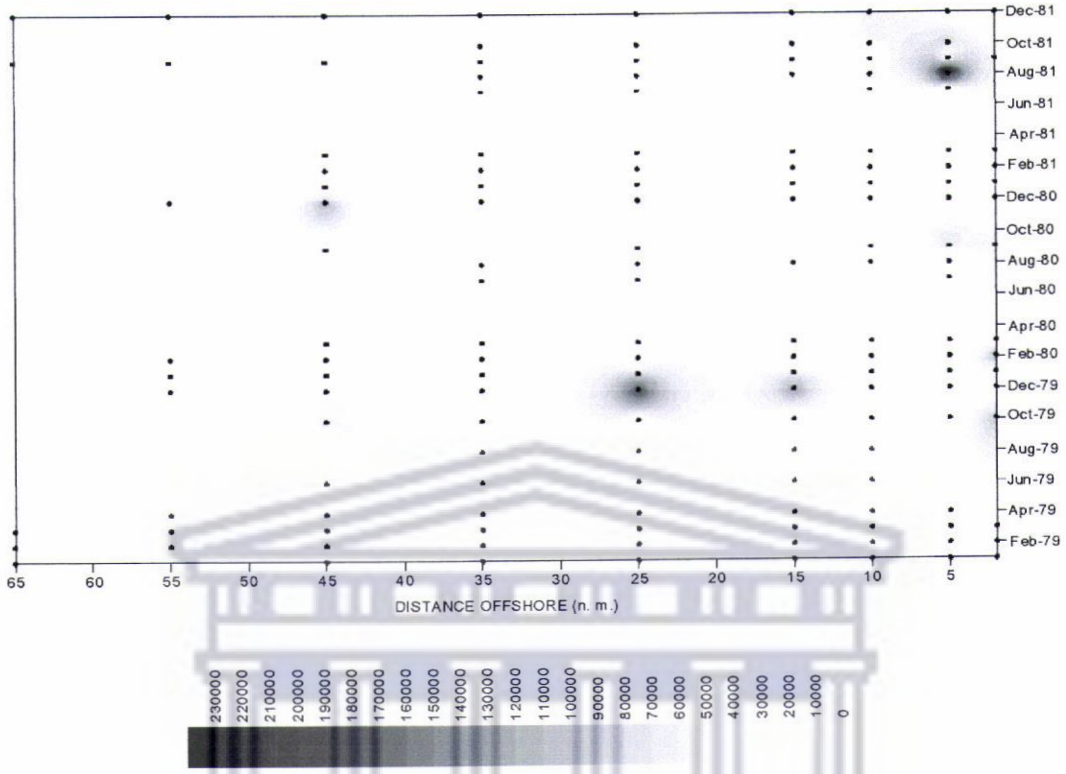

Fig. 13: Spatial and temporal distribution of total copepod abundance (ind. m^{-2}) along transect 70 (23° S) over a period of three years (1979-81). Dots indicate positions of sampling stations along the transect

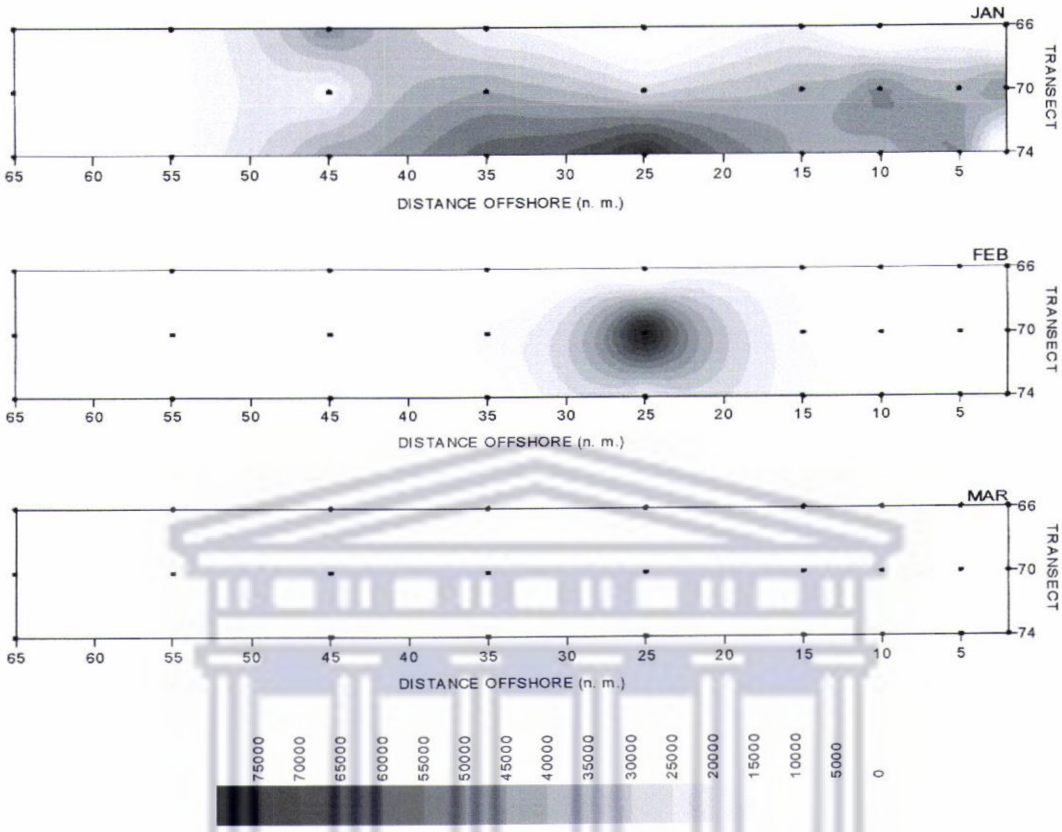

Fig. 14: Total copepod abundance (ind. m^{-2}) distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979. Dots indicate positions of sampling stations along the transects

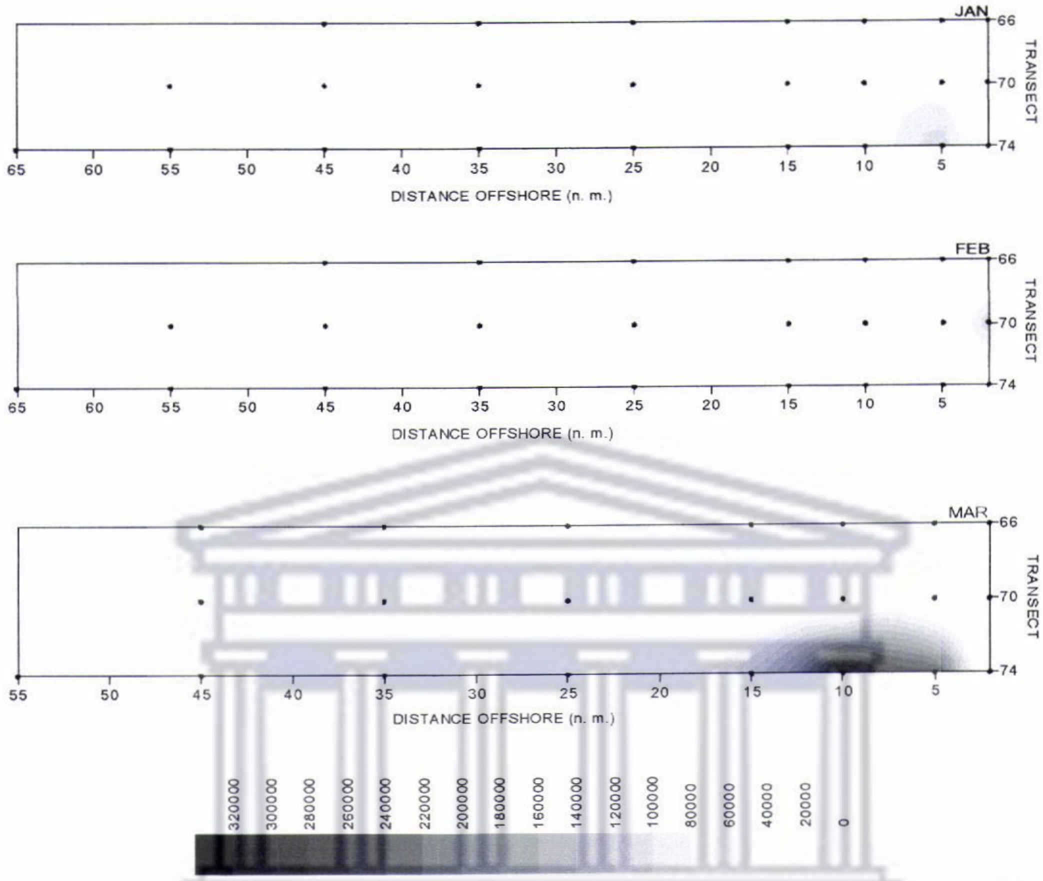

Fig. 15: Total copepod abundance (ind. m^{-2}) distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Dots indicate positions of sampling stations along the transects

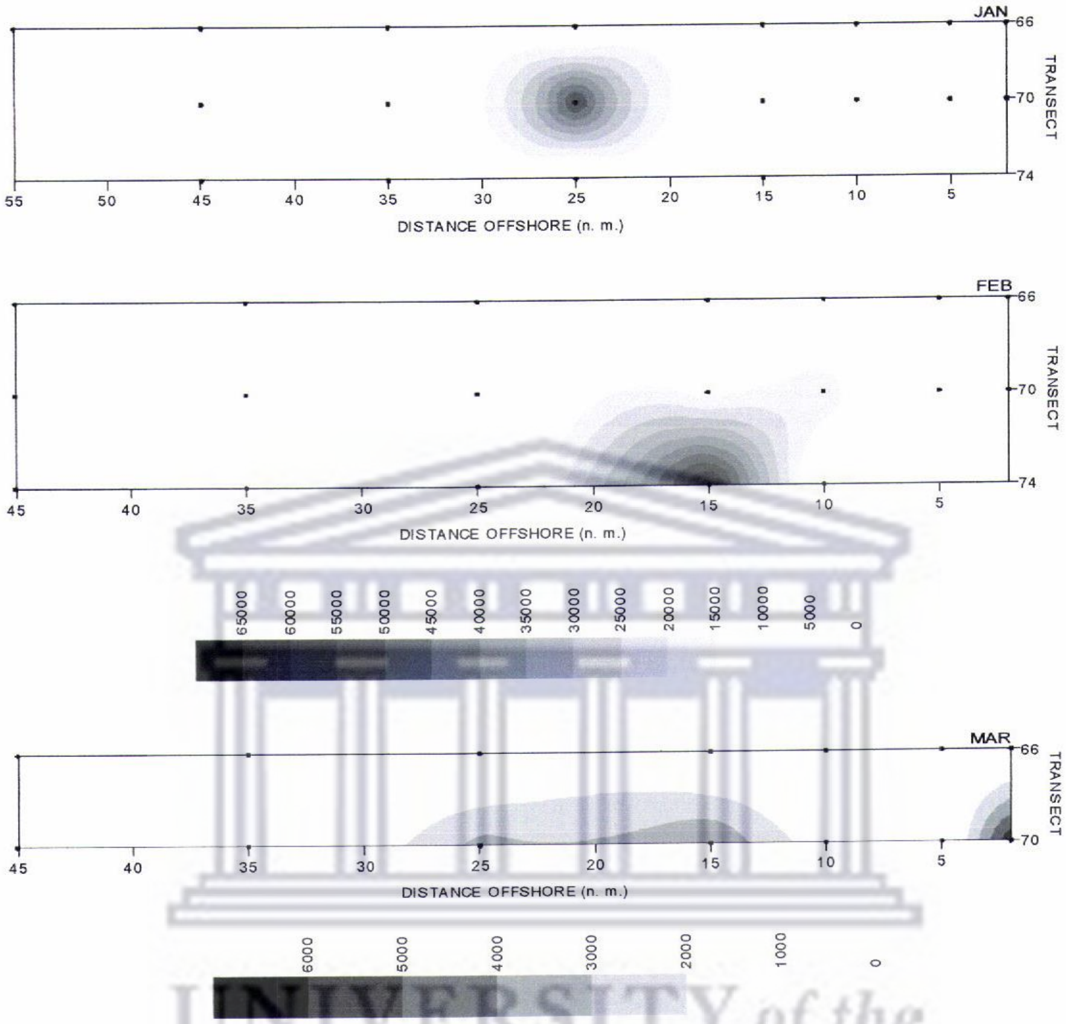

Fig. 16: Total copepod abundance (ind. m^{-2}) distribution along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Note that the map for March has been assigned a separate colour scale due to the exceptionally low abundances in comparison to January and February. Dots indicate positions of sampling stations along the transects

3.4 Copepod species abundance

A table of the entire dataset used in this study is shown in Appendix A. As far as abundances are concerned, only the adult stages of the copepods were considered for this study. That is, for each sample, abundances for both males and females were added together to give a single abundance value for that species.

3.4.1 Alongshore and cross-shelf distributions

In order to identify spatial patterns in the copepod communities, cluster analysis was performed on a month-by-month basis. Therefore, time (month) was kept constant, thereby precluding any effects it may have on the grouping of communities. It is important to note that the month-by-month cluster analysis was performed only where data were available for all three transects. Therefore, these analyses covered the months January, February and March of each year (1979/80/81). However, clusters for some months were deemed unreliable to deduce any meaningful spatial trends from: due to the small number of samples used in the analyses; or due to the inconclusive (result meaningless) dendrogram outputs (see Appendix C).

The cluster analyses revealed copepod communities grouped according to both alongshore (transect position) and cross-shelf (station position) distributions. In January 1979, groups B, C and D were clumped according to transects 74, 70 and 66, respectively (Fig. 17a). Mixed cluster groups (A, E and F) were dominated by inshore (group A) and offshore stations (E and F), with mean bottom depths at 109, 241 and 244 m, respectively (Fig. 17b). The results of the BIOENV procedure indicated that bottom depth was shown to be the most important environmental variable (Fig. 17c). Even though SST was the least important environmental variable (Fig. 17c), there were significant differences ($p < 0.05$, not shown) in SST between groups (A and E). Not considering the outlier group X, A ('inshore' group) had the lowest mean SST at 14.23 °C, whereas E ('offshore' group) had the highest at 16.93 °C (Fig.17b). Using the SIMPER procedure, the copepod assemblages proved to be different, with *C. brachiatus* contributing the most to the similarity (as well as abundance) of E, whereas *C. carinatus* was most dominant in A (Fig. 17d). Also, in terms of abundance, *M. lucens* was "demoted" to fourth rank by

Oncaea spp., whereas in A – and in the other groups – *M. lucens* ranked third. All the groups differed significantly ($p < 0.05$, not shown) in terms of abundance. Among the transects, line 74 had the highest mean abundance (44 259 ind. m^{-2}) and line 70 the lowest at 13 738 ind. m^{-2} (Fig. 17b). There was a significant negative correlation between SST and salinity, and salinity was also strongly correlated to depth (Fig. 17e).

In March 1979 (Fig. 18a), and not considering outlier groups X, Y and Z, only group A was clustered together by transect (70), while C was characterised by offshore stations with mean bottom depth at 216 m (Fig. 18b). The result of the ANOVA showed that with respect to all the variables (biotic and abiotic), there were no significant differences ($p > 0.05$) among the groups. Nevertheless, the results of the BIOENV procedure indicated that bottom depth was still the most important variable in the clustering of the groups (Fig. 18c), albeit at a low correlation value of 27%. The only significant ($p < 0.05$) relationship between the variables was between bottom depth and species richness (referred to in the figures as number of species). These two variables were positively correlated, at 65.76% (Fig. 18e).

Both alongshore and cross-shelf patterns emerge in January 1980 (Fig. 19a). Firstly, group A was comprised of offshore stations with a mean depth of 149 m at a relatively low standard deviation of 10 m (Fig. 19b); secondly, even though it was mixed in terms of stations, group B comprised predominantly transect 66 samples with a mean depth of 105 m, and a relatively high standard deviation of 38 m (Fig. 19b); eight out of the eleven samples in C came from the inshore region; finally, no spatial similarities could be read into the grouping of cluster D (Fig. 19a). Even though the BIOENV procedure indicated that depth was the most important variable in the clustering of the samples (Fig. 19c), statistically there were no significant ($p > 0.05$) differences between the groups with respect to depth. However, there were significant differences ($p < 0.05$) in the abundances of groups A and C, and C and D. Also, the combination of depth and salinity ranked second in the BIOENV procedure (Fig. 19c), and the negative correlation between these two variables was marginally significant ($p = 0.055$), as shown in Fig. 19e.

Two clusters – notwithstanding the outlier group X – emerged from the analysis of the February 1980 samples (Fig. 20a), namely groups A and B. Both these clusters were grouped according to station position along the transects, resulting in an 'inshore' group (A) and an 'offshore' group (B). Furthermore, it was evident from the dendrogram that within these two clusters, there were sub-groups that were clumped according to transect. ANOVA showed that B was significantly ($p < 0.05$) deeper than A, the respective depths being 185 and 93 m (Fig. 20b). The shallow group A had a significantly ($p < 0.05$) higher abundance than the deeper inshore group B (Fig. 20b). The importance of bottom depth in the grouping of these clusters emerged again in the BIOENV procedure, in which depth ranked as the most important environmental variable (Fig. 20c). The SIMPER procedure indicated the existence of two communities corresponding to the groups A and B (Fig. 20d). The exceptionally high mean copepod abundance in group A (24 493 ind. m^{-2}) – compared to group B (3 661 ind. m^{-2}) – as depicted in Fig. 20b, is attributed to *C. brachiatus* and to a lesser extent to *C. carinatus* (Fig. 20d). The most important species in the grouping of cluster B is *M. lucens*, followed by *Oncaea* spp. and *R. nasutus*.

Two groups were identified for March 1980, and both were to a large extent clustered according to distance offshore (i.e. station number). Group A mostly comprised the offshore stations, while B comprised two inshore stations and one offshore station (Fig. 21a). However, mean bottom depths of the two groups were not significantly different. The two groups did not differ significantly from each other with respect to any of the variables given in Fig. 21b. This was likely to be caused by the low resolution due to a small number of samples used in the analysis. Unlike in the previous months discussed above, in March 1980 salinity was the most important variable, with the combination of salinity and SST ranked second (Fig. 21c). The communities represented by these clusters differed as well. Even though group A was dominated by the large (see Appendix B) calanoid copepod species, group B was represented by *Oncaea* and *Oithona*, as well as *M. lucens* (Fig. 21d). Furthermore, during this month, SST was strongly correlated to species evenness (82.75%, $p < 0.05$), and there was a significant negative correlation between evenness and abundance (Fig. 21e).

(c)

No of variables	Correlation	Selections
1	0.502	bottom depth
2	0.484	salinity, bottom depth
3	0.472	all
2	0.454	SST, bottom depth
2	0.295	SST, salinity
1	0.260	salinity
1	0.191	SST

(d)

Group A	Group B	Group C	Group D	Group E	Group F
C. carinatus(9935)	*C. carinatus* (27229)	*C. carinatus* (9189)	*C. Carinatus* (13959)	*C. brachiatus* (3319)	*C. carinatus* (1175)
C. brachiatus (5424)	*R. nasutus* (9338)	*C. brachiatus* (1544)	*C. brachiatus* (3493)	*C. carinatus* (1859)	*C. brachiatus* (770)
M. lucens (4708)	*C. brachiatus* (4765)	*M. lucens* (2429)	*M. lucens* (2657)	*M. lucens* (208)	*R. nasutus* (226)
R. nasutus (2115)			*R. nasutus* (1260)	*Oncaea* (283)	
Oithona (2553)					

Mean abundances shown in parentheses

(e)

	No. of spp.	Abundance (ind. m^{-2})	Evenness (*J*)	SST (°C)	Salinity
Abundance (ind. m^{-2})	-.1050				
	p=.669				
Evenness (*J*)	.1459	.0733			
	p=.551	p=.766			
SST (°C)	.1465	-.0172	-.1466		
	p=.550	p=.944	p=.549		
Salinity	-.0523	-.0184	-.4273	**-.5846**	
	p=.832	p=.940	p=.068	**p=.009**	
Bottom depth (m)	-.0427	-.4342	.4310	.4508	**-.6108**
	p=.862	p=.063	p=.065	p=.053	**p=.005**

Fig. 17: Multivariate analysis of samples collected during January 1979 along transects 66, 70 and 74 off Walvis Bay: (a) dendrogram based on Bray-Curtis similarity (sample labels depict transect-station-bottom depth, e.g. 74-04-118); (b) summary table; (c) BIOENV results showing the abiotic variables (bottom depth, SST and salinity) and their importance (as indicated by correlations) to the grouping of the clusters (d) SIMPER results showing species in order of decreasing contribution to the similarity of each dendrogram group; (e) matrix showing correlations between several variables

(e)

	No. of spp.	Abundance (ind. m^{-2})	Evenness (J)	Bottom depth (m)	Salinity
Abundance (ind. m^{-2})	.2724				
	p=.392				
Evenness (J)	-.1718	-.2929			
	p=.593	p=.355			
Bottom depth (m)	.1069	**.6576**	-.2811		
	p=.741	**p=.020**	p=.376		
Salinity	.0520	-.3548	.0230	-.5290	
	p=.873	p=.258	p=.943	p=.077	
SST (°C)	-.1610	-.0007	.0287	.3038	-.0919
	p=.617	p=.998	p=.929	p=.337	p=.776

Fig. 18: Multivariate analysis of samples collected during March 1979 along transects 66, 70 and 74 off Walvis Bay: (a) dendrogram based on Bray-Curtis similarity (sample labels depict transect-station-bottom depth, e.g. 74-10-158); (b) summary table; (c) BIOENV results showing the abiotic variables (bottom depth, SST and salinity) and their importance (as indicated by correlations) to the grouping of the clusters (d) SIMPER results showing species in order of decreasing contribution to the similarity of each dendrogram group; (e) matrix showing correlations between several variables

(d)

Group A	Group B	Group C	Group D
C. carinatus (7037)	*C. carinatus* (10421)	*C. carinatus* (26332)	*Oithona* (874)
C. brachiatus (780)	*M. lucens* (4968)	*C. brachiatus* (5375)	*M. lucens* (354)
Oncaea (535)	*C. brachiatus* (3593)	*M. lucens* (4110)	*Oncaea* (844)
	Oncaea (680)		

Mean abundances shown in parentheses

(e)

	No. of spp	Abundance (ind. m^{-2})	Evenness (*J*)	SST (°C)	Salinity
Abundance (ind. m^{-2})	.2363				
	p=.302				
Evenness (*J*)	-.1855	-.4032			
	p=.421	p=.070			
SST (°C)	.2249	.0318	-.1104		
	p=.327	p=.891	p=.634		
Salinity	.0165	.1138	.0784	.1792	
	p=.944	p=.623	p=.736	p=.437	
Bottom depth (m)	.1610	-.2874	.0801	.3559	-.4244
	p=.486	p=.206	p=.730	p=.113	p=.055

Fig. 19: Multivariate analysis of samples collected during January 1980 along transects 66, 70 and 74 off Walvis Bay: (a) dendrogram based on Bray-Curtis similarity (sample labels depict transect-station-bottom depth, e.g. 74-10-160); (b) summary table; (c) BIOENV results showing the abiotic variables (bottom depth, SST and salinity) and their importance (as indicated by correlations) to the grouping of the clusters (d) SIMPER results showing species in order of decreasing contribution to the similarity of each dendrogram group; (e) matrix showing correlations between several variables

(d)

Group A	Group B
C. carinatus (8861)	*M. lucens* (2396)
C. brachiatus (13485)	*Oncaea* (234)
M. lucens (1619)	*R. nasutus* (108)
	C. carinatus (355)

Mean abundances shown in parentheses

(e)

	No. of spp.	Abundance (ind. m^{-2})	Evenness (*J*)	SST (°C)	Salinity
Abundance (ind. m^{-2})	-.4170				
	p=.085				
Evenness (*J*)	.2343	-.5035			
	p=.349	p=.033			
SST (°C)	.2230	.1193	.1406		
	p=.374	p=.637	p=.578		
Salanity	-.2531	.0209	-.0788	-.1790	
	p=.311	p=.934	p=.756	p=.477	
Bottom depth (m)	.3747	-.2587	-.0581	.1297	-.1457
	p=.126	p=.300	p=.819	p=.608	p=.564

Fig. 20: Multivariate analysis of samples collected during Februay 1980 along transects 66, 70 and 74 off Walvis Bay: (a) dendrogram based on Bray-Curtis similarity (sample labels depict transect-station-bottom depth, e.g. 70-01-040); (b) summary table; (c) BIOENV results showing the abiotic variables (bottom depth, SST and salinity) and their importance (as indicated by correlations) to the grouping of the clusters (d) SIMPER results showing species in order of decreasing contribution to the similarity of each dendrogram group; (e) matrix showing correlations between several variables

(d)

Group A	Group B
M. lucens (8447)	*M. lucens* (346)
Oncaea (586)	*R. nasutus* (28)
Oithona (126)	*C. carinatus* (35)
	C. brachiatus (589)

Mean abundances shown in parentheses

(e)

	No. of spp.	Abundance (ind.m^{-2})	Evenness (*J*)	SST (°C)	Salinity
Abundance (ind. m^{-2})	.1316				
	p=.756				
Evenness (*J*)	-.3158	**-.8212**			
	p=.446	**p=.012**			
SST (°C)	-.5128	-.5337	**.8275**		
	p=.194	p=.173	**p=.011**		
Salinity	.3751	.0207	.0706	-.0499	
	p=.360	p=.961	p=.868	p=.907	
Bottom depth (m)	.3904	.3346	-.6338	-.4549	-.4944
	p=.339	p=.418	p=.092	p=.257	p=.213

Fig. 21: Multivariate analysis of samples collected during March 1980 along transects 66, 70 and 74 off Walvis Bay: (a) dendrogram based on Bray-Curtis similarity (sample labels depict transect-station-bottom depth, e.g. 70-08-144); (b) summary table; (c) BIOENV results showing the abiotic variables (bottom depth, SST and salinity) and their importance (as indicated by correlations) to the grouping of the clusters (d) SIMPER results showing species in order of decreasing contribution to the similarity of each dendrogram group; (e) matrix showing correlations between several variables

3.4.2 Overall cluster analysis

This Section explores whether there are any temporal patterns in the copepod community structure, over the three years (1979-81). Cluster analysis was performed on the entire data set, and a dendrogram (Fig. 22) was constructed. Ten pairs of clusters were identified according to similarity level, referred to here as levels A-H. No clear seasonal patterns could be discerned. An MDS was performed on the same data set in order to display the dendrogram clusters in a more visually informative format. Clarke and Warwick (1997) recommended that for higher values of stress (stress > 0.1) an MDS should be performed in combination with cluster analysis. The MDS obtained had a stress value of 0.22 (Fig. 23), and no distinct groups could be clearly identified. This was still the case even when the MDS was viewed in three dimensions (not shown here). Thus, it can be concluded that there is no overriding variable (such as season, in particular) that is strong enough to cause the samples to group into distinct groups.

Even though level A samples were all collected in mid-summer, they differed in terms of species richness, with group AI having more species than group AII (Table V). Both groups were dominated by *C. carinatus*. Group AI individuals were more evenly distributed among the species than group AII individuals (Table V), signifying high dominance by *C. carinatus* and *R. nasutus* in AII.

There was evidence of a cross-shelf pattern in the level B structure of the dendrogram, with group BI comprising high salinity (35.35), deep stations and BII dominated by moderate-depth, offshore stations (Table V). *M. lucens* was the dominant copepod in group BI, whereas *C. carinatus* dominated in BII (Table VI). Other taxa (not shown) that featured in BI but not in BII were *Oncaea* and *Oithona* spp..

Even though CII was richer in species than CI, the former was strongly dominated by *C. carinatus* (Table VI), whereas in the latter group individuals were relatively evenly distributed among the different species, as indicated by the higher evenness (Table V). Of note was the prominence of *Oithona* spp. in CI.

Temporal differences could be observed in level D (Table V). Group DI was characterised by mid-autumn samples, whereas DII was a mid-summer group. The season was reflected in the differences in mean SSTs between the two groups, with samples from the cooler waters belonging to the 'autumn' group.

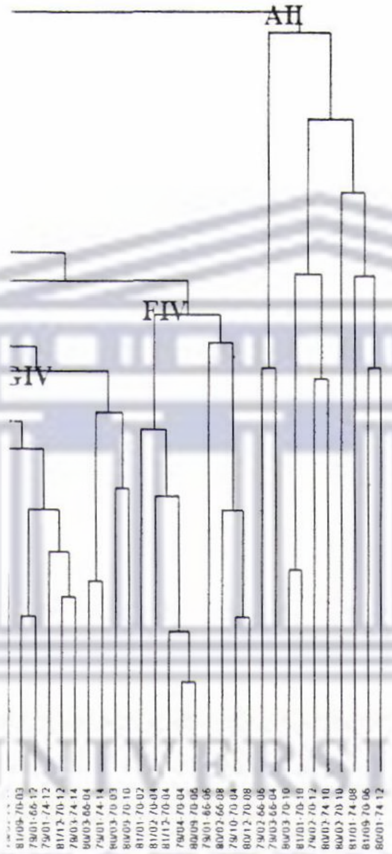

Fig. 22: off the coast of Walvis Bay (in

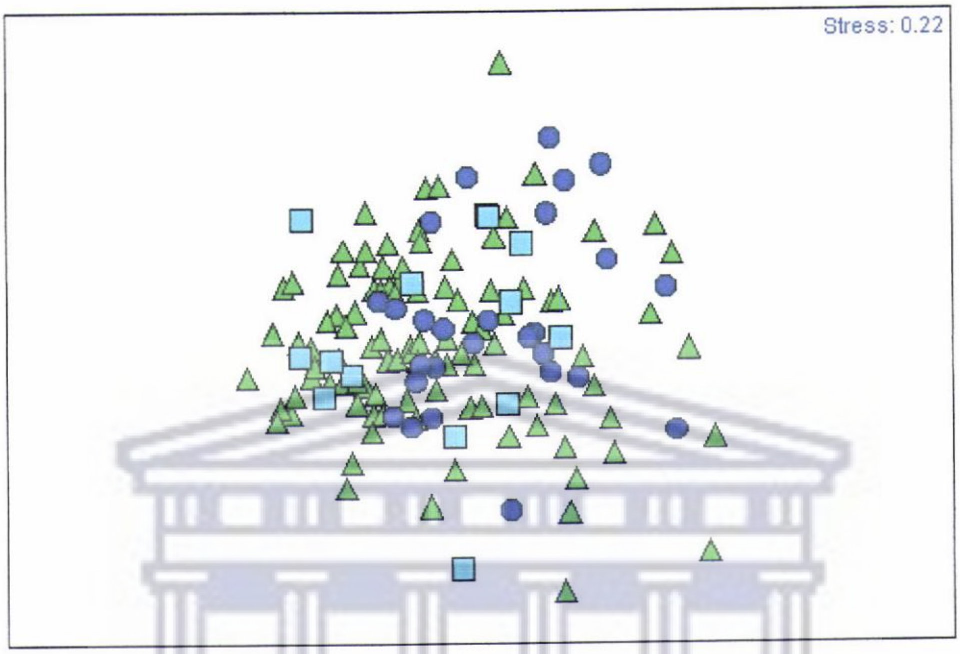

Fig. 23: MDS ordination of SWAPELS samples collected along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S) during the period 1979-81. The MDS is based on root-root transformed abundance data, using the Bray-Curtis similarity index. The stress value is indicated. The triangles denote summer; the circles denote autumn; and the squares denote spring

Table V: Summary of characteristics of each cluster identified in Fig. 22 (*SD* = standard deviation, numbers in bold denote significant differences)

Group	No. of stations	Abundance (ind. m^{-2})		No. of spp.		Evenness (*J*)		Salinity		SST (°C)		Season		Bottom depth (m)	
		Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
AI	132	17608	22806	**5**	1	**0.69**	0.15	35.18	0.13	15.83	1.44	1.5	0.9	141	74
AII	10	11634	11498	**4**	1	**0.49**	0.25	35.23	0.16	16.45	0.92	1.5	1.0	168	64
BI	6	16703	8733	6	1	0.65	0.15	**35.35**	0.14	16.18	0.82	1.7	0.5	**225**	91
BII	126	17651	23280	5	1	0.69	0.15	**35.17**	0.13	15.82	1.47	1.5	0.9	**137**	71
CI	10	11968	20060	**5**	1	**0.78**	0.10	35.19	0.16	15.18	1.89	1.6	1.0	105	95
CII	116	18141	23549	**6**	1	**0.68**	0.15	35.17	0.12	15.87	1.42	1.5	0.9	140	68
DI	7	11464	9612	5	1	0.63	0.12	35.21	0.15	**14.85**	1.59	**2.4**	1.5	126	76
DII	109	18570	24131	6	1	0.68	0.16	35.17	0.12	**15.94**	1.39	**1.4**	0.9	141	68
EI	70	19265	27213	**5**	1	0.68	0.17	35.16	0.12	15.79	1.36	**1.3**	0.7	**124**	41
EII	35	18490	18038	**6**	1	0.66	0.14	35.18	0.13	16.17	1.48	**1.7**	1.1	**170**	83
FI	66	19090	27883	**5**	1	0.69	0.17	35.17	0.12	15.80	1.35	1.3	0.8	121	29
FII	4	22160	13254	**7**	1	0.62	0.12	35.08	0.08	15.53	1.67	1.0	0.0	166	134
FIII	24	17671	19390	6	1	**0.70**	0.11	35.15	0.12	**15.69**	1.51	1.8	1.2	152	70
FIV	9	20751	17126	6	1	**0.58**	0.18	35.24	0.16	**17.20**	0.74	1.3	0.5	225	104
GI	9	**52585**	52269	**5**	1	0.60	0.16	35.10	0.07	16.06	2.08	1.7	1.3	120	36
GII	57	**13801**	17417	**5**	1	0.70	0.17	35.18	0.12	15.76	1.22	1.2	0.6	121	29
GIII	5	28045	30340	6	1	0.65	0.11	35.13	0.07	**14.20**	1.15	**2.4**	0.9	166	77
GIV	19	14941	15430	6	1	0.71	0.11	35.16	0.13	**16.08**	1.36	**1.7**	1.2	148	70
HI	26	15741	18355	5	1	0.66	0.17	**35.13**	0.08	15.43	1.26	1.3	0.8	124	26
HII	31	12174	16718	5	1	0.73	0.16	**35.22**	0.13	16.04	1.13	1.2	0.4	119	30

Table VI: Species composition in the ten pairs of clusters identified in Fig. 22, and the contribution of each species to the similarity of each cluster level. Numbers in parentheses show ranking (i. t. o. % contribution) of species within each cluster. All results were obtained using the SIMPER routine of PRIMER

Level	Species	Abundance (ind. m^{-2})				Contribution (%)
		I	II	III	IV	
A	*C. carinatus*	9974(1)	201(1)			21
	C. brachiatus	3603(3)	89			18
	M. lucens	2250(2)	150(3)			15
	R. nasutus	1431(4)	134(2)			11
	Oithona spp.	573	0			11
B	*C. carinatus*	14	10448(1)			27
	C. brachiatus	219(4)	3765(3)			13
	M. lucens	6068(1)	2068(2)			12
	R. nasutus	105	1494(4)			11
C	*C. brachiatus*	0	4089(2)			25
	C. carinatus	929(3)	11269(1)			17
	Oithona spp.	1311(2)	532			14
	R. nasutus	961	1540(4)			13
	Oncaea spp.	365(4)	715			11
D	*M. lucens*	0	2101(3)			22
	Oithona spp.	2931(1)	378			18
	C. carinatus	4705(4)	11690(1)			16
	Oncaea spp.	2181	248			14
E	*C. carinatus*	17291(1)	1713(1)			22
	C. brachiatus	5898(2)	1222(2)			15
	R. nasutus	2193	452(4)			13
	M. lucens	2922(3)	652(3)			12
	Oithona spp.	493	177			12
	Oncaea spp.	282	160			10
F	*Oithona* spp.	323	3300			21
	R. nasutus	2315	201			17
	Oncaea spp.	217	1365			14
	Calanus spp.	74	477			11
	C. brachiatus	5821(2)	7165(3)			11
	C. carinatus	17835(1)	8294(1)			11
F	*C. brachiatus*			1139(2)	1528(3)	18
	C. carinatus			1942(1)	1349(1)	14
	Oncaea spp.			147	204	14
	R. nasutus			604(4)	98	14
	Oithona spp.			214	114(4)	12
	Calanus spp.			246	27	10
G	*R. nasutus*	1030	2518			21
	C. brachiatus	4352(2)	15129(2)			18
	Harpacticoids	327	122			16

	C. carinatus	17206(1)	17935(1)			13
	Oncaea spp.	249	15			11
G	*C. carinatus*			4310(1)	1319(1)	17
	C. brachiatus			2176(3)	866(3)	16
	M. lucens			944(4)	716(2)	13
	Oithona spp.			201	217	12
	Oncaea spp.			85	163	12
	R. nasutus			734(2)	570(4)	11
H	*R. nasutus*	4968(4)	462			18
	C. carinatus	28781(1)	8839(1)			17
	Oithona spp.	808	10			15
	C. brachiatus spp.	6324(2)	2697(3)			12
	Oncaea spp.	324	185			12

Season was significantly correlated to salinity and abundance (Table VII). Bottom depth and SST were positively correlated. There was a positive relationship between bottom depth and richness as well, suggesting that the number of copepod species increased with distance offshore. However, there was no significant relationship between bottom depth and abundance.

TableVII: Correlation matrix of relationships among biotic and abiotic variables based on data (*N* = 142) collected off Walvis Bay, during SWAPELS (1979-81). Each entry shows *r* (correlation coefficient) and *p* values

	SST (°C)	Salinity	Bottom depth (m)	Abundance (ind. m^{-2})	No. of spp.	Evenness (*J*)
Salinity	.0485					
	p=.566					
Bottom depth (m)	.2551	-.0275				
	p=.002	p=.745				
Abundance (ind. m^{-2})	**.2083**	-.0704	.0197			
	p=.013	p=.405	p=.816			
No. of spp.	.0565	.0306	**.2313**	-.0943		
	p=.504	p=.718	**p=.006**	p=.264		
Evenness (*J*)	-.0803	.0368	-.0836	**-.3556**	.1030	
	p=.342	p=.664	p=.323	**p=.000**	p=.222	
*Season	-0.112	**0.191**	0.017	**0.179**	-0.059	-0.153

* Correlations calculated using Spearman rank correlation

There was no single overriding factor responsible for structuring the dendrogram clusters. The BIOENV analysis produced weak correlation values, with the highest correlation resulting from combining all the variables (Table VIII). Bottom depth, SST and season were the second-most important combination. This suggests an important interaction between these three variables, with SST being the dependent variable. However, season did not feature as a solitary variable, and bottom depth was not as important in this overall analysis as it was in the month-by-month analysis (see Section 3.4.1).

In summary, month-by-month cluster analysis grouped samples according to position along the transect. It was also observed that samples belonging to the same transect tended to fall into the same dendrogram groups. Barring groups D, E and GIII and IV, in which there were significant differences between the samples with respect to season, there was no marked seasonal signal in the data set. In other words, only three out of ten pairs of cluster groups displayed a seasonal pattern. In both the month-by-month and the overall cluster analyses, the four large calanoid copepod species (namely, *C. carinatus*, *C. brachiatus*, *M. lucens* and *R. nasutus*) were responsible for structuring most of the dendrogram groups, implying that these species govern the structuring of copepod communities in this region.

Table VIII: BIOENV results obtained from analysing the entire SWAPELS dataset (i.e. all three transects were included), over a period of three years (1979-81). Only the best nine correlations were selected in the analysis

No. of variables	Correlations (%)	Selections
4	20.4	All
3	20.3	SST, bottom depth, month
3	20.3	SST, salinity, bottom depth
3	20.3	salinity, bottom depth, month
2	20.1	SST, bottom depth
2	20.1	bottom depth, month
2	20.1	salinity, bottom depth
1	20.0	bottom depth
1	11.3	salinity

3.5 Spatio-temporal patterns in the distribution of the dominant copepod species

In Section 3.4 it emerged that *C. carinatus*, *C. brachiatus*, *M. lucens* and *R. nasutus* were the most important species in structuring the copepod communities off Walvis Bay. Percentage contributions of these species to total copepod abundance along transect 70 during the study period 1979-1981, are shown in Table IX. The four species mentioned above collectively contribute 23% to the total abundance in 1979 and 1980, but only 6% in 1981. It should be noted that the total copepod abundances include also copepod developmental stages, as well as other copepod taxa (see Appendix A), whereas the abundances of the individual species represent only the adult stages. It could thus be assumed that these species, combined, constituted a much larger component of the copepod community in this area during the study period, especially during 1979 and 1980. Consequently, in this section the distribution patterns of these species on both temporal and spatial scales are briefly explored. It must be noted that for the purpose of comparing seasonal distribution patterns of these species over a period of three years, only transect 70 samples were considered. Maps showing distributions along all three transects are also presented here.

Table IX: Combined percentage contributions per year of the most dominant copepods species (adults), including abundances and contributions (in parentheses) of each species to the total copepod abundance

Year	Total copepod abundance (ind. m^{-2})	*C. carinatus*	*C. brachiatus*	*M. lucens*	*R. nasutus*	Combined contribution (%)
1979	1 337 568	95 764 (7%)	139 052 (10%)	47 091 (4%)	27 864 (2%)	23
1980	940 252	77 050 (8%)	47 249 (5%)	57 744 (6%)	34 864 (4%)	23
1981	1 275 016	13 533 (1%)	18 700 (1%)	25 977 (2%)	31 055 (2%)	6

3.5.1 *Calanoides carinatus* (Krøyer 1849)

Throughout the study period, adult *C. carinatus* were often observed to occur predominantly within 30 n. m. of the coast (Figs 24-27). From Fig. 24, it can be seen that the major concentrations of this species corresponded to the seasonal distribution of relatively cool, low-salinity water (see Figs 5a and b). Even though abundances generally ranged around 3 000 ind. m^{-2}, high values of up to 13 000 ind. m^{-2} were recorded in early autumn, spring and summer. However, in 1981 abundances were generally low (< 500 ind. m^{-2}), and exceeded 500 ind. m^{-2} only in summer. The near-shore distribution of *C. carinatus* is depicted again in the intertransect comparisons (Figs 25-27). Populations were observed as far offshore as 45 n. m. in January 1979 (transects 66 and 74, Fig. 25), March 1980 (transects 66 and 70, Fig. 26), January and March 1981 (transects 74 and 70, respectively, Fig. 27). Also, of note was the occurrence of relatively low abundances in March 1980 (< 27 ind. m^{-2}, Fig. 26) and 1981 (< 340 ind. m^{-2}, Fig. 27).

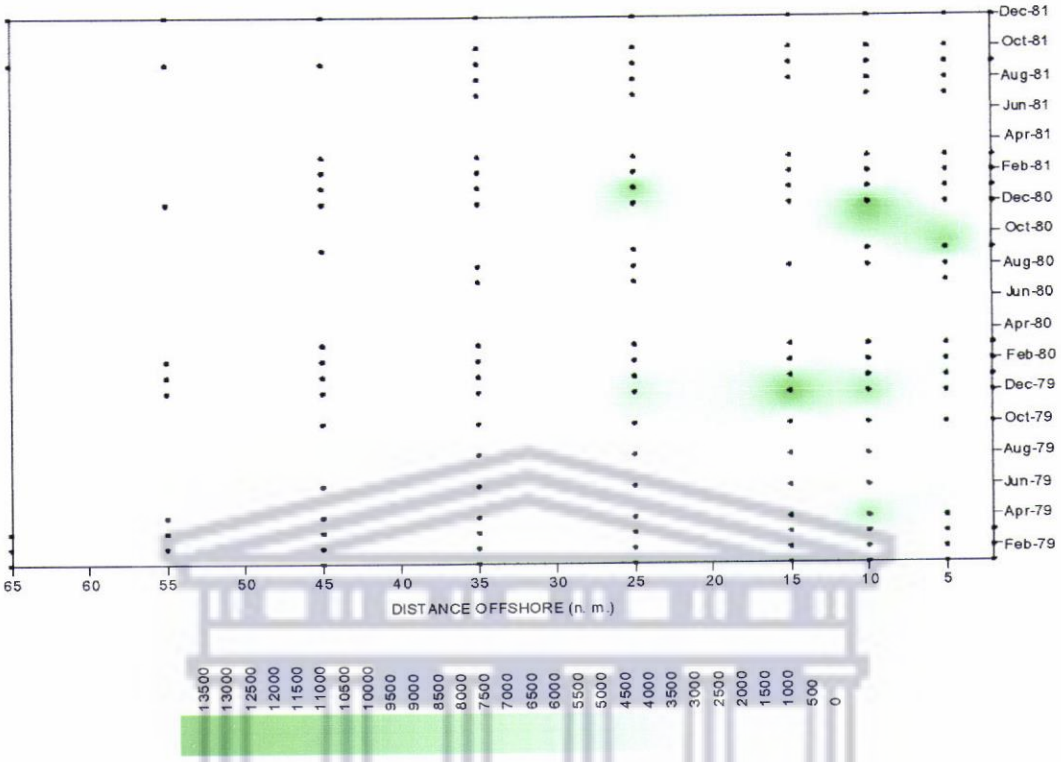

Fig. 24: Spatial and temporal distribution of *Calanoides carinatus* (adults) abundance (ind. m^{-2}) along transect 70 (23° S) over the period 1979-1981. Dots indicate positions of sampling stations along the transect

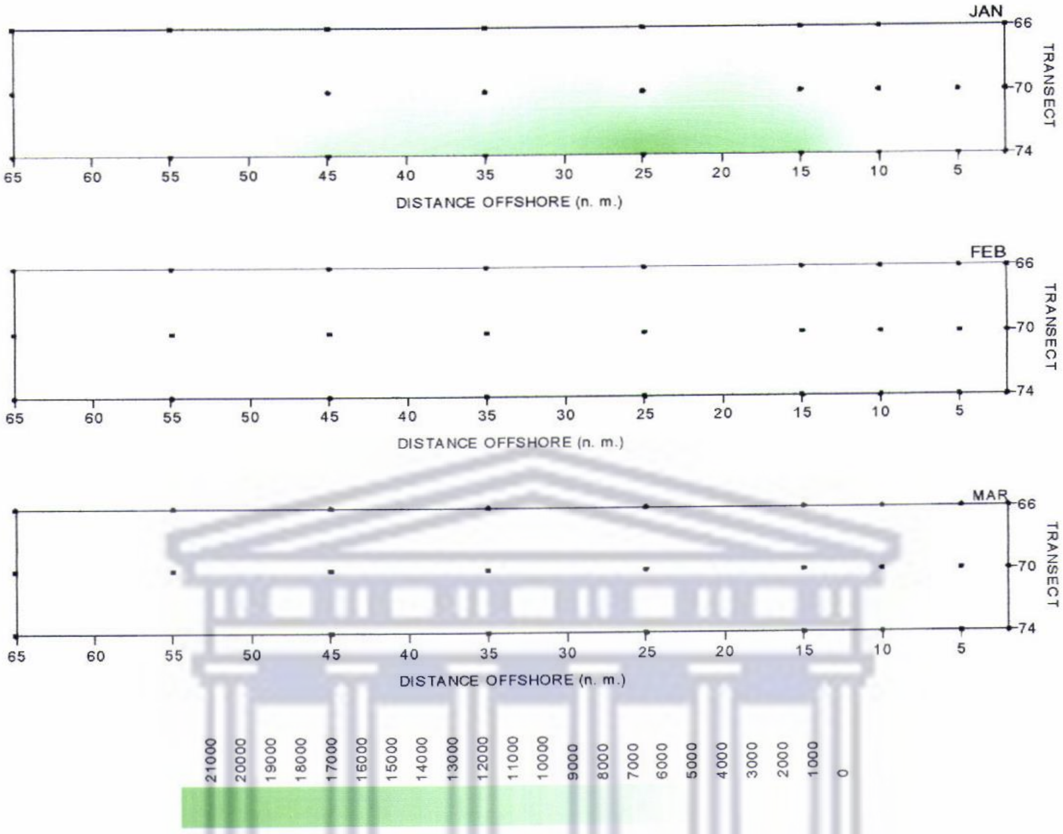

Fig. 25: Distribution of *Calanoides carinatus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979. Dots indicate positions of sampling stations along the transects

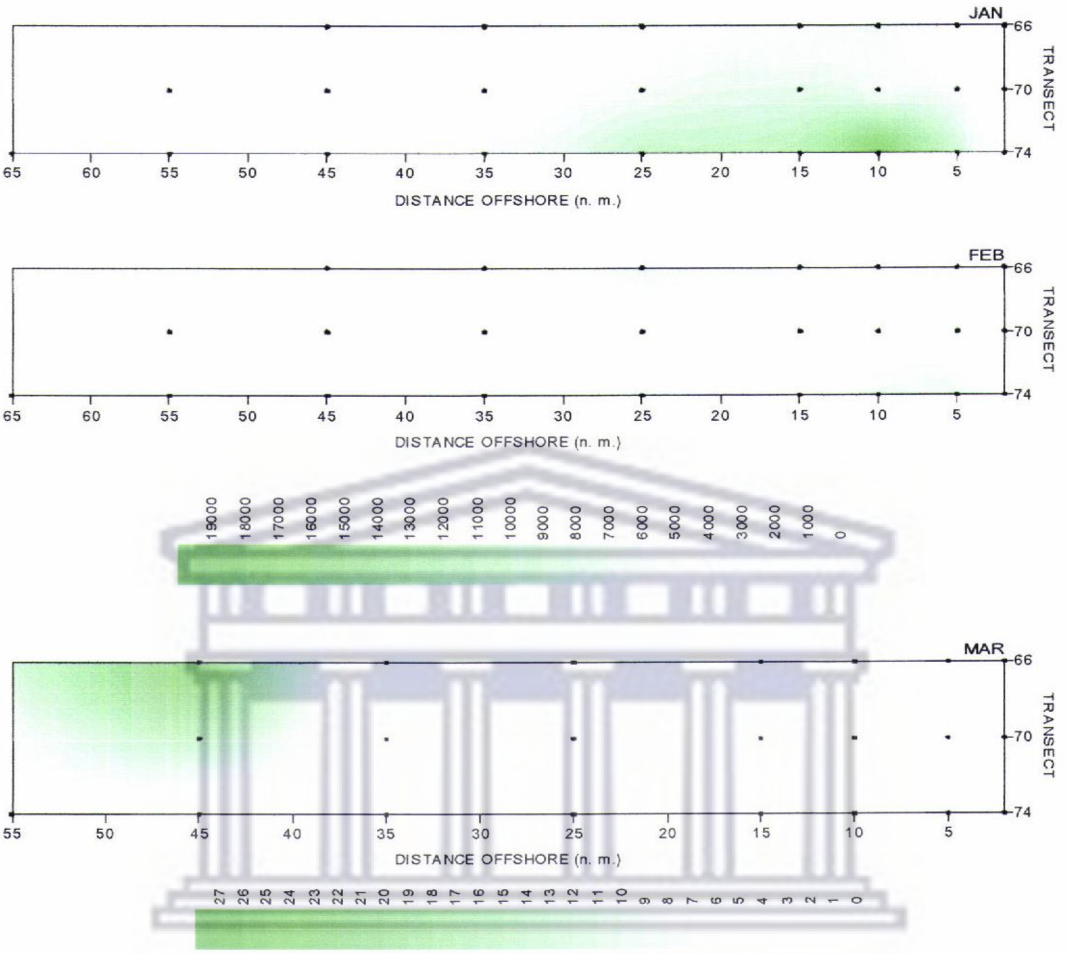

Fig. 26: Distribution of *Calanoides carinatus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Note that the map for March has been assigned a separate colour scale due to the exceptionally low abundances in comparison to January and February. Dots indicate positions of sampling stations along the transects

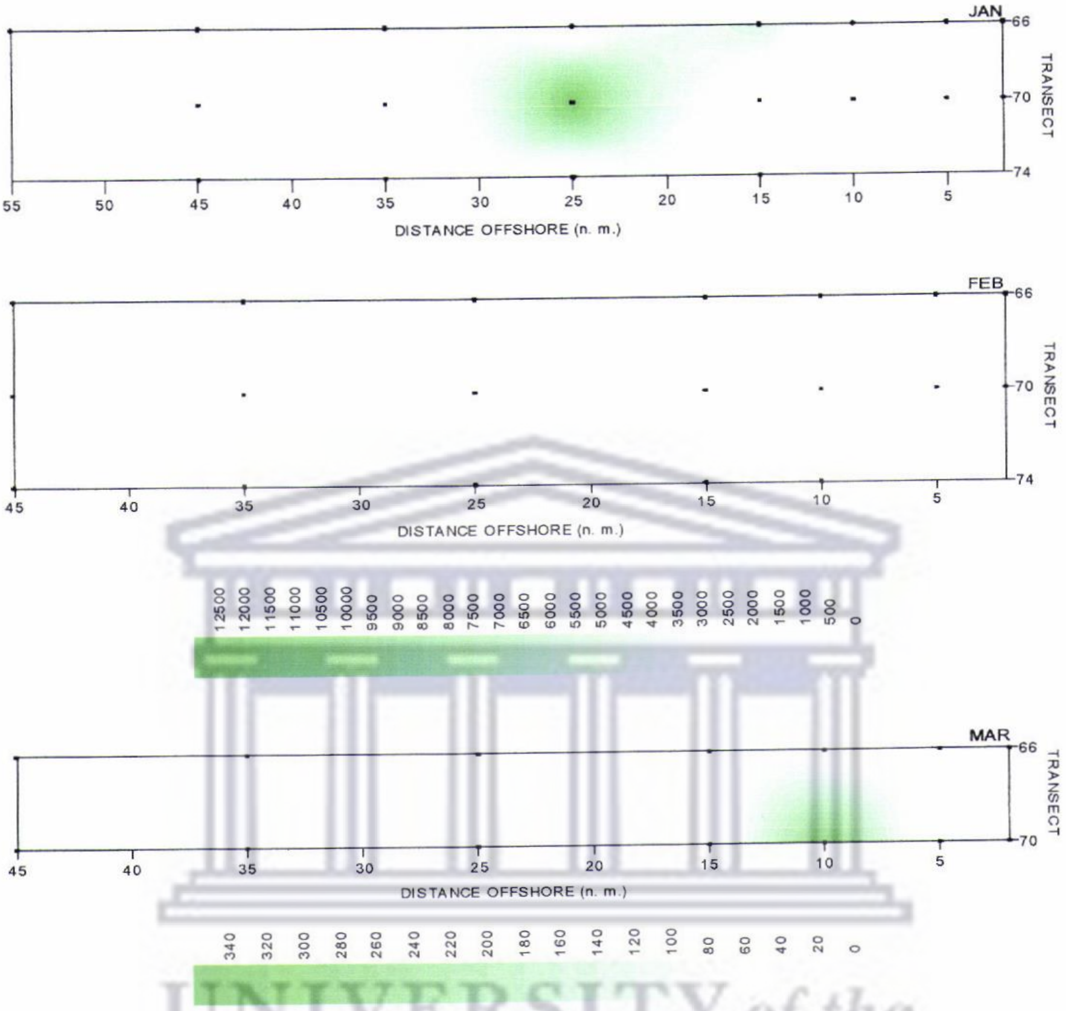

Fig. 27: Distribution of *Calanoides carinatus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Note that the map for March has been assigned a separate colour scale due to the exceptionally low abundances in comparison to January and February. Dots indicate positions of sampling stations along the transects

3.5.2 *Centropages brachiatus* (Dana 1848)

Generally, adult *C. brachiatus* were prominent only during 1979 (Fig. 28). Their distribution extended over most of transect 70 (up to 50 n. m. offshore). There was, however, no seasonal pattern observed during the study period. Of note were the exceptionally high abundances recorded in December 1979, when abundances soared to c. 20 000 ind. m^{-2} – an order of magnitude higher than observed throughout the year. There was also no uniformity in abundance among the transects, with each transect showing a unique distribution in comparison to the other transects (Figs 29-31). The observation that the maximum for March 1981 was more than 100 fold lower than those recorded for January and February 1981 (Fig. 31), is noteworthy.

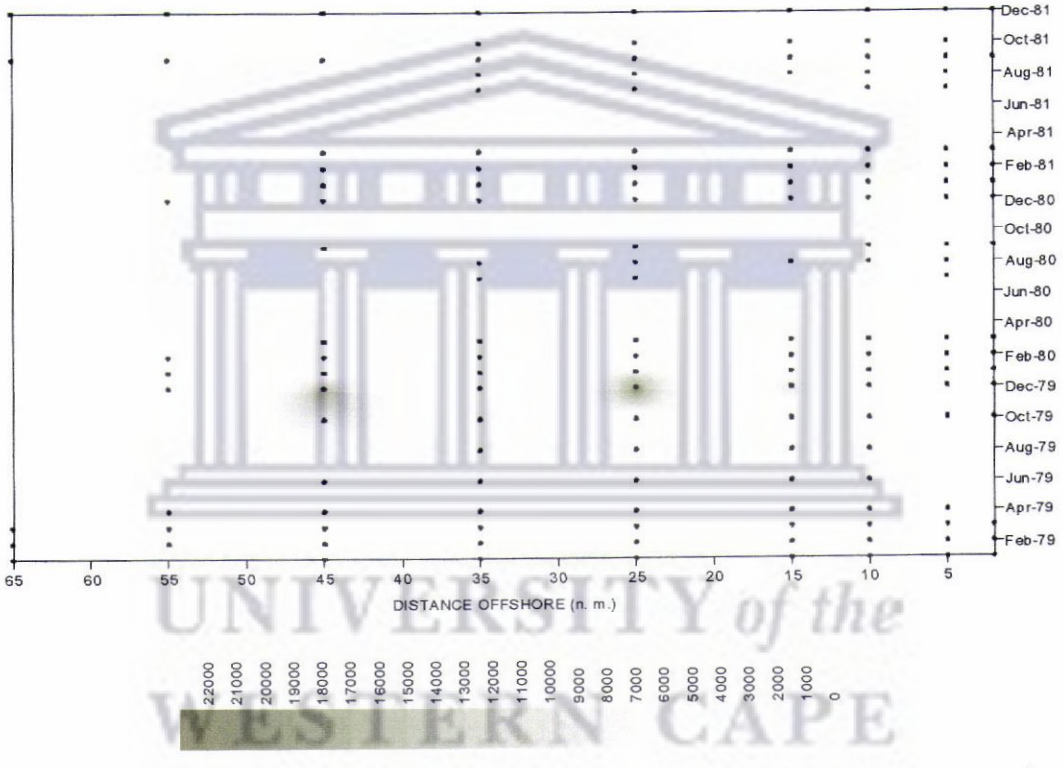

Fig. 28: Spatial and temporal distribution of *Centropages brachiatus* (adults) abundance (ind. m^{-2}) along transect 70 (23° S) over the period 1979-1981. Dots indicate positions of sampling stations along the transect

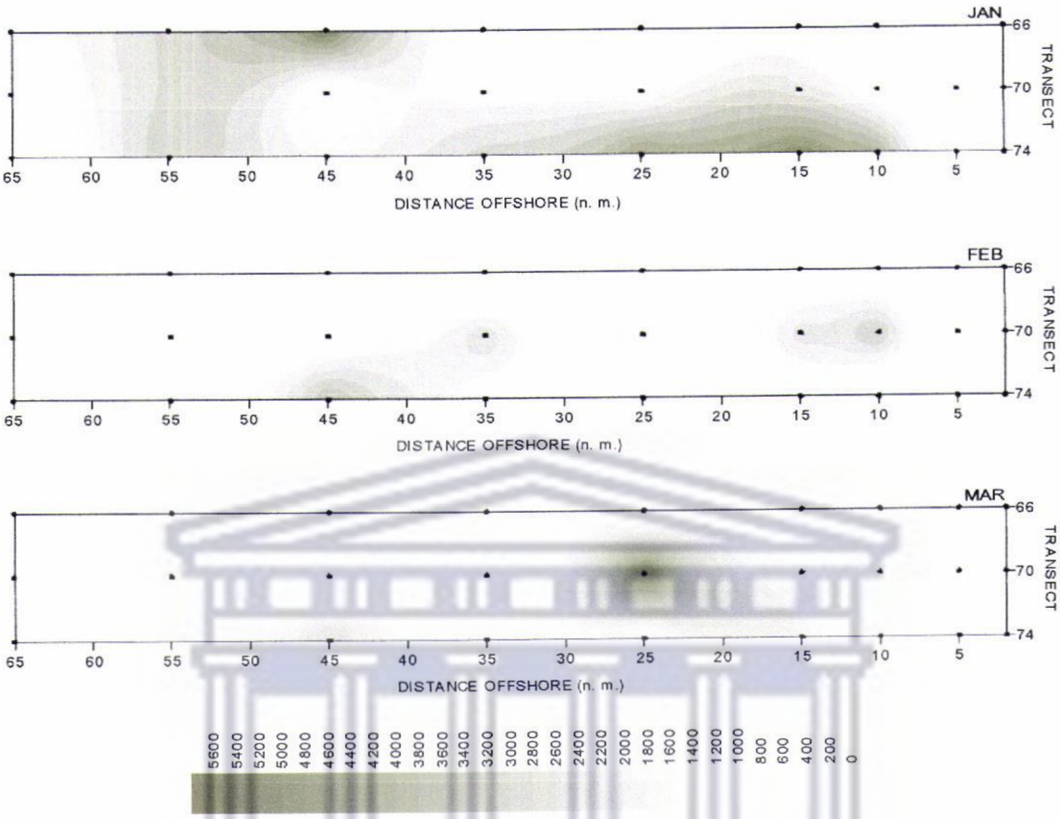

Fig. 29: Spatial and temporal distribution of *Centropages brachiatus* (adults) abundance (ind. m^{-2}) along transect 70 (23° S), from January to March 1979. Dots indicate positions of sampling stations along the transect

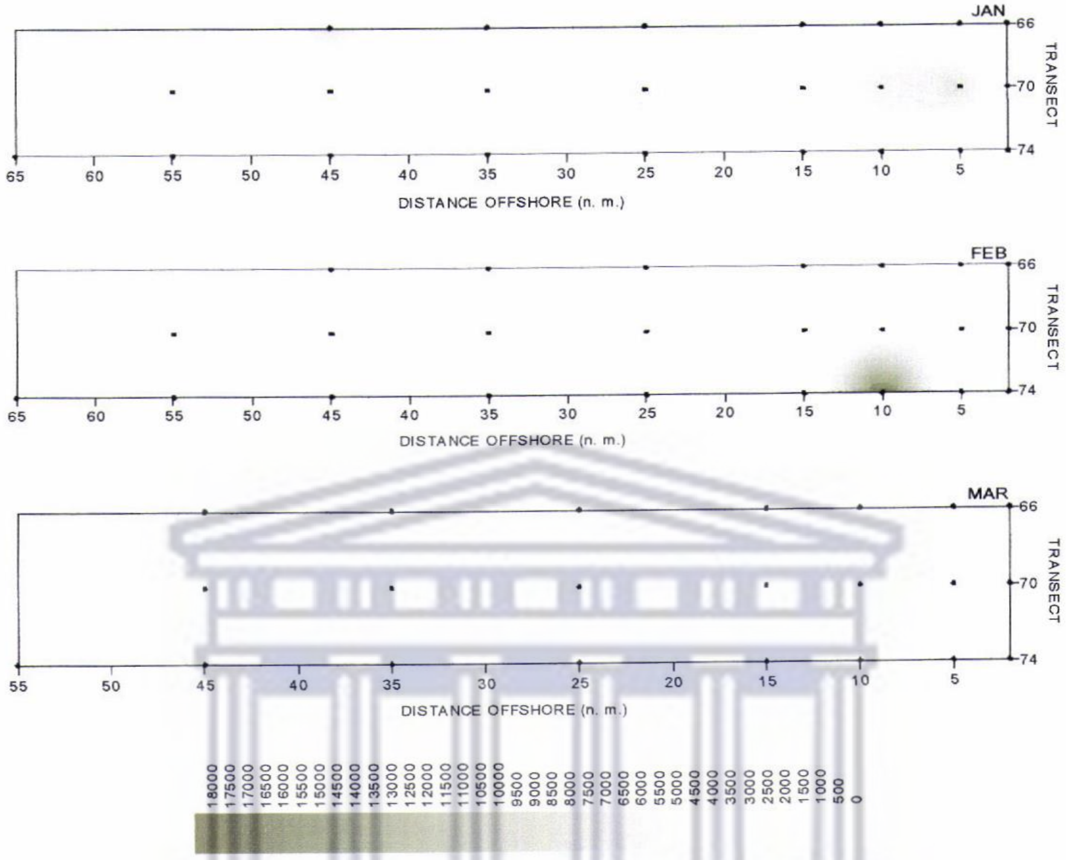

Fig. 30: Distribution of *Centropages brachiatus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Dots indicate positions of sampling stations along the transects

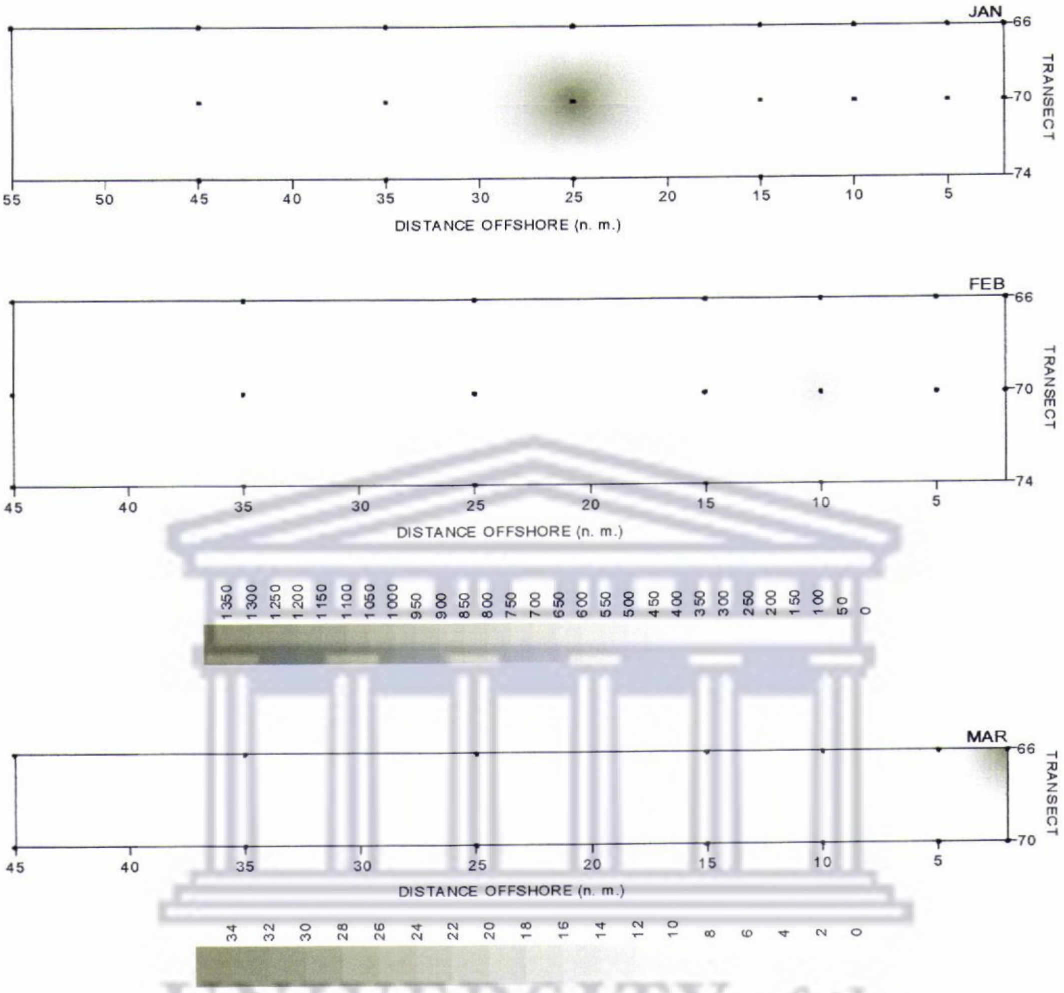

Fig. 31: Distribution of *Centropages brachiatus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Note that the map for March has been assigned a separate colour scale due to the exceptionally low abundances in comparison to January and February. Dots indicate positions of sampling stations along the transects

3.5.3 Metridia lucens (Boeck 1964)

Even though *M. lucens* occurred almost throughout the period 1979-1981, it was most abundant (4500-6500 ind. m^{-2}) during summer to early autumn, i.e. December-March (Fig. 32). However, there was no discernable seasonal cross-shelf pattern, except that this species was mostly observed between 15 and 45 n. m. offshore. During the summer months of 1980 and 1980-81, however, *M. lucens* populations also occupied the inshore region, i.e. within 15 n. m. of the coast. This was during the period when warm (> 15.5 °C) water pushed shorewards (see Fig. 5a). With respect to intertransect comparison, there was no discernible pattern in the distribution of *M. lucens* (Figs 33-35).

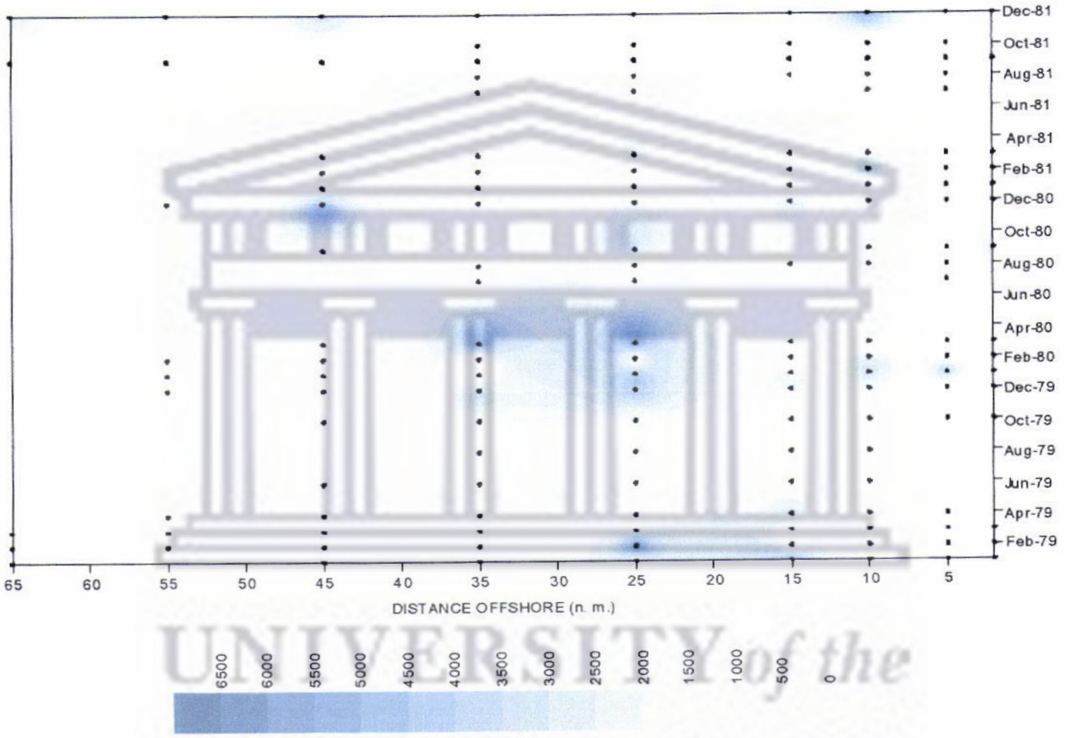

Fig. 32: Spatial and temporal distribution of *Metridia lucens* (adults) abundance (ind. m^{-2}) along transect 70 (23° S) over the period 1979-1981. Dots indicate positions of sampling stations along the transect

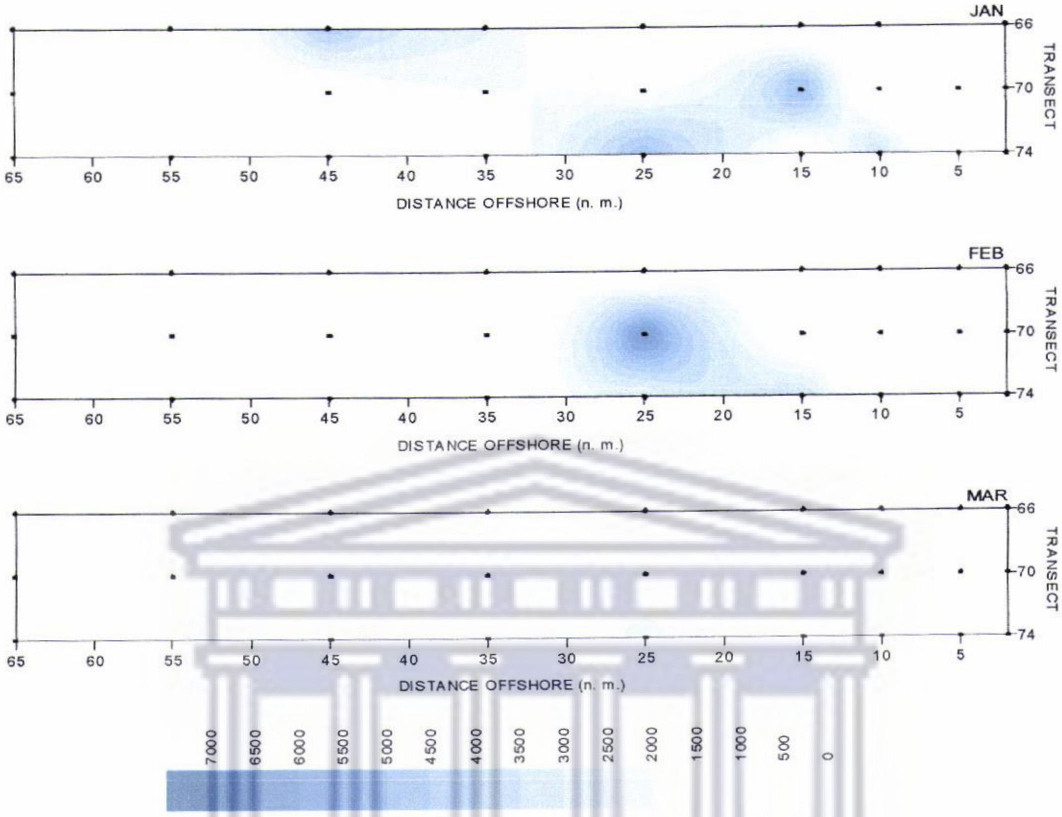

Fig. 33: Distribution of *Metridia lucens* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979. Dots indicate positions of sampling stations along the transects

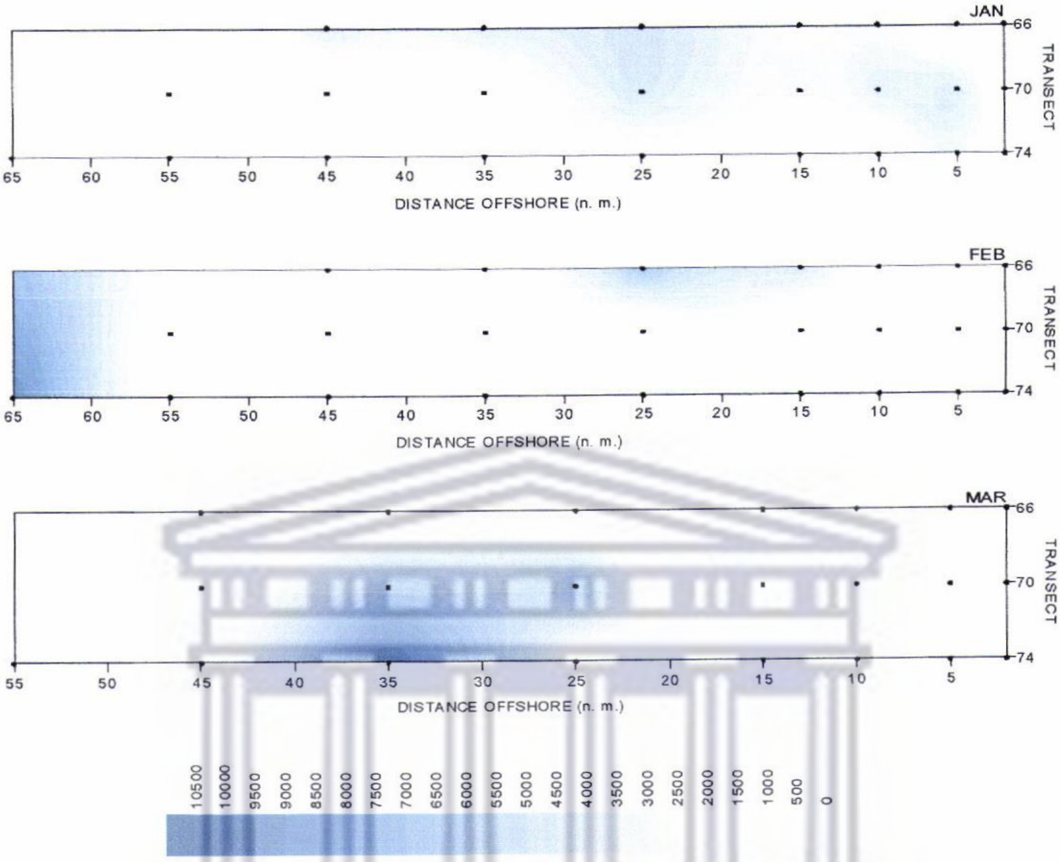

Fig. 34: Distribution of *Metridia lucens* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Dots indicate positions of sampling stations along the transects

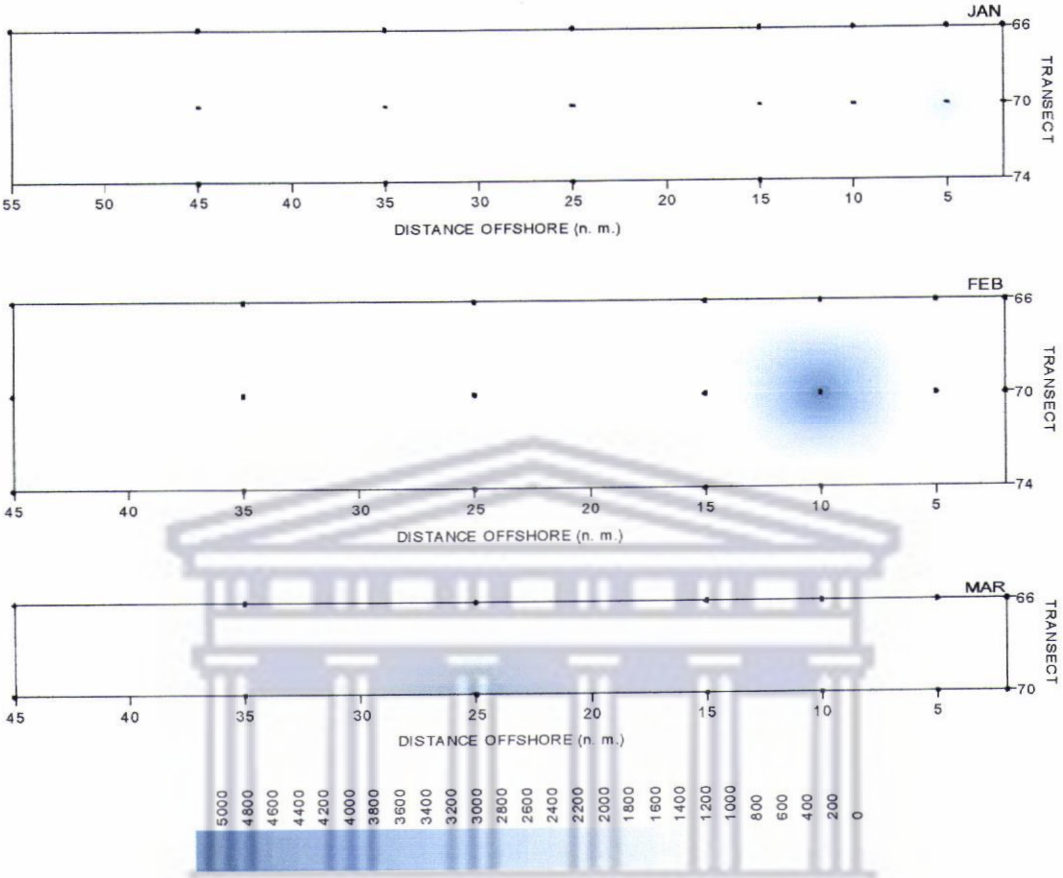

Fig. 35: Distribution of *Metridia lucens* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Dots indicate positions of sampling stations along the transects

3.5.4 *Rhincalanus nasutus* (Giesbrecht 1888)

This copepod was also present along most of transect 70 (Fig. 36). As was observed for *C. carinatus*, relatively high (1 500-2 000 ind. m^{-2}) abundances occurred during spring and summer of each year. However, the cross-shelf distribution of *R. nasutus* extended as far as 45 n. m. offshore, and was not restricted to the inshore region (i.e. within 15 n. m. offshore). Moreover, in spring and summer of 1980, abundances for this species were the highest recorded during this study, ranging between 7 000 and 9 000 ind. m^{-2}. Again, there was variability among the transects in the distribution of *R. nasutus* abundance (Figs 37-39).

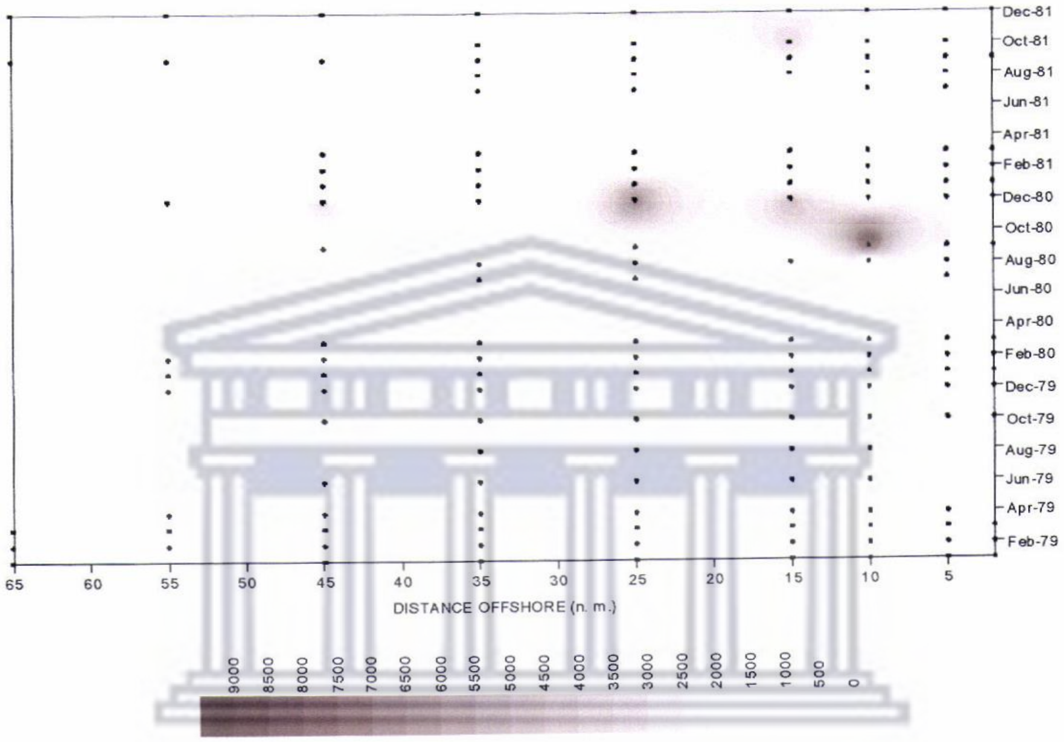

Fig. 36: Spatial and temporal distribution of *Rhincalanus nasutus* (adults) abundance (ind. m^{-2}) along transect 70 (23° S) over the period 1979-1981. Dots indicate positions of sampling stations along the transect

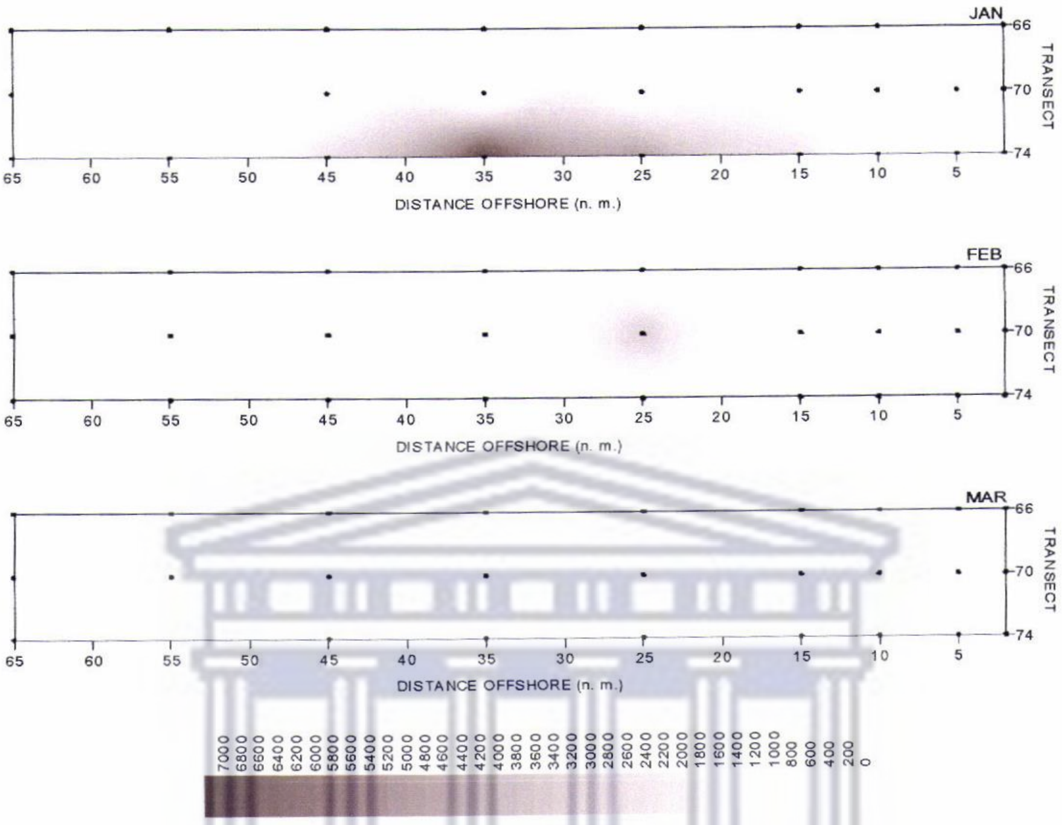

Fig. 37: Distribution of *Rhincalanus nasutus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1979. Dots indicate positions of sampling stations along the transects

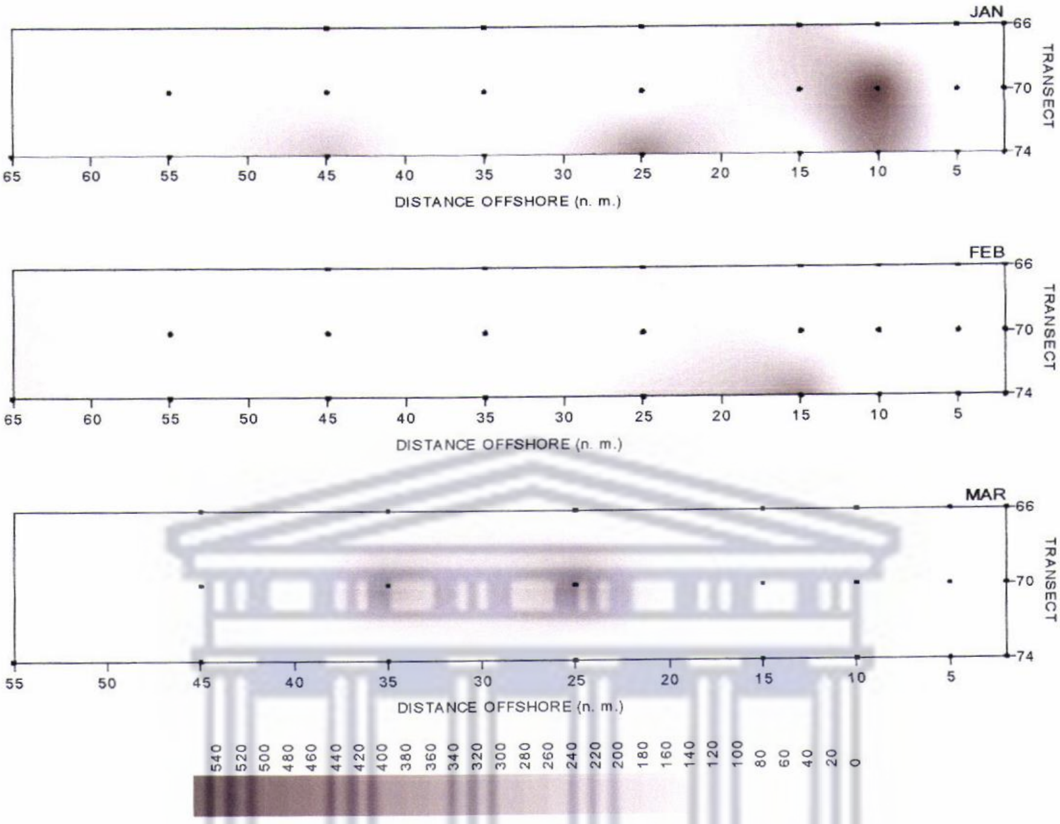

Fig. 38: Distribution of *Rhincalanus nasutus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1980. Dots indicate positions of sampling stations along the transects

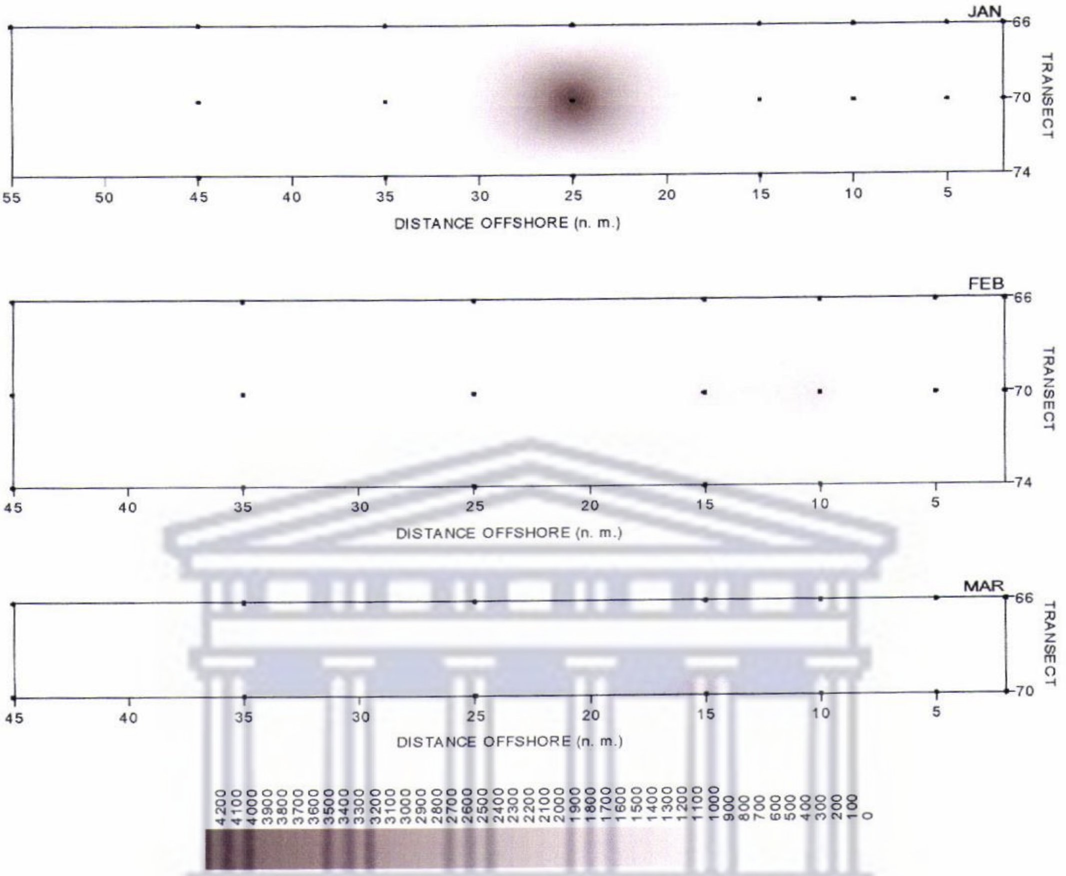

Fig. 39: Distribution of *Rhincalanus nasutus* (adults) abundance (ind. m^{-2}) along transects 66 (22°67 S), 70 (23° S) and 74 (23°33 S), from January to March 1981. Dots indicate positions of sampling stations along the transects

4 Discussion

4.1 The physical environment

The area off Walvis Bay (transects 66, 70 and 74, between 22°67 S and 23°33 S) was highly variable temporally and spatially with respect to SST and salinity distribution during the 1979-81 SWAPELS surveys. Nevertheless, it has been shown in this study that despite the observed variability in SST, the most frequently occurring SSTs were in the 15-16 °C range (Fig. 4). It is likely that this overall range of moderate to warm SSTs was attributable to the predominance of high SSTs mainly offshore, with the offshore region constituting the largest area (covering a distance of c. 45 n. m. of the 65-n. m. transect). With respect to salinity, waters of varying salinities were observed over the three-year period. In 1979 salinities ranged mostly between 35.1 and 35.2, whereas in 1980 and 1981 modal salinities fell within the 35.0-35.1 and 35.2-35.3 ranges, respectively. The generally warm, saline waters recorded in 1981 are indicative of the dominance of oceanic water that year, possibly derived from the mixing of Benguela and Angola Current waters (O'Toole 1980, Le Clus and Kruger 1982).

A clear seasonal pattern in the cross-shelf distribution of SST and salinity was observed in 1979-80, wherein, generally, warm, high-salinity water covered most of transect 70 – nearshore surface water was relatively cool – in summer to early autumn. The warm water during January-March – with peak SSTs mostly in February – has been suggested to be the result of prevailing conditions during this time of the year, namely, weaker upwelling winds, reduced vertical mixing and strong insolation (Boyd *et al.* 1987a). In spring the cool inshore water extended seaward, to recede again into summer. Consistent with observations by O'Toole (1980) and Hansen *et al.* (2005), the existence of cool inshore surface water from mid-winter to mid-spring, warming up into summer and extending offshore, was indicative of a typical upwelling season off Walvis Bay. This upwelling season was particularly evident in 1979.

It appears that the presence of two distinct water masses – warm, high salinity (> 35.2) water offshore, and cool, low salinity (< 35.1) water inshore – with relatively sharp boundaries, is characteristic of the Namibian coast (Currie 1953, as cited in O'Toole 1980, Stander 1964). Furthermore, O'Toole (1980) suggested the existence of three, fairly distinct bodies of surface water: firstly, cold, low-salinity, recently-upwelled water; secondly, warm, highly saline water of Angolan origin; and thirdly, water of intermediate SST and salinity magnitudes, thought to form as a result of the mixing between the Angola and Benguela Currents – this water mass usually advanced from the west shorewards. The last two water masses could explain the atypical SST distributions encountered in 1981. More data are required in order to confidently determine the sources of water masses found in the Walvis Bay area during the study period. This study makes use of surface measurements of temperature and salinity, which is not sufficient to adequately explain movements of water bodies.

Disregarding seasonality, the offshore reaches were generally characterised by warm surface waters, and nearshore reaches tended to be cool. Ekman transport of coastal water westwards is expected to affect trends in offshore SSTs (Walker 1987). Of importance as well to the oceanography of an area, is the local wind regime. Stander (1963) reported on seasonal and interannual variability in SST, and related it to wind. He found that over the period 1958-1961, notwithstanding interannual variations, the weakest winds prevailed during mid-summer, while in mid-spring the highest wind velocities were recorded. Furthermore, the general wind direction in summer was south-westerly, while in spring it was west-south-westerly (between 225° and 270°). Wind stress, combined with the effect of Coriolis forces, can result in a seasonal cross-shelf movement of surface waters, away from the coast, most importantly creating suitable conditions for upwelling. Even though the winter season is not well represented in the data coverage of this study, it is expected that the diurnal southerly winds that typically occur in winter in the Walvis Bay area (Stander 1963, Boyd 1983), would not have resulted in a significant seaward movement of coastal surface waters. Hence upwelling is not pronounced during most part of winter.

It emerges from this study that there was variability from year to year with regard to the timing of the seasonal cycle, as well as the levels of SSTs and salinities, over the period 1979-1981 (see Section 3.1, and figures therein). Similarly, seasonality and interannual variability in both SST and salinity off Walvis Bay have been reported in works by, *inter alia*, Kruger and Boyd (1984), and Boyd *et al.* (1987a). Moreover, intra-annual changes in the structure and location of the Angola-Benguela front, as well as episodic warm and cool anomalies – as discussed in Chapter 1 – are possible contributing factors to the interannual variability of the system off Walvis Bay.

Monthly comparisons of the three transects with respect to SST and surface salinity were done only for January-March of each year. Therefore, any spatial variability presented in Section 3.1 should be discussed only for these three months, taking into account the climatological and hydrological conditions that typically prevail during these months. There was generally heterogeneity among the transects with respect to the distribution of especially SST, and to a lesser extent salinity. These results therefore suggest that transect 70 is not suitable to use as a proxy for measuring hydrological parameters off Walvis Bay, due to the very dynamic, and therefore very variable, nature of this area, as it lies downstream from the Lüderitz upwelling cell.

The results from the intertransect comparisons discussed above (January-March each year) are not sufficient – they cover a limited area – to draw conclusions on latitudinal gradients. However, a discussion on latitudinal variability in SST and salinity is still relevant. Even though this was supported by weak evidence, SST tended to display a north-to-south decrease, whereas there were no consistent patterns in the alongshore distribution of salinity. Coastal upwelling off Walvis Bay has been found to be more active and intense south of 23° S, as far south as Lüderitz (Le Clus and Kruger 1982, Kruger and Boyd 1984, Walker 1987). This is likely to result in the distribution of relatively cooler water mostly south of 23° S, as observed in the SST profiles of the three transects (Figs. 6-8). A southerly gradient of decreasing SST is observed also during the episodic intrusions of warm Angolan water from the north, which tend to occur in summer and early autumn (Kruger and Boyd 1984, Boyd *et al.* 1987a). However, even though Walvis Bay lies within range of these intrusions (Le Clus and Kruger 1982, Boyd *et al.* 1987a), the observed uniform pattern in alongshore salinity distribution, as well as the low levels in salinity values, cast a doubt on the existence of such an intrusion during January-March – these intrusions are characterised by relatively high salinities (35.5-35.7). Moreover, the more extreme versions of these intrusions – named the *Benguela Niños* – to occur closer to the study period, 1979-1981, was the 1984 event (Boyd *et al.* 1987a). However, the 1984 event did not start forming until December 1983 (Mainoane, in prep.).

Seasonal patterns in the distribution of SST and surface salinity presented in this work cover almost three seasons in each year, namely: summer, early autumn (to mid-autumn in 1979), and early to mid-spring. The entire winter season was not accounted for in the data set, due to the timing of the SWAPELS cruises (as discussed in Section 2.2). Even though biological (ichthyo- and zooplankton) data collected on ships-of-opportunity during the winter months were available, corresponding SST and salinity data could not be retrieved. Nevertheless, seasonal and interannual variability in SST and surface salinity distribution could still be described in this work.

4.2 Zooplankton biomass and total copepod abundance

4.2.1 Seasonal variability

The peaks observed in zooplankton biomass (biovolume) from year to year occurred mostly during early autumn, and during late winter/spring and early summer, taking into account interannual variability in spatial and temporal patterning. Similarly, Unterüberbacher (1964) reported on peaks in settled volumes during summer 1960, winter 1961, and spring 1962, in the Walvis Bay area. A discussion on the relationship between biomass and hydrology will follow.

Total copepod abundance seemed to respond, both spatially and temporally, to SST and salinity dynamics. Firstly, total abundances were generally distributed within, at the most, 45 n. m. off the coast – the maximum distance seaward to which cool water was generally distributed during the course of 1979-1981. Secondly, the seasonal peaks in total abundances displayed a 'delayed' response to the surge of cool, low-salinity water in late autumn and spring (September and/or October), which signalled the occurrence of upwelling. For instance, in the springs of 1979 and 1980, copepods accumulated inshore, with total abundances soaring to high levels in December, and extending offshore. Unterüberbacher (1964) found a similar 'delayed' response – albeit in total zooplankton settled volumes rather than total copepod abundances – whereby peaks were observed two months after periods of low water temperatures, and also corresponded to the periods of high phytoplankton production reported by Kollmer (1962). Thus, this points to the critical role upwelling plays in stimulating both primary and subsequently secondary production off Walvis Bay.

The fact that the patterns observed in zooplankton biomass distribution were not mirrored in total copepod abundance, can be explained by pointing to variability in the composition of zooplankton collected during sampling. Apart from copepods, there were other large-sized zooplankton contained in the samples, such as euphausiids, chaetognaths, amphipods, decapod larvae, polychaetes, and occasionally fish eggs and larvae – nearly all fish eggs and larvae were already extracted from the samples during previous analysis (e.g. Le Clus and Kruger 1982, Le Clus 1985). The presence of these groups in varying proportions through time obscured the relationship between total copepod abundance and total zooplankton biomass. Determination of total copepod biomass could probably reveal more clearly to what extent copepods and total zooplankton biomass were related. For instance, Fearon *et al.* (1986) described copepods to make up 40% of the total zooplankton biomass between 23° and 23°30 S, in January 1985. Barange (1989) found that during the winters of 1983 and 1984, 50% of the total zooplankton biomass measured from Walvis Bay to the Orange River mouth, was made up of groups larger than 2 000 µm (TL), such as euphausiids, hyperiid amphipods and chaetognaths. Copepods dominated (i.t.o. biomass) in all other size classes.

The seasonal patterns in zooplankton biomass described in this study are in agreement with previous observations by Kruger (1983), Fearon *et al.* (1986), Timonin (1990, 1991 and 1992), Timonin *et al.* (1992), Hansen *et al.* (2005). These authors showed cross-shelf distribution patterns of zooplankton biomass that exhibited multiple peaks (mostly bimodal). This is consistent with the findings in this work. These peaks have been attributed to the effects of coastal upwelling (Timonin 1990, 1991 and 1992, Hansen *et al.* 2005). Generally, in the absence of upwelling – from autumn to winter – there is low zooplankton abundance close inshore, increasing in the midshelf region, and peaking between 20 and 80 n. m. from the coast (Hansen *et al.* 2005). Following active upwelling in spring to summer, there is development of zooplankton populations inshore. This inshore aggregation becomes displaced offshore upon relaxation of upwelling in November- January.

In conclusion, as previously suggested by Timonin (1992) and Hansen *et al.* (2005), the observed multiple peaks in biomass off Walvis Bay during the study period (1979-81), are likely to be linked to the pulsed nature of upwelling – which follows a seasonal cycle – which results in increased herbivorous zooplankton populations inshore in response to enhanced phytoplankton production there.

4.2.2 Decadal variability

The zooplankton biomass and total copepod abundance data obtained in this study can be put within a context of long-term variability, examining decadal changes in the northern Benguela. To that extent, additional 'initial' biovolume data from other SWAPELS cruises (Mainoane, pers. comm., and data currently acquired from retrospective analysis under the umbrella of the BENEFIT and BCLME programmes), published historical data (Kollmer 1963), and data acquired during Namibia's current monthly monitoring programme (courtesy of R. Cloete and A. Kreiner, Ministry of Fisheries and Marine Resources) were combined to reconstruct a 4-5 decade time-series. Characteristics of each of these data sources are summarised in Table X, and maps showing the survey grids are illustrated in Fig. 40.

Annual means of log-transformed total zooplankton biovolume and total copepod abundance are shown in Figs. 41a and b, respectively. The time-series cover a period of five decades. The data indicate an increasing trend in zooplankton biomass in the northern Benguela over the past 50 years. This upward trend is also reflected in total copepod abundance.

Studies on long-term changes in zooplankton abundance and/or biomass are useful in understanding the importance of zooplankton as indicators of changes in trophodynamic links (Verheye and Richardson 1998, Verheye *et al.* 1998, Verheye 2000, Hutchings *et al.*, in press) and the physical environment (Roemmich and McGowan 1995, Lavaniegos *et al.* 1998, Planque and Taylor 1998). The decade-scale data presented in this work allow for only tentative – thus far, there are only limited data for particular years, with large gaps inbetween, which we are filling through BCLME, and *inter alia*, this study – conclusions to be drawn as to the long-term variability of zooplankton biomass and abundance over the period 1959-2004. As is common in many interdecadal comparisons, the data were collected during a variety of sampling surveys. These surveys differed in design, driven by their respective specific objectives. Therefore, the time-series, as presented here, should be viewed with caution, taking into account the following limitations:

1. Different sampling nets with different mesh sizes, towed in different modes over varying depth ranges, were used (Table X). Using Pillar's (1984b) correction factor assumes that the zooplankton communities in this study and Pillar's study were similar.

Table X: Sampling time, strategy and information source for each sampling programme considered in this study's interdecadal comparison. Samples were collected off and around Walvis Bay (23° S) between 1959 and 2004

Parameter	1959	1978-1985	2000-2004
Time	January-December	January-December (including one winter month each year)	January-December
Target sampling depth (m)	100	50	200
Gear type	N70V	Bongo and N50V (winter samples)	WP-2
Towing mode	Vertical	Oblique; N50V vertical	Vertical
Mouth area (m^{-2})	0.385 (Kemp *et al.* 1929)	Bongo - 0.255; N50V - 0.196	0.255 (UNESCO 1968)
Mesh size (µm)	200	Bongo - 300; N50V - 80	200
Flowmeter	None	Calibrated digital	Calibrated digital
Information Source	Kollmer 1963	This study	Hansen *et al.* 2005

Note: for the purpose of interdecadal comparison, to standardise between the different mesh sizes used during the various sampling programmes, all N50V net samples were washed through a 200-µm mesh sieve; to compensate for the larger 300-µm Bongo net mesh, settled volumes from this net were multiplied by a correction factor of 1.85 (Pillar 1984b); settled volumes from all the sampling programmes were standardised to biovolume, in ml m^{-2}.

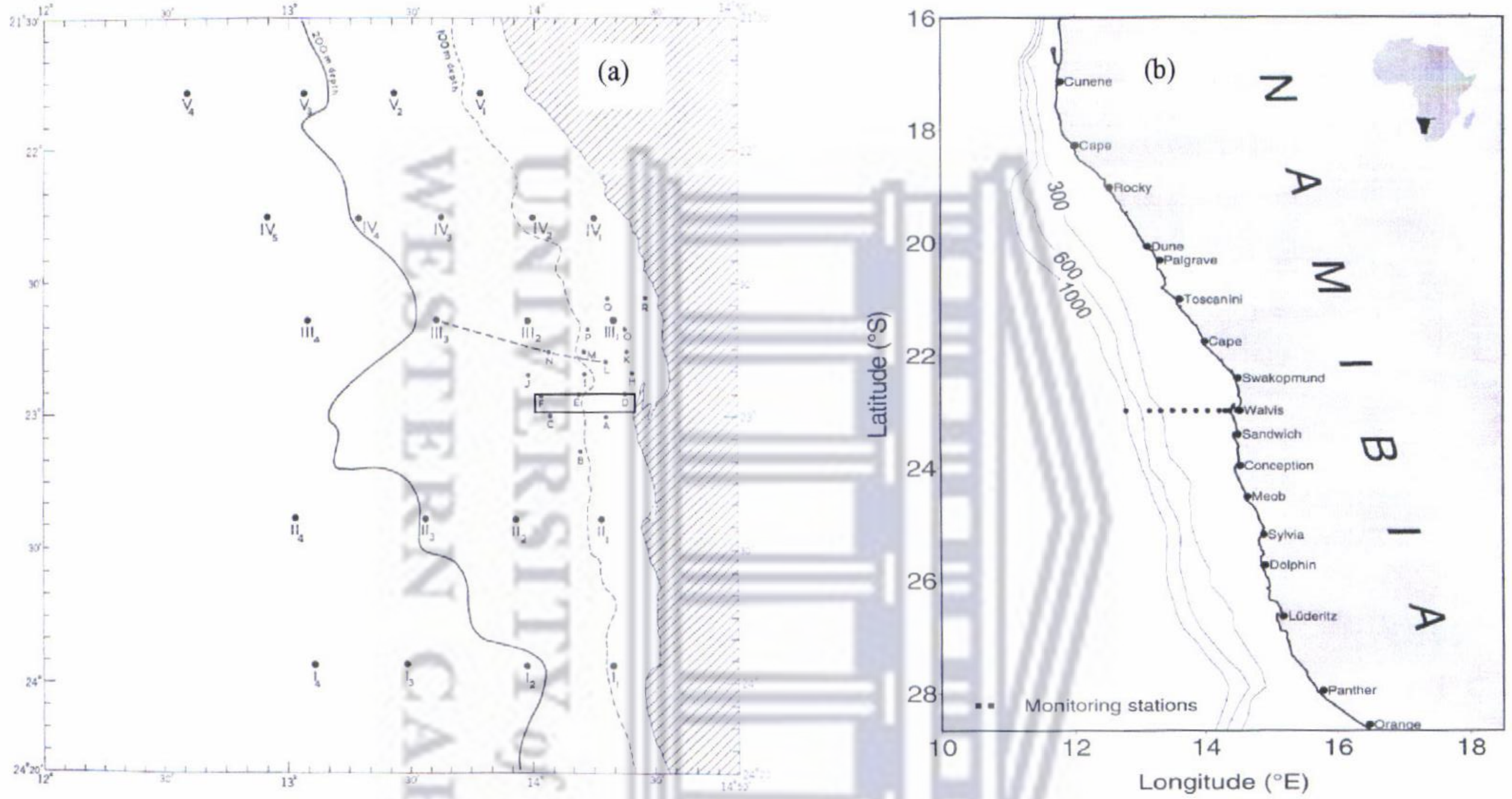

Fig. 40: Zooplankton stations during Namibia's monthly surveys in 1959 (a) and 2000-04 (b), from Kollmer (1963) and Hansen *et al.* (2005), respectively. The frame in Fig. 40a highlights the 1959 stations off Walvis Bay considered in this study

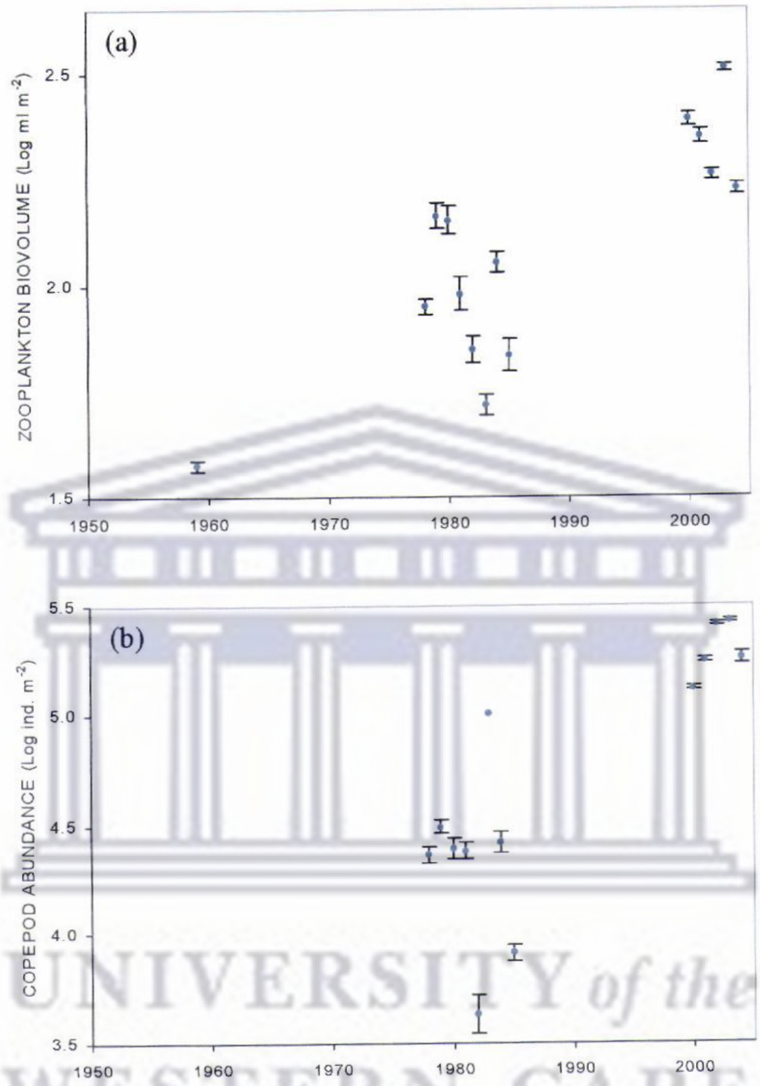

Fig. 41: Time-series of annual means of (a) 'initial' zooplankton biovolume and (b) total copepod abundance measured within 30 and 70 n. m. off the coast of Walvis Bay (23° S), respectively

2. In order to standardize spatial coverage, only samples collected within 30 n. m. and 70 n. m. offshore of Walvis Bay (23°) were considered for interdecadal comparison of biomass and total copepod abundance, respectively. However, there was no standardization for sampling depth for reasons explained below.

3. Various sampling depths were targeted during the various sampling programmes (see Table X). It is assumed that sampling the upper 50, or 100, or 200 m probably does not make much of a difference, given that sampling took place day and night, thereby taking into account, to some extent, diel vertical migration.

4. The data shown in this study (Figs. 41a and b) are annual means of each year in the time-series, computed by averaging monthly means of all stations (< 30 n. m of the coast – biomass, and < 70 n. m. of the coast – total copepod abundance) on the same transect, from that particular year. Therefore, annual means of years in which data for only a few months (or not all stations) are available may be under- or over-estimates. However, in this work it was observed that the data used in the time-series were mostly acquired from samples collected during summer and spring, and it was during these seasons that the highest biovolumes were recorded. Therefore, the inclusion of more monthly data in a year will most probably not result in a different annual mean. Be that as it may, it is envisaged that with continuing analysis of the SWAPELS collection, the improvement in the volume of the acquired data will allow for better interpretation.

5. The data points in the time-series are quite staggered in time, thus these results should be cautiously interpreted. Nevertheless, the available data are sufficient to suggest an upward trend in total zooplankton biovolume and total copepod abundance over the past five decades. This trend of increasing zooplankton over the past 50 years is in agreement with observations in the southern Benguela (Verheye *et al.* 1998, Verheye and Richardson 1998, Verheye 2000).

As discussed in Chapter 1, trends in zooplankton abundance and biomass have been attributed to either top-down or bottom-up control, or a combination of both. Catch and survey data for the small pelagic fish (sardine, anchovy and horse mackerel) indicate a general decline over the past three decades (Fig. 42) likely to be due to fishing mortality before the 1990s (Boyer and Hampton 2001), and a combination of total mortality (Fossen *et al.* 2001) and environmental anomalies – such as intrusions of warm, poorlyoxygenated Angola Current water into the Walvis Bay region in the 1990s (Boyer *et al.* 2001 and references therein).

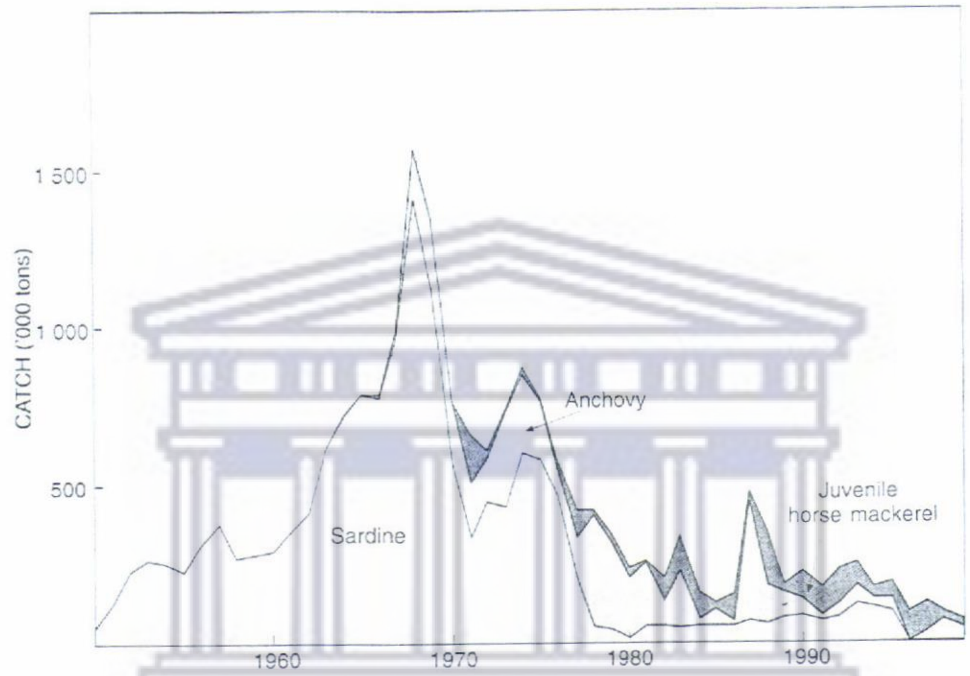

Fig. 42: Purse-seine catches in the Namibian region of the Benguela Current over the past five decades (from Boyer and Hampton 2001)

This consequent long-term reduction in predation pressure by pelagic fish is likely to result in a long-term increase in zooplankton, as has been observed in the southern Benguela, as reported by Verheye *et al.* (1998), Verheye and Richardson (1998), and Verheye (2000). Copepods are numerically the most dominant zooplankton taxa in the region (Verheye and Hutchings 1988, Timonin 1990, Timonin *et al.* 1992, Verheye *et al.* 1992, Hansen *et al.* 2005), and form an important component of the diet of commercial small pelagic fish (Fearon *et al.* 1986, James 1987, Richardson *et al.* 2003). So, although the two sub-systems (northern and southern Benguela) have been seen to differ in terms of physical oceanography as well as the dynamics of the pelagic ecosystem (Cury and Shannon 2004), the data presented here for the northern Benguela allow for the tentative conclusion that the increasing trend in zooplankton biomass may be indicative of ailing stocks of the small pelagic fish species (sardine and anchovy).

4.3 Copepod distribution and community structure

4.3.1 Community structure

4.3.1.1 Alongshore and cross-shelf patterns

Month-by-month cluster analysis revealed copepod communities grouped according to both cross-shelf and alongshore distribution. These results were to be expected as it has been shown not only in the Benguela region (Timonin 1992, Hansen *et al.* 2005), but also in other systems, such as the North Atlantic and the Baltic Sea (Sherman *et al.* 1998 and Vuorinen *et al.* 1998, respectively), that hydrological conditions, such as SST and salinity, are important in structuring zooplankton communities. However, in this study bottom depth (a proxy for distance offshore) features as the most important variable in the structuring of copepod communities found in the study area (22°67-23°33 S). In fact, SST and salinity were found to be of little importance, except in March 1980, when the BIOENV procedure ranked salinity first, and the combination of SST and salinity, second. Moreover, the correlation values for the physical variables given in the BIOENV procedure were generally low.

It is proposed that the observations mentioned above are attributable to the sampling strategy employed during the SWAPELS surveys. The fact that temperature and salinity measurements were taken at the surface of the water column (see Section 2.2.1), and that the depth from which zooplankton samples were collected was 50 m, may have resulted in a discrepancy in the relation between SST/salinity and copepod communities. There is probably, to some extent, discontinuity between conditions at, say, 50 m, and at the surface. It is thus suggested that SST and salinity data corresponding to the water column – as sampled by the net – would have been a better representation of conditions in which the copepods were found. Moreover, due to the reasons stated in Section 3.4.1, the months (January-March) considered in the month-by-month cluster analyses fall in the period when there is a relaxation in upwelling. Therefore, it is likely that the variability in SST and salinity was not so great as to significantly affect copepod communities.

In this study bottom depth represents distance along the transect. Taking into account the shortcomings discussed above, hydrological conditions should be viewed in the context of spatial distribution, as described and discussed in Sections 3.1 and 4.1, respectively. For instance, it was observed that generally the communities in which *C. carinatus* dominated were associated with cool, inshore (shallow bottom depth) waters, whereas, *M. lucens*, *C. brachiatus*, *Oithona* spp. and *Oncaea* spp. were important in offshore communities – not much can be discussed with respect to *R. nasutus*. The spatio-temporal distribution of some copepod species will be discussed in the next section. It also emerged from the cluster analyses that communities were to a large extent distributed according to positions of the transects, suggesting an alongshore pattern in the distribution of copepod communities. It is envisaged that with the ongoing analysis of the SWAPELS collection – thereby increasing the spatial coverage – more knowledge on latitudinal patterns in the distribution of copepod communities, will be acquired.

4.3.1.2 Seasonal patterning

Because the sampling of zooplankton during winter on board ships-of-opportunity was not accompanied by the collection of any hydrographic data (temperature and salinity), multivariate analysis in this study was limited to only summer, autumn, and spring samples. This is because PRIMER software procedures, such as BIOENV, require physical data corresponding to the biological data. This had a bearing on investigating seasonal patterns using cluster analysis.

Using cluster analysis and MDS, a clear seasonal signal could not be detected in the SWAPELS data set. This is attributable to the methods used for sample collection and analysis. For instance, the samples were collected using a 300-µm-mesh Bongo net, and Pillar (1984b) found that this mesh was inefficient in retaining small copepods (0.87-1.14 mm in total length). These small copepods included *Oncaea* spp., *Oithona* spp., *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus* spp., *Centropages brachiatus* juveniles, and *M. lucens* juveniles. In this study, barring the juveniles, all of the small copepod species referred to by Pillar (1984b), as well as harpacticoids, and many other unidentified species, were grouped into one category of "small copepods". This category was not included in the multivariate analyses, resulting in a limited number of species being used in the analyses. It is believed that any seasonal signal was blurred due to the omission of many individual species in the analysis. Furthermore, the temporal coverage of the samples was limited, in that at best nine months per year were sampled during SWAPELS, and that winter samples were not included in the multivariate analyses. Even though some seasonal patterning was observed in the overall cluster analysis (Fig. 22), it was "confused", to an extent that no seasonality could be deduced. Unterüberbacher (1964) reported on spatial patterns in copepod community structure off Walvis Bay, which, to a degree, indicated the existence of inshore and offshore communities. Moreover, seasonal changes in copepod community structure were related to a seasonal shoreward intrusion of oceanic water. It was against this backdrop that, in this study, it became expected that the overall cluster analysis would reveal spatio-temporal patterning in copepod community structure.

From this study it can be concluded that the four large calanoid species, *C. brachiatus*, *C. carinatus*, *M. lucens* and *R. nasutus* were the most numerically dominant species in the Walvis Bay area. These four species appeared in all of the dendrogram groups (Fig. 22) from the overall cluster analysis, and were numerically dominant in the majority of the groups (Table VI). A discussion on the distribution of these species is thus warranted, and is provided in the next section.

4.3.2 Spatio-temporal patterns in the distribution of the dominant copepod species

4.3.2.1 Seasonal distribution over the period 1979-1981

C. carinatus is known to be an upwelling species, as it responds strongly to upwelling in terms of reproduction (Unterüberbacher 1964, Armstrong *et al.* 1991, Verheye *et al.* 1992, Huggett 2003, Hansen *et al.* 2005). Findings in this study corroborate this, as the main concentrations of *C. carinatus* were found to correspond to the seasonal distribution of cool water (< 14.5 °C). High abundance values were recorded mainly in spring to summer, signalling a bloom in *C. carinatus* populations following active upwelling. Moreover, this species was found to occupy mainly the inshore area, or remaining within 30 n. m. of the coast.

The omnivorous (Hansen *et al.* 2005) species, *M. lucens* and *C. brachiatus*, tend to be distributed across the shelf, as they are not directly dependent on upwelling for enhanced feeding conditions (Hansen *et al.* 2005). Unterüberbacher (1964) found *M. lucens* to have a distribution similar to *C. carinatus*. In this study *M. lucens* was mostly abundant during summer to early autumn, at a distance of 15-45 n. m. offshore. This suggests then that this omnivore thrived after a period of high productivity, as it foraged on the resultant high concentrations of plankton that were swept offshore in late summer to autumn. However, high abundances of this species were again observed inshore (within 15 n. m. of the coast), during the summers of 1980 and 1980/81, when relatively warm (> 15.5 °C) waters extended inshore. It is likely that this warm, highly saline water carried with it some oceanic zooplankton species, which *M. lucens* exploited.

The other omnivorous species, *C. brachiatus*, on the other hand, was remarkably abundant during the summer of 1979, but almost disappeared during 1980-81. Although it is not clear why this species became extremely scarce in 1980-81, it was observed that 1979 was comparatively a cool year, and it was during this year that the lowest salinities over the study period were observed. Also, this year saw the highest variability in both SSTs and salinities. It is in this variability that this species thrived.

Like *C. carinatus*, *R. nasutus* has been reported to be associated with cold water inshore, where intense upwelling occurs (Timonin *et al.* 1992, Hansen *et al.* 2005). Unterüberbacher (1964) also reported that *R. nasutus* was common in the cool waters (south-eastern part of the Walvis Bay coast). Observations in this study also point to a spring to summer bloom in this species.

4.3.2.2 Long-term variability

In the context of long-term variability, the annual mean abundances of the four species discussed above are illustrated in Fig. 43. After combining the SWAPELS data (1978-1985) together with data (2000-2004) collected by the Namibian Ministry of Fisheries and Marine Resources (R. Cloete and A. Kreiner, pers. comm.), it was found that *C. carinatus* and *M. lucens* showed an increase over the period 1978-2004, whereas *C. brachiatus* and *R. nasutus* did not. The former two species therefore mirrored the increasing trend observed for both total zooplankton biomass and total copepod abundance (Figs. 41a and b, respectively) during this period.

Over the past five decades, several workers have described copepod communities of the Walvis Bay region, from which some long-term changes in copepod species composition and dominance can be derived. Table XI summarises variations in rank order of dominance of the major copepod species in this region during the period 1961-2000. In this study *C. carinatus*, *M. lucens*, *C. brachiatus*, and *R. nasutus*, were the most dominant copepods, with the first two occupying the same rank. Though in different rank orders, Timonin *et al.* (1992) and Hansen *et al.* (2005) found these four species also to be dominant during the 1980s and in 2000, respectively. Earlier work by Unterüberbacher (1964), who surveyed the waters around the Walvis Bay area in the early 1960s, indicated that the much smaller copepod, *Paracalanus parvus*, ranked second after *C. carinatus*. This species featured prominently again in the mid-1970s, with another small copepod, *Paracalanus scotti*, "demoting" *C. brachiatus* to fifth place in the rank order (Brenning 1985, as cited in Hansen *et al.* 2005). It has been suggested that shifts in zooplankton composition in the Benguela (Verheye *et al.* 1998, Verheye 2000, Hansen *et al.* 2005), and in other parts of the world (e.g. Roemmich and McGowan 1995, Vuorinen *et al.* 1998), are controlled by either environmental forcing or by altered predator-prey interactions.

The 300-μm mesh used during the SWAPELS surveys most likely undersampled smaller copepods such as *Oithona* spp. and *Oncaea* spp. considerably. In addition, for this study all other small-sized copepods were grouped into the category "small copepods". As a result, there was both sampling and analytical bias in favour of the larger-sized copepods, preventing a comprehensive analysis of copepod community structure and its variability to be done.

Nevertheless, it is believed that from the early 1960s to 2000, at least three of the four large calanoid copepod species, namely *C. carinatus*, *C. brachiatus*, *M. lucens* and *R. nasutus*, were indeed always among the most dominant species (Table XI), and that variable sampling gear and strategy would not have significantly impacted on this finding.

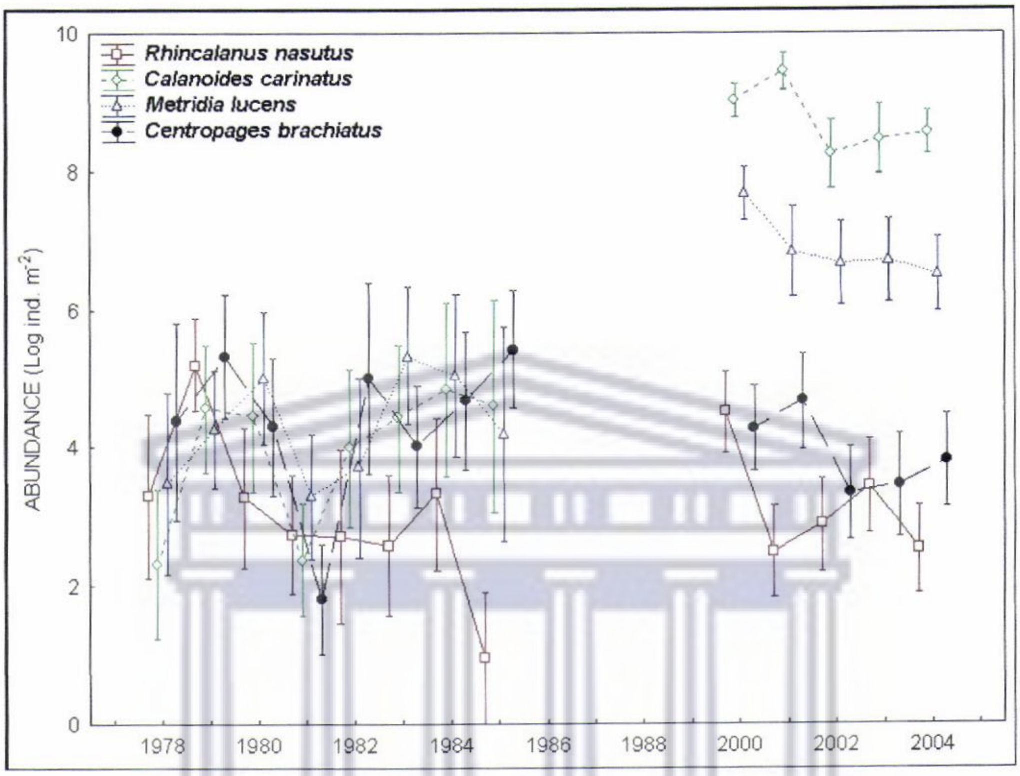

Fig. 43: Long-term variability in annual mean abundances of major copepod species, measured within 70 n. m. off Walvis Bay, during the period 1978-2002

Table XI: Rank order of dominance of major calanoid species from different studies off Walvis Bay (modified after Hansen *et al.* 2005)

Reference	Unterüberbacher (1964)	Brenning (1985)	This study	Timonin *et al.* (1992)	Hansen *et al.* (2005)
Sampling years	1961, 1962	1976	1979-81	1985, 1986, 1988	2000
Depth sampled (m)	0-300 (initially 0-100)	0-30	0-50	0-1500	0-200
Mesh size (µm)	200-460	200	300	180	200
Rank: 1	*Calanoides carinatus*	*Calanoides carinatus*	*Calanoides carinatus**	*Calanoides carinatus*	*Metridia lucens*
Rank: 2	*Paracalanus parvus*	*Paracalanus parvus*	*Metridia lucens**	*Rhincalanus nasutus*	*Calanoides carinatus*
Rank: 3	*Metridia lucens*	*Metridia lucens*	*Centropages brachiatus*	*Metridia lucens*	*Rhincalanus nasutus*
Rank: 4	*Centropages brachiatus*	*Paracalanus scotti*	*Rhincalanus nasutus*	*Centropages brachiatus*	*Centropages brachiatus*
Rank: 5	-	*Rhincalanus nasutus**	-	-	-
	-	*Centropages brachiatus**	-	-	-

* Both species had same ranking

5 Conclusion

1. The hydrography was characterised by seasonally variable cross-shelf distribution of SST, and to a lesser extent salinity, as well as some interannual variability in terms of modal SST and salinity values.

2. Multiple peaks, mostly bimodal, were observed in the cross-shelf distribution of zooplankton biomass, attributable to the effects of coastal upwelling. Total copepod abundance showed a 'delayed' response to the surge of cool, low-salinity water in late autumn and spring commonly observed during upwelling. However, variability in spatio-temporal distribution of total copepod abundance was not necessarily mirrored in the distribution of total zooplankton biomass.

3. Month-by-month cluster analyses revealed copepod communities grouped according to cross-shelf and/or alongshore distribution. However, no clear seasonal patterns could be discerned from the overall cluster analysis, probably due to loss of information caused by shortfalls during sample collection and analysis.

4. The copepod communities were dominated by four species, namely, *Calanoides carinatus*, *Centropages brachiatus*, *Metridia lucens* and *Rhincalanus nasutus*. These species displayed some specific distribution characteristics. *C. carinatus* was associated with cool waters, occurring mainly close to the shore, and was most abundant during the upwelling season. *M. lucens* also increased in numbers after upwelling, but was also present in the absence of upwelling. *C. brachiatus* was abundant during 1979, and was almost absent during 1980-81. *R. nasutus* also increased in numbers during spring and summer, but was not necessarily restricted to the inshore region. This spatio-temporal patterning in the distributions of these four species was indicative of their respective life history strategies

5. There is tentative evidence for a long-term increase in both zooplankton biomass and total copepod abundance, similar to observations made in the southern Benguela. This increase may be attributed to the demise of commercial pelagic species such as anchovy and sardine in the northern Benguela, or it may be linked to changes in the physical driving forces of the upwelling in this region – however, these were not examined in any detail in this study.

6. The increasing trend was also reflected in the abundances of *C. carinatus* and *M. lucens*, but not *C. brachiatus* and *R. nasutus*, suggesting long-term changes in community structure.

The abundance data here were analysed using multivariate statistics, and information on copepod communities was obtained, including a description of the distribution of the dominant species. It is clear that *C. carinatus*, *C. brachiatus*, *M. lucens*, and *R. nasutus* are signature species of the Walvis Bay region, and of the northern Benguela as a whole. Using the SWAPELS collection, the next step subsequent to this study would be to do, where possible, a detailed analysis of the developmental stages of these dominant species covering several years, in order to examine the role of secondary production in structuring these copepod communities. Some data on developmental stages of *C. carinatus* are already available. Presently, the analysis of the developmental stages of *R. nasutus* is underway (I. Kauvee, pers. comm.). The information acquired will then indicate whether there are any major changes in populations of individual copepod species over time, and bring attention to the possible physical and/or biological causes of such changes.

Monitoring of the environment in Namibia has for long been focused on the Walvis Bay area. Oceanographic surveys are commonly conducted along transects placed at 23° S. However, in this study it has been shown that transect 70 (23° S) is not representative of the entire Walvis Bay coast, as there was variability in both the hydrological conditions as well as the zooplankton along all three transects. Though probably not logistically feasible, routine sampling over a wider spatial scale (latitudinally) would give a more reliable account of zooplankton dynamics off Walvis Bay.

In the past decade there has been an increasing interest in long-term time series of zooplankton. Even though most of the work is done in the northern hemisphere, more especially the North Atlantic Ocean (e.g. Dickson *et al.* 1988, Aebischer *et al.* 1990, Planque and Taylor 1998, Sherman *et al.* 1998, Stephens *et al.* 1998, Beaugrand 2004), there are long-term zooplankton data sets based on samples collected in other systems in the southern hemisphere, including the southern Benguela and to a lesser extent the northern Benguela (see Perry *et al.* 2004). It is important that similar research in southern Africa, and other regions of the continent, be given the prominence it enjoys in other parts of the world. Associations of zooplankton with climate change should be explored in order to improve our understanding of climate change and its effect on marine ecosystems.

South Africa has a major fishing industry, and fisheries research, under the auspices of mainly M&CM, has long been steering the management of the fisheries. Currently, the scientific community, as well as the fisheries authorities, are looking into the applicability of Ecosystem Approach to Fisheries (EAF) Management in South Africa (Cochrane *et al.* 2004, Shannon *et al.* 2004, Shannon and Moloney 2004). Because zooplankton is seen as a major component in the control of small pelagic fish (Cury *et al.* 2000), as well as its role in mediating the strong interactions between primary production and pelagic fish (Moloney 1992, Cury *et al.* 2000), there is thus no doubt as to the importance of, and the role a long-term zooplankton research programme would play in this approach to fisheries management. Moreover, such a programme can go a long way in improving our ability not only to understand marine ecosystems, but also to detect and anticipate any modifications in such ecosystems, be they anthropogenic and/or symptomatic of the effects of global climate change.

It is strongly recommended that zooplankton – copepods in particular – be analysed in greater detail at M&CM. It has been seen that the placing of species into broad taxonomic groups often precludes meaningful information on community structure and seasonality. It is acknowledged that research done at M&CM is directed at fisheries management. This means that attention is paid only to data that pertains to the major copepod species which are important as a food source for fish. However, with the rising awareness of climate change (see Beaugrand *et al.* 2002, Richardson and Schoeman 2004), it is globally becoming increasingly crucial to report on as many species as possible, in order to detect any significant changes in ecosystems.

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APPENDICES

Key to **APPENDIX A**

f = female
m = male
j = juvenile
C = Calanus
Cc = Calanoides carinatus
Cb = Centropages brachiatus
Cop naup = copepod nauplii
Cor = Corycaeus
Ml = Metridia lucens
Oi = Oithona
Onc = Oncaea
Ot cal = other calanoids
P = Pleuromamma
R = Rhincalanus
S cop = small copepods
Cten = Ctenocalanus
Claus = Clausocalanus
Pp = Paracalanus parvus
Ps = Paracalanus scotti
Tot no = total number

Note: missing biovolumes are excluded from Appendix A to show that they were not used in the time-series. See Section 2.2.2 for details.

APPENDIX A: SWAPELS data set

Transect 70

				C	C	C	C	C	C	C	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cb	Cb	Cb	Cop	Cor	Harp	Ml	Ml	Ml	Oi	Onc	Ot Cal	P	P	P	R	R	R	S	Cten	Clau	Pp	Ps	Tot No
DATE	Distance offshore (n. m.)	Station no.	Biovolume (ml m^{-2})	f	m	C5	C4	C3	C2	C1	f	m	C5	C4	C3	C2	C1	f	m	j	naup			f	m	j				f	m	j	f	m	j	Cop					
Aug-81	5	2	867	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8045	0	4022	0	0	0	44246	239333	0	0	0	0	0	0	0	239333	0	0	0	0	534980
Aug-81	10	3	449	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1527	0	2037	0	0	0	1527	80957	0	0	0	0	0	0	509	42770	0	0	0	0	129328
Aug-81	15	4	71	0	0	0	0	0	0	178	0	0	0	0	0	0	0	0	0	0	4099	0	4812	0	0	0	4812	2851	178	0	0	0	0	0	0	8376	0	0	0	0	25305
Aug-81	25	6	20	0	0	0	0	0	0	119	0	0	0	0	0	0	0	0	0	0	357	0	2780	0	0	0	874	40	0	0	0	0	40	79	0	4766	0	0	0	0	9055
Aug-81	35	8	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug-81	45	10																																							
Aug-81	55	12																																							
Aug-81	65	14																																							
Sep-81	2	1		0	0	0	0	0	0	0	345	0	0	0	0	345	1378	0	345	0	0	0	0	0	1378	0	5858	3446	689	0	0	0	0	0	0	41004	0	0	0	0	54787
Sep-81	5	2	193	0	0	0	0	0	0	0	546	0	0	0	0	546	0	273	546	273	0	0	0	0	0	0	2455	1091	0	0	0	0	0	273	0	6001	0	0	0	0	12002
Sep-81	10	3	34	0	0	80	240	0	0	80	80	0	0	0	0	0	160	160	639	160	1917	0	80	80	240	0	479	319	80	0	0	0	0	319	0	1358	0	0	0	0	6469
Sep-81	15	4	120	0	0	278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11379	0	0	0	0	278	0	0	0	0	0	0	1388	1110	1388	1943	0	0	0	0	17762
Sep-81	25	6	174	206	0	0	0	0	0	0	206	0	0	0	0	0	0	0	206	0	0	0	0	0	0	0	0	0	0	0	0	0	206	412	206	0	0	0	0	0	1442
Sep-81	35	8	244	1335	1869	267	267	0	267	0	267	0	0	0	0	0	267	801	1068	0	0	0	0	267	267	0	267	0	534	0	0	0	0	0	534	1869	0	0	0	0	10147
Sep-81	45	10	454	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	313	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	313
Sep-81	55	12	57	0	0	0	0	0	0	0	106	106	0	0	0	0	0	211	950	0	106	0	0	0	0	0	422	422	0	0	0	0	211	317	528	1583	0	0	0	0	4961
Sep-81	65	14	60	146	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	98	0	488	0	0	0	0	488	0	0	0	0	0	0	0	0	0	0	0	0	1219
Oct-81	2	1																																							
Oct-81	5	2	337	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1095	0	547	0	0	0	13136	126438	0	0	0	0	0	0	547	27915	0	0	0	0	169679
Oct-81	10	3	214	0	0	0	0	0	0	0	0	0	0	0	0	0	356	0	0	0	3921	0	3208	0	0	0	6772	57026	0	0	0	0	0	356	1069	21029	0	0	0	0	93737
Oct-81	15	4	77	0	0	0	0	0	0	0	0	0	2648	331	0	1324	1986	0	1986	0	10922	0	5295	0	0	0	4633	11584	0	0	0	0	0	7281	7612	11914	0	0	0	0	67515
Oct-81	25	6	15	0	0	0	0	0	102	51	0	0	0	0	0	0	51	0	102	0	102	0	2342	0	0	51	916	662	0	0	0	0	0	204	153	2342	0	0	0	0	7077
Oct-81	35	8	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oct-81	45	10																																							
Oct-81	55	12																																							
Oct-81	65	14																																							
Dec-81	2	1		0	0	0	0	0	0	0	0	0	0	0	0	0	177	0	0	0	147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2357	0	0	0	0	3
Dec-81	5	2	199	0	0	0	0	0	0	0	6387	0	0	0	0	1219	929	0	0	0	5110	0	0	0	9291	1742	2090	15678	0	0	0	0	174197	78389	0	5226	0	0	0	0	300
Dec-81	10	3	191	0	0	0	0	0	0	0	93814	0	0	0	0	0	682	0	0	0	11258	0	0	36843	136457	5117	8187	15351	5117	0	0	0	307028	46054	0	32408	0	0	0	0	698
Dec-81	15	4	138	0	0	0	0	0	0	0	23660	3925	10324	1667	0	0	0	0	1075	0	215	0	0	11615	12905	17745	430	0	0	0	0	0	225842	14518	8066	2151	0	0	0	0	334
Dec-81	25	6	304	0	0	0	0	0	0	0	124029	31658	27755	8066	0	1214	0	2168	13877	3122	0	0	0	0	0	2602	0	0	2602	0	0	0	156120	210763	143110	7806	0	0	0	0	735
Dec-81	35	8	280	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dec-81	45	10	87	0	0	0	0	0	0	0	8626	40070	50185	9723	0	3842	941	11762	17251	2823	1490	0	0	93156	25093	7057	2196	4705	4705	0	0	0	47049	190547	305815	6273	0	0	0	0	833
Dec-81	55	12	58	2979	1622	1430	0	0	0	0	3244	0	2831	457	0	0	0	14746	17696	1991	44	0	0	11148	8258	6193	295	8405	1770	0	0	0	4424	0	0	5751	147	0	0	147	94
Dec-81	65	14	111	26028	14173	6249	2964	0	1160	0	14173	4703	24739	1997	0	2706	1031	6442	3865	1739	0	0	0	27832	67002	5798	11339	38655	5798	0	0	0	19327	69579	0	12241	0	0	644	0	370
	Transect 66																																								
Jan-79	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	36	0	0	0	0	55
Jan-79	5	2		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1618	180	0	0	0	0	0	0	0	0	0	0	0	1798
Jan-79	10	3	152	0	0	97	581	0	0	194	968	387	3969	4162	97	581	1839	678	968	387	0	0	0	0	97	194	0	0	0	0	0	0	0	0	290	4259	0	0	0	0	19747
Jan-79	15	4	57	0	0	0	0	0	0	0	492	281	632	983	0	140	351	0	70	140	0	0	0	70	0	0	0	0	0	0	0	0	0	70	0	421	0	0	0	0	3652
Jan-79	25	6	95	0	0	160	0	160	0	160	2083	481	2404	3205	320	2404	641	641	160	0	160	0	0	801	1763	1122	0	160	160	0	0	0	0	961	641	801	0	0	0	0	19389
Jan-79	35	8	85	235	0	470	0	0	0	0	3055	1645	3290	2350	470	2820	1880	940	4465	3760	2350	0	235	705	3760	705	0	0	235	0	0	0	0	470	705	10105	0	0	0	0	44648
Jan-79	45	10	184	0	0	341	68	0	0	0	0	0	273	341	136	0	0	409	2522	1023	0	0	68	0	136	68	409	545	136	0	68	0	0	68	136	5590	0	0	0	0	12339
Jan-79	55	12	320	529	0	132	132	0	132	0	0	0	0	264	0	264	0	132	1322	529	264	0	0	0	0	0	529	0	132	0	0	0	132	0	397	2644	0	0	0	0	7536
Jan-79	65	14	418																																						
Feb-79	2	1	14	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	12	0	23	0	0	0	0	0	0	0	0	0	0	0	0	47
Feb-79	5	2	15	36	0	0	0	0	0	0	253	0	0	0	0	36	0	0	0	0	72	0	0	0	0	0	0	72	36	0	0	0	0	0	0	0	0	0	0	0	506
Feb-79	10	3	114	0	0	0	0	0	0	0	832	0	951	357	0	0	0	238	238	119	0	0	0	0	238	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2972
Feb-79	15	4	147	0	0	0	297	0	0	0	1632	148	2966	3411	0	890	0	148	445	297	0	0	0	742	297	297	0	0	1038	0	0	0	0	297	148	297	0	0	0	0	13349
Feb-79	25	6	31	0	0	193	0	0	0	0	0	0	97	0	0	0	0	0	0	0	0	0	48	0	48	0	0	0	0	0	0	0	0	48	0	0	0	0	0	0	435
Feb-79	35	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-79	45	10	70	0	0	0	366	0	122	0	244	366	1706	4266	122	1828	122	0	122	366	0	0	0	0	0	0	0	0	731	0	0	0	0	0	0	1706	0	0	0	0	12067
Feb-79	55	12	40	0	0	0	60	0	0	0	0	0	0	0	0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	119
Feb-79	65	14	51	0	0	0	0	0	0	0	0	63	824	3107	0	507	317	444	697	888	0	0	0	63	63	63	63	63	507	0	0	0	0	63	0	1141	0	0	0	0	8877
Mar-79	2	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	94	0	0	0	0	96
Mar-79	5	2	17	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	328	0	0	0	0	0	0	0	0	0	0	0	0	365
Mar-79	10	3	8	37	0	112	37	0	0	0	205	0	75	19	0	0	0	0	0	0	0	0	0	19	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	523
Mar-79	15	4	47	0	0	0	0	0	0	0	386	97	97	0	97	0	97	0	0	0	0	0	97	0	97	386	0	0	0	0	0	0	97	0	0	0	0	0	0	0	1448
Mar-79	25	6	66	0	0	0	0	0	0	0	0	0	478	119	0	119	0	119	0	0	0	0	0	0	119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	956
Mar-79	35	8	16	0	0	78	233	0	0	0	233	156	2256	622	0	0	0	156	233	467	0	0	0	467	311	156	0	0	156	0	0	0	156	156	78	389	0	0	0	0	6301
Mar-79	45	10	35	0	0	0	0	0	0	0	0	0	86	0	0	0	0	0	0	0	0	0	0	86	0	0	0	0	0	0	0	0	86	0	0	0	0	0	0	0	258
Mar-79	55	12	13	0	0	0	0	0	0	0	28	0	0	14	0	0	0	0	0	0	0	0	85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	128
Mar-79	65	14	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
Jan-80	2	1	27	0	0	0	0	0	0	0	0	0	0	0	0	0	52	0	0	0	0	0	0	0	209	731	157	0	2557	0	0	0	0	0	0	2035	0	0	0	0	5740
Jan-80	5	2	90	0	0	227	0	0	0	0	227	114	568	0	0	0	0	0	0	0	0	0	0	0	0	0	0	114	0	0	0	0	0	0	0	0	0	0	0	0	1249
Jan-80	10	3	158	0	247	0	0	0	0	0	4698	1731	12116	2967	247	1731	1484	989	1484	1484	0	0	0	247	2473	4945	0	0	1731	0	0	0	0	0	0	0	0	0	0	0	38572
Jan-80	15	4	197	0	0	0	0	0	0	0	2801	1400	4435	4668	467	5135	2334	1167	1400	0	0	0	700	1400	700	233	467	0	4201	0	0	0	0	233	0	10737	0	0	0	0	42480
Jan-80	25	6	322	0	0	0	0	0	197	0	2362	787	1771	1574	0	2362	787	0	984	1378	0	0	197	3149	1574	787	394	197	0	0	0	0	0	0	0	3739	0	0	0	0	22240
Jan-80	35	8	199	0	0	194	0	0	0	0	1357	776	4653	2327	0	194	194	388	194	582	194	0	0	1939	2133	388	0	194	582	0	0	0	0	0	776	2908	0	0	0	0	19970
Jan-80	45	10	180	0	0	0	267	0	0	0	133	667	1334	1601	0	267	0	3469	3736	2802	0	0	133	1868	2001	133	0	1067	133	0	0	0	0	133	400	3335	0	0	0	0	23481
Jan-80	55	12																																							
Jan-80	65	14																																							
Feb-80	2	1	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	299	0	0	0	0	299
Feb-80	5	2	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-80	10	3	181	0	0	0	0	0	0	0	1224	245	3182	2448	245	490	0	7832	12973	8077	0	0	245	245	1224	0	0	0	1224	0	0	0	0	0	0	3671	0	0	0	0	43324
Feb-80	15	4	243	0	0	0	0	0	0	0	3539	1011	18200	11628	0	1011	0	4550	15166	18200	0	0	506	0	1517	0	0	0	506	0	0	0	0	0	0	7078	0	0	0	0	82910
Feb-80	25	6	259	0	0	0	0	0	0	0	6576	329	1315	164	0	164	0	2466	4932	2959	0	0	329	1315	329	164	0	0	0	0	0	0	0	164	0	2795	0	0	0	0	24003
Feb-80	35	8	69	0	0	0	0	0	0	0	1120	118	118	0	0	0	0	0	0	0	0	0	0	236	354	236	0	295	59	0	0	0	0	59	0	0	0	0	0	0	2593
Feb-80	45	10	73	0	0	0	0	0	0	0	182	0	0	0	0	0	0	0	91	0	0	0	91	455	727	91	91	727	0	0	0	0	0	0	273	91	0	0	0	0	2818
Feb-80	55	12																																							
Feb-80	65	14																																							
Mar-80	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-80	5	2	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	525	600	826	0	0	0	38	188	113	0	0	38	0	0	0	0	0	0	38	0	0	0	0	2364
Mar-80	10	3	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	190	381	476	0	0	0	0	286	95	0	0	0	0	0	0	0	0	0	1143	0	0	0	0	2572
Mar-80	15	4	24	0	0	0	0	0	0	0	0	0	37	37	0	0	0	110	366	549	0	0	0	0	220	110	146	0	0	0	0	0	0	37	0	37	0	0	0	0	1648

APPENDIX A: SWAPELS data set

Transect 70

				C	C	C	C	C	C	C	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cb	Cb	Cb	Cop	Cor	Harp	Ml	Ml	Ml	Oi	Onc	Ot Cal	P	P	P	R	R	R	S	Cten	Clau	Pp	Ps	Tot No
DATE	Distance offshore (n. m.)	Station no.	Biovolume (ml m^{-2})	f	m	C5	C4	C3	C2	C1	f	m	C5	C4	C3	C2	C1	f	m	j	naup			f	m	j				f	m	j	f	m	j	Cop					
	Transect 66																																								
Mar-80	25	6	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	420	761	131	0	0	0	0	53	26	0	0	79	0	0	0	0	0	0	79	0	0	0	0	1549
Mar-80	35	8	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-80	45	10	16	0	0	0	0	0	0	0	27	0	0	0	0	0	0	0	27	0	0	0	0	82	0	0	0	0	27	0	0	0	0	0	0	27	0	0	0	0	192
Mar-80	55	12																																							
Mar-80	65	14																																							
Jan-81	2	1	57	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0	0	0	0	0	0	0	0	0	0	0	93	0	0	0	0	0	0	93	0	0	0	0	279
Jan-81	5	2	16	0	0	0	0	0	0	0	34	0	168	168	34	67	34	0	0	0	134	0	0	0	201	201	67	34	402	0	0	0	0	0	0	536	0	0	0	0	2078
Jan-81	10	3	71	0	0	0	0	0	0	0	361	0	1322	1082	240	361	120	0	0	0	0	0	0	240	120	120	0	0	240	0	0	0	120	120	120	481	0	0	0	0	5048
Jan-81	15	4	81	0	0	0	0	0	0	0	4906	392	981	1177	0	0	0	0	0	0	0	0	0	1177	196	785	0	0	0	0	0	0	0	0	196	0	0	0	0	0	9812
Jan-81	25	6	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan-81	35	8	71	458	0	0	0	0	0	0	2597	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3055
Jan-81	45	10	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan-81	55	12	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan-81	65	14																																							
Feb-81	2	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	59	0	0	0	0	0	0	0	0	0	0	0	82
Feb-81	5	2		0	0	0	0	0	0	0	152	152	0	0	0	912	152	0	0	0	0	0	0	152	304	608	0	0	608	0	0	0	0	0	0	1064	0	0	0	0	4106
Feb-81	10	3	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-81	15	4	153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	361	361	361	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1084
Feb-81	25	6	187	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-81	35	8	152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-81	45	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-81	55	12																																							
Feb-81	65	14																																							
Mar-81	2	1	9	0	0	0	0	0	0	0	0	0	17	0	0	0	0	17	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	286	0	0	0	0	353
Mar-81	5	2	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-81	10	3	22	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
Mar-81	15	4	21	0	0	46	0	0	0	0	46	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	92	0	0	0	0	0	0	0	230
Mar-81	25	6	37	0	0	79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79
Mar-81	35	8	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	188	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	188
Mar-81	45	10	62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-81	55	12																																							
Mar-81	65	14																																							
	Transect 74																																								
Jan-79	2	1	128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	221	0	221	0	0	0	0	0	0	0	0	0	0	0	0	0	442
Jan-79	5	2	578	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3693	12309	4924	0	0	0	0	0	0	0	24619	0	0	0	0	45545
Jan-79	10	3	141	0	0	0	0	0	0	0	1397	1118	2236	1118	0	0	0	1677	2515	1956	1397	0	279	0	3633	1956	2236	1118	1118	0	0	0	0	279	279	11737	0	0	0	0	36048
Jan-79	15	4	232	0	0	0	0	0	0	0	11569	3254	2169	362	0	0	0	2892	2169	2531	0	0	723	0	362	1085	362	362	0	0	0	0	362	2169	723	7592	0	0	0	0	38684
Jan-79	25	6	291	0	0	0	0	0	0	0	13219	7626	8135	2034	0	1525	1017	2034	2542	3559	2034	0	0	2542	2542	1017	0	0	2034	0	0	0	0	4576	2542	10168	0	0	0	0	69144
Jan-79	35	8	294	0	0	0	0	0	0	0	7015	5011	7015	3508	0	501	1503	1503	1503	501	1002	0	0	0	1002	0	0	501	3508	0	0	0	0	7015	6514	5011	0	0	0	0	52616
Jan-79	45	10	203	0	0	0	0	0	0	0	4715	4421	9136	2358	0	1179	1768	295	1768	589	589	0	0	295	0	0	295	589	589	0	0	0	0	2652	4715	3242	0	0	0	0	39196
Jan-79	55	12	119	0	0	134	0	0	0	0	0	0	940	1343	134	537	269	1343	1880	1746	0	0	0	0	134	0	134	269	1209	0	0	0	0	0	0	2149	0	0	0	0	12220
Jan-79	65	14	43	0	0	0	0	0	0	0	0	0	117	0	0	0	0	39	78	0	0	0	0	39	39	39	78	0	352	0	0	0	0	39	39	0	0	0	0	0	860
Feb-79	2	1	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	689	0	0	0	0	689
Feb-79	5	2	133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	145	145	145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	579	0	0	0	0	1013
Feb-79	10	3	115	0	0	0	0	0	0	0	1440	144	1296	288	0	0	0	288	288	576	0	0	0	288	0	144	0	288	144	0	0	0	0	576	144	1584	0	0	0	0	7489
Feb-79	15	4	144	0	0	0	0	0	0	0	2075	1436	1915	798	160	0	0	319	638	0	0	0	0	1915	1756	1436	0	160	479	0	0	0	160	160	319	2394	0	0	0	0	16119
Feb-79	25	6	217	0	0	0	0	0	0	0	2564	1602	3205	1602	320	0	0	0	0	0	0	0	0	320	1923	2564	0	320	320	0	0	0	0	641	961	3205	0	0	0	0	19550
Feb-79	35	8	127	0	0	0	240	0	0	0	480	960	1200	1680	0	720	0	240	1200	0	480	0	0	240	0	0	0	240	960	0	0	0	0	240	240	1680	0	0	0	0	10799
Feb-79	45	10	212	0	0	0	0	0	0	0	416	208	416	2082	208	833	625	833	2915	2915	416	0	0	0	208	625	0	833	416	0	0	0	0	0	416	2499	0	0	0	0	16866
Feb-79	55	12	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0	0	0	32	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	95
Feb-79	65	14	6	0	0	0	50	0	0	0	151	0	302	403	101	151	0	353	151	202	0	0	0	302	50	50	0	50	252	0	0	0	0	101	50	857	0	0	0	0	3577
Mar-79	2	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-79	5	2	59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	54
Mar-79	10	3	82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	110	0	0	0	0	0	0	0	0	110	0	0	0	0	0	0	551	0	330	0	0	0	0	1101
Mar-79	15	4	57	0	0	89	0	0	0	0	533	444	1066	178	0	0	0	1332	710	799	89	0	178	89	89	710	0	0	266	0	0	0	0	178	444	888	0	0	0	0	8082
Mar-79	25	6	32	0	0	72	0	0	72	0	1443	433	1659	433	0	0	0	289	361	794	0	0	0	1299	1010	1299	144	0	361	0	0	0	0	0	72	1154	0	0	0	0	10894
Mar-79	35	8	8	0	0	0	0	0	0	0	45	0	45	45	0	134	45	312	802	1248	490	0	0	89	178	356	178	45	178	0	0	0	0	0	0	3342	0	0	0	0	7530
Mar-79	45	10	86	0	0	0	0	0	0	0	0	0	449	897	150	150	150	1196	1495	449	598	0	449	0	0	0	1495	150	0	0	0	0	0	150	598	2093	0	0	0	0	10466
Mar-79	55	12		0	0	0	56	0	0	0	56	0	0	279	56	279	279	502	837	1116	223	0	0	0	167	0	335	390	279	0	0	0	0	0	223	948	0	0	0	0	6024
Mar-79	65	14	67																																						
Jan-80	2	1	58	0	0	0	0	0	0	0	83	0	0	0	0	0	0	0	0	0	0	0	0	0	83	413	1323	83	0	0	0	0	0	0	0	12403	0	0	0	0	14388
Jan-80	5	2	302	0	0	0	421	0	0	0	8004	2106	4213	1685	0	1264	1264	421	0	421	0	0	421	421	2949	2528	5055	1264	0	0	0	0	0	0	0	84257	0	0	0	0	116696
Jan-80	10	3	189	0	0	0	0	0	0	0	13809	5686	2437	2031	0	3655	812	406	2437	6905	406	0	0	0	406	2437	812	406	406	0	0	0	0	406	0	13403	0	0	0	0	56862
Jan-80	15	4	150	0	0	0	0	0	0	0	9567	2160	3086	2160	617	2469	1852	0	309	1234	0	0	0	0	1234	926	0	0	309	0	0	0	0	0	309	5864	0	0	0	0	32095
Jan-80	25	6	170	0	0	0	0	0	0	0	7757	3017	6033	5171	431	5602	3017	1293	2155	431	431	0	0	1293	431	862	431	862	862	0	0	0	0	431	0	6895	0	0	0	0	47404
Jan-80	35	8	180	0	0	0	0	0	0	0	5055	202	2224	6268	1213	9907	4246	607	404	1011	202	0	202	202	607	607	0	0	607	0	0	0	0	0	0	11929	0	0	0	0	45493
Jan-80	45	10	315	0	0	0	0	0	0	0	0	0	278	972	0	2082	1110	139	416	278	0	0	139	0	0	0	278	278	0	0	0	0	0	278	278	3609	0	0	0	0	10132
Jan-80	55	12	285	0	0	0	0	0	0	0	0	0	0	139	0	139	0	0	69	69	0	0	0	0	0	0	0	69	0	0	0	0	0	69	139	208	0	0	0	0	903
Jan-80	65	14	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	0	0	0	0	54
Feb-80	2	1	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	148	0	0	2224	0	0	0	0	2372
Feb-80	5	2	55	0	0	128	0	0	0	0	6249	893	383	0	0	128	0	128	255	383	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25505	0	0	0	0	34049
Feb-80	10	3	536	0	0	0	0	0	0	0	5792	827	0	827	0	0	0	8275	9930	9930	827	0	827	0	0	827	0	0	0	0	0	0	0	0	0	15722	0	0	0	0	53787
Feb-80	15	4	335	0	0	0	0	0	0	0	1243	207	414	207	0	207	0	414	622	414	0	0	829	1243	829	1451	0	207	207	0	0	0	207	207	0	1658	0	0	0	0	10568
Feb-80	25	6	33	0	0	0	0	0	0	0	1912	637	6375	1169	0	106	0	0	0	319	0	0	106	319	212	531	0	106	212	0	0	0	0	212	212	744	0	0	0	0	13175
Feb-80	35	8	12	0	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34
Feb-80	45	10	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	86	0	172	0	0	0	172	0	343	0	86	0	0	0	0	0	86	0	258	0	0	0	0	1202
Feb-80	55	12	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	46
Feb-80	65	14	124	0	0	0	0	0	0	0	161	0	0	0	0	0	0	0	0	0	0	0	0	5957	4508	5152	2576	483	161	0	0	0	0	161	0	1127	0	0	0	0	20286
Mar-80	2	1	164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	232	232	0	0	0	0	0	0	0	0	0	0	0	0	0	0	464
Mar-80	5	2	760	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1232	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	246388	0	0	0	0	247620
Mar-80	10	3	863	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1554	1554	0	0	0	0	0	1554	1554	0	0	0	0	0	0	0	0	0	310829	0	0	0	0	317046
Mar-80	15	4	471	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	613	0	0	0	0	0	613	613	0	0	0	0	0	0	0	0	0	122690	0	0	0	0	124530

APPENDIX A: SWAPELS data set

Transect 70

				C	C	C	C	C	C	C	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cb	Cb	Cb	Cop	Cor	Harp	Ml	Ml	Ml	Oi	Onc	Ot Cal	P	P	P	R	R	R	S	Cten	Clau	Pp	Ps	Tot No
DATE	Distance offshore (n. m.)	Station no.	Biovolume (ml m^{-3})	f	m	C5	C4	C3	C2	C1	f	m	C5	C4	C3	C2	C1	f	m	j	naup			f	m	j				f	m	j	f	m	j	Cop					
	Transect 74																																								
Mar-80	25	6	90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	158	158	158	0	0	0	0	1579	316	0	158	0	0	0	0	0	0	0	0	0	0	0	0	2527
Mar-80	35	8	79	0	0	0	0	0	0	0	0	0	87	0	0	0	0	0	0	433	346	0	87	3463	7099	10389	87	346	0	0	0	0	0	0	0	3550	0	0	0	0	25886
Mar-80	45	10	59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	98	0	131	558	721	1804	131	230	98	0	0	0	0	0	0	1049	0	0	0	0	4854
Mar-80	55	12	51	0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	45	0	0	0	135	1570	987	2513	179	808	135	0	45	0	0	45	45	1167	0	0	0	0	7717
Mar-80	65	14																																							
Jan-81	2	1																																							
Jan-81	5	2																																							
Jan-81	10	3																																							
Jan-81	15	4	92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	155	0	0	0	0	0	0	0	0	0	0	0	155
Jan-81	25	6	76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	99	0	0	0	0	0	0	0	0	0	0	0	0	99
Jan-81	35	8	248	0	4	0	4	4	0	0	50	14	171	193	7	78	18	4	11	11	0	0	0	4	7	4	0	7	14	0	0	0	4	4	0	160	0	0	0	0	770
Jan-81	45	10	86	0	0	0	0	0	0	0	1287	0	643	322	0	0	0	161	322	0	2895	0	161	483	483	161	0	965	483	0	0	0	161	322	161	804	0	0	0	0	9811
Jan-81	55	12																																							
Jan-81	65	14																																							
Feb-81	2	1																																							
Feb-81	5	2																																							
Feb-81	10	3	689	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	815	0	0	0	0	0	0	815	0	0	0	0	1631
Feb-81	15	4	919	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12043	51614	0	0	0	0	0	0	0	0	0	0	0	0	63658
Feb-81	25	6	123	0	0	0	0	0	0	0	671	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	671
Feb-81	35	8	99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb-81	45	10	90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	169	0	0	0	0	1694	0	508	0	0	0	0	0	0	0	0	0	9996	0	0	0	0	12368
Feb-81	55	12																																							
Feb-81	65	14																																							
Mar-81	2	1	82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar-81	5	2	89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	54
Mar-81	10	3	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	110	0	0	0	0	0	0	0	0	110	0	0	0	0	0	0	551	0	330	0	0	0	0	1101
Mar-81	15	4	37	0	0	89	0	0	0	0	533	444	1066	178	0	0	0	1332	710	799	89	0	178	89	89	710	0	0	266	0	0	0	0	178	444	888	0	0	0	0	8082
Mar-81	25	6	126	0	0	72	0	0	72	0	1443	433	1659	433	0	0	0	289	361	794	0	0	0	1299	1010	1299	144	0	361	0	0	0	0	0	72	1154	0	0	0	0	10894
Mar-81	35	8	25	0	0	0	0	0	0	0	45	0	45	45	0	134	45	312	802	1248	490	0	0	89	178	356	178	45	178	0	0	0	0	0	0	3342	0	0	0	0	7530
Mar-81	45	10	230	0	0	0	0	0	0	0	0	0	449	897	150	150	150	1196	1495	449	598	0	449	0	0	0	1495	150	0	0	0	0	0	150	598	2093	0	0	0	0	10466
Mar-81	55	12																																							
Mar-81	65	14																																							

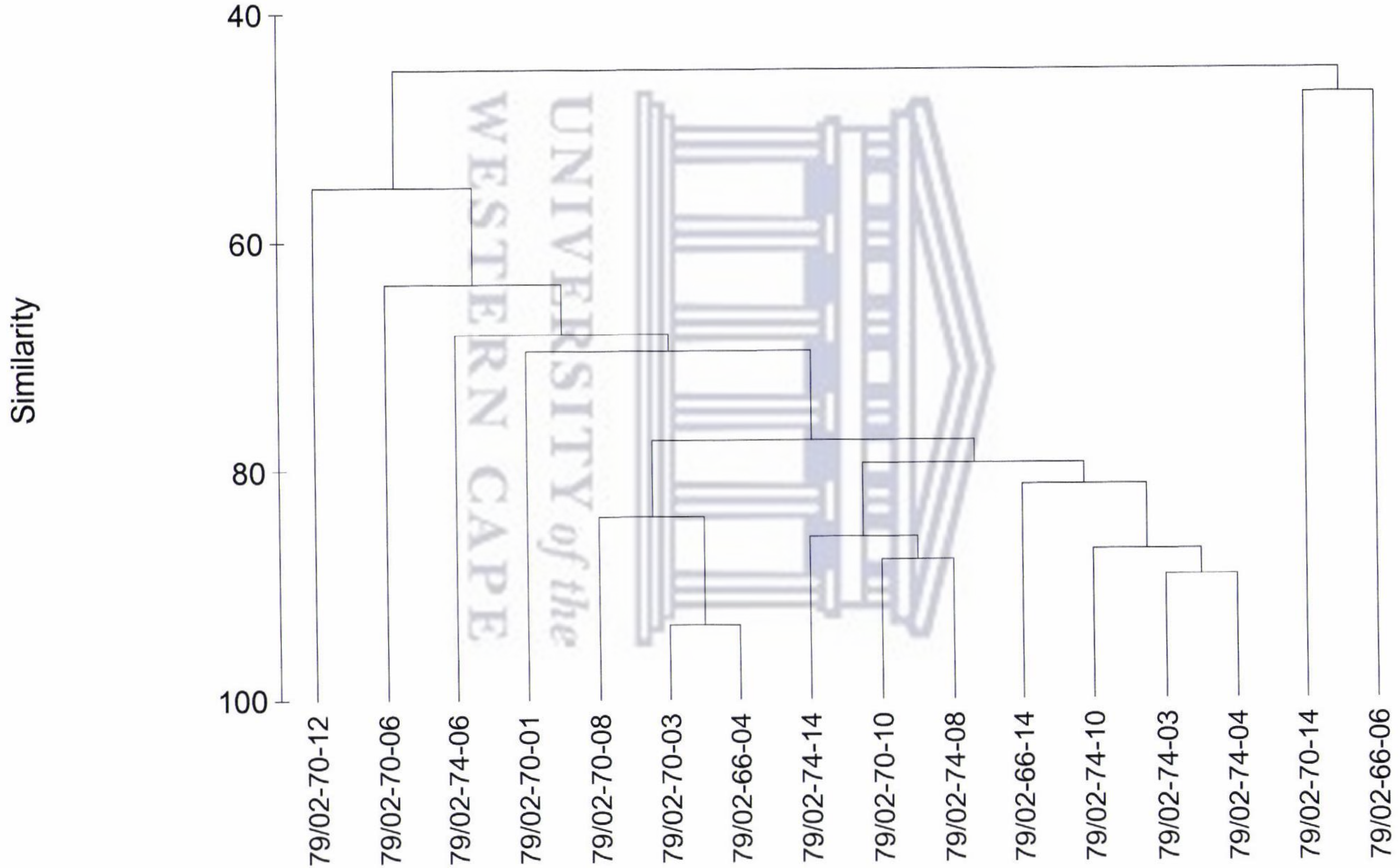
APPENDIX B: Copepod abundance data used in the multivariate analysis

Station	*C. carinatus*	*Calanus* spp	*Centropage. brachiatus*	*Metridia lucens*	*Rhincalanus nasutus*	*Pluero-mamma* spp	*Oncaea* spp	*Oithona* spp	Harpacti-coids
79/01-70-02	0	0	553	0	553	0	10511	8298	0
79/01-70-04	6582	0	2531	7088	2531	0	2025	5063	1013
79/01-70-06	16788	0	1975	1481	1975	0	0	0	494
79/01-70-08	11036	0	2030	3932	254	254	127	0	254
79/01-70-10	7342	0	1058	926	0	0	132	0	132
79/01-70-14	1603	0	1033	285	0	285	36	36	0
79/02-70-01	513	0	930	545	32	449	32	0	0
79/02-70-03	7430	425	3609	1274	212	0	0	0	0
79/02-70-06	46400	0	2456	10099	7779	546	0	0	0
79/02-70-08	7321	0	2892	813	2892	0	0	0	0
79/02-70-10	1169	292	1023	146	365	0	146	0	73
79/02-70-12	85	0	256	85	0	0	85	0	0
79/02-70-14	0	203	203	294	23	158	0	271	0
79/03-70-02	253	0	0	161	46	0	413	918	0
79/03-70-04	2034	0	2122	1326	265	0	0	88	0
79/03-70-06	2246	0	5911	1891	355	0	118	0	0
79/03-70-08	1989	0	398	1194	398	0	0	0	0
79/03-70-10	76	0	672	304	87	0	98	33	0
79/04-70-02	5126	0	814	1871	163	0	41	81	41
79/04-70-03	20143	0	2553	1135	3972	0	142	284	0
79/04-70-04	12712	0	138	3592	1382	0	0	553	0
79/04-70-08	5582	0	7792	291	1221	0	116	174	0
79/04-70-10	2145	0	2423	159	119	0	159	79	0
79/04-70-12	505	0	487	36	144	0	108	198	0
79/10-70-02	2578	0	0	184	2394	0	921	1105	0
79/10-70-04	604	0	40	644	805	0	40	0	0
79/10-70-06	7712	0	5036	1259	3620	0	0	0	0
79/10-70-08	11592	0	11264	1637	2751	0	0	0	65
79/10-70-10	30799	0	14552	424	4380	0	0	0	141
79/12-70-01	1740	0	224	168	898	0	112	56	0
79/12-70-02	4611	0	256	0	2562	0	2818	1793	0
79/12-70-03	29138	0	5254	1911	6210	0	0	239	0
79/12-70-04	98108	0	12400	2188	5835	0	365	365	0
79/12-70-06	106694	0	41778	9641	1500	0	0	214	0
79/12-70-08	15232	0	7495	4956	1451	0	484	242	0
79/12-70-10	1774	0	23845	1664	0	0	776	665	0
80/01-70-01	7310	0	1985	3790	90	0	0	0	0
80/01-70-02	24227	0	11964	8076	0	0	0	1196	0
80/01-70-03	17569	283	8076	5526	567	0	0	0	0
80/01-70-04	39792	0	5247	2624	219	219	219	0	656
80/01-70-06	44061	0	8140	6193	354	0	708	1062	885
80/01-70-08	11803	0	521	434	174	0	694	0	0
80/01-70-10	4865	0	987	141	71	0	635	141	0
80/01-70-12	71	0	566	212	0	212	1628	425	0
80/02-70-01	1714	0	8568	571	0	190	0	0	0
80/02-70-02	4253	0	1251	584	83	0	0	0	0
80/02-70-03	2084	321	4489	3206	0	0	0	0	0
80/02-70-04	548	0	228	183	46	46	91	0	137
80/02-70-06	187	0	94	56	112	0	19	37	37
80/02-70-08	293	0	226	25	17	0	59	0	17
80/02-70-10	9	0	9	0	17	0	9	0	0
80/02-70-12	109	0	73	675	109	0	109	529	18
80/03-70-03	14	28	740	384	14	0	14	43	0
80/03-70-06	0	0	601	6616	401	0	501	0	200
80/03-70-08	0	0	0	6516	465	0	1047	233	0
80/03-70-10	16	0	0	323	32	0	32	0	0
80/09-70-02	20783	0	577	0	3464	0	0	5773	0
80/09-70-03	10583	0	331	1984	23811	0	0	0	0
80/09-70-06	4379	0	137	3558	3011	0	0	684	0
80/09-70-10	160	32	160	736	64	32	192	64	0
80/12-70-02	1582	0	0	1384	1384	0	1582	396	0
80/12-70-06	33804	0	2561	3585	8195	0	0	0	0
80/12-70-08	1523	0	76	1447	1219	0	305	0	0
80/12-70-10	60130	0	4854	6835	6538	0	396	5944	198
80/12-70-12	0	116	0	395	116	0	93	162	23
81/01-70-02	1132	0	0	1767	226	0	0	136	0
81/01-70-06	33542	0	2346	235	7271	0	0	0	0
81/01-70-10	18	0	0	35	18	0	106	0	0
81/02-70-03	6676	0	668	5842	1419	0	83	417	584
81/02-70-04	3741	0	150	150	1197	0	0	299	449
81/03-70-03	408	0	0	783	0	0	0	68	68
81/09-70-02	1091	0	1091	0	273	0	1091	2455	0

APPENDIX B: Copepod abundance data used in the multivariate analysis

Station	*C. carinatus*	*Calanus* spp	*Centropage. brachiatus*	*Metridia lucens*	*Rhincalanus nasutus*	*Pluero-mamma* spp	*Oncaea* spp	*Oithona* spp	Harpacti-coids
81/09-70-03	240	399	958	319	319	0	319	479	80
81/09-70-06	206	206	206	0	824	0	0	0	0
81/09-70-08	534	4005	1869	534	534	0	0	267	0
81/09-70-12	211	0	1161	0	1056	0	422	422	0
81/12-70-02	1161	0	0	435	2177	0	1306	1306	0
81/12-70-03	2559	0	0	5544	2985	0	1279	5117	0
81/12-70-04	1210	0	134	2151	2151	0	0	269	0
81/12-70-06	6071	0	2819	217	5638	0	0	0	0
81/12-70-10	6273	0	4117	3529	7253	0	392	1372	0
81/12-70-12	221	111	4240	1032	37	0	700	184	0
81/12-70-14	3221	1288	1611	3221	805	0	3221	7087	0
79/01-66-04	12003	871	2033	290	290	0	0	0	0
79/01-66-06	2879	0	211	70	70	0	0	0	0
79/01-66-08	11537	481	801	3686	1602	0	160	0	0
79/01-66-10	15509	705	9165	5170	1175	0	0	0	235
79/01-66-12	750	409	3954	205	205	68	545	409	68
79/01-66-14	529	925	1983	0	529	0	0	529	0
79/02-66-04	9048	297	890	1335	445	0	0	0	0
79/02-66-06	97	193	0	48	48	0	0	0	48
79/02-66-14	4819	0	2029	190	63	0	63	63	0
79/03-66-04	772	0	0	483	97	0	0	0	97
79/03-66-08	3267	311	856	933	389	0	0	0	0
80/01-66-03	24973	247	3956	7665	0	0	0	0	0
80/01-66-04	21240	0	2567	2334	233	0	0	467	700
80/01-66-06	9644	197	2362	5511	0	0	197	394	197
80/01-66-08	9500	194	1163	4459	776	0	194	0	0
80/01-66-10	4002	267	10006	4002	534	0	1067	0	133
80/02-66-03	7832	0	28882	1469	0	0	0	0	245
80/02-66-04	35388	0	37916	1517	0	0	0	0	506
80/02-66-06	8549	0	10357	1808	164	0	0	0	329
80/02-66-08	1356	0	0	825	59	0	295	0	0
80/02-66-10	182	0	91	1273	273	0	727	91	91
80/03-66-04	73	0	1025	330	37	0	0	146	0
81/01-66-02	503	0	0	402	0	0	34	67	0
79/01-74-03	5868	0	6148	5589	559	0	1118	2236	279
79/01-74-04	17354	0	7592	1446	3254	0	362	362	723
79/01-74-06	33555	0	8135	6101	7118	0	0	0	0
79/01-74-08	24554	0	3508	1002	13530	0	501	0	0
79/01-74-10	23576	0	2652	295	7368	0	589	295	0
79/01-74-12	3223	134	4969	134	0	0	269	134	0
79/01-74-14	117	0	117	117	78	0	0	78	0
79/02-74-03	3168	0	1152	432	720	0	288	0	0
79/02-74-04	6384	0	958	5107	638	0	160	0	0
79/02-74-06	9294	0	0	4807	1602	0	320	0	0
79/02-74-08	5040	240	1440	240	480	0	240	0	0
79/02-74-10	4789	0	6663	833	416	0	833	0	0
79/02-74-14	1109	50	705	403	151	0	50	0	0
79/03-74-04	2220	89	2842	888	622	0	0	0	178
79/03-74-06	3968	144	1443	3607	72	0	0	144	0
79/03-74-08	312	0	2362	624	0	0	45	178	0
79/03-74-10	1794	0	3140	0	748	0	150	1495	449
79/03-74-14	948	56	2454	167	223	0	390	335	0
80/01-74-01	83	0	0	496	0	0	83	1323	0
80/01-74-02	18537	421	843	5898	0	0	1264	5055	421
80/01-74-03	28431	0	9748	2843	406	0	406	812	0
80/01-74-04	21911	0	1543	2160	309	0	0	0	0
80/01-74-06	31028	0	3879	2586	431	0	862	431	0
80/01-74-08	29116	0	2022	1415	0	0	0	0	202
80/01-74-10	4442	0	833	0	555	0	278	278	139
80/01-74-12	278	0	139	0	208	0	69	0	0
80/02-74-03	7447	0	28135	827	0	0	0	0	827
80/02-74-04	2279	0	1451	3523	414	0	207	0	829
80/02-74-06	10200	0	319	1062	425	0	106	0	106
80/02-74-10	0	0	258	515	86	0	86	0	0
80/02-74-14	161	0	0	15617	161	0	483	2576	0
80/03-74-08	87	0	433	20951	0	0	346	87	87
80/03-74-10	0	0	33	3083	0	0	230	131	131
80/03-74-12	0	45	45	5070	90	45	808	179	135
81/01-74-08	531	11	25	14	7	0	7	0	0
81/01-74-10	2252	0	483	1126	643	0	965	0	161

APPENDIX C: February 1979



January 1981